Reproductive Success and Survival of Swallows (*Hirundo rustica*): Effects of Age and Body Condition

Maimie L P Thompson

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Avian Ecology Group
Department of Biological and Molecular Sciences
University of Stirling

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For Dave

for his encouragement and patience

&

For Ross, Margaret and Sharon

without their love, support and practical help I would
never have finished this year

BUT MOST OF ALL

For mum and Katharine

who have given me so much yet asked for so little. I love you more than words
can ever say. Thank-you for always being there

Abstract

This thesis presents the results of a study on the Swallow *Hirundo rustica* carried out in Central Scotland between April 1986 and August 1989. Their social behaviour and life history are described. Adults were found to be markedly faithful to both their mate and site. Notable differences between results observed here and with other similar studies were the apparent lack of any sexually selected infanticide or intra-specific nest parasitism. These results were attributed to differences in colony size.

Intra- and inter-sexual variation in adult body size was measured and the presence of any age-related trends identified. Older birds had significantly bigger wing and outer-tail lengths but skeletal measures and inner tail-length did not vary in size. Swallows were found to be sexually size dimorphic for several parameters and these findings were discussed in relation to three hypotheses.

Variation in reproductive performance between years and individuals was described. Clutch size and number of young fledged was lower for second- than first-broods but even after controlling for this, breeding performance still declined seasonally. Possible mechanisms associated with this common finding were explored. The number of broods attempted in a season made an important contribution to seasonal reproductive performance. Double brooded Swallows: (i) bred earlier, (ii) were older and (iii) were more successful during their first brood (*cf.* single-brooded). Since any measure of seasonal performance is likely to be an incomplete measure of fitness, attention was also given to understanding what factors affected adult and juvenile survival. Offspring which hatched earliest and from first broods were most likely to be recruited. There was no evidence to support a positive association between fecundity and parental survival in Swallows studied here, however.

The role of individual characteristics in shaping reproductive performance was examined. Body size was only weakly associated, whereas parental age was strongly correlated with breeding success; yearlings laid later, had smaller clutch sizes and fledged fewer young during a season. Although females which were monitored over two successive seasons laid earlier in their second season they did not differ significantly for any other parameter compared. Data from other studies were reviewed and possible hypotheses to explain age-related trends were considered. It was concluded that the improved performance of older Swallows was related at least in part to individual differences and selective mortality.

In an attempt to manipulate reproductive effort brood sizes were experimentally altered by adding (Enlarged) or removing (Reduced) one, two or three nestlings shortly after hatch. Un-manipulated broods served as Controls. The size of the first brood reared affected the probability that a second clutch would be laid as well as the timing (IBI) and, (iii) success (but not size) of the second clutch. The effect of manipulation on the IBI and occurrence of second brood was asymmetrical. Temporal variation, however, could not explain differences in future fecundity between first brood treatment categories. Early desertion in relation to clutch or brood reduction was discussed in relation to the "Concorde Fallacy".

Although most pairs were able to rear additional young, nestling quality was adversely affected. Juvenile survival was related to brood size such that parents which reared Control broods were most likely to produce recruits. Manipulation of brood size also had an effect on adult survival but the effect differed between sexes and broods. The clearest and most significant result was that Swallows which reared Reduced broods (first or second) were more likely to survive (*cf.* Control or Enlarged broods). These findings were not attributed to differential dispersal of adults. A review of the literature indicated that this was the first study to publish results on the possible effects of manipulation of second broods for parental survival.

The pattern of adult body mass during the nesting cycle was described. Males and females reached a minimum mass when the nestlings were aged between Days 9 and 16 (NP II) and Days 17-23 (NP III) respectively. Only during these two stages were males heavier than females. Possible implications associated with a decrease in mass while feeding nestlings (*cf.* incubation) were discussed. Analyses of a sample of adult carcasses enabled body condition to be determined precisely. Quantitative methods of assessing the condition of live birds in the field were developed and validated against carcass analysis results. Muscle thickness as measured by a portable ultra-sound device and body mass were both considered to give reliable estimates of condition.

A number of predictions following from the assumption that parental condition was related to current and future fecundity or overwinter survival were tested. There appeared to be no significant relationship between condition while feeding first brood nestlings and, a) the IBI or b) occurrence of second broods. This applied to parents rearing both natural and experimental broods. There was some evidence to suggest that the condition of parents after the brood had fledged might be of greater importance. More data are necessary to confirm this finding, however.

Female condition at any stage in the nesting cycle (1st or 2nd brood) was not related to overwinter survival. Data for males, however, supported the prediction such that birds in poorer condition during NP II were less likely to survive. Possible reasons for differences between the sexes were explored. One suggestion proposed was that females were better able to regulate their effort to maximise fitness and and so males were possibly "victims" of their partners variability. The possibility that single- and double-brooded species may vary in their allocation of resources was considered and there was some evidence to support this suggestion for Swallows observed here.

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Chapter one

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General Introduction

1. GENERAL INTRODUCTION

1.1 VARIATION IN REPRODUCTIVE SUCCESS

Individuals within populations exhibit considerable variation in their reproductive success, both within years and across lifespans and it has been commonly reported that a minority in a population raise a majority of the next generation (Clutton-Brock 1988; Newton, I. 1989). Moreover, it has been demonstrated that parents can usually raise additional young when these are added to broods (for review see Dijkstra *et al.* 1990). One challenge for avian ecologists is, therefore, to evaluate the factors that normally impose an upper limit to clutch size (which is clearly an important component of fitness), and to account for the differences between the most and least successful breeders within a population.

1.2 HYPOTHESES TO EXPLAIN VARIATION IN CLUTCH SIZE

Three hypotheses have been proposed to explain the ultimate factors responsible for both the evolution and the maintenance of variation associated with clutch size (for review see Nur 1987): (i) the "individual optimisation" hypothesis (*sensu* Perrins & Moss 1975; Boyce & Perrins 1987; Pettifor *et al.* 1988); (ii) the "trade-off " hypothesis (Williams 1966) and, (iii) the "year to year fluctuation" hypothesis (Nur 1987). Tests of these hypotheses, particularly in the field, have proven difficult, not least because they require that both reproductive effort and life-history parameters be measured accurately (Lessells 1991). Moreover, any measure of fecundity is confounded by the possible co-variance with parental quality (Högstedt 1980; Smith 1981; Askenmo 1982; Nur 1988a) so that the number of offspring reared, whilst being an adequate measure of reproductive output, may be a poor measure of reproductive effort. In addition, there remains the problem of whether the number of young reared to fledging is an appropriate unit of success (Clutton-Brock 1988). A more rigorous test is to experimentally manipulate reproductive effort (but see Reznick 1992a,b and Partridge 1992 for recent discussion of this topic) which in bird studies has primarily involved altering brood size (Dijkstra *et al.* 1990).

1.2.1 THE "INDIVIDUAL OPTIMISATION" HYPOTHESIS

The principal tenet of this hypothesis is that individuals adjust their clutch size (in an adaptive fashion) to their own circumstances and ability, so that each female has her own optimal clutch size. This is an attractive idea since there is a substantial body of data linking the number and quality of young raised each season to both extrinsic (eg. habitat quality, Högstedt 1980, and food resources, Bryant 1975b; Hussell & Quinney

1987; Korpimaki 1990a,b), and intrinsic factors, such as age, experience, body size, dominance and body condition (Coulson & Thomas 1985; for reviews see Clutton-Brock 1988; Newton, I. 1989). Since the initial clutch size should correspond to that which is best for the individual, it is predicted that experimentally increasing or decreasing clutch (or brood) size should result in a lower fitness payoff for the individual concerned.

1.2.2 THE "TRADE-OFF" HYPOTHESIS

The trade-off hypothesis proposes that different clutch sizes achieve the same net payoffs as a result of current effort reducing the residual reproductive value. The key assumption underpinning this hypothesis is that reproduction entails costs (Calow 1979; Bryant 1988a; Reznick 1992a,b). The notion of costs implies that reproduction at any one stage may have deleterious consequences, immediately or at some later date for an individual. As a result an individual needs to "decide" (see Krebs & Davies 1991) the allocation of resources between current and future fecundity. Two crucial questions concerning this hypothesis are unresolved, however: (i) are individuals able to estimate the likely consequences of their reproductive decisions and, (ii) if so, how do they make this estimate ? Useful accounts of these problems have been given by Dawkins & Carlisle (1976), Maynard-Smith (1977) and more recently by Winkler (1991). These authors have argued that animals should base their reproductive decisions on the expected benefits of each behavioural strategy available rather than using what they had already committed to their offspring (but see Trivers 1972, 1974). The two might not be exclusive if past investment is an accurate indication of future prospects.

Costs of reproduction lead to a predicted inverse relationship between current and future fecundity. Natural selection should favour both a reduction in reproductive effort (see Hirshfield & Tinkle 1975), if this increases lifetime success (Williams 1966; Charnov & Krebs 1974), and an increase in effort as future breeding opportunities decline (Pianka & Parker 1975). These ideas have also been supported by other theorists (Stearns 1976; Calow 1979; Charlesworth 1980; Sibly & Calow 1983; Bell & Koufopanou 1986). Since different clutch sizes represent different means of achieving the same lifetime reproductive success, individuals which rear clutch sizes which are smaller or larger than the original would still be expected to have a similar fitness.

1.2.3 THE "YEAR TO YEAR FLUCTUATION" HYPOTHESIS

Unlike the other two hypotheses, this hypothesis does not require an overall "best" clutch size nor that different clutch sizes produce equivalent fitness payoffs (*cf.* trade-off hypothesis, Nur 1987). It does require, however, that in any given year there is a "best" clutch size and that, depending on selection pressures, this will vary from year to year. It is further predicted that the genotypic variability of clutch size is maintained via fluctuating selection pressures and so the range of commonly occurring clutch sizes should, therefore, closely correspond to the range of selected-for clutch sizes (Nur 1987).

1.3 REPRODUCTIVE COSTS

Although the exact relationship between brood size and fitness remains unclear, and allowing for some equivocal results, current evidence does favour the existence of reproductive costs (see reviews Lindén & Møller 1988; Dijkstra *et al.* 1990; Orell 1990; Lessells 1991). Even so, the specific mechanism or currency (*viz* Reid 1987), through which such costs are manifest has yet to be clearly established. More importantly, it is still not known if the "costs" are sufficiently severe to alone explain why the most frequent clutch size is commonly smaller than the most productive (Nur 1987). If mortality occurs outside the breeding season then the mechanism which induces such costs is particularly difficult to identify. Alternative ways of measuring costs have, therefore, been sought such as testing for short-term reproductive costs (Bryant 1988b). If measurable short-term costs do indeed reflect longer-term costs (see Sibly & Calow 1984) then this approach offers at least three important advantages for studies concerned with evaluating costs or reproduction: (i) it is more amenable to manipulation of reproductive effort; (ii) it more easily identifies the exact stage of the nesting cycle during which costs are incurred and, (iii) it may prove to be more powerful for discovering the causal agent(s) involved.

1.3.1 CORRELATES OF COSTS AND THEIR MEASUREMENT

Measures such as body mass (Bryant 1988a), "condition" indices (Newton 1966; Hussell 1972; Winkel & Winkel 1976; Askenmo 1977; Bryant 1979) and energy expenditure (Drent & Daan 1980; Bryant & Westerterp 1983a; Bryant *et al.* 1984; Ricklefs & Williams 1984; Reyer & Westerterp 1985, for review see Bryant 1988a) are often presumed to be correlates of short-term reproductive costs. Theoretically, at least, these parameters may be indicators by which individuals determine their situation during the current breeding attempt and evaluate their longer term prospects. The accurate measurement of body "condition" of live individuals in the field is, therefore, central to predictions of this nature. There is little agreement, however, on how best this may be achieved. A particular area of debate stems from definitions of body mass as a measure of body condition. Body mass may vary independently of the status of body reserves so the validity of such a definition is questionable.

Even though condition may be assessed from measurements of size-corrected body mass (Owen & Cook 1977; Johnson *et al.* 1985) or from a combination of other techniques (Baldassare *et al.* 1980; Bryant & Westerterp 1983a; Lewis *et al.* 1986; Jones 1987a; Bryant 1988a), precise measures of condition can only be obtained from a knowledge of body composition as determined by carcass analysis (Evans & Smith 1975; Davidson *et al.* 1986). This method also enables the testing of alternative non-destructive field methods. If body mass and condition are found to be covariates, such that a change in body mass also implies a change in body condition, mass may be used by researchers as a field measure of condition.

Over the last decade the interpretation of parental mass loss during the breeding season has generated considerable debate. Two conflicting hypotheses have been proposed: the " stress" (*sensu* Silverin 1982; Westerterp *et al.* 1982; Murphy & Haukioja 1986) and "adaptive" hypotheses (Freed 1981, Norberg 1981). The "stress" hypothesis proposes that a loss of mass during breeding implies a loss of "condition" and is symptomatic of a fitness cost. The "adaptive" hypothesis, on the other hand, states that there is no loss in condition with a loss in mass and that mass loss may be neutral or indeed beneficial. Others have argued that these hypotheses are not necessarily mutually exclusive but rather the significance of mass change depends on both the amount and timing of mass changes observed (Jones 1987e,f; Gaston & Jones 1988, but also see Nur 1984a). This third idea has been termed the "threshold" hypothesis.

Investigations of variation in reproductive success, and reproductive costs ideally require data relating to ecological, behavioural and physiological aspects of breeding for known individuals. Moreover, to properly assess the fitness consequences of different strategies, a knowledge of the subsequent survival of parents and their offspring is desirable. This is a formidable challenge for field ecologists but one that can be eased through choosing an appropriate study species. Much relevant research has been performed on nest-box populations, but the full value of such studies made on "artificial" populations has been questioned (Møller 1989d). Any species which offers similar practical benefits but which occupies natural nest sites might, therefore, be considered more appropriate.

1.4 THIS STUDY: THE STUDY SPECIES

This study was carried out exclusively on the Swallow (*Hirundo rustica*) which meets seven important criteria desirable for life-history studies: (i) Swallows were common in the study area and readily observable. They nested in accessible, almost entirely indoor, sites permitting the use of micro-computers and electronic nest-balances on mains power to monitor nests. Data collection was rarely interrupted by inclement weather conditions; (ii) adult birds were easily caught, handled, measured and sexed. The majority of the breeding population was uniquely marked. Non-breeding birds also occupied breeding sites so they too could be observed and captured. Predation was very low. The high degrees of site- and mate-fidelity, enabled population changes and the fate of individuals to be investigated; (iii) Swallows were tolerant of disturbance, which together with the high degree of breeding synchrony, facilitated efficient execution of clutch and brood manipulations; (iv) the complete dependence of adults and juveniles on aerial insect food meant that food availability could be readily quantified by using suction traps; (v) fecundity may be related to territory quality in some species (Perrins & Moss 1975; Högstedt 1980, 1981a; Nur 1986), complicating data interpretation. Although Swallows have nest territories they do not have feeding territories and since nest sites were not limiting, the role of territory quality in shaping fitness is assumed to be unimportant in this study; (vi) multi-brooded species show several characteristics which assist researchers in their understanding of life-history strategies. Investigation of variation in the number of broods attempted each season offers insight into the factors which underpin the decision to breed. Moreover, fecundity responses to natural or experimental variation in reproductive effort during the first brood can be detected within the same season. This may be useful when attempting to relate short- to long-term costs of reproduction and finally, (vii) detailed studies have already been carried out on aspects of the behaviour and ecology of the Swallow both within this study area (Turner 1980, 1982, 1983a; Jones 1985, 1987b,e,f, 1988,1989) and on other populations (Cramp 1988; Turner & Rose 1989). These provide an ideal background to this study and a good source of comparative data.

1.4.1 POTENTIAL DRAWBACKS

There are three main drawbacks associated with the Swallow as a study species: (i) adults cannot be aged, other than through their ringing history; (ii) as migrants, data could only be gathered during the breeding season which limits the interpretation of, for example, factors affecting survival and (iii) adult birds are not amenable to supplementary feeding experiments.

1.5 OUTLINE OF CHAPTERS

All methods, assumptions, equations and definitions of terms used in the thesis are described in Chapter 2. Methods, experiments or techniques specific to particular parts of the study are described in detail within each chapter. A general background to the breeding biology, social behaviour and behavioural activities of the species is provided (Chapter 3). Intra- and inter-sexual variation in adult body size was measured and quantified. The presence of age-related trends in size was explored and the possible the relationship of body size and adult survival examined (Chapter 4). Variation in the reproductive success of Swallows is investigated, in particular the role of age, individual differences and body size (Chapter 5).

The effect of natural and manipulated (reduced and enlarged) brood size on the fitness of parents and their offspring was analysed. Specifically, the effect of first brood size on nestling quality and survival and the occurrence, timing, size and success of second broods was measured. The relationship of parental survival to fecundity was also considered

(Chapter 6). Changes in adult body mass during the nesting cycle were described and quantitative body condition measures of live birds in the field developed. An important area of research was the evaluation of body mass as an indicator of condition and the implications of body mass variation for fitness. In Part III, the relationship of adult body mass and other condition indices to fecundity and survival was explored (Chapter 7). Finally, Chapter 8 discusses the findings of the previous chapters and the result are reviewed in light of the hypotheses outlined in Chapter 1).

Chapter two

(pp 7-14)

General Methods

2 GENERAL METHODS

2.1 INTRODUCTION

Most data were collected from 1987 to 1989 at over forty sites in Central Scotland, all within 10 km of the University of Stirling G.R. NS 808 965 (Appendix 2.1, Fig 2.1). A small number of birds (17 adults and 33 juveniles) was ringed in 1986 over a two day period (15th and 16th July). All dates are given as the nth day after 1st April (1st April=1; 1st May=31; 1st June=62 and so on).

2.2 PRE-LAYING OBSERVATIONS

From early April onwards most farms were visited at least three times a week to monitor the pattern of arrival and occupation of buildings. Some birds were caught, ringed and colour marked at this time to investigate movement between farms and or buildings prior to breeding. This was done only on a limited scale, however, to minimise any movements which might have been caused by disturbance alone. Birds entering buildings during the day or roosting in them at night were useful indications of breeding intention. The firmest evidence, however, came from observing birds engaged in nest building.

2.3 DATA COLLECTED ON BREEDING PAIRS AND THEIR OFFSPRING

2.3.1 LAYING DATES AND CLUTCH SIZE

Most potential nest sites were checked daily until laying had commenced. First egg dates were predicted to the nearest two days using the behaviour of the pair, the mass of the female, the stage of nest building, or by the type and amount of nest lining. Based on the predicted first egg dates, nests were then checked regularly, often daily, to determine actual laying date (to the nearest day). The date of the first egg was considered to be the day that an egg first appeared in the nest and the date of clutch completion the day that the last egg of the clutch was laid. Clutch size was determined by counting the eggs six days after the appearance of the first. Where laying intervals were not monitored or first egg dates were unknown, eggs were assumed to have been laid daily and the number of eggs in the nest on inspection equal to the original clutch size. Since predation of eggs and clutches of seven were very rare this was a safe assumption.

2.3.1.1 Estimating laying date

Where exact laying date was unknown, estimates suitable for some sections of the analysis were calculated. If the date of hatch (Dh) was known, it was assumed that the clutch size (CL) on finding was equal to the original clutch size, that the eggs were laid

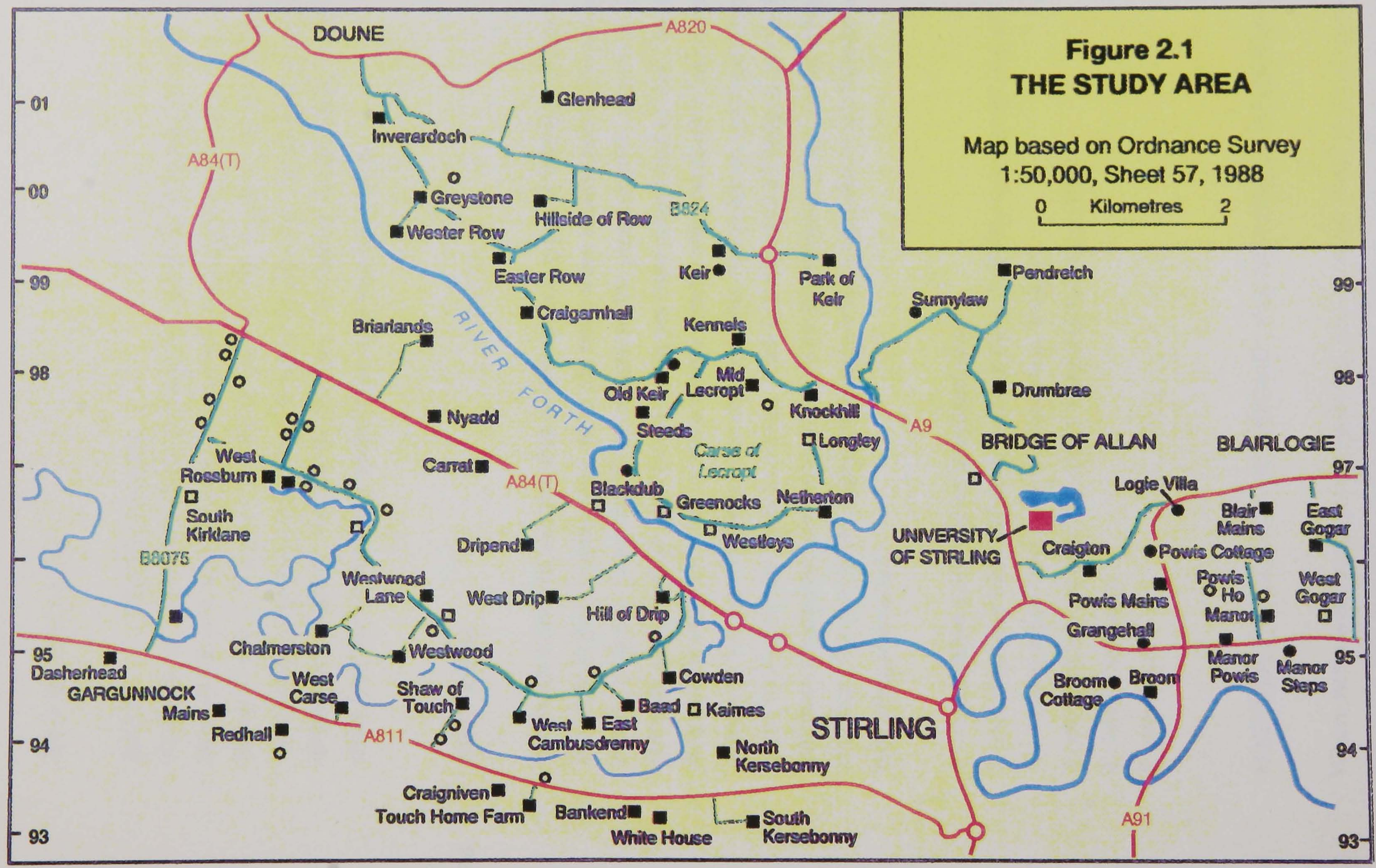

Figure 2.1
THE STUDY AREA

Map based on Ordnance Survey 1:50,000, Sheet 57, 1988 daily and that the incubation period (IP), which was defined as the period between the day that the last egg of the clutch was laid until the date of hatch, was equal to 15 days, then the estimated date of the first egg (Ee) was calculated from the following equation:

$$Ee = Dh - [(IP-1)+CL]$$

2.3.1.2 Laying intervals

Accurate determination of laying intervals requires that nests are checked daily and at a time which was later than that during which an egg may be laid. Only some nests were checked daily. Where a nest was found with one egg and four days later contained five, for example, daily intervals were reasonably inferred. Both these methods have been termed as 'complete' checks. In contrast, 'incomplete' checks refer to nests where the exact interval between only some of the eggs was confirmed.

2.3.2 NEST TYPES

Swallows nested in various sites within several types of building. Prior to the arrival of the birds at their nesting sites, most old nests were located and their contents and condition noted. Once the birds had arrived the presence of new nests or the addition to old ones was recorded. First brood nest types were categorised as 'old', 'new' or unknown. Inspections of active nests continued until shortly after incubation had commenced. Although the nest contents were checked after this point no particular attention was given to the nest structure or lining. After first broods had fledged or a breeding attempt had been terminated, nests were checked for the presence of second (or subsequent) clutches. Choice of nest type at this stage was categorised in accordance with the following five codes:

1 - re-occupied their first (or previous) nest
2 - occupied any other old nest; no distinction made between an old nest of the current season and those from previous seasons
3 - occupied an old nest: categories 1 and 2 not distinguished
4 - built a new nest
5 - unknown

2.3.3 HATCHING DATES, BROOD SIZE AND THE NUMBER OF YOUNG FLEDGED

Where nests were located during laying, approximate dates of hatch were calculated by assuming that incubation lasted for at least 15 days. Daily visits to the nest were resumed at this time until all eggs had hatched, enabling accurate estimation of dates of hatch, incubation period and nestling age.

Table 2.1 Summary of age classification of adult Swallows in 1988 and 1989[a]

Category	Age class[b] code	Description
1	1	"known one year old" birds or yearlings
2	1*	"assumed one year old" birds
3[c]	**1****	"known plus assumed one year old" birds (categories 1 and 2 combined)
4	≥1	"at least one year old" birds
5	2	"known two year old" birds
6[c]	≥ 2	"equal to or older than two year old" birds
7	≥3	"equal to or older than three year old" birds^^
8	≥ 4	"equal to or older than four year old" birds ^^
9[c]	**≥≥3**	all birds which were known to be at least three^^ years old (categories 7 and 8 combined)
10[c]	**≥≥2**	all birds which were known to be at least two years old (categories 5 to 8 combined)

a - adults were not aged in 1987, only in 1989 were data for ≥ 3 or ≥ 4 collected

b - combined age categories are given in bold text

c - most age-related analyses were carried out on categories 3 and 10 in both years and also on categories 3, 6 and 9 in 1989

Hatching was usually synchronous (i.e on the same day) but where a spread in hatch occurred, usually over two days, the date of hatch was taken as the day that ≥ 50% of the brood hatched. Hatching day was designated as Day 0 of the nestling period and brood size as the number of young in the nest on Day 2. Young were later counted on Days 13 and 18 (±1 day). The number of young in the nest on Day 18 was assumed to represent the number of young which fledged. The length of the nestling period was not accurately determined in most cases because fledging is a gradual process and nest visits may induce premature nest departure.

2.3.3.1 Estimating hatching date

If a nest was found with young but the exact date of hatch was not known then the hatch date could be calculated (see Equations below, Section 2.3.4.1). By estimating the age of the brood an estimated date of hatch (Ed) could be derived by back calculation. Where clutch completion dates (Dc) were also known, the above estimates could be further refined using the following equation:

Ed = Dc + (IP-1); where IP is equal to the incubation period

2.3.4 NESTLING AGE AND GROWTH

All nestlings within a nest were given the same age and were taken as having age Day 0 on the day they hatched (see 2.3.3). From Days 5 to 18 ± 2 days, daily measurements of mass, wing length, head-to-bill length and tarsus length were made on a sample of broods. In general, measurements were taken between 1000h and 1300h. Age-growth curves were constructed for each parameter. Most broods were ringed and also measured on Day 13 ±1 day, when peak nestling mass usually occurred. A few individuals were also measured at and after fledging. All adult measurements were made on fledged individuals. Details are given in the methods section of Chapter 4.

2.3.4.1 Ageing nestling and fledgling Swallows

The age of nestlings assumed to be less than five days old could be determined to the nearest day by eye. Equations for calculating nestling age between Day 2 and Day 10, used mass (Day = (Mass(g)+0.13)/2.12, $r^2_{258} = 0.88$); between Day 2 and Day 20 used wing length (Day = (Wing(mm)+5.79)/5.88, $r^2_{374} = 0.97$); and between Day 21 and Day 30 used outer tail length (Day = (Outer tail(mm)-6.31)/2.11, $r^2_{214} = 0.77$).

2.3.5 POST-FLEDGING OBSERVATIONS OF JUVENILES

After fledging, the nest and surrounding buildings were checked for dead birds. Carcass wing length was measured, where possible, to determine the age at death and possible cause. Some fledglings were caught after they had left the nest, which enabled local inter-seasonal dispersal and post-fledging development to be monitored.

2.3.6 MALE - FEMALE PAIRINGS

Adults were caught whilst attending the nest, measured, ringed and colour-marked. Both male and female were identified for most nests. Birds often entered buildings other than their own (*pers obs*), so it was necessary to confirm that pairings were correctly assigned and that they had been attributed to the right nest. This was ideally achieved by re-catching individuals at the nest site. Where this was not possible, the colour-marked birds were observed. Where several pairs nested together in close proximity, the brood-patches of incubating females were sometimes coloured using non-toxic "felt" pens so that eggs were stained, thus ensuring that each female was matched with the correct nest.

2.3.7 REPLACEMENT BIRDS

Where one member of a pair was known to have died early in the season and a new pair was formed, the "new" bird was considered to be making its first breeding attempt of the season but its partner was classed as having a re-lay (see 2.3.8). If death occurred late in the season then the new bird was entered as having an unknown number of attempts.

2.3.8 RE-LAYING

Pairs were considered to have had a replacement clutch (a re-lay), if previous attempts failed before Day 8. Those which failed after Day 14 and made a subsequent attempt were considered as having a second brood. In analyses these were distinguished from second broods following a successful first brood. Similarly, nests which failed as a result of human disturbance were distinguished from natural failures.

2.3.9 PAIR-BOND

Ringed adults which kept the same mate from the previous year were classified as having the 'same' partner; those which had a new partner were classified as having 'changed'. Reasons for change were 'separation', where both the male and the female survived but a new pairing was formed by one or both, and 'loss', where a new pair formed as a result of one member of the pair dying or assumed to have died.

2.3.10 SECOND BROODS

Regular visits continued at each site throughout the season to record second or third brood attempts. A second clutch was defined as at least two eggs laid. The presence of just one egg was inadequate due to the possibility of "egg-dumping" (Møller 1989c) or "stray layings". Both male and the female were recaptured and identified for each new breeding attempt. Where capture was not successful but birds remained at the same nest or building and the duration of the inter-brood interval was not unusually long, the pairing was assumed to be the same. Few birds were known to have changed partners within a season during the course of the study. If no subsequent broods were found at a site pairs were classified as single-brooded (birds rarely bred at more than one site)

2.3.10.1 Number of breeding attempts

Swallows arrived at farms throughout the breeding season. It was assumed that these birds had not bred elsewhere (see 3.2.8 and 3.2.9). If a site had been monitored regularly then the possibility of undiscovered nests could be discounted and each new nest located was considered to be the first breeding attempt. Where nest checks or adult capture was not thorough, pairs were not assigned a brood number but classified as unknown. Similarly, where the total number of breeding attempts per season was not accurately determined, an 'unknown' category was used, though retaining a distinction between those pairs which had at least two broods from those that had only one.

2.4 ADULT AGE CLASSES

In 1987, most trapped birds were unringed and of unknown age. Only 1988 and 1989 data could be used, therefore, for age analyses. Birds were assigned to one of ten age classes (see Table 2.1). In 1989, there were sufficient "known three year-old" birds. Using this system of age classes produces an overlap of bird ages within ≥ 2 and ≥ 3 of an unknown scale. For some analyses, age classes were combined as follows: 1 and 1*; 2 and ≥ 2; and 2, ≥2 and ≥ 3 (Table 2.1). An attempt was also made to distinguish between unringed birds which were likely to be new recruits from those which were unringed through evading capture in the previous season. As the study started in full in 1987, this rationale could only be applied to the unringed birds of 1988 and 1989. When an unringed bird was captured at a site (x) it was assigned a code based on the level of observation and the percentage of birds estimated to be captured at that site (x) in the previous season. The following five codes were used:

1 - All birds caught at site in previous season.
2 - No birds present at site in previous season.
3 - No birds present in building being occupied in year(n) and all other birds at the site captured in previous season.
4 - Not all birds caught at the site in previous season; typical of larger colonies.
5 - No catching carried out in the site in the previous season.

Birds falling into categories, 1, 2 or 3 were, for most cases, grouped together and assumed to be new recruits to the area (i.e one year old). Birds coded as 4 or 5 were classed as being "at least one year-old".

2.5 ESTIMATING SURVIVAL

To estimate the survival of adults and nestlings (juveniles) from one year to the next an attempt was made to catch all adults within the study area.

2.5.1 JUVENILES

The survival of nestlings ringed in 1987 and 1988 was determined on the basis of whether or not they were recaptured in the following season.

2.5.2 ADULTS

For the purposes of this study each adult was assigned to one of the following categories:
1 - Known to have survived from year (n) to year (n+1) (see 2.5.2.1 below).
2 - Known to be dead.
3 - Uncertain whether to have survived or not (see 2.5.2.3 below).

2.5.2.1 Survival

All birds which were known to have survived were allocated to one of five breeding classes for the previous season:

1 - Single-brooded.
2 - Double-brooded.
3 - Known to breed but unknown number of attempts.
4 - Non-breeding.
5 - Unknown.

2.5.2.2 Mortality

Birds which were ringed in one year but not recaught in subsequent year(s) were considered not to have survived when:

1 - All birds had been caught at site in year (n+1).
2 - No bird were present at site in year (n+1).
3 - No birds present in the building that they occupied in the previous season but all other birds at site were captured in year (n+1).
4 - Known to be dead in previous season from natural causes.

2.5.2.3 Survival or mortality not determined

Codes were devised which took into account the likelihood of an individual surviving from one year (n) to the next (n+1) but not being re-caught in year (n+1) and so incorrectly categorised. All birds at site (x) which were not recaptured in year (n+1) were coded according to: a) had the site (x) changed and, b) the intensity of trapping at site (x) in the following season:

1- Structural disturbance at site by year (n+1); no longer suitable for breeding.
2- Did not catch at site or building in year (n+1).
3- Caught only once in year (n), not known to have bred at site where caught.
4- Survived but captured outside the study area.
5- Survived but not recaptured until year (n+2).

Although Code 4 birds survived, trapping within the study area did not record this. These individuals were, therefore, classified as having unproven survival for some analyses. Code 5 birds were included as survivors when data for 1987 were analysed alone but excluded when data for this year were combined with 1988. Birds which were known to be dead in year (n) for reasons other than starvation, such as predation or injury, have also been excluded. Any individual which was assigned to one of the above categories was classified of unknown survival status, and where necessary excluded from calculations of annual survival to minimise any bias favouring mortality as opposed to survival. Mortality is assumed to occur mainly outside the breeding season (Møller 1989b).

2.6 MEASURING FOOD AVAILABILITY

Food availability for breeding Swallows was sampled using an aerial insect suction trap (Johnson 1950; Taylor 1962). The device was sited at the University, 2-10km from the study sites (Fig 2.1). Samples were removed daily from the suction trap at 1000h, stored in 10:1 methanol/glycerol solution and the settled volume in a measuring cylinder recorded. The trap sampled aerial insects at a height of 12.2m, through a 1mm mesh gauze. The method is considered to be non-selective with regard to insect size and taxon (Johnson 1950; Taylor 1962; Taylor and Palmer 1972; Bryant 1973) so it is particularly suitable for estimating the food availability for aerial feeding birds. All values of insect abundance (n) were log-transformed (ln (n+1), Bryant 1973; Turner 1980; Jones 1985).

2.7 WEATHER DATA COLLECTION

Standard weather data were collected daily from the Parkhead Meteorological station situated at Stirling University.

2.8 STATISTICAL ANALYSES

Data were analysed on the University of Stirling mainframe using the Statistical package SPSSx. Histograms were plotted to determine the distribution of each variable (Zar 1974). Parametric analyses were used on normally-distributed data. Non-normal data was transformed to a normal distribution before parametric analysis. Non-parametric analyses were used where transformation was unsuccessful and for small samples.

Significance values are two-tailed unless otherwise stated. The following symbols were used in some tables and figures to indicate significance levels:

ns =$p>0.05$; * =$p<0.05$; ** =$p<0.01$;*** =$p<0.001$.

2.9 NOMENCLATURE

In general only English names have been cited in the text. A full list of English and scientific names of all bird species mentioned are listed in alphabetical order (English name) in Appendix 1.1

Chapter three
(pp 15 - 31)

Social Patterns, Life History and Breeding Biology of the Swallow

3 SOCIAL PATTERNS, LIFE HISTORY AND BREEDING BIOLOGY OF THE SWALLOW

3.1 INTRODUCTION

The Swallow belongs to the family Hirundinidae, within the order Passeriformes. It is a summer migrant to temperate breeding grounds, wintering in southern Africa where the annual moult takes place (Palmer 1972; Kasparek 1981). Major reviews of their breeding biology and life history are given by Vietinghoff-Riesch (1955), Glutz von Blotzheim & Bauer (1985) and Cramp (1988). A detailed study has been performed on a Danish population by A. P. Møller. This ongoing project, which started in 1970, has concentrated on reproductive strategies, in particular the behaviour of parents during the pre-laying and laying periods (Møller 1985, 1987c,d,e, 1988c, 1989c, 1991a,d). More generally, Møller has presented data on nest site selection, costs and benefits of colonial living, sexual selection, breeding biology, life history and long-term population changes (Møller 1987a,b,g, 1988a, 1989a,b, 1990a,e, 1991a,b,c reviewed by Cramp 1988 and Shields *et al.* 1988).

In Britain, relatively little has been published on the breeding biology or behaviour of swallows despite their familiarity and abundance. Early accounts are given by Uchida (1932), Boyd (1935,1936), Adams (1957), Witherby *et al.* (1940), Hartley (1941), Davis (1965) and Davies (1976). More recent contributions are those of McGinn & Clark (1978), McGinn (1979) and Tate (1981). Breeding and feeding ecology have been described in detail by Waugh (1978), Bryant & Turner (1982), Turner (1980, 1982, 1983a) and Jones (1985, 1987b,e,f, 1988, 1989). Pre-migratory and migratory movements of Swallows have been analysed by Ormerod *et al.* (1991).

Two other hirundines also breed in Scotland and winter in Africa: the House Martin (*Delichon urbica*) and the Sand Martin (*Riparia riparia*). A different sub-species, the Barn Swallow *Hirundo r. erythrogaster*, breeds in North America. All are aerial insectivores. It is believed that the North American population of Barn Swallows was derived from the European one but is now reproductively isolated (Mayr & Bond 1943). There are two notable differences between the populations. North American males: (i) participate in incubation (Ball 1983a,b; Turner & Rose 1989) and, (ii) have shorter outer tails or "streamers" (Cramp 1988). General accounts of breeding biology and behaviour of Barn Swallows are reviewed by Shields *et al.* (1988) and Turner & Rose (1989). The aims of this chapter are twofold: firstly to provide a broad overview of the social patterns and behaviour of Swallows from arrival at the breeding grounds to departure, and secondly, to present general breeding data. Comparisons are made with the Barn Swallow and other members of the Hirundinidae.

3.2 BREEDING CYCLE

The breeding cycle of the Swallow comprises pair formation, mating, nest-building, brood provisioning and post-fledging care by both sexes. Egg formation, laying, incubation and brooding is carried out by the female and nest-site selection, mate guarding and any involvement in extra-pair fertilization (EPF), is by the male (Møller 1985,1987c,d,e,f). These activities may differ in their duration and energetic cost (Ricklefs 1974; Bryant & Westerterp 1980; Ettinger & King 1980). Multi-brooded individuals repeat much of the behaviour described above.

3.2.1 ARRIVAL

Swallows arrived on their breeding grounds from the middle of April onwards. Birds were first observed at farms in the study area on the 20th, 10th and 14th of April in 1987, 1988 and 1989 respectively. Males arrived, on average, two days earlier than females but the difference was not significant. Some birds appeared at sites already paired. Elsewhere, females tended to arrive on the breeding grounds one week later than males and to visit a number of males before making their choice of mate (Møller 1988a, 1989a, 1990a).

Other studies on hirundines have shown that date of arrival is age-related. This was also thought to be the case during this study. Out of a total of 124 birds caught between 26th April and 1st May in 1988, 66% were at least two years old, 33% were unringed and 1% were known to be yearlings. Birds which appeared on the breeding grounds for the first time from June onwards were typically yearlings. Some late arrivals may have visited other sites earlier in the season but breeding was almost certainly not attempted. Birds were observed to arrive at some sites consistently earlier than others (*pers obs*). Arrival date was also significantly correlated with date of first egg (*pers obs*).

3.2.2 NEST-SITE SELECTION

Most pairs nested on farms and all nests (except one) were inside buildings. Traditional stone walled barns were the commonest sites and were usually occupied first. More modern buildings, although occasionally used, were among the last to be utilised. Garden sheds, domestic garages, derelict houses, kennels and stables were also occupied, but less frequently. Most nests were supported by a rafter, unsupported nests were built against wooden or stone walls or at the apex of rafters. Nearly all nests were situated close to an entrance. Where several pairs nested in the same building, more than one entrance, or a particularly large entrance was usually available. Nest-site selection and the role of micro- and macro-habitat have been described in detail by Møller (1983), who found that 87% of all pairs bred inside buildings which contained livestock, in particular cows or pigs. This was found to be much less important during this study; less than 1% of nests were located within buildings containing livestock. Moreover, only 25% of the sites visited actually carried sheep or cattle. Of the colonies which had ten or more pairs only one had livestock.

At larger colonies, several pairs nested in the same building even when other seemingly suitable sites were available (see Shields 1984a; Shields & Crook 1987). Møller (1987b) suggested that the presence of Swallows may attract others to nest at a particular site. Consistent with Møller's suggestion, most late-arriving yearlings observed here settled at sites with three or more breeding pairs. None settled at sites with single pairs or no breeding pairs.

In this study, surviving adults usually returned to the same site and the same building, as found for other Swallow species (Freer 1979; Cramp 1988; Turner & Rose 1989). The use of traditional sites is often discussed with philopatry and site tenacity (Rowley 1983). The usual site tenacity hypothesis proposes that experience at a particular site will most profit those birds that re-use the site. The presence of breeders may indicate a safe site more suitable than nearby empty sites. Yearlings observed during this study usually settled at traditional "active" sites, supporting this idea (Møller 1987a; Shields 1984b).

Nest-site selection is usually initiated by males (Turner 1980; Vietinghoff-Riesch 1985; Glutz von Blotzheim & Bauer 1985; Cramp 1988). Nests may be continuously or intermittently used over a considerable number of years (Vietinghoff-Riesch 1955; Shields 1984b), thus pairs have the "choice" of building a new, or refurbishing an old, nest. Refurbishment, usually by adding a layer of mud to the rim, and the subsequent re-use of old nests has commonly been reported for Swallows (for review see Shields *et al.* 1988; Barclay 1988).

In this study new nests were built for 24% of first broods and 39% of second broods. Trends were similar between years (Table 3.1a). Two thirds (68%, n=85) of double-brooded pairs whose first brood was in an old nest also attempted a second brood in an old nest. Only 16% (20/126) re-used their first brood nest (Table 3.1b). More notable was the finding that only a quarter of double-brooded pairs built a new nest for their first brood (37/163 = 23%). More single-brooded pairs occupied a new nest. Of the 37 pairs which had a first brood in a new nest, 62% also used a new nest for their second brood. Elsewhere it has been reported that when old nests are available, between 40% and 90% of pairs refurbish rather than build a new one (references in Shields *et al.* 1988). Pairs which built new nests in the present study (n=49) started laying about four days later than those which re-used an old nest (Z_{168}=-3.54, p<0.001). Birds arriving earlier also tended to be older so nest choice may be age-related. This possibility was not investigated here, however.

Table 3.1a Swallow nest types in 1988 and 1989, by brood number

Brood	Nest	1988		1989		Both years	
number	type	n	%	n	%	n	%
First	Old	84	73.0	92	80.0	176	76.5
	New	31	27.0	23	20.0	54	23.5
	Total	115	-	115	-	230	-
Second	Old^{a}	15	16.3	9	11.4	24	14.0
	Old^{b}	41	44.6	40	50.6	81	47.4
	Old^{c}	56	60.9	49	62.0	105	61.4
	New	36	39.1	30	38.0	66	38.6
	Total	92	-	79	-	171	-

a - same as first brood nest
b- old nest but changed from first brood
c - a+b

Table 3.1b Nest types used by double-brooded Swallows

	Second-brood nest type				
First-brood nest type	Old^{a} n	Old^{b} n	Old n	New n	Total
Old	20	65	85	41	126
New	2	12	14	23	37
Total	22	77	99	64	163

3.2.3 NEST BUILDING

The nests, principally mud and straw, are usually built by the female although the male may assist (Purchon 1948; Turner 1980; Cramp 1988). Nest construction averaged nine days (9.3±0.9, n=16, range 6-17) from the first mud pellet to the last (inclusive of the lining) and six days (5.7±0.7, n=20, range 3-16) when strengthening the outside of an old nest. Very few clutches were initiated in nests without any apparent additional construction (see also Barclay 1988).

Nests were usually lined with dry grass, hair and feathers. Green vegetation was rarely observed (see Turner 1980 and Barclay 1988). The time taken to fully line a nest varied from two to ten days. Grass usually appeared five days, and feathers three days, before laying commenced. The state of the lining could be used to predict laying dates to within one or two days. Some pairs also continued to line their nest during laying and through the early stages of incubation. Absence of lining (n=4) was associated with desertion early in incubation. Three pairs lined over clutches which they had earlier deserted. Lining in relation to the nesting cycle has been described by Møller (1987a, 1991b).

3.2.4 PRE-LAYING AND LAYING PERIOD

The fertile period during which sperm can be stored by the female and still fertilise eggs (Lake 1975), is generally considered to extend from approximately five days before the start of laying until the day when the penultimate egg is laid (Tienhoven 1983). In Swallows, copulatory activity is prolonged with a marked peak ten days before laying commences (Møller 1985). The male can increase his certainty of paternity and thus his fitness, by mate-guarding during the fertile period, a widespread tactic in birds (Birkhead & Møller 1992). A male engaging in extra-pair copulations (EPCs) and a monogamous breeding attempt is commonly described as showing a mixed reproductive strategy (Trivers 1972). There has been intensive study of the factors which influence mate guarding behaviour and extra-pair copulations in the Swallow, showing that these activities are more frequent in early breeders and at larger colonies (Møller 1985, 1987a, 1988c). Increased guarding behaviour at larger colonies is probably a response to increases in attempted EPCs (Møller 1985). Although mate guarding and EPC behaviour were not measured during this study, it was noted that neither sex spent much time around the nest. Particularly in the larger colonies, males were observed to closely guard their partners, often chase intruders, and occasionally fight with them.

3.2.4.1 Intra-specific nest parasitism (INP)

Females can increase their fitness by laying one or more eggs in a nest of a conspecific. This behaviour, known as intra-specific nest parasitism (INP) or "egg dumping", is quite common in some hirundines (Andersson 1984; Brown 1984; Møller 1987f). In Swallows, egg types can be distinguished by size, shape, colour and spot pattern (Møller 1987f,1989c) so it should be possible to detect "dumped" eggs through regular inspection of the clutches. During this study 66 nests were checked daily from three days before egg laying but there was no evidence of INP based on egg types. Moreover, two eggs never appeared on the same day and there were no unusually large (>7) clutches. A more detailed study of the same population also failed to detect any "dumped" eggs (Ward 1992). These findings contrast sharply with the 16% incidence of INP recorded in Denmark (Møller 1987f).

3.2.4.2 Laying times

All eggs were recorded as laid before 1000h, the majority between 0600h and 0800h. Møller (1987f) reported that most eggs were laid between between 0400h and 0800h, and all before 0900h. Accurate laying times are difficult to ascertain as checking nests may disturb the normal pattern of laying. During the laying period females roosted on, or close to, the nest, usually with the male nearby. The female left her roost prior to laying for ~ 30 mins, presumably to defecate as there was a mass loss. The male usually accompanied his mate back to the nest and perched in or just outside the building .

3.2.5 EGG SIZE

Egg mass(g), length(mm) and breadth(mm) (n=192, mean ±se) were: 1.95±0.01, 19.7±0.06 and 13.8±0.03 respectively. All eggs were measured by Sally Ward at the start of incubation in 1989 (Ward 1992). Egg-size varied between, and to a lesser extent within, clutches. Egg-size was not related to female body size but individually marked females were found to lay similar sized eggs in successive seasons (Ward 1992).

3.2.6 INCUBATION

Incubation usually commenced with the last or penultimate egg. Intermittent incubation of incomplete clutches sometimes occurred during the earlier or latter parts of the day. Incubation usually lasts 15-16 days (review in Turner 1980). Only the female was observed incubating in this study. Males were never observed to cover the eggs but did occasionally perch on the nest edge. Throughout incubation males often perched inside or just outside the nest building and 'escorted' their mates to the foraging grounds during inattentive periods. In North America, males incubate to varying degrees up to a quarter of the total incubation (Ball 1983a,b).

3.2.7 POST-HATCHING

3.2.7.1 Nestling period (NP I) Days 1-7

The majority of clutches hatched on the same day, few over two days and very few over three days. At hatching, nestlings were poikilothermic, blind and naked except for a few downy feathers. Females brooded nestlings for the first few days, leaving the nest for only short periods. The male usually fed the young during her absence but was never observed to brood them. Nestlings opened their eyes at Day 4 . From Day 7 onwards they developed a dense coat of down, initiating homeothermy (Marsh 1979). As nestlings grew, they were brooded less frequently and fed at an increasing rate. Night brooding by the female continued until about Day 7-8 with the male usually roosting nearby. The loss of one of the parents during these stages always caused the remaining parent to abandon.

3.2.7.2 NP II - Days 8-16

Sexes shared brood feeding equally during this period. Feeding rates were highest between 1000h and 1700h (Turner 1980; Jones 1985 and this study). If a mate died or deserted when the young were > Day 10, the brood was still successfully reared (on two occasions by a female and once by a male).

3.2.7.3 NP III - Days 17-23

Young usually fledged on Day 20 (±1, range Day 17-23), but the exact date of fledging was usually not determined (Section 2.3.3). Nestlings sometimes fledged individually but more usually fledged together.

3.2.7.4 Post-fledging

Fledglings generally remained as a family group in or around the nest building for about a week and were often fed by their parents. Parents were not observed to feed their offspring later than seven days after fledging but detailed observations were not made during this period. Medvin & Beecher (1986) have reported feeding up to ten days after fledging. Fledglings rarely returned to their nest during the day but often returned to roost at night (see Medvin & Beecher 1986).

Bank and Cliff Swallow parents recognise their young by voice (Beecher *et al.* 1981a,b; Stoddard & Beecher 1983; Beecher *et al.* 1986). In the Swallow, however, parents apparently have no means of identifying their offspring though the offspring themselves are thought to show some signs of parental recognition (Medvin & Beecher 1986). Fledglings of various ages frequently entered buildings occupied by other breeding Swallows, usually unrelated. No aggression by parents to alien fledglings was observed and indeed they often roosted alongside each other (see Medvin & Beecher 1986). Since parents may mistakenly reject their own chick instead of an unrelated chick (Beecher *et al.* 1981b), selection may favour parents which accept all young in or around the nest (for discussion on this topic see Medvin & Beecher 1986).

Family groups occasionally remain together in Swallows throughout incubation of the second brood (Berndt & Berndt 1942). In the present study fledglings sometimes roosted with the female until laying of the second clutch commenced. Detailed observations of Barn Swallows showed that complete families had all broken up by two weeks after fledging. Occasionally, however, parents and some fledglings from the first clutch were still together after the second clutch had been started (Medvin & Beecher 1986). Although in a number of early studies it was reported that fledglings, assumed to be progeny of a first brood, helped to feed second brood siblings (eg. Williamson 1941; Bent 1942 in Crooks & Shield 1987) there was no evidence to support such an assumption. A later study reported that at one third of nests observed, 'extra' birds contributed 6%-29% of total feeding visits (Myers & Waller 1977). Contrary to earlier studies, however, these helpers were found to be non-breeding adults unrelated to the pairs which they attended (also see Medvin *et al.* 1987). Only at one nest was it confirmed that offspring from the first clutch assisted in feeding newly hatched second brood nestlings (Myers & Waller 1977). Medvin *et al.* (1987) suggested that the 'extra' attendants reported in earlier studies may also have been adults but which were mistakenly identified as juveniles. There were no records of juveniles, related or otherwise, feeding second brood nestlings during this study.

3.2.8 INTRA- SEASONAL ADULT BEHAVIOUR

Adult Swallows usually roosted and nested in the same building for first and subsequent breeding attempts. Some pairs, however, consistently changed buildings between broods. Shortly after completion of the first brood, single-brooded adults dispersed from the study area. Occasional individuals or pairs remained at the breeding site throughout the period during which a second brood could have been attempted and were caught at their regular roost site or entering other buildings. It was not clear why second broods were not attempted when the pair remained, particularly as some built new nests. Body condition may be important (Chapter 7). It was not known if, single birds remained at active breeding sites to gain access to another partner or, in the case of males, to attempt EPC's.

Double-brooded males and females also varied in time of dispersal. Some departed in August while others stayed until October. A few pairs remained together and roosted at their regular sites for many weeks after the second brood had fledged but they did not attempt a third brood. Others moved away soon after the second brood had fledged. No explanation for these post-fledging patterns was evident.

3.2.9 INTRA- SEASONAL DISPERSAL

3.2.9.1 Fledglings

Most nestlings in the study area were ringed so any unringed fledglings probably came from outside the study area. Only five ringed nestlings were re-caught the following year at other sites within the study area (Appendix 3.1a). These moved about 1.5 km (range 0.6- 2.5km). The following season, two of these were recaptured and both had returned to the site to which they had dispersed. Also, four of the five birds which were ringed for the first time as fledglings (thus of unknown origin) had returned to the same or a neighbouring site when recaptured the following season. It is possible that intra-seasonal dispersal helps fledglings gain familiarity with their social and physical environment, which may increase their chance of securing a mate or breeding site the following season. This theory has been termed the "discovery" hypothesis (Begon *et al.* 1986). Indirect support for this hypothesis is provided by Crook & Shields (1987) who found that 90% of all 'extra' adults nested in the area they had attended the previous season. Similar trends have been found in other studies (Shields 1984b; Lombardo 1986a,b).

Fledgling Swallows observed during the present study remained within the natal area for varying lengths of time. First-brood fledglings were re-caught at Day 45 and 80 at neighbouring sites to those where they were ringed, whilst another was caught 150km away from the nest site 23 days after it had fledged. Fledglings were also caught at their natal site from Day 30 onwards. Møller (1989b) described fledglings as dispersing a couple of weeks after having left the nest. Ormerod (1991) examined the distance, direction and timing of movements of 437 juvenile Swallows in Britain and Ireland between July and November. He showed (excluding fledglings which dispersed after ten days or which had moved less than five kilometres away), that directional movement was influenced by the month of ringing. Non-directional wandering occurred in August but movement became increasingly South-easterly from September onwards. Northerly and Westerly movements averaged 25-38km, the maximum being 270km (Ormerod 1991).

3.2.9.2 Adults

In the three year study, of the 800 plus ringed adults only ten (5 males, 5 females) were known to have moved sites during a breeding season (1.2± 1.2 km, range 0.4 - 4.1km, Appendix 2.1b). The majority of movements were to neighbouring farms. There was little difference between the sexes (1.1±0.7 vs 1.4±1.6, for males and females respectively). Two females moved during the inter-brood interval and gained new partners. It was assumed that their previous partner had died. On one occasion, a male feeding young during a spell of very bad weather was caught at a neighbouring farm indicating that, at least temporarily, he had deserted his brood. The remaining seven were first caught in the pre-laying period. Although such individuals could have been prospecting for breeding sites, it is possible that catching them during this period induced a change of site.

3.3 NON-BREEDING POPULATION

There was some evidence of a non-breeding population. Firstly, following the death of one member of a pair, prompt re-pairing indicated the presence of "spare" birds. Secondly, some adults were caught at roost in possible nesting buildings shortly after their arrival and were observed at the same site throughout the season without an apparent breeding attempt. This was particularly clear in the case of females known to have bred the previous season because a brood patch was not formed. There were two instances of birds actually roosting in the nest which they had occupied in the previous season, so they were not prevented from breeding by competition for nest sites. Finally, one quarter of known yearlings were captured just once and were not known to have bred within the study area. Four were captured for the first time late in the season, two of which had paired following the death of one of a pair. Some birds (n=7) were ringed as nestlings and caught for the first time aged two. These may not have bred during their first year, increasing the probability of evading capture. Møller (1989b) estimated that on average one eighth of all males remained unmated for the entire breeding season. No comparable value was calculated here, but it was not envisaged to be as large a fraction.

3.4 COLONY SIZE

In Britain, the Swallow usually breeds solitarily or in small loose colonies (Cramp 1988). In this study the term 'colony' was used to describe the number of breeding pairs occurring at one site. At larger colonies, where several buildings were occupied, breeding pairs were in close proximity and interacted regularly. Solitary sites held only one breeding pair and were isolated from other sites by about ≥ 300m (Møller 1987b). These pairs were not observed to visit occupied territories of neighbouring sites.

From 1987 to 1989 colony size varied from 1 to 14 pairs, with half having only one or two pairs (Table 3.2). Only two to four farms censussed within the study area had ≥ 10 pairs each season. These sites were, nevertheless, important as they held 20% of the total breeding population studied. These figures contrast with other European (Vietinghoff - Riesch 1955, Møller 1987b, 1989b) and North American studies (Shields & Crook 1987), where colonies of up to 100 pairs have been recorded. In the majority of these studies pairs nested semi-colonially, with some solitary sites (5-15%) and small colonies (15-33%), but with a majority breeding in moderately sized colonies of 9 to 35 pairs (review by Shields *et al.* 1988).

There were an average of 3.2 and 3.6 breeding pairs per site during first broods in 1987 and 1989 respectively, with 4.4 in 1988 (Table 3.3, *cf.* 1.1 in Southern England, Davies 1976). The population increase in 1988 was matched by an increase in the number of middle-sized colonies (≥5) and a decrease in the number of solitary sites; only half as many sites and colonies were located in 1987 and 1989 as were present in 1988. Usually only one or two, occasionally three or four and rarely a maximum of ten pairs nested in each building. In Denmark, although the mean number of breeding pairs was the same as observed here (Møller 1983), it was reported that the majority of pairs at most colonies nested within a single building. In one particular study site, 56 pairs nested together under one roof (Møller 1983, 1987b).

Table 3.2 Swallow colony sizes from 1987 to 1989

Colony Size	No. of sites in each year 1987	1988	1989	All years	Total No. of pairs
1	13	7	13	33	33
2	11	10	5	26	52
3	8	4	5	17	51
4	3	5	8	16	64
5	5	5	3	13	65
6	2	3	0	5	30
7	1	2	4	7	49
8	1	0	1	2	16
9	0	3	0	3	27
10	1	2	0	3	30
14	1	2	2	5	56
Total No. of pairs	143	188	142	473	473
Total No. of sites	46	43	41	130	

Table 3.3 Number of breeding pairs of Swallows at each site, by year and brood number

	1987		1988		1989	
	First	Second	First	Second	First	Second
No. of sites	45	45	43	43	40	40
No. of pairs	143	111	188	133	142	101
Mean No. of pairs	3.2	2.5	4.4	3.1	3.6	2.5
Range	1-10$^+$	1-10	1-14	1-14	1-10^a	1-10^a

a - at least ten pairs

Third broods attempted were: 1987 (n=2), 1988 and 1989 (n=2)

One female attempted three broods in each year of the study.

3.5 SITE FIDELITY

Breeding site tenacity is well known in the Swallow (Shields 1984b) and other Swallow species (Freer 1979). Dispersal, usually defined as the distance between consecutive breeding sites, is similar in most adults (Greenwood *et al.* 1979a). Studies of other bird groups have indicated that age (Austin 1949), sex (Greenwood 1980, 1983), local habitat, nest site stability (McNicholl 1975, Freer 1979) and prior breeding experience at a particular site or with a particular partner (review in Rowley 1983) may affect the degree and magnitude of dispersal.

Established breeders were site-faithful, usually returning to the same building. Less than 5% of adults were known to move sites (Table 3.4a). Mean dispersal distance was 1.1±0.5km, range 0.5 - 2.2km, with no difference between sexes. Over half moved to farms less than one kilometre away (Appendix 3.2). Other studies on Swallows (references in Cramp 198; Møller 1987b) and Barn Swallows (Shields 1984a; Crooks & Shields 1987b) have also found that adults are extremely site faithful though pairs which had a failed breeding attempt tended to have a higher probability of dispersing (Shields 1984b). Although dispersal has been incompletely analysed, this finding was not supported by my data. Of fourteen birds which were attempted breeding but which dispersed in the following season, nine were successfully double-brooded, thirteen raised at least one brood and only one female dispersed having failed to rear any young (Table 3.4b).

The proposed advantage of dispersal for failed breeders would only occur if failure was attributable to specific habitat factors which are likely to affect future attempts. As there can be no guarantee of 'success' and since the dispersing individual will also be unfamiliar with the new site, in general Swallows should benefit from 'staying' rather than 'dispersing'. There was no evidence of individuals being displaced from their former nest-site by an incomer. Disturbance at their former site, the loss of their partner or other chance factors seem the most likely reasons why both successful and unsuccessful breeders occasionally changed sites.

3.6 MATE FIDELITY

Both male and female identity was known for 53 and 97 breeding pairs in 1987 and 1988 respectively. Overall 15% of pairs remained together from one season to the next but this varied slightly between years; only two pairs were together for three successive seasons (Table 3.5). A change of partner usually resulted from the death or disappearance of the mate. Only three instances of 'change' were observed; in all cases these birds re-mated. Changing farms between broods was also accompanied by a change in partner. Other studies have found that pair-bonds usually continue during successive breeding attempts though they may break-up following nest failure or adult mortality between breeding

Table 3.4a Inter-seasonal adult Swallow dispersal to new breeding sites: 1986-87, 1987-88 and 1988-89

Dispersal Category	1986-87 M	1986-87 F	1987-88 M	1987-88 F	1988-89 M	1988-89 F	All[a] M	All[a] F
Total No. survivors	3	6	105	98	168	173	276	277
Total No. moved	0	1	7	4	2	6	9	11
Total No. moved to neighbouring site	0	0	4	4	2	4	6	8
Percentage (%) dispersed	0	16.7	6.7	4.1	1.2	3.5	3.3	4.0
Percentage[b] dispersed	0	0	57.1	100	100	66.7	66.7	72.7

a - one male and one female dispersed in two successive seasons:
b - includes only those which dispersed to neighbouring sites; none moved further than two sites away

Table 3.4b Inter-seasonal adult dispersal in relation to breeding success in the first season, for each sex

Category of br success[a]	Male	Female	Total
Successfully double brooded	2	7	9
Failed during the second brood	2	1	3
Successfully single brooded	1	-	1
Failed during first brood	-	1	1
Non-breeding	4	1	5
Site disturbed	-	1	1
Total No. moved site	9	11	20
Total No. attempted breeding	5	9	14

a - category of breeding success relates to the season prior to dispersal all birds which were categorised as non-breeding were only caught once in the study area.

seasons (Shields 1984b; Crook & Shields 1985). In this study pair-bond maintenance, within or between seasons, did not seem to be related to breeding performance. The probability of separation was not related to the success of the first brood. A shortage of alternative partners was not thought to be important in restricting separation.

3.7 NATAL SITE FIDELITY

The size of the study area limited the discovery of local recruits although additional records came via the BTO ringing scheme. Forty-nine pulli were known to survive overwinter; 47 were recaptured in the study area between 1986 and 1988 and the remaining two were trapped outside the study are. Of the 47, two were of unknown sex, 28 were male and 17 were female (Table 3.7). Five of these returns were ringed as fledglings and thus of unknown origin. Of the five, one stayed at the site of ringing (male), and three others (all male) moved to a neighbouring farm (x=0.9±0.4km). No breeding records were obtained for pulli which were ringed in the study area but which bred elsewhere. Only one bird was caught which was not ringed in the study area; a male ringed as a juvenile in June 1986 at a large communal roost in Grampian region. Very few juveniles were ringed in 1986 so it is possible that this bird was reared in the study area then dispersed North after fledging to be trapped while roosting. The fate of the remaining recruits is described below.

3.7.1 DISPERSAL DISTANCES

3.7.1.1 Males versus females

The mean distance moved from the natal site by yearlings was two and a half kilometres (±0.3; range 0-7.3km, Table 3.6). Males dispersed shorter distances than females (1.8km vs 3.8km, Z_{44}=-2.8, p<0.005). Four of twenty seven males, but no females, returned to their natal site but even excluding these birds males still dispersed shorter distances than females (2.1km±0.2 vs 3.8km±0.6; Z_{40}=-2.3, p=0.023). Overall, less than ten percent remained at their natal site. Other studies have also found that first year birds can return to within 3km of their natal site, most within 30km (Davis 1965; Davies 1976; Christensen 1981; Cramp 1988), but some up to 360 km away. Similarly Barn Swallow fledglings rarely return to their natal colonies (references in Crook & Shields 1987). Most settled within 6-15km of their natal site (Shields 1984b). Only 5% of nestlings returned to their natal area but none to their natal colonies (Shields 1984b). Male nestlings are more faithful to their natal area than females (Cramp 1988).

3.7.1.2 First versus second broods

First brood pulli which were later recruited moved the same distance from their natal site as those which were recruited from second broods (2.3km vs 2.9km; Z=-1.2, p=0.24). When analysed by sex the differences were still not significant (Males Z=-1.7, p=0.08; Females Z=-0.5, p=0.6).

Table 3.5 Mate-fidelity between 1987 and 1988, and 1988 and 1989

Number of pairs	1987/88	1988/89	Both years
Identified in year (n)	53	9.7	150
Identified as being the same in year (n+1)	11	12	23
% Faithful from year (n) to year (n+1)	20.8	12.4	15.3
Identified as being the same in year (n+2)	2	-	-
% Faithful Year (n) to Year (n+2)	3.8	-	-

Table 3.6 Inter-seasonal juvenile dispersal (km), by sex and brood number, for nestlings ringed in 1986, 1987 and 1989

Sex	Brood	mean (se)	median	range	n
All[a]	All	2.52 (.29)	2.25	0.0[b] - 7.3	44
	1st	2.30 (.41)	2.20	0.0 - 7.3	25
	2nd	2.91 (.44)	2.38	0.0 - 6.3	14
Male	All	1.81 (.24)	2.00	0.0 - 4.4	27
	1st	1.40 (.34)	1.25	0.0 - 4.4	14
	2nd	2.41 (.40)	2.30	0.0 - 4.3	9
Female	All	3.80 (.55)	4.15	0.4 - 7.3	16
	1st	3.45 (.72)	2.50	0.4 - 7.3	11
	2nd	4.41 (.93)	4.78	1.9 - 6.3	4

a - All included 1st, 2nd and also recruits which came from unknown brood numbers or relay attempts

b - 0.0 refer to recruits which returned to natal site

3.8 ADULT MORTALITY DURING THE BREEDING SEASON

Mortality is assumed to occur primarily outside the breeding season (Møller 1989b). Some birds may die during breeding but the exact number is difficult to quantify. Predation accounted for about 70% of all known casualties (Table 3.8). Additionally the remains of 5-10 killings were found each season, though they were possibly injured or already dead before being taken by a ground scavenger. The main mammalian predators in the study area were the Domestic cat and the Rat. The main avian predators were the Tawny Owl and the Sparrowhawk.

Three females and two birds of unknown sex were found dead early in the season with no apparent injuries. Two of the females had a full brood patch and were found beneath their nests; one had been incubating whilst the other had laid a pygmy egg on the previous day. The remaining birds were found in April. These birds were found to have poor body condition (see Chapter 7). Starvation was suspected as a contributory cause of death on several occasions but there was only one definite record; a male (age class 3-3+) rearing an artificially enlarged first brood (+3 nestlings) was found dead in the nest among the brood on Day 16 of the nestling period. It weighed only 14g, whereas on Day 12 and 14 it weighed 18.2g and 17.9g respectively. Seven of the eight young were dead on inspection and the eighth died later that day. The male may have died feeding the brood or when roosting at night (other records were made of one or both parents burying themselves under their broods while roosting). The mate may have abandoned the brood earlier as she was observed with a new partner two days after his death and successfully reared a second brood. On Days 12 and 14 the female weighed 17.4g and 17.0g respectively (incubation mass was 20.5g).

3.9 ANNUAL ADULT AND JUVENILE SURVIVAL ESTIMATES

3.9.1 ADULTS

Males survived slightly better than females (Table 3.9a,b). Only a small sample of birds was ringed in 1986, so comparisons are only made between 1987-88 and 1988-89. Male and female survival was lower for 1988-1989 than for 1987-1988 (Table 3.9a). This decrease coincided with a population drop in 1989. Such fluctuations in survival rates are consistent with estimates presented elsewhere. Forty five per cent of breeding Barn Swallows returned to the same colony to breed the next year (Crook & Shields 1987).

3.9.2 JUVENILES

Juvenile survival values are minimum estimates, indicative only of the number of recruits which returned to their natal area (Table 3.10). Of 1600 pulli ringed and fledged only 49

Table 3.7 Sex of pulli which survived over winter, analysed by the year in which they were ringed

Sex of Pullia	Year nestling ringed 1986	1987	1988	All years
Male	3	15	10	28
Female	1	10	16	17
Unknown	0	1	1	2
Total	4	26	27	47[b]
% Males[c]	75	60	38	62.2
% Females	25	40	62	37.8

a - sex was determined on recapture the following season(s)

b - two pulli survived overwinter but were retrapped outside of the study area; these are not included in the above figures (see Table 3.10).

c - percentages were calculated excluding yearlings of unknown sex

Table 3.8 Intra-seasonal adult mortality[a] observed between 1987 and 1989

	Cause	Males	Females	Adults
Predation	1	10		11
Injured	1	-		1
Starvation	1	-		1
Unknown	-	3		3
Total	3	13		16

a - the above figures represent only those cases where carcasses were found. Remains (mainly feathers) of an additional 5-10 birds were also located around farms. Four females and four broods were predated at one farm during a 48 hr period. Estimates presented above may be biased towards breeding females since the area around the nest was checked most frequently and so remains were more likely to be found.

Table 3.9a Estimates of minimum[a] adult survival over the periods: 1986-87, 1987-88 and 1988-89

Category	Sex	No adults ringed/recaptured 1986-87	1987-88	1988-89	All
Ringed in the study area	M	6	109	169	384
	F	11	99	188	298
Known to be dead in year (n)	M	-	4	1	5
	F	-	1	15	16
Total assumed to be alive in year (n)	M	6	105	168	279
	F	11	98	173	282
Recaptured for the first time in year (n+1)	M	2	51	55	108
	F	6	42	43	91
Recaptured for the first time in year (n+2)	M	1	1	no	(2)
	F	-	3	no	(3)
Total number known to have survived to year (n+1)	M	3	52	55	110
	F	6	45	43	94
Percentage (%) survival[a]	M	33.3	48.6	32.5	-
	F	54.5	42.9	24.9	-
Percentage (%) survival[b]	M	50.0	49.5	-	-
	F	54.5	45.9	-	-

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a - based on minimum estimates (i.e bird recaptured or not in the following year

b - based on maximum estimate (i.e excluding birds which were dead in year (n) or which were unlikely to be recaptured in year (n+1) as a consequence of catching not being carried out at a particular site

1- birds which were recaptured for the first time in year (n+2) represented < 1% of the total population recaptured: Males = 2/279; Females=3/283 One adult (male) was recaptured outside the study area

Table 3.9b Estimates[a] of maximum adult survival over the periods: 1986-87, 1987-88 and 1988-89

Category	Sex	No adults ringed/recaptured 1986-87	1987-88	1988-89	All
Ringed in the	M	6	91	133	230
study area	F	11	80	133	224
Recaptured	M	3	52	55	110
	F	6	45	43	94
Percentage	M	50.0	57.1	41.4	47.8
survival	F	54.5	56.3	32.3	42.0

a - Maximum estimates were calculated by eliminating birds which were known to be dead in year (n) or where disturbance had taken place at buildings which previously has contained nests (these birds were less likely to be recaptured). Additionally, birds caught only once during the breeding season in year (n), but which were known not to have bred at that site were also assigned to an unknown survival status and so excluded from the above estimates (also see Chapter 2).

Table 3.10 Estimates of minimum juvenile survival over the periods: 1986-87, 1987-88 and 1988-89

Category	No pulli ringed/recaptured 1986-87	1987-88	1988-89	All
Ringed in the nest	30	645	993	1668
Ringed out of the nest	3	26	40	69
Known to be dead in year (n)	-	22	62	84
Total assumed to be alive in year (n)	33	649	971	1653
Recaptured for the first time in year (n+1)	3	21	17	41
Recaptured for the first time in year (n+2)	1	5	na	6
Controlled outside the study area	-	2	-	2
Total number known to have survived	4	28	17	49
Survival S^a (%)	9.1	3.3	1.8	2.5
Survival S^b (%)	12.1	4.0	no	2.8
Survival S^c (%)	12.1	4.3	no	3.0

a - No recap year (n+1) / total assumed to be alive year (n)

b - Total recap within study area / total assumed to be alive year (n)

c - Total pulli known to be alive / total assumed to be alive year (n) were recaptured as adults during the study, of which two were caught outside the study area and six were first recaptured two years after ringing. Three survival estimates which exclude and include the above values have been calculated, to give minimum and maximum estimates of return rates of juveniles to their natal area. Despite more young being ringed in 1988, 1988-1989 return rates were almost half those of in 1987-1988. In 1987-1988, 7% of all nestlings recaptured were caught outside the study area and 18% were first trapped the second year after ringing. By including all available data on returns, the maximum survival estimate was 4.3%. If birds caught outside the area or two years after ringing were excluded, the survival estimate decreased to 3.3%. Shields (1984b) estimated that 5% of ringed nestling Barn Swallows returned to the study area.

3.10 BREEDING BIOLOGY

A summary of breeding data analysed by brood number (first or second) is given in Table 3.11. Variability between years and broods is investigated later in Chapter 5.

3.10.1 TIMING OF BREEDING

In Britain, the main breeding season of the Swallow is between April and August, depending on the latitude, earlier in the South (March) and later in the North (Bent 1942; McGinn & Clark 1978; Cramp 1988). In this study the earliest laying date was the 4th May. Only two clutches were started in September but neither of these hatched. Mean laying dates for first and second broods were the 23rd May and 19th July. Breeding span, defined as the period between the first and last egg-laying of the season, was 109 days. Laying always commenced by Week 6 and continued until Week 20.

The peak of first-brood egg laying was in Week 8 when a third (36.2%) of all laying started. Three quarters (78%) of all first broods attempts commenced in Weeks 7, 8 and 9 (Fig 3.1). Second-brood egg laying peaked during Weeks 15 and 16 when about half the second clutches were initiated. Twenty per cent started in Week 17 (Fig 3.1). All laying was completed by Week 21.

3.10.2 LAYING INTERVALS

Most hirundines usually lay their eggs daily (Bryant 1979; Turner & Rose 1989, Chapter 3) but interruptions in laying, termed as anomalies, are also known to occur (Bryant 1979). A laying suspension refers to a female which lays her eggs at an interval of greater than one day but less than five days, and an interrupted laying is where there is an interval of more than five days between eggs (Bryant 1979). In this study the interval (days) between eggs was checked daily at 66 nests, termed here as 'complete' checks, and

Table 3.11 **Breeding parameters (mean, se and range), by brood number. Data are 1987, 1988 and 1989 combined**

Breeding parameters	Brood number	mean	se	range	n
Date of first egg[a]	1st	54.9	0.5	34-83	290
	2nd	109.8	1.0	82-146	167
Clutch size	1st	4.9	0.1	3-7	286
	2nd	4.4	0.1	2-6	167
Brood size	1st	4.6	0.6	1-7	271
	2nd	4.1	0.1	1-6	151
Hatching success[b]	1st	92.2%	-	-	271
	2nd	93.0%	-	-	151
No. fledged	1st	4.1	0.2	0-6	167
	2nd	3.4	0.1	0-5	105
No. fledged[c]	1st	4.2	0.2	1-6	162
	2nd	3.8	0.1	1-5	94

a - nth day after April 1st; 55= 25th May

b - hatching success = clutch size/brood size

c - complete nest failures are excluded (i.e no young fledged).

Table 3.12 **Frequency of laying anomalies observed in Swallows in 1988 and 1989**

	"Complete[a]" checks			" Incomplete[b]" checks		
Total	1988	1989	Both years	1988	1989	Both years
No. nest inspected	23	43	66	25	30	55
No. of Intervals	84	155	239	151	54	205
No of Intervals > 1 day	3	3	6	6	3	9

a - "Complete" = nests inspected daily during laying

b - "Incomplete" =not checked daily

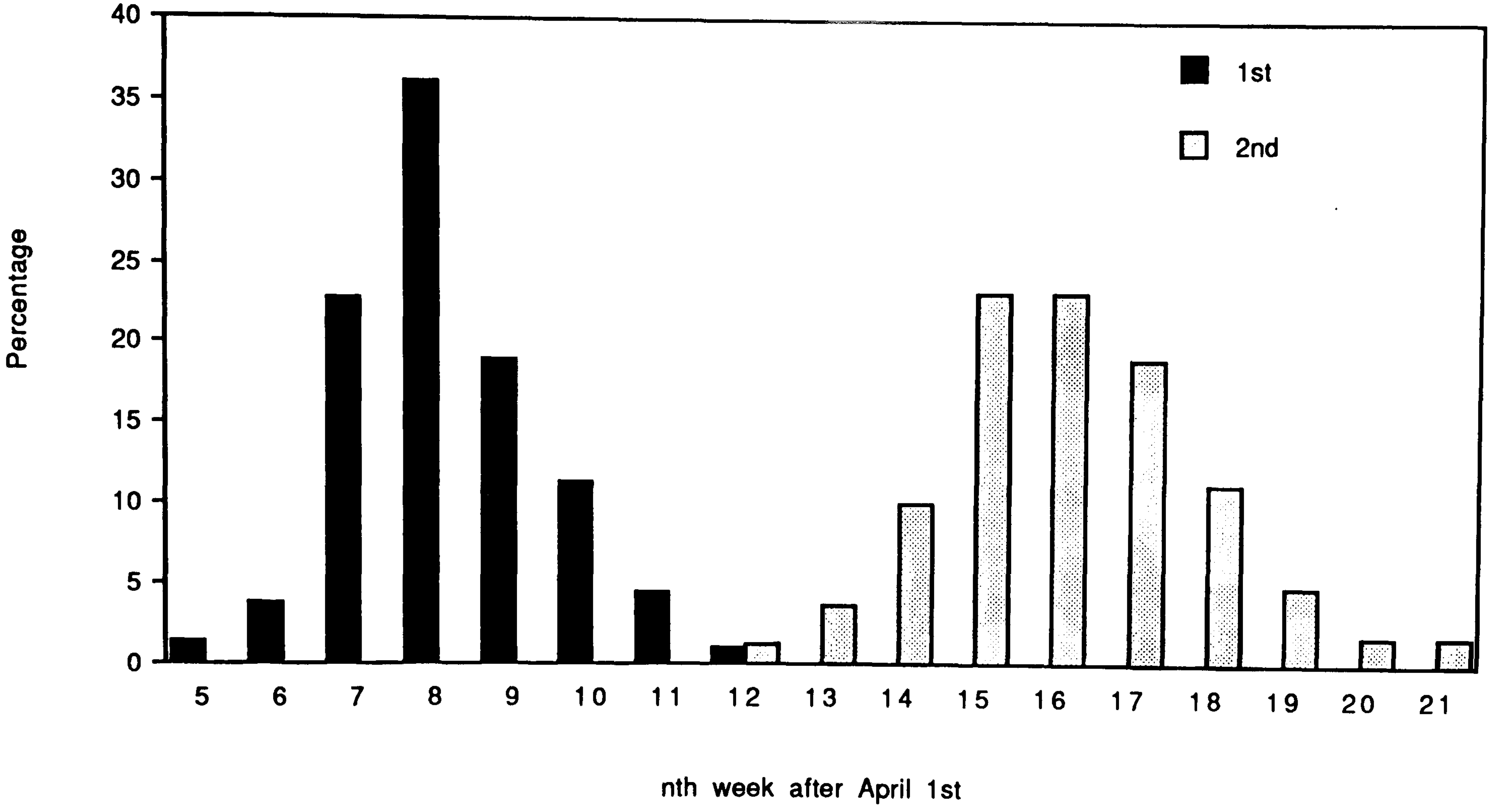


Fig 3.1 Frequency (%) of laying dates during first (n=290) and second (n=167) broods. Data are for 1987 to 1989

intervals longer than one day were detected at six nests (Table 3.12). 'Incomplete' checks were made at 55 nests and nine more anomalies identified. Anomaly duration varied from one to fourteen days (mean 3 days, Fig 3.2a). Interrupted laying occurred on four occasions and had a mean interval of nine days. These delays were not attributed to there having been a change in female. On one occasion a female (ringed) laid the second egg of her second brood 14 days after the first egg was laid. A clutch of six was eventually laid (all of which hatched), demonstrating that the first egg laid was still viable even though it had not been incubated until eighteen days after it was laid. Half of all anomalies occurred between the first and the second egg (53.3%, Fig 3.2b). None was identified after the fourth egg (but see Ward 1992). Anomalies were detected in both first and second broods but only on two occassions were they linked with reduced food availability (Ward 1992). The apparent lack of importance of food resources in causing laying interruptions could be because: a) the suction trap was unable to detect small but important differences in food abundance or quality between sites (also see Chapter 5) or, b) females laid an egg at some other location, perhaps due to disturbance around the building (Ward 1992).

3.10.3 CLUTCH SIZE

Eighty-five percent of clutches had four or five eggs (Fig 3.3a). First-brood clutch size varied from three to seven eggs (4.9±0.1, n=286, Table 3.11; Fig 3.3b), second-brood clutch size from two to six (4.4 ±0.1, n=167, Table 3.11; Fig 3.3b). Clutches of five or six eggs were rarer in second broods (52.1% versus 78.6%) whereas clutches of two or three were more common (10% vs 3%, Fig 3.3b). For general reviews of Swallow or Barn Swallow clutch sizes see Turner (1980), Cramp (1988) and Turner & Rose (1989). Some of these data are summarised in Appendix 3.5. Brood number and season effects on clutch size are analysed in Chapter 5. Clutch size increases with nest volume (Møller 1982) and the size of the second clutch decreases with increasing latitude (Møller 1984a).

3.10.4 HATCHING "SUCCESS"

From 1987 to 1989, 1415 first clutch eggs were laid (286 nests); average hatching success was similar (above 90%) for all years, and consistent with that reported for Swallows and other hirundines (Cramp 1988; Turner & Rose 1989). Only 7.8% of eggs failed to hatch as a result of presumed natural causes (infertile, chick dead in egg). No predation of eggs was recorded but four females were predated during incubation (carcasses or remains found) and six nests fell down, resulting in hatch failure. Infertile clutches were laid by four females. These clutches were incubated for 19 or more days before they were deserted, and were always followed by a new, successfully hatched, clutch. Hatch failure due to infertile eggs has been estimated at 7.2 % (Boyd 1936, 10% and McGinn & Clark 1978, 7.2%). Hatch failure in the study population has been investigated in detail by Ward (1992).

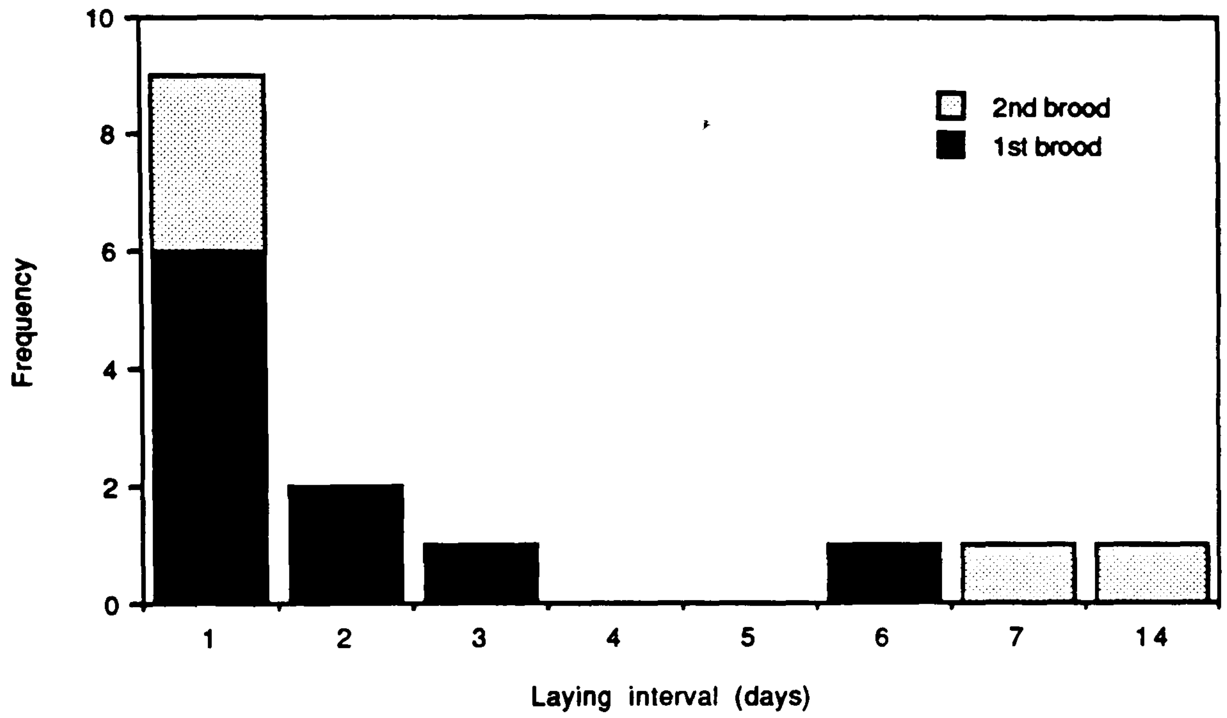


Fig 3.2a Duration of interval between eggs for laying anomalies during first and second broods

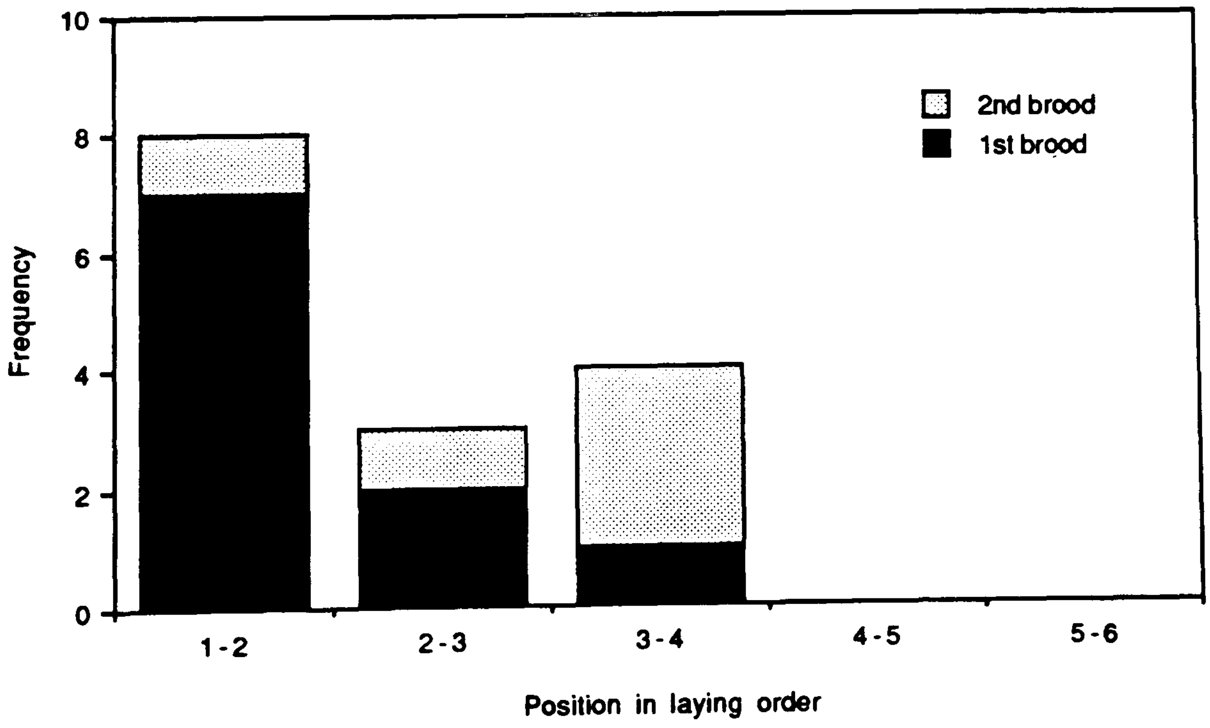


Fig 3.2b Position in laying order where a laying anomaly was recorded

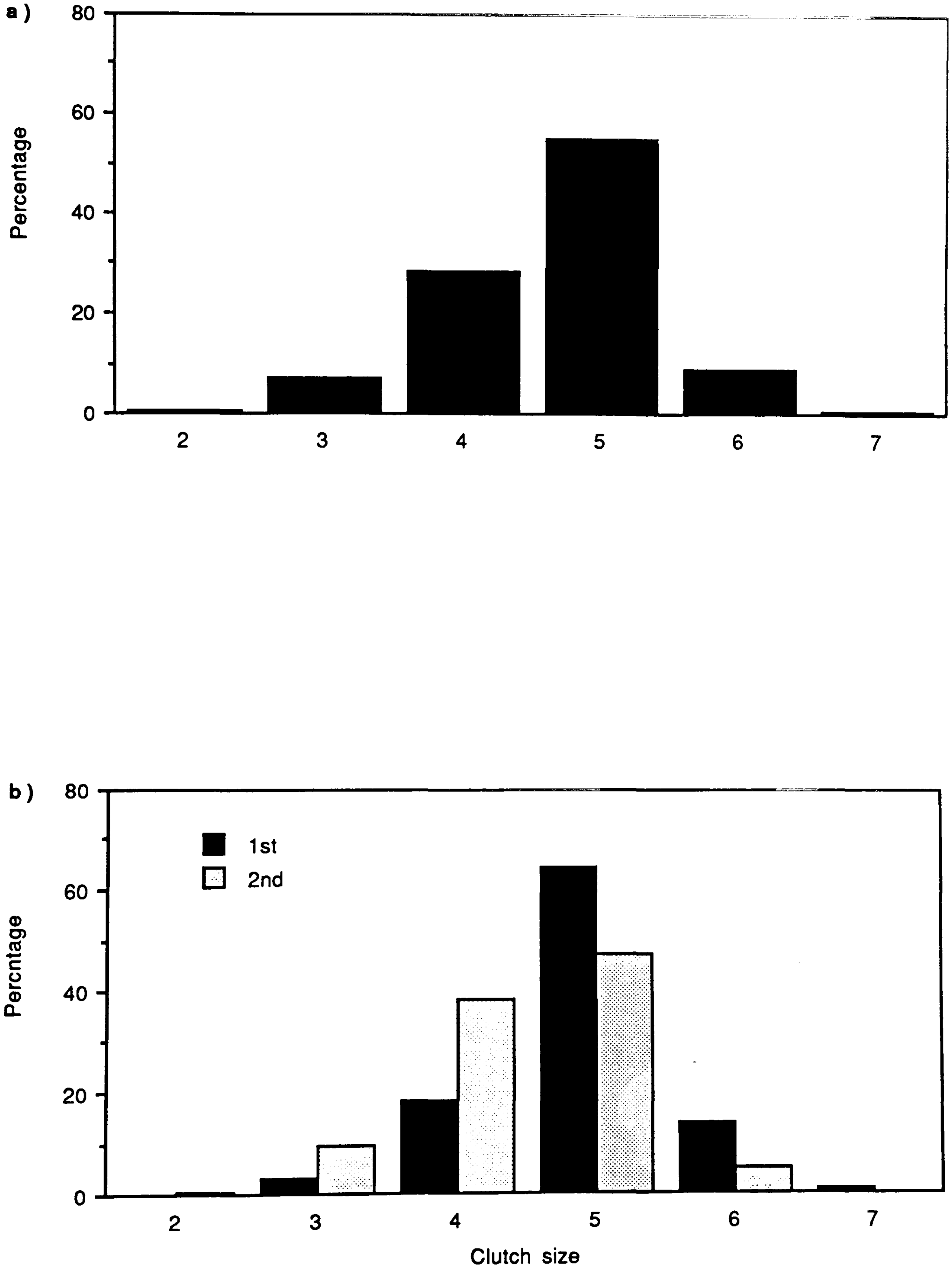


Fig 3.3 Frequency (%) of clutch sizes laid between 1987 and 1989: a) All clutches (n=453) and b) First (n=286) and Second (n=167) clutches

Hatching success varied considerably between individuals. Two females observed in all three years differed in their hatching success. One which laid a total of 39 eggs with a hatching success of only 49%: (1987: 3/6, 4/6; 1988: 3/6, 1/4, 3/5; 1989: 2/6, 3/6, first and second broods respectively). The other, double-brooded in each season with six clutches of five eggs, successfully hatched all 30 eggs. Both females had two different partners but hatching success was the same with both. Complete hatching success (i.e 100%) was recorded for 110 females known to be double-brooded and ten pairs double-brooded in successive seasons. McGinn & Clark (1978) found that clutches of six hatched better than clutches of two or three. Though not tested in this study the majority of clutches of six were laid early in the season by older females. The quality of eggs may vary with incubation behaviour, age, mate fertility, individual or season (also see Ward 1992). A tendency for higher hatching success in northern latitudes, present in House Martins, was not significant in Swallows (Møller 1984b).

3.10.5 NEST "FAILURE"

Half of nest failures (i.e where no young fledged) were prior to hatching, three quarters prior to the midpoint of the nestling period (Table 3.13). Failure during laying was uncommon. Where eggs hatched at least one young usually fledged. A third of nest failures were attributed to disturbance (23%) and predation of a parent (11%). The stage of nest failure differed between first and second broods. More first brood nests failed during incubation (40% vs 29%). Total nest failure during the nestling period was similar (52% vs 59%, first and second broods respectively) but the exact stage at which they failed differed, most first-brood failures (64%) occurred before Day 10 whereas most second-brood failures (61%) occurred after Day 10.

3.10.6 NESTLING MORTALITY

Predation of parents or nestlings, disturbance and nest falls accounted for almost one quarter (23.8%) of total nestling mortality (Table 3.14a). The importance of other causes of mortality have been calculated by excluding this percentage. These new figures show that starvation accounted for 21% of mortality, 70% of which were the result of complete brood starvation. Mortality was highest from Day 0 to Day 5 (39%, Table 3.14) though exact causes of death were uncertain. Where nests were checked on Day 1, individuals were often found to be chilled or dead in the nest. These dead or moribund young had been removed on later inspection with eight found below the nest. Twenty-two percent of nestlings disappeared between hatching and Day 12, probably dying early on in this period through starvation or nest falls, which in some cases might be connected. Of 72 nestlings found dead in or below the nest, 62 came from complete broods (17 nests). Only five post-fledging deaths were recorded, all had very low peak nestling mass and died shortly after fledging (carcasses were found in the natal building). It is doubtful

Table 3.13 Number of pairs which failed during breeding, by stage in the nesting cycle and brood number. Data are for 1987 and 1988 combined

Stage in the nesting cycle	Brood number First n	 Second n	 Both n
Laying	4	4	8
Incubation	19	9	28
Nestling period I[a]	9	11	20
Nestling period II[b]	16	7	23
Clutch reduction[c]	7	3	10
Brood reduction[d]	4	7	11
Total	59	41	100
Predation[e]	11	6	17
Disturbance[f]	14	20	34
Total	25	26	51
Overall Total	**74**	**67**	**151**

a - nestlings age 0 - 7 days (inclusive)

b - nestlings age 8 -16 days (inclusive)

c - eggs removed by author during laying or incubation for experiments

d - nestlings removed by author during nestling period I for experiments

e - Predation: males, females or nests

f - Disturbance includes birds which were caught but which subsequently deserted; destruction of barn, entrances blocked or doors closed and broods or clutches removed for experiments.

Table 3.14a Causes of nestling mortality[a] in Swallow nests inspected between 1987 and 1989

Cause and time[b] of death	Total No. of Nestlings	% Total	% Total[c]
Dead in or below nest ≤ age 5 days	72	30.6	39.1
Dead in or below nest > age 5 days	22	9.4	12.0
Disappeared from nest (days 0-15)	41	17.4	22.3
Starvation	38	16.2	20.6
Nest fall	6	2.6	3.3
Disturbance	33	14.0	-
Parent predated	5	2.1	-
Nest predated	13	5.5	-
Found dead post-fledging	5	2.1	2.7
Total	235	100	100

a - only nestlings from Control broods included, 235 nestlings from 84 nests; at 38 nests no nestlings fledged

b - stage in the nesting cycle

c - nestlings which died as a result of disturbance or predation are excluded

Table 3.14b Mortality of 131 nestlings in 308 Swallow broods from 1982-1986; Table 1, p367, Møller (1988)

Cause of death	Total %
Infanticide	32.1
Starvation	29.0
Mite infection	13.7
Female dead	6.9
Nest fall	6.1
Unknown	12.2

that these birds should be classified as fledged. The post-fledging mortality identified in this study is probably an underestimate but more precise data is not available.

Major causes of nestling mortality in Denmark were starvation (29%) and mite infection (14%) while female death and nest falls accounted for only 13% (*cf*.4.7% this study). Mite infection was not investigated during the present study. Nestling predation was not recorded (*cf*.5.5%, this study) and the cause of death was undetermined in 12% of cases (Møller 1988b, data in Table 3.14b here). Møller attributed the absence of predation to inaccessibility of nests for ground predators and as most nests were inside buildings he suggested that they were defended against other types of predation. In this study a Sparrowhawk was observed (A Newton *pers comm*) and a Tawny Owl suspected of predating nests, undermining Møller's assumption.

More important are the different interpretations of nestling mortality from Day 1 to 5 (31% this study vs 32%, Møller 1988b). Møller (1988b) attributed nestling mortality during this period entirely to male infanticide, that is the killing of young by a male in order that he might increase his probability of gaining a mate, as he directly observed a non-resident remove chicks three times. Furthermore, since entire broods disappeared during this period Møller argued that these findings could not be explained by starvation. Similar conclusions have been made for the Tree Swallow (Robertson & Stutchbury 1988) and the Barn Swallow (Crook & Shields 1985). Myers & Waller (1977) and Medvin *et al.* (1987) did not, however, observe any instances of infanticide in Barn Swallows, and nestling mortality from Day 1 to 5 was not attributed to infanticide in the present study for two reasons. Firstly, nestlings were often chilled or dead in the nest on Day 0 or Day 1. On later inspection these dead or moribund young had been removed and were usually beneath the nest. Secondly, when complete broods disappeared, the pair re-laid without changing partner. It is suggested, therefore, that nestlings were removed during this period because one or two nestlings died shortly after hatch. The nest was then abandoned and a new attempt was made in the same or in a new nest.

While such an interpretation might explain the " 9 cases where all nestlings during the first few days of their lives disappeared from one day to another " (Møller 1988b, p 366), it does not explain the infanticides he directly observed at three nests "where three different unmated males removed all nestlings within a single hour by visiting the nest when it was unattended, picking up a nestling, flying away and dropping it on the ground" (Møller 1988b, p 366). In most cases the male disappeared, presumed dead, prior to infanticide. It was assumed that the unmated male later mated with the widowed female. Re-nesting took place in 12 of the 14 cases.

3.10.7 NUMBER OF BREEDING ATTEMPTS

Eighty-four percent of pairs attempted at least two broods in a season, ten percent had a replacement clutch during the first or the second brood but less than one percent incurred

Table 3.15 **Breeding attempts (%) made each season. Data are for 1987, 1988 and 1989**

Broods attempted[a]	% Total
First brood only	18.6
First + second	60.4
First + second + third	1.1
First + first relay (r) only	2.7
First + first (r) + second	2.7
First + second + second (r)	1.9
First + first (r) +second + second (r)	0.5
First + first (r) + first (r)	1.3
Unknown	8.1
Unknown but at least first + second	2.7
All double-brooded[b]	83.2[c]

a - results are for all observed nesting attempts including those which relayed as a result of some form of disturbance or predation and also includes those which were experimentally manipulated

b - summary result for percentage pairs double brooded; pairs which reared manipulated first broods or which had an unknown number of breeding attempts are not included

c - 88.9%, 82.% and 75% were double brooded in 1987,1988 and 1989 respectively.

Chapter four
(pp 32 - 46)

Body Size Variation in the Adult Swallow

4 BODY SIZE VARIATION IN THE ADULT SWALLOW

4.1 INTRODUCTION

Morphometric data have served an important role in a wide range of avian studies and are crucial in shaping the ecology and life history of individuals (Peters 1983). Body-size has a strong heritable component (Boag & Grant 1978; Smith & Zach 1979; Dhondt *et al.* 1979; van Noordwijk *et al.* 1980; Garnett 1981; Moss & Watson 1982; Boag 1983) but non-genetic environmental factors are also important (James 1983) yet in field studies it is commonly assumed that phenotypic variation closely reflects underlying genetic variation (Grant *et al.* 1976). Within any species, body size and other phenotypic characteristics may vary between individuals, sexes, populations, seasons, years, locations (James 1970; Mosimann & James 1979) and in relation to climate (Mayr 1956; Johnston & Fleischer 1981; Jones 1987c). Natural selection can act on this variation to influence individual fitness. Darwin (1871) first proposed that sexual dimorphism in body size or ornament is often a product of inter- or intra-sexual selection. This theory has been supported more by recent research (Searcy 1979a; Price 1984a; Andersson 1982; Møller 1988a,1990a).

4.1.1 SEXUAL SELECTION

Sexual selection occurs in response to competition for resources (intra-sexual selection), or through mate choice (inter-sexual selection), directly or indirectly affecting reproductive success. Much work has focussed on identifying possible agents for mate choice and understanding how such preferences might evolve. The theory of sexual selection predicts greater sexual dimorphism in polygynous than monogamous species (Clutton-Brock 1983) because polygyny produces greater competition for mates. Female mate choice has been associated with the evolution of secondary sexual characteristics such as exotic plumage colouration, ornamentation such as tail feathers, comb characteristics, and colouration as well as elaborate courtship displays and vocalisations (Andersson 1986; Zuk 1991, also see section 4.1.2). Both observational (Trail & Adams 1989) and experimental studies (Andersson 1982; Schantz *et al.* 1989) support this conclusion.

4.1.2 COSTS AND BENEFITS ASSOCIATED WITH VARIATION IN BODY SIZE

During the annual cycle or lifespan of individuals, body-size variation has been related to several life history traits and dominance and territoriality (Fretwell 1969; Kikkawa 1980; Smith *et al.* 1980; Rohwer *et al.* 1981; Ulfstrand *et al.* 1981; Jarvi & Bakken 1984; Desrochers *et al.* 1989; Newton, S.F. 1989, but see Schantz *et al.* 1989), individual recognition (Whitfield 1987), foraging ecology (Møller 1989a; Morton & Morton 1987; Gosler 1987), mate choice (Andersson 1982; Røskaft & Jarvi 1983; Brodsky 1988; Møller 1988a, 1990a; Schantz *et al.* 1989; Barnard 1990; Hill 1990; Höglund *et al.* 1990; Zuk *et al.* 1990), flight dynamics (Pennycuick 1969; Andersson & Norberg 1981; Alatalo *et al.* 1984), energetics (Downhower 1976; Johnston & Fleischer 1981; Bryant & Westerterp 1982, 1983a,b; Lehikoinen 1986b; Røskaft *et al.* 1986; Bryant & Tatner 1988) and physiology (Downhower 1976; Langston *et al.* 1990). Many of these factors have also been shown to be directly or indirectly related to the probability of survival (Fleischer & Johnston 1982, 1984; Lehikoinen 1986a; Monaghan & Metcalfe 1986, but see Jones 1985, 1987c; Langston *et al.* 1990) and components of reproductive success (see Chapter 5).

Accurate body-size measures are important to resolving these problems, prompting researchers into investigating what might reflect the best measure of overall or 'basic' body size. It has been suggested that any single parameter is unlikely to accurately represent basic body size. Instead, indices derived from a combination of size characters (Sibly *et al.* 1987; McGillvray & Johnston 1987; Rising 1987b), or multivariate measures such as Principal Component Analyses (Johnston & Selander 1971; Zink 1986; Rising 1988), are likely to give a more accurate measure of size. Applications of such techniques in ornithological studies are discussed by Mosimann & James (1979) and Bookstein *et al.* (1985).

4.1.3 CHANGES IN ADULT BODY SIZE BETWEEN YEARS

Early studies commonly assumed that adult body size was constant in birds. Although skeletal measures do not appear vary in adult birds, other parameters, such as wing-length (reviewed by Alatalo *et al.* 1984), tail-length (Banbura 1986; Møller 1988a, 1990a, Cherry 1990) or bill measures (Price & Grant 1984; Gosler 1987; Morton & Morton 1987; Matthysen 1989) may vary annually and seasonally. Evidence of a change in size with age has come from comparisons of yearling size with adult size. This may be misleading, however, as any observed differences may also result from differential mortality with respect of size, immigration or a shift in the mean age of the population. Direct evidence requires that individually marked birds are measured in successive years (Leverton 1989; Francis & Wood 1989).

4.1.4 RELATIONSHIP BETWEEN NESTLING AND ADULT SIZE

The relationship of nestling to adult size, and the effects of variation in adult size in a wild population of birds, are difficult to discern because mortality and dispersal usually occur between birth and attainment of adult size. Few studies have demonstrated categorically that the size of nestlings or fledglings is maintained into adulthood. Studies of laboratory populations, where such relationships can be examined more precisely, have shown that both food availability and "quality" can influence growth rates and that these effects may persist until adulthood (Boag 1987a; Johnston 1990).

4.1.5 AIMS

The aims of this chapter are to accurately measure intra- and inter-sexual variation in the adult body size of Swallows and in particular, to test for age-related trends. This study did not specifically examine the relationship of nestling size to yearling size but some data were collected to provide a better understanding of variation in adult body size. Two questions were addressed: (i) is nestling size related to adult size? and (ii) do the date, brood number or year of hatching affect adult body size? The relationship of survival to body size was also analysed.

4.2 METHODS

Adult Swallows were captured during daytime using mist-nets and at roost using a hand-net on an extendible pole. Individuals were sexed using their brood patch. Where pairings were confirmed, the relationship between male and female size was examined.

4.2.1 ADULT BIOMETRICS

Seven body-size measures were taken at each capture. A second tail-length measure was used in 1988 and 1989.

1. Wing-length: 150mm stopped rule (nearest mm). Flattened maximum chord recorded.

2. Outer tail-length: 150mm unstopped rule (nearest mm). Pygostyle tip to the tip of the outermost tail-streamer. Flattened, straightened, measured along the edge of the rule.

3. "Second" tail-length: 150mm unstopped rule (nearest mm). Pygostyle tip to tip of the second longest tail feather. Flattened,straightened, measured along the edge of the rule.

4. Inner tail-length: 150mm unstopped rule (nearest mm). Pygostyle tip to tip of the inner most tail feather. Flattened, straightened, measured along the edge of the rule.

5. Head-to-bill length: Dial callipers (nearest 0.1mm). Maximum length from the back of the head to bill tip.

6. Keel-length: Dial callipers (nearest 0.1mm). Length from tracheal pit to the posterior edge of the sternum.

7. Tarsus-length: Dial callipers (nearest 0.1mm). Distance from beneath the elbow to the uppermost point of the tarsus.

Wing, outer, "second" and inner tail-length measures were nearly always taken on the right-hand side (Smith & Montgomerie 1991). Where feathers were broken or abraded the left-hand side was measured. When both sides were damaged no measure was recorded. No comparisons between right and left hand side parameters were made (*cf*. Møller 1990e). Mean values were used in analyses where individuals were captured several times in a season. All measures were highly repeatable except tarsus-length which was excluded from some analyses (see text).

4.2.2 SIZE CLASSES

Individuals were categorised as "small", "medium" or "large" by splitting the size range of each parameter into three groups. Upper and lower outliers were not included. Measures were normally distributed so the medium was usually larger than the small or large size class.

4.2.3 PLUMAGE VARIATION

Three plumage characters were colour-scored during the study (P1=Under tail coverts; P2= Breast and belly; P3=Chest-band). All three were scored on a 0-5 point scale, with increments of 0.5 (where 0 represents the dullest individuals). P1 and P2 were scored from dull white to a rich rufous brown. P3 was scored from a pale dull blue to a very dark and shiny blue/black colour. Only birds scored during daylight hours were included in analyses. Mean values were used for individual caught more than once in a season.

4.2.4 CHANGE IN ADULT BODY SIZE MEASURES

When individuals were measured in successive years the change in size (ΔS) of each parameter was calculated by subtracting the size in Year (n) from the size in Year (n+1). Initial size may influence the size of the change so ΔS was also expressed as a percentage of size at Year (n).

4.2.5 MEASURING NESTLINGS AND FLEDGLINGS

Nestlings and fledgling measurements are described in Chapter 2. Brood means were combined for all years to obtain a mean for each age (days). Inner- and outer-tail-length, and keel-length were usually measured after Day 15.

Nestlings usually fledged from Day 18 to 21 days so most data were collected to this age. After Day 25, some fledglings were caught away from the nest and in general represent a single measure (rather than a brood mean). Few birds were caught after Day 40 so a mean was calculated for all birds caught between Days 40 to 84 .

4.2.6 STANDARDISED BODY SIZE

From Day 10 to Day 30, standardised size at a certain age (days) was calculated for each body-size measure for each individual using the mean and standard deviation (SD) for each age (Days 1-30) of the population (pop_n) in a given year. Standardised individual size for each day was calculated as follows:

$$Size_{std} = (size_{indiv} - size_{popn\ mean}) / SD_{popn}$$

The size of surviving nestlings was compared to the mean of the population. A mean standardised score was calculated for individuals measured more than once. Similarly, a standardised size was computed for yearlings.

4.2.8 ADULT SURVIVAL

All adults were assigned to a survival class at the end of the study (Chapter 2). Body size of survivors (Survived) and non-survivors (Died) was compared. Birds which reared experimentally manipulated broods were excluded because the degree of manipulation affects survival (Chapter 6). Age and brood number also affected survival (Chapter 5) and so were also analysed separately.

4.3 RESULTS

From 1987 to 1989, 396 males and 442 females were caught and measured. Year data are not independent because some birds survived from one year to the next. In 1987, 206 birds were caught of which 17% were recaptured in 1989 (Table 4.1). Body-size parameters were normally distributed (Fig 4.1a to 4.1f) so parametric analyses were used. Plumage scores were not normally distributed (Fig 4.2a,b,c), even after transformation, so they were analysed by non-parametric tests.

4.3.1 VARIATION OF ADULT BODY SIZE AND PLUMAGE WITH AGE

The exact age composition of the two year-old age class (≥ 2) was unknown, but it almost certainly contained some birds older than two. "Known one year-old" and "assumed one

Table 4.1 Adult Swallow catches by year and age class

Year	Sex	Age classes 1	≥ 1	2	≥ 2	≥3	Total
1986[b]	M	6	-[a]	-	-	-	6
	F	11	-	-	-	-	11
	U[c]	-	-	-	-	-	-
1987	M	3	102	-	2	1	108
	F	-	92	-	6	-	98
	U	-	1	-	-	-	1
1988	M	12	101	2	46	3	164
	F	9	133	1	38	3	184
	U	-	2	-	-	-	2
1989	M	9	58	7	25	23	122
	F	7	99	3	21	19	149
	U	1	3	1	-	-	5
All years		58	591	14	182	5	850

a - no data collected

b - in 1986 fieldwork was carried out on the July 15th & 16th to ring a sample of adults and nestlings at key sites so that some marked birds would be present in the study area when the field work began in proper in 1987

c - undetermined sex

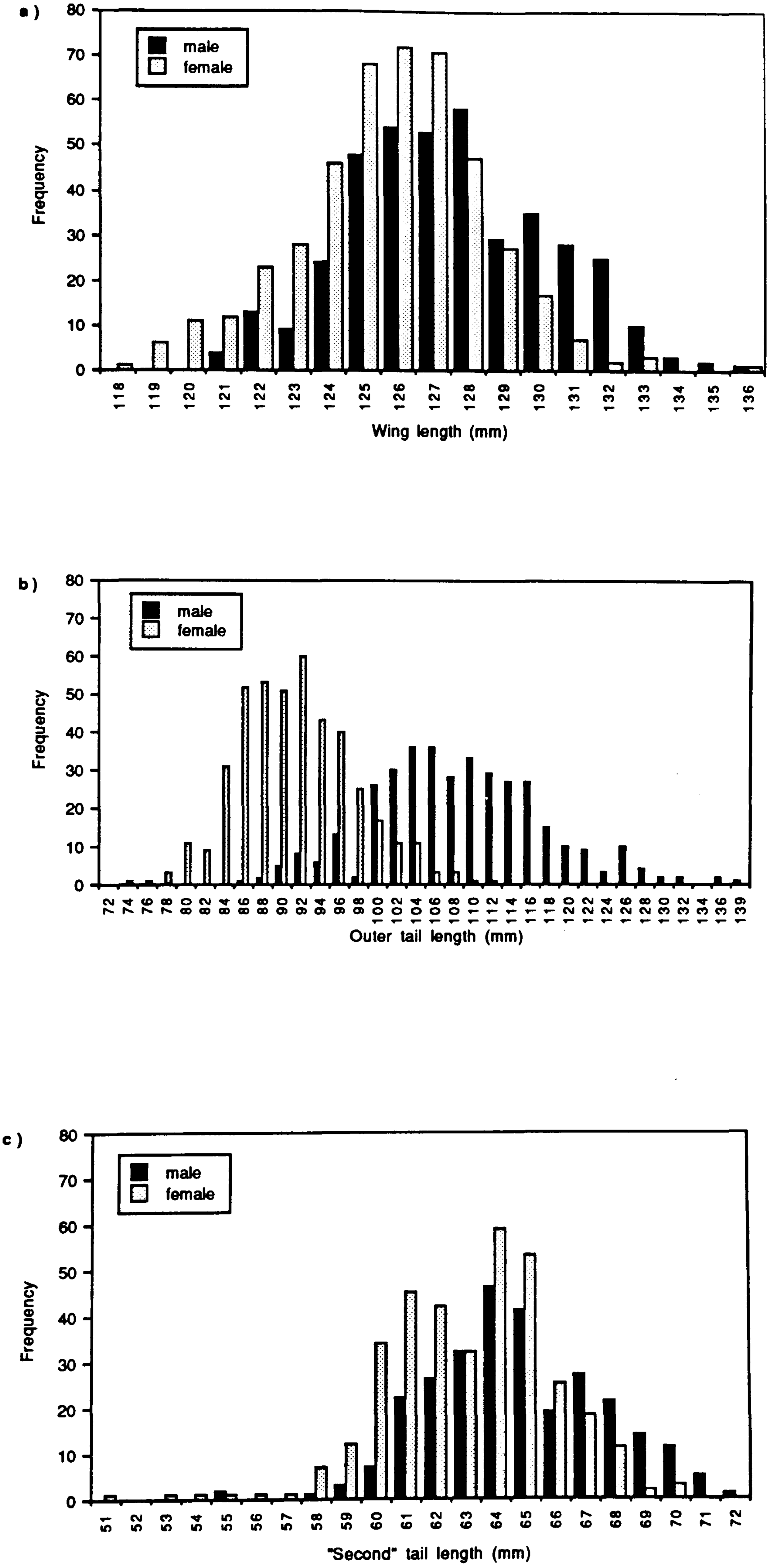


Fig 4.1 Frequency distribution of: a) wing, b) outer tail and c) second tail length in male and female Swallows

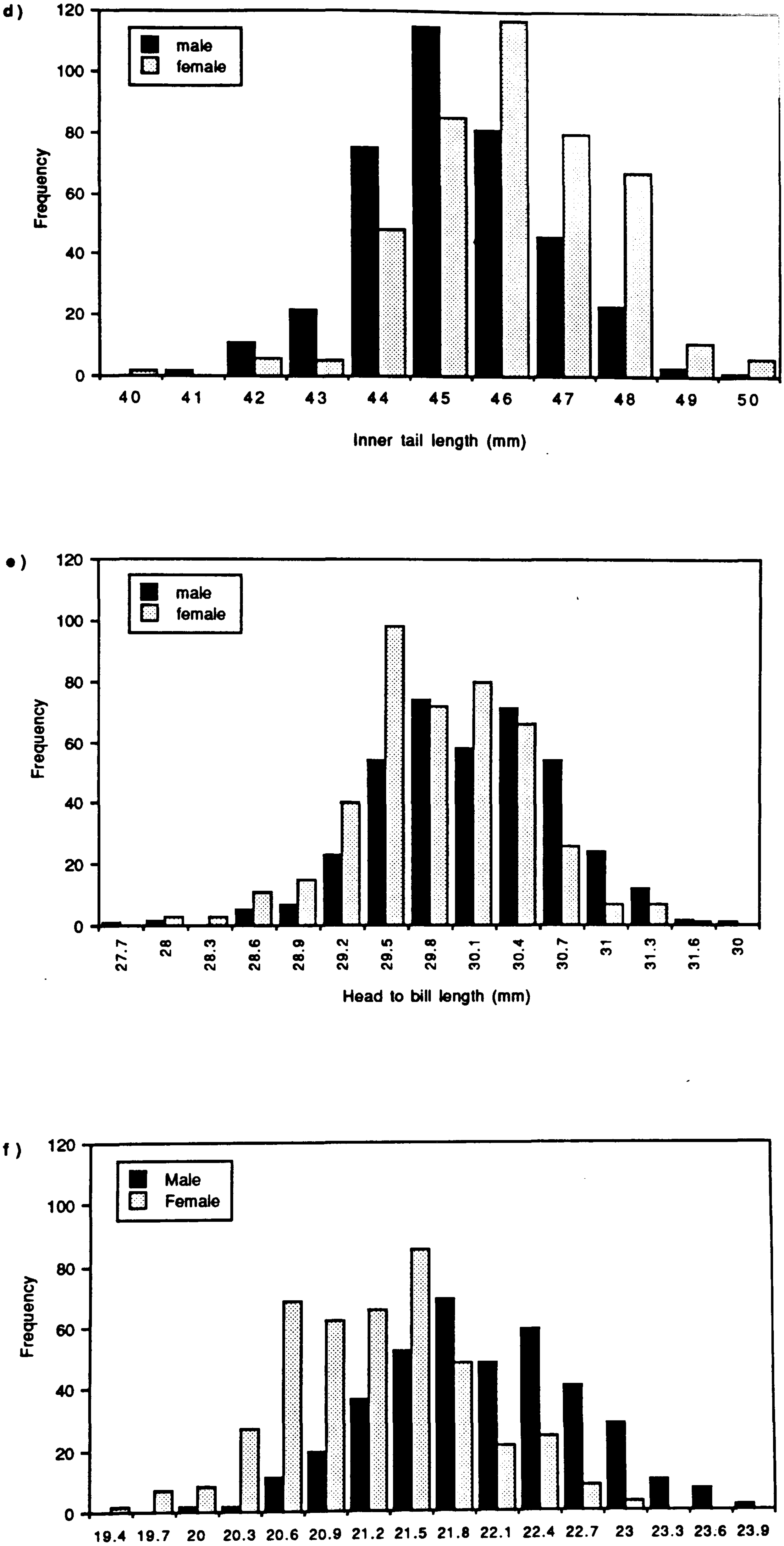


Fig 4.1 Frequency distribution of: d) inner tail, e) head to bill and f) keel length in male and female Swallows

year-old" birds did not differ in size , except that male outer tail-length was longer for "assumed one year-old" males (Table 4.3). There was no significant difference in plumage scores between these two age categories (Table 4.5) Given their overall similarity in size and plumage "known" and "assumed one year-old" birds were combined for subsequent analyses.

4.3.1.1 Males

Wing, outer tail and "second" tail-length increased with age (Table 4.2a). Plumage brightened with age (Table 4.4). One and two year-old birds differed most with respect to outer tail-length and plumage (P3) (Fig 4.3a,b). Skeletal measures (head-to-bill and keel-length) and inner tail-length did not significantly vary with age (Table 4.3). Re-analyses including only known-aged birds confirmed these trends.

4.3.1.2 Females

Tails of ≥ two year-old females were longer (outer tail: $p<0.001$; second tail: $p<0.05$, Table 4.3) and plumage more brightly coloured (Table 4.5) than those of yearlings and three year-old birds. Plumage scores did not differ between ≥ 2 and ≥ 3 ages (Table 4.5). Although yearlings and three year-old birds did not differ in size, younger birds were significantly duller (P3). Head-to-bill, keel- and inner tail-length did not vary with age. Wing-length showed an insignificant trend to increase with age.

4.3.2 AGEING MALES BASED ON BODY SIZE AND PLUMAGE

Outer tail-length and male plumage score (P3) varied with age but there was considerable overlap between the age classes (Fig 4.3a,b). Using only outer tail-length, a third of males could be categorised as yearlings or ≥ two year-old. Males of outer tail-length ≤ 90mm were yearlings and those ≥ 114mm "at least two years-old". Exclusion of a single yearling overlapping with the ≥ two year-old birds meant that less than half (43%) the males were assigned to their correct age class. For all parameters older males tended to be bigger, except for head-to-bill, and brighter (P1,P2 and P3).
Discriminant Function Analyses (DFA) were used to determine the percentage of known-age birds correctly aged using their morphometric characteristics. Direct entry and Wilks Method were used. In the direct method, all variables passing the tolerance test are entered into the function (SPSSx, Norusis 1990).

Seven parameters (wing, outer, "second" and inner tail, head-to-bill, keel-length and P3) were entered in the equation. All yearlings and 92% of ≥2 year-old were assigned to their correct age class with 93% correctly aged overall. The discriminant function, based on unstandardised derived canonical coefficients was:

$D= -1.668-(0.12*wing)+(0.02*OT)+(0.04*ST)-(0.08*IT)+(0.44*HB)-(0.21*keel)+ (0.92*P3)$, where OT, ST and IT =outer, "second" and inner tail resp; HB =head-to-bill length.

Table 4.2a Male Swallow body size for different age classes, 1988 and 1989 combined

	Male age classes											
	1^{a}		1^{*b}		$1^{\cdot\,\cdot c}$		2^{d}		$\geq 2^{e}$		$\geq 3^{f}$	
Parameter(mm)	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
n	23		84		107		9		105		25	
Wing	126.4	0.8	127.8	0.3	127.4	0.3	126.7	0.8	127.8	0.3	128.4	0.5
Outer tail	101.5	1.4	106.8	1.0	105.7	0.9	110.4	2.5	111.4	0.8	113.3	1.7
"Second" tail	63.2	0.5	64.5	0.3	64.3	0.3	64.6	0.9	65.4	0.3	66.4	0.6
Inner tail	45.1	0.4	45.4	0.1	45.3	0.1	45.0	0.3	45.3	0.1	45.4	0.2
Head-to-bill	30.0	0.1	30.1	0.1	31.1	0.1	30.4	0.1	30.1	0.1	30.0	0.1
Keel	21.9	0.2	21.8	0.1	21.8	0.1	21.9	0.3	21.8	0.1	21.9	0.2

a - "known one year-old"
b - "assumed one year-old"
c - "known+assumed one year-old"
d - "known two year-old" birds
e - "equal to or older than two year-old"
f - "equal to or older than three year-old"

Table 4.2b Female Swallow body size for different age classes, 1988 & 1989 combined

	Female age classes											
	1[a]		1 *[b]		1 * *[c]		2[d]		≥ 2[e]		≥ 3[f]	
Parameter(mm)	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
n	16		128		144		4		84		22	
Wing	126.0	0.5	125.6	0.3	125.6	0.3	127.3	0.3	126.1	0.3	125.7	0.6
Outer tail	90.6	1.3	90.0	0.58	90.0	0.5	96.8	3.5	93.6	0.2	92.1	1.4
"Second" tail	63.4	0.6	62.6	0.1	62.7	0.2	64.5	0.5	63.6	0.4	63.7	0.6
Inner tail	46.4	0.4	46.0	0.1	46.0	0.1	46.3	1.1	46.3	0.2	46.1	0.3
Head-to-bill	30.1	0.4	29.9	0.1	29.9	0.1	30.0	0.2	29.9	0.1	30.0	0.1
Keel	21.3	0.1	21.1	0.1	21.1	0.1	21.2	0.2	21.1	0.1	21.2	0.1

a -f see Table 4.2a

Table 4.3a Comparison of body size between age classes for male and female Swallows, using the Students t-test

		1 vs 1*		1 vs 2		1 vs ≥2		1 vs ≥3		1** vs ≥≥2	
Parameter	sex	t	p	t	p	t	p	p	t	p	t
Wing	M	-1.68	0.104	-0.24	0.815	-1.77	0.087	-1.45	0.151	-0.89	0.373
	F	0.59	0.554	-[a]		-0.16	0.873	-0.17	0.862	-1.33	0.185
Outer tail	M	-2.54	0.013	-3.22	0.003	-5.16	0.000	-3.72	0.000	-4.54	0.000
	F	0.43	0.670			-1.70	0.093	-1.63	0.105	-4.15	0.000
"Second" tail	M	-1.87	0.065	-1.38	0.180	-2.98	0.003	-3.44	0.001	-2.79	0.006
	F	1.16	0.246	-		-0.21	0.832	-1.79	0.075	-2.21	0.028
Inner tail	M	-0.92	0.360	0.08	0.938	-0.81	0.420	-0.63	0.533	0.00	1.000
	F	1.06	0.290	-		0.48	0.631	-0.28	0.777	-1.01	0.312
Head-to-bill	M	-0.58	0.562	-1.68	0.103	-0.36	0.719	0.68	0.533	0.07	0.940
	F	1.13	0.259	-		1.10	0.276	-0.53	0.594	-0.08	0.937
Keel	M	0.78	0.438	0.18	0.855	0.75	0.455	-0.22	0.823	0.20	0.841
	F	0.93	0.356	-		0.87	0.385	-0.56	0.579	0.20	0.844

a - sample sizes were too small to allow comparisons to be made

Table 4.3b **Comparison[a] of male and female Swallow plumage scores between age classes using the Mann-Whitney U-test**

		Age classes compared[a]									
Plumage		1 vs 1*		1** vs ≥2		1** vs ≥3		1** vs ≥≥2		≥2 vs ≥3	
area	sex	Z	p	Z	p	Z	p	Z	t	Z	p
P1	M	-1.10	0.271	-0.85	0.396	-2.91	0.004	-1.82	0.069	-2.29	0.021
	F	-0.69	0.489	-1.30	0.194	-1.47	0.143	-1.69	0.091	-0.64	0.523
P2	M	-0.98	0.326	-1.28	0.200	-1.02	0.307	-1.44	0.149	-0.15	0.879
	F	-0.32	0.746	-2.16	0.031	-1.69	0.092	-2.50	0.013	-0.257	0.797
P3	M	-1.74	0.082	-3.70	0.000	-3.84	0.000	-4.51	0.000	-1.65	0.100
	F	-0.04	0.970	-3.88	0.000	-3.30	0.001	-4.59	0.000	-0.733	0.46

a - Results of Kruskal-Wallis one-way ANOVAs of 1** vs ≥ vs ≥3, were:
Males : P1 $X=8.54$, $p<0.014$; P2 $X=2.11$, $p<0.349$; P3 $X=22.59$, $p<0.000$
Females: P1 $X= 3.22$, $p\leq0.199$; P2 $X=6.31$, $p<0.043$; P3 $X=21.60$, $p<0.000$

Table 4.4 **Adult Swallow plumage score by age class and sex (Mean(x) and se), 1988 and 1989 combined**

Plumage	Age[a]		Males			Females	
areas	class	x (se[b])	Median	Range	x (se)	Median	Range
P1	1	5.10 (.38)	6	2-8	4.06 (.48)	4	2-8
	1 *	5.59 (.20)	6	2-9	4.32 (.15)	4	2-9
	1 * *	5.49 (.18)	6	2-9	4.29 (.14)	4	2-9
	≥2	5.78 (.20)	6	2-9	4.69 (.23)	4	2-9
	≥3	6.76 (.35)	7	3-9	4.95 (.43)	5	1-9
	≥≥2	6.02 (.18)	6	2-9	4.75 (.20)	4	1-9
P2	1	2.20 (.45)	5	2-9	4.00 (.16)	3	2-8
	1 *	5.68 (.20)	6	2-9	4.06 (.16)	4	2-9
	1 * *	5.59 (.19)	6	2-9	4.06 (.15)	4	2-9
	≥2	5.95 (.21)	6	2-9	4.55 (.20)	4	2-9
	≥3	6.00 (.36)	6	2-9	4.71 (.38)	4	2-9
	≥≥2	5.96 (.18)	6	2-9	4.59 (.18)	4	2-9
P3	1	6.10 (.35)	6	2-8	4.31 (.33)	4	2-6
	1 *	6.74 (.16)	7	2-9	4.34 (.33)	4	2-8
	1 * *	6.62 (.11)	7	2-9	4.34 (.12)	4	2-8
	≥2	7.44 (.11)	8	5-9	5.33 (.20)	5	3-9
	≥3	7.84 (.17)	8	6-9	5.52 (.32)	6	3-9
	≥≥2	7.53 (.10)	8	5-9	5.38 (.17)	5	3-9

a - see Table 4.2a for definition of age classes

b - sample sizes are given in Tables 4.2a,b for males and females respectively

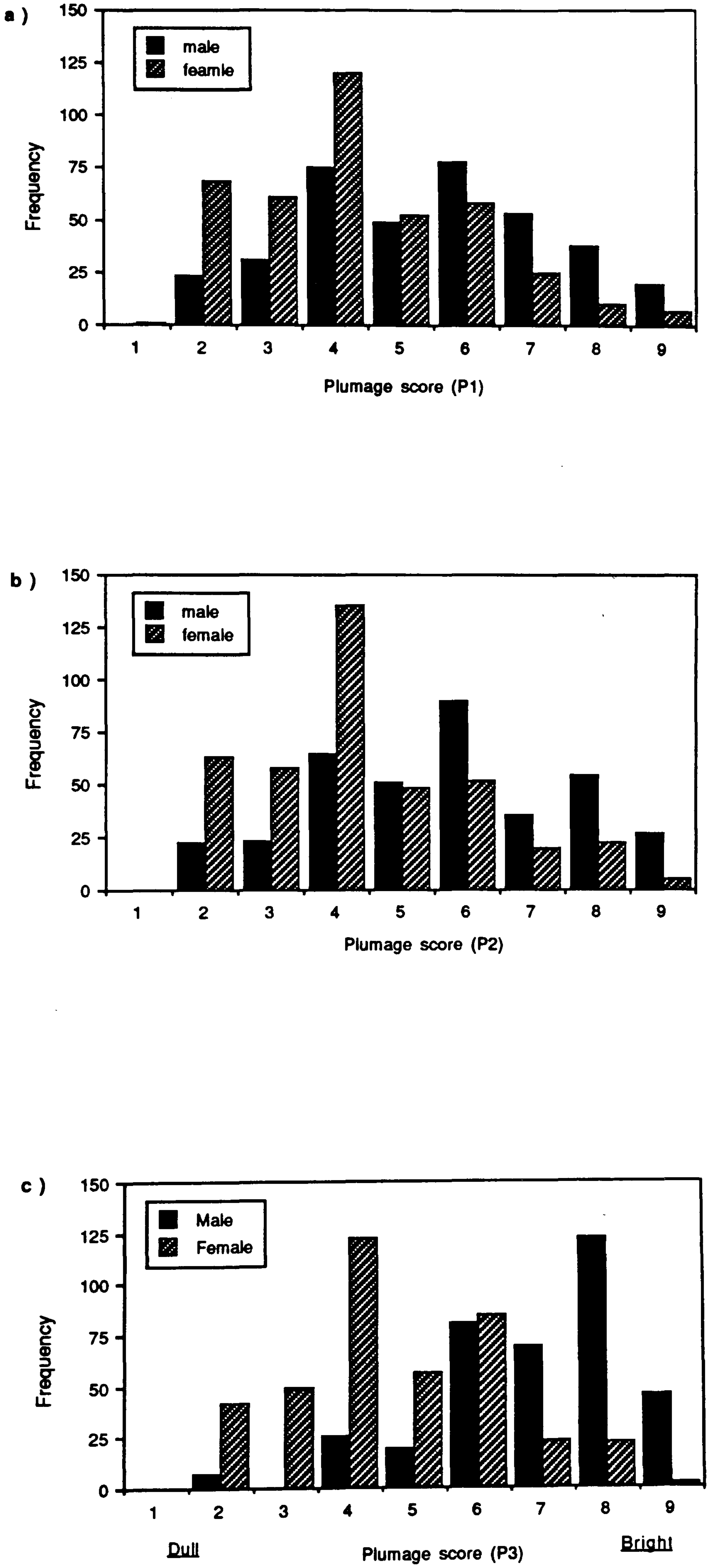
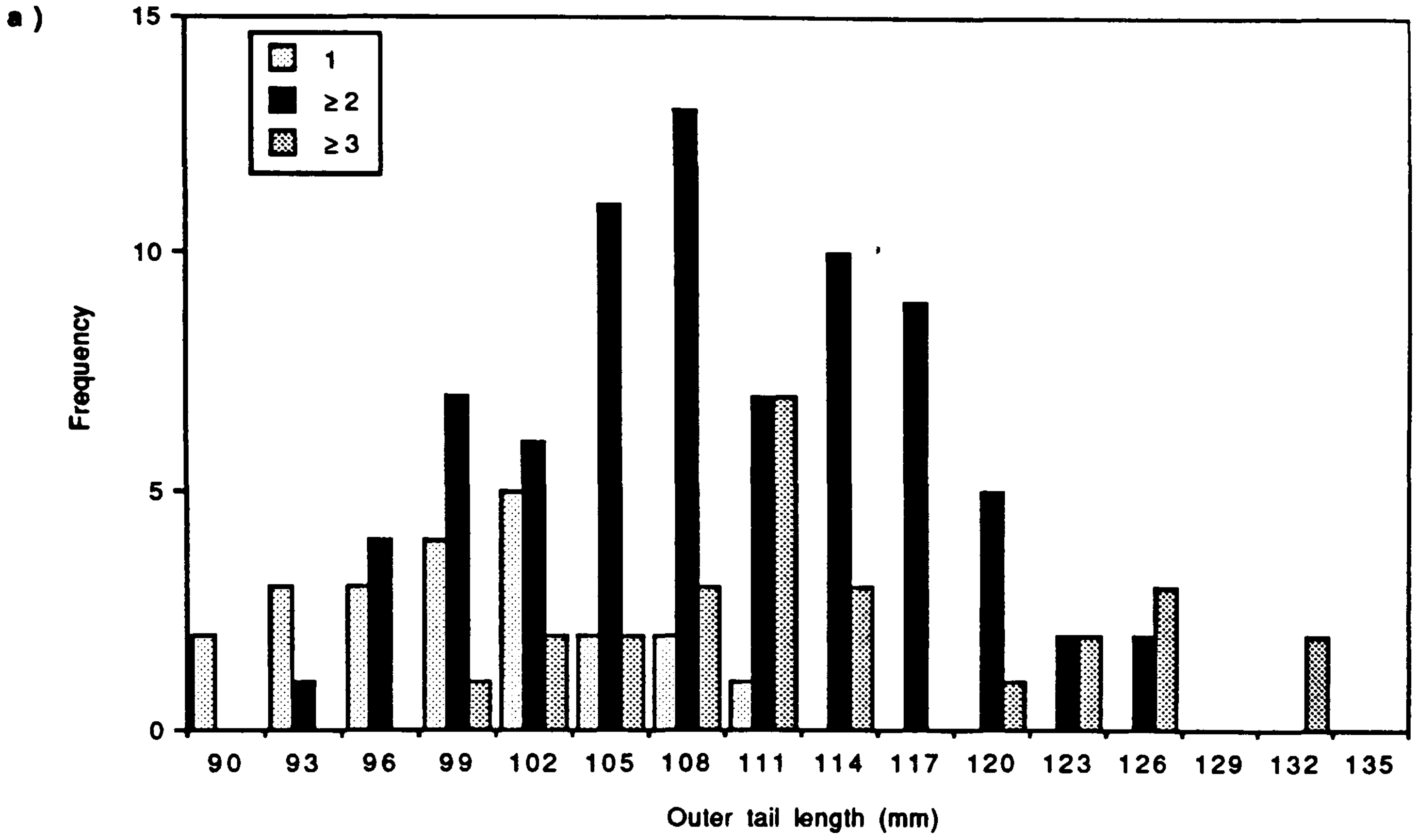


Fig 4.2 Frequency distribution of plumage scores: a) P1, b) P2 and c) P3 in male and female Swallows



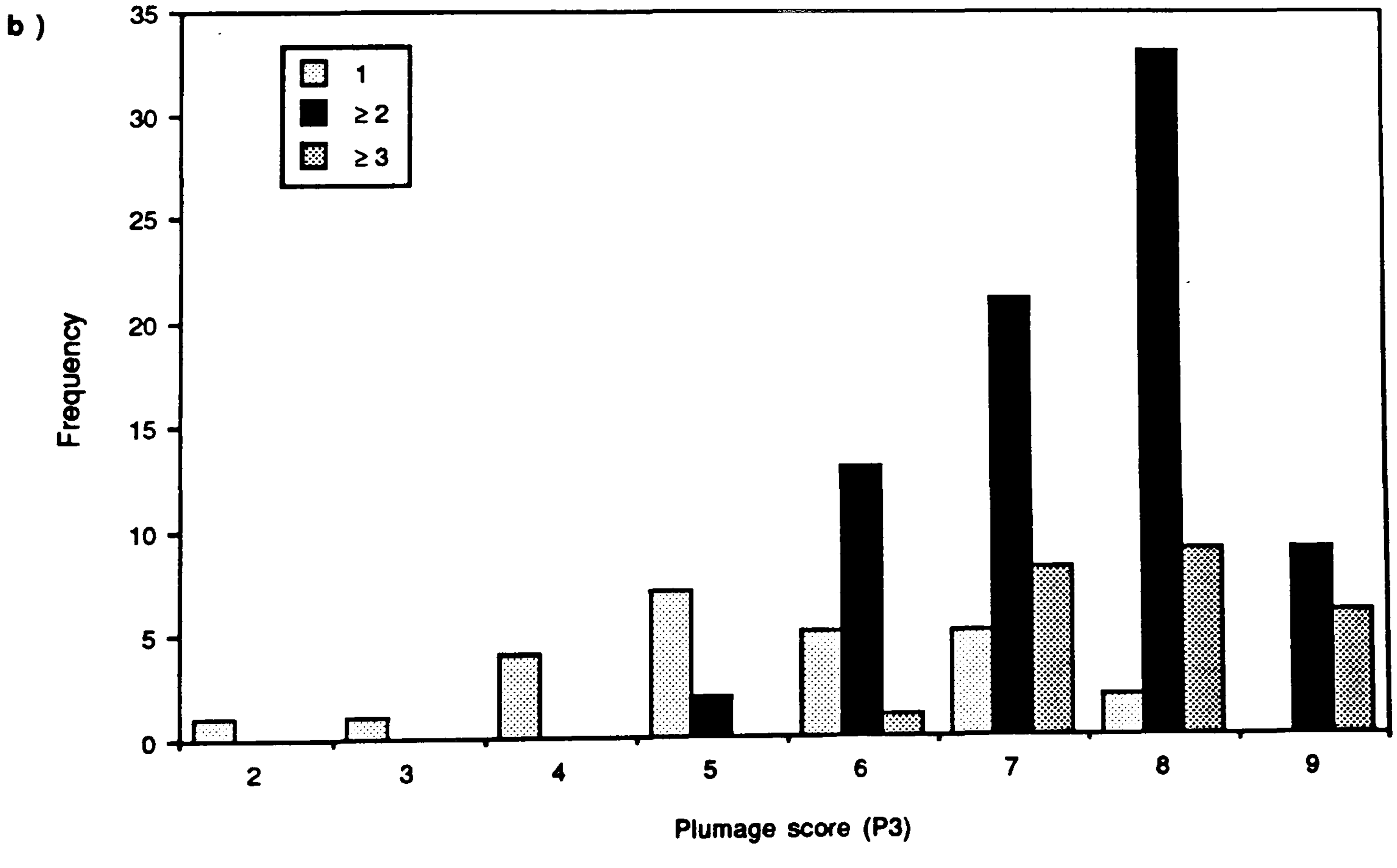


Fig 4.3 Frequency distribution of: a) outer tail length and b) plumage score (P3), analysed by age class in male Swallows

When only wing, outer , "second" tail and P3 were used, 87% of males and all yearlings were correctly aged:

$$D= 3.377-(0.124*wing)+(0.0249*OT)+(0.0473*ST)+(0.9203*P3)$$

4.3.3 RELATIONSHIP BETWEEN ADULT BODY SIZE MEASURES

A Pearson correlation matrix (Table 4.6a) showed that six body-size parameters were correlated significantly. Inter-relationships were generally similar for both sexes except head-to-bill length which was significantly correlated with all three tail measures for females, but only with the inner tail of males ($p<0.001$).

PCA was used to calculate overall size (PC1). All measures, except "second" tail-length (not measured in 1987), were included in analyses. Each of the measures was significantly and positively correlated with PC1; strongest for wing-length (Table 4.6a). 'Shape' (PC2) correlations were more varied (Table 4.6a). A partial correlation, controlling for the effects of age: 1, ≥ 2 and ≥ 3 yielded similar results (Table 4.6b).

4.3.4 SEX DIFFERENCES IN MORPHOLOGY

All size parameters were sexually size dimorphic (Table 4.7a). Males were significantly larger and more variable than females except for inner tail feathers where the reverse was true (Tables 4.8). A Dimorphism index was used to summarise sex differences. Outer tail (19%) and "second" tail (7.5%) differed most, head-to-bill the least (Table 4.9). Within age-class differences were also most pronounced for outer tail-length; 17, 19 and 23 % for ≥1, ≥2 or ≥3 respectively. Inner tail, head-to-bill and keel-length did not differ between sexes. Coefficients of variation did not differ between years. Analyses of plumage scores showed that males were significantly brighter than females (Table 4.8).

4.3.5 SEXING ADULT SWALLOWS

Swallows could be reliably sexed using brood patch development, however, as it was not developed in pre-, post- and non-breeding females, accurate sexing could not always be achieved. Even though sexes differed significantly in all parameters there was some overlap (Fig 4.1a to 4.1f). Using Principal Component Analysis although male and female groups were apparent 10% of birds could not be separated (Fig 4.4).

Including five parameters in a Discriminant Function Analysis (wing, outer tail, "second" tail, inner tail & head-to-bill) 261 adult Swallows were sexed with 95% accuracy. When only the two tail measures were used, 94.3% of birds (n=264) were

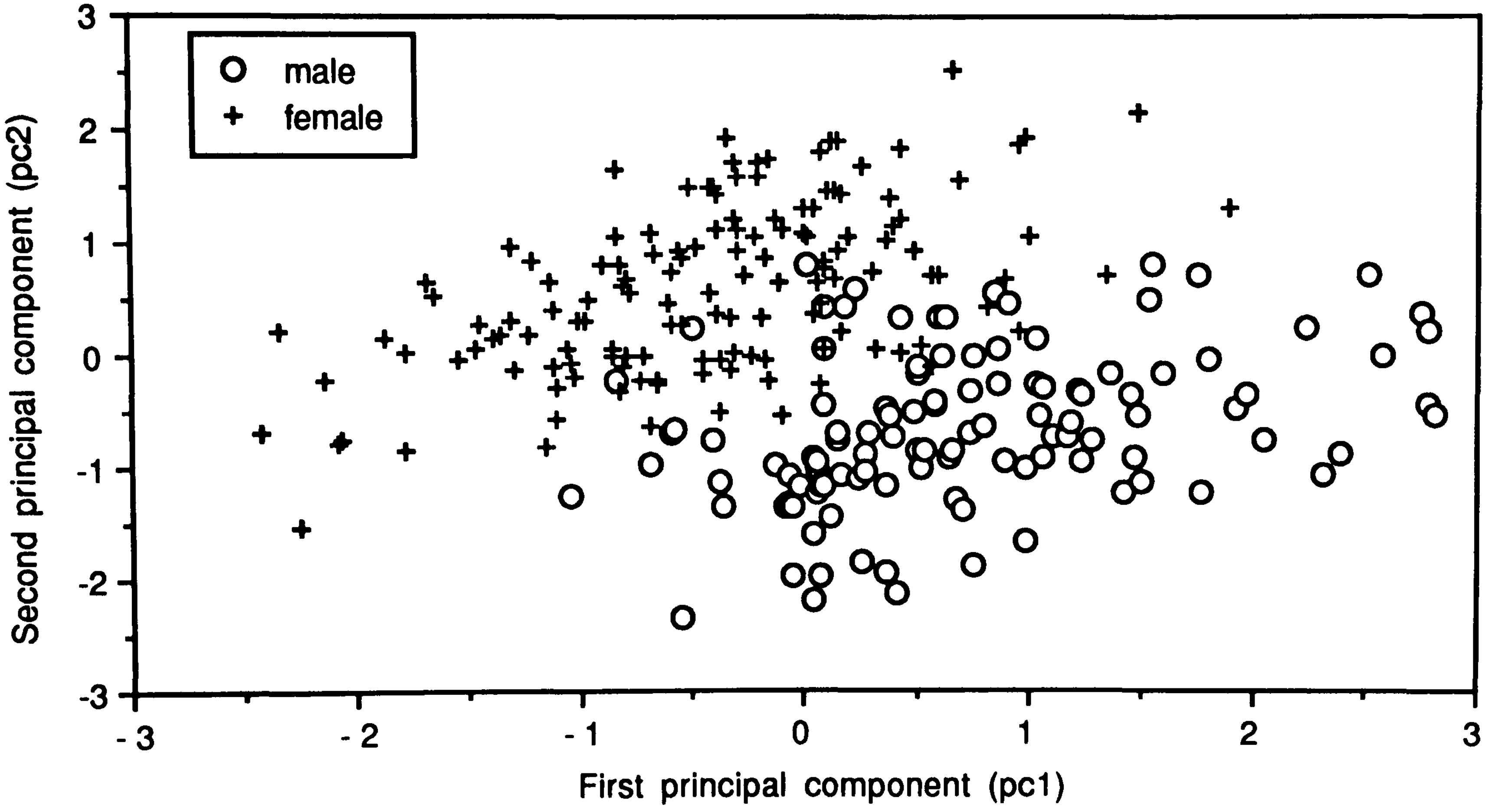


Fig 4.4 Principal component analysis: plot of pc1 versus pc2 categorised by sex for adult Swallows measured in 1989

Table 4.6a Pearson correlation coefficient matrix (coefficients and significance level) of adult body size parameters with principal components[a](PC1,PC2) by sex, years and age classes pooled. Male (n=371)values are given in plain and female (n=424) in bold text

Parameter	W	OT	ST	IT	HB	K	PC1	PC2
Wing (W)	-	0.38 ***	0.37 ***	0.45 ***	0.25 ***	0.30 ***	0.81 ***	-0.18 ***
Outer tail (OT)	**0.50** ***	-	0.60 ***	0.26 ***	0.08 ns	0.04 ns	0.55 ***	-0.53 ***
"Second" tail (ST)	**0.46** ***	**0.59** ***	-	0.32 ***	0.05 ns	0.04 ns	-	-
Inner tail (IT)	**0.49** ***	**0.38** ***	**0.47** ***	-	0.15 **	0.12 *	0.67 ***	-0.33 ***
Head-to-bill (HB)	**0.35** ***	**0.29** ***	**0.27** ***	**0.27** ***	-	0.35 ***	0.55 ***	0.59 ***
Keel (K)	**0.15** **	**0.08** **ns**	**0.07** **ns**	**0.10** *	**0.28** ***	-	0.54 ***	0.62 ***
PC1	**0.80** ***	**0.72** ***	-	**0.73** ***	**0.63** ***	**0.35** ***	-	-
PC2	**-0.18** ***	**-0.28** ***	-	**-0.27** ***	**0.39** ***	**0.83** ***	-	-

a - PC1, the first principal component, and PC2, the second principal component were calculated from wing, outer and inner tail; head-to-bill and keel length and represent 'size' and 'shape' respectively

Table 4.6b [as Table 4.6a but with age as a partial correlate (n=198 males, n=221 females)]

Parameter	W	OT	ST	IT	HB	K
Wing (W)	-	0.39 ***	0.33 ***	0.52 ***	0.33 ***	0.27 ***
Outer tail (OT)	**0.51** ***	-	0.61 ***	0.25 ***	0.10 ns	0.05 ns
"Second" tail (ST)	**0.47** ***	**0.62** ***	-	0.26 ***	0.02 ns	0.03 ns
Inner tail (IT)	**0.49** ***	**0.40** ***	**0.52** ***	-	0.21 **	0.16 *
Head-to-bill (HB)	**0.36** ***	**0.36** ***	**0.34** ***	**0.32** ***	-	0.43 ***
Keel (K)	**0.22** **	**0.08** **ns**	**0.04** **ns**	**0.14** *	**0.31** ***	-

Table 4.7a **Male and female Swallow body size, parameters and principal components (PC1,PC2), years combined**

	Males				Females			
Parameter[a]	Mean	se	Range	cv[b]	Mean	se	Range	cv
Wing	127.5	0.1	121-136	2.2	125.7	0.1	118-136	2.1
Outer tail	107.9	0.5	86-139	8.4	90.9	0.3	74-111	6.7
"Second" tail	64.7	0.2	55-72	4.5	63.0	0.2	51-70	4.4
Inner tail	45.3	0.1	41-50	3.2	46.1	0.1	40-50	3.4
Head to bill	30.0	0.0	27.5-31.8	2.1	29.8	0.1	27.9-31.6	2.0
Keel	21.8	0.0	19.7-23.8	3.3	21.1	0.3	19.2-23.0	3.2
PC1	0.54	0.05	-2.48-2.96	-[c]	-0.48	0.04	-2.56-2.03	-
PC2	-0.55	0.04	-3.09-2.01	-	0.49	0.04	-3.02-2.97	-

a - all measurements are in mm
b - CV % = (sd/x)•100 : sd =standard deviation
c - not calculated
Male sample sizes: 396,385,278,379,388,385,371,371; for wing to pc2
Female sample sizes: 442,427,329,427,429,428,424,424; for wing to pc2

Table 4.7b **Male and female Swallow plumage scores, years combined**

Plumage	Males				Females			
score	Mean	se	median	Range	x	se	Median	Range
P1	5.5	0.1	6	2-9	4.3	0.1	4	1-9
P2	5.7	0.1	6	2-9	4.4	0.1	4	2-9
P3	7.0	0.1	7	2-9	4.7	0.1	4	2-9

Male sample sizes: 367,367,367; for P1 to P3
Female sample sizes - 403,403,400; for P1 to P3

Table 4.8 Sex differences in adult Swallow body size and plumage scores[a]

Parameters	t	df	p
Wing	9.6	836	0.000
Outer tail	30.9	661.4	0.000
"Second" tail	7.6	605	0.000
Inner tail	-7.8	804	0.000
Head-to- bill	3.6	815	0.000
Keel	13.8	811	0.000
PC1	16.6	76.7	0.000
PC2	-17.2	78.9	0.000
Plumage score		Z[b]	P
P1		-8.70	0.000
P2		-9.75	0.000
P3		-16.64	0.000

a - data are for all years combined
b - Mann-Whitney test

Table 4.9 Indices of sexual dimorphism in Swallow body size

Measures of body size	Difference[a] (mm)	Dimorphism[a] index (%)
Wing	1.8	1.43
Outer tail	17.0	18.7
"Second" tail	4.7	7.5
Inner tail	-0.8	1.7
Head-to-bill	0.2	0.7
Keel	0.7	3.3

a - [size (male) - size (female)]
b - [((D/size (female)) * 100]

correctly sexed with males (8.6%) slightly more likely to be incorrectly sexed than females (3.4%). Only 0.7% of discriminatory power was lost using only outer and inner tail-lengths so this was used as the best 'working' method for sexing adult Swallows outside breeding:

D = 7.76 + (0.14*outer tail)- (0.47* inner tail), where, at 95% confidence limits, $D \leq -1.07$ is female and $D \geq 0.85$ is male.

4.3.6 CHANGES IN ADULT MORPHOLOGY

Adult body size was compared between years (Table 4.10). Head-to-bill length of both sexes ($p<0.001$) and the outer tail-length of males ($p<0.05$) increased each year. "Second" tail was also significantly longer in 1988 than 1989. The difference in outer tail-length between 1988 and 1989 persisted even when analysed within age classes so differences were not as a result of a shift in the mean age of the population.

4.3.7 DO ADULT SWALLOWS GROW WITH AGE?

Individuals which survived from one year to the next changed size between 1987 and 1988 (Period 1) and between 1988 and 1989 (Period 2). The pattern was similar for both periods and so these data were combined to calculate the mean change from Yr (n) to Yr (n+1) (Table 4.11). Trends were similar for both sexes. Male and female wing- , outer tail- and head-to-bill length increased significantly from one summer to the next (Table 4.11). Outer tail-length change showed most variation between years: -2 to 13mm and -1 to 10mm for males and females respectively, whereas inner tail and keel-length did not change significantly. Eighty-four percent of all males increased in outer tail-length between years. A similar trend was evident for females. Wing-length decreased in 15% of females but in only 5% of males.

4.3.8 NESTLING GROWTH

Nestling growth and percentage of adult size (yearling) reached in the year of hatch are described for each parameter (Table 4.12).

Wing (Fig 4.5a) and outer tail feather (Fig 4.5b) growth were similar, showing linear growth until Day 28-30 when a slight leveling occurred. Wing-length was 80% of adult size at fledging (Day 21+), whereas outer tail was only half it's eventual yearling size (Table 4.12). The wing was almost fully developed and the outer tail 70% developed ten days after fledging. Beyond this age, although the sample size was small, there was no apparent growth of either parameter.

Table 4.10 Male and female Swallow body-size by year and ANOVA of year differences

Parameter	Sex	1987		1988		1989			
		Mean	se	mean	se	mean	se	F[a]	sig level
Wing	M	127.4	0.3	127.4	0.2	127.9	0.3	1.2	ns
	F	125.4	0.3	125.9	0.2	125.7	0.2	0.8	ns
Outer tail	M	106.4	0.9	107.8	0.7	109.3	0.9	2.9	*
	F	89.9	0.6	91.4	0.5	90.9	0.5	1.8	ns
"Second" tail	M	-[b]	-	64.6	0.2	65.0	0.3	2.0	*
	F	-	-	62.9	0.2	63.0	0.2	0.7	ns
Inner tail	M	45.3	0.2	45.3	0.1	45.2	0.1	0.3	ns
	F	46.0	0.2	46.0	0.1	46.3	0.1	1.2	ns
Head-to-bill	M	29.8	0.1	30.0	0.1	30.1	0.1	7.5	* *
	F	29.6	0.1	29.9	0.0	30.0	0.1	16.6	* * *
Keel	M	21.8	0.1	21.7	0.1	21.9	0.1	1.8	ns
	F	21.2	0.1	21.1	0.1	21.1	0.1	1.2	ns

a - df_M = 2,387, (2,275 for "Second" tails); df_F = 2,428, (2,326 for "Second" tails)

b - "Second" tail not measured in 1987

Table 4.11 Yearly size change in adult male and female Swallows

Parameter	Sex[b]	year[a] (n)		year (n+1)		Paired t-test		
		mean	se	mean	se	D	t	p
Wing	M	127.5	0.3	128.0	0.3	-0.4	-5.4	0.000
	F	125.7	0.3	126.1	0.3	-0.3	-3.3	0.002
Outer tail	M	106.9	0.9	111.3	0.9	-4.4	-11.7	0.000
	F	90.8	0.8	93.4	0.8	-2.5	-10.0	0.000
Inner tail	M	45.2	0.1	45.3	0.1	-0.1	-0.6	0.561
	F	46.0	0.2	46.2	0.2	-0.1	-1.4	0.181
Head-to-bill	M	29.9	0.1	30.1	0.1	-0.3	-5.0	0.000
	F	29.7	0.1	29.9	0.1	-0.2	-5.4	0.000
Keel	M	21.8	0.1	21.8	0.1	0.0	0.6	0.573
	F	21.1	0.1	21.1	0.1	0.0	0.4	0.691

a - 1987 to 1988 and 1988 to 1989

b - sample size, 96 males and 79 females; 19 males and 17 females were measured in all three years.

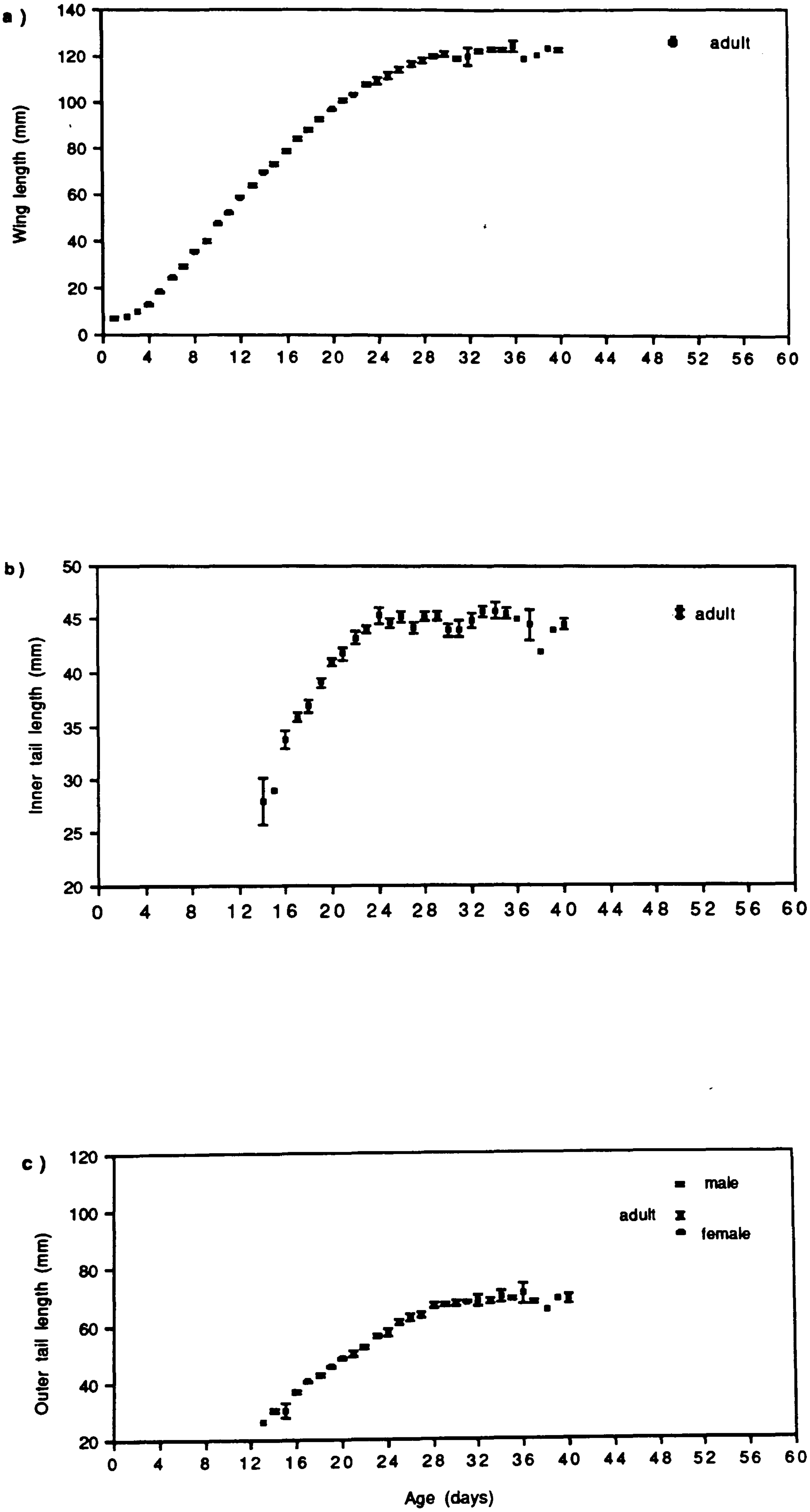


Fig 4.5 Plot of mean (±se): a) wing, b) inner tail and c) outer tail length in nestling (0-21days) and fledgling (22++ days) Swallows, 1987 to 1989

note: mean male, female and adult size are given on the right hand side of the plot; sexes are not always distinguishable

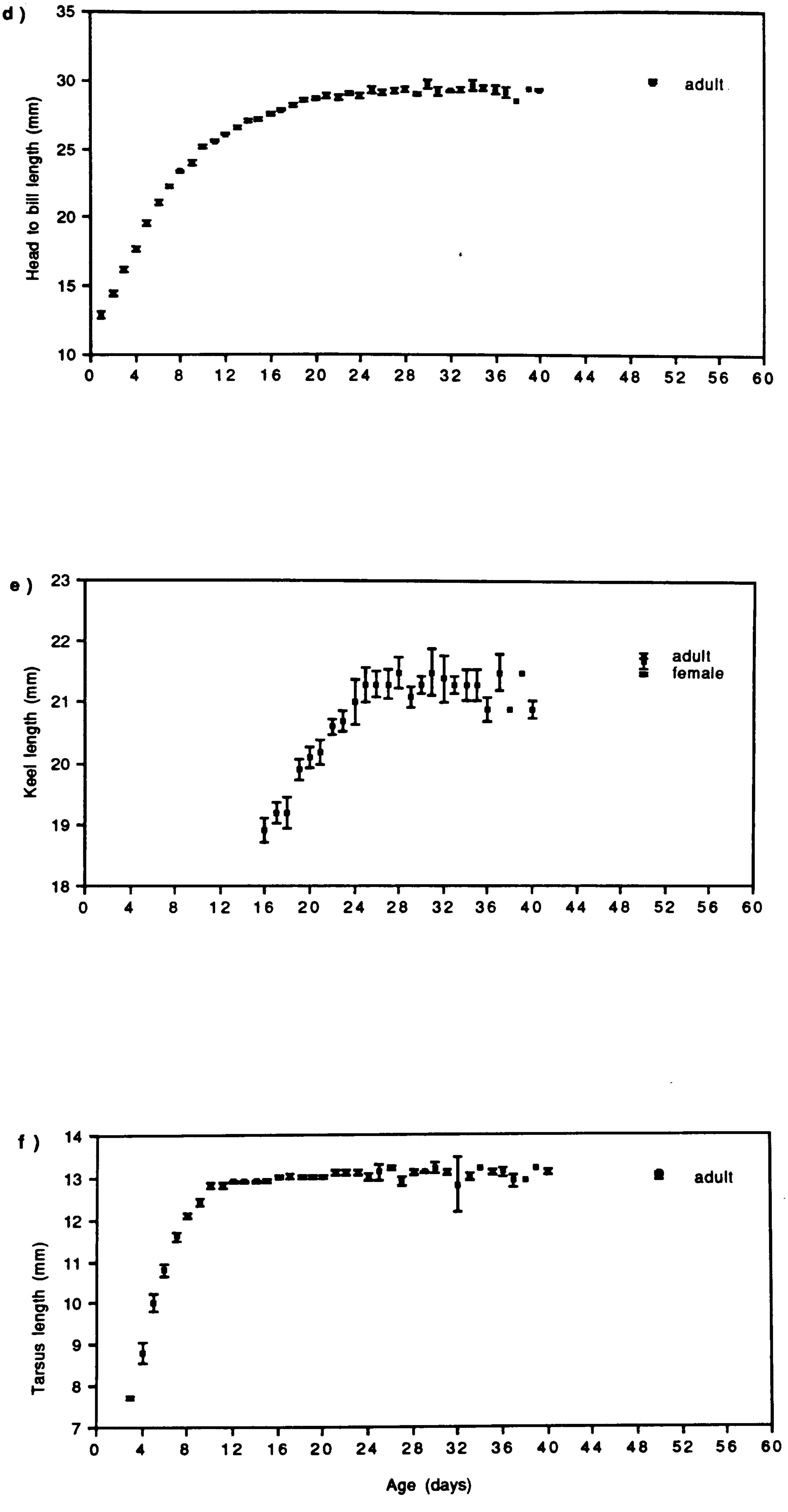


Fig 4.5 Plot of mean (±se): d) head to bill, e) keel and f) tarsus length in nestling (0-21 days) and fledgling (22++ days) Swallows, 1987 to 1989

note: mean male, female and adult size are given on the right hand side of the plot; sexes are not always distinguishable.

Table 4.12 **Swallow nestling and fledgling^a size as a percentage of mean yearling size (yearlings). Sample sizes in parentheses**

Age class (days)	Wing	Outer tail	Inner tail	Head-to-bill	Keel	Tarsus
			Measures of body size			
10	37.6 (72)	-^{a}	-	83.8 (39)	-	98.5 (29)
15-17	61.7 (138)	39.6 (30)	76.2 (21)	91.7 (109)	88.7 (23)	99.9 (88)
20-24	80.3 (103)	53.9 (94)	93.1 (80)	95.9 (97)	94.9 (94)	100.5 (74)
25-29	92.4 (38)	66.4 (37)	98.7 (37)	97.3 (36)	99.0 (31)	100.7 (31)
30-34	96.2 (27)	70.9 (27)	98.8 (27)	98.1 (29)	99.1 (27)	100.5 (23)
35-39	97.1 (15)	70.9 (150	98.7 (15)	97.9 (15)	98.9 (15)	100.5 (13)
40++	97.7 (08)	70.6 (06)	98.7 (07)	97.3 (07)	98.3 (07)	100.8 (07)
Fledglings^b	94.7 (68)	67.9 (66)	97.8(66)	98.5 (64)	99.1 (68)	100.8 (59)

a - outer and inner tail and keel length were measured from day15 onwards

b- fledglings are those which were not ringed in the nest and are thus of unknown (mixed) age, but were at least 25 days old.

Table 4.13a **Comparison of yearling size between years of hatch (1987 vs 1988) for male and female Swallows**

Variable	Sex^a	1987 mean (se)	1988 mean (se)	t	sig level
Wing	Male	125.1 (.8)	127.9 (1.6)	-1.8	ns
	Female	126.9 (.6)	124.9 (.8)	2.1	*
	Both	125.8 (.5)	126.3 (.9)	-0.6	ns
Outer tail	Male	103.4 (1.9	101.8 (3.4)	0.5	ns
	Female	92.6 (2.0)	88.0 (.9)	2.1	0.061
	Both	99.2 (1.8)	95.1 (2.4)	1.4	ns
Inner tail	Male	44.9 (.4)	45.3 (.6)	-0.5	ns
	Female	46.3 (.6)	46.6 (.4)	-0.3	ns
	Both	45.5 (.3)	45.8 (.4)	-0.7	ns
Head-to-bill	Male	30.0 (.2)	30.0 (.3)	0.1	ns
	Female	30.3 (.2)	29.8 (.1)	1.6	ns
	Both	30.1 (.1)	29.9 (.2)	1.2	ns
Keel	Male	21.9 (.2)	22.2 (.3)	-0.6	ns
	Female	21.5 (.2)	21.0 (.2)	1.6	ns
	Both	21.7 (.2)	21.6 (.2)	0.5	ns

a - sample sizes were 14, 8 and 9,7 for males and females in 1987 and 1988

By Day 15 inner tail was three quarters of its adult size (Fig 4.5c, Table 4.12), after which it grew to 90% of the mean yearling size by Day 24 and to 99% by Day 40.

Head-to-bill grew fastest to Day 10 (Fig 4.5d) and a ninety-six percent of final size was reached by the end of the nestling period (Table 4.12). There was little change in size during the fledging period, when individuals were about 98% of adult size.

Keel growth was similar to that of the inner tail; rapid from Day 16 to Day 24 (Fig 4.5e) and fully developed by Day 29 (99%, Table 4.12).

Tarsus grew rapidly to almost full size by Day 10. From Day 10 to 15 it grew slowly to full adult size (Fig 4.5f, Table 4.12).

4.3.8.1 Sexing fledgling Swallows

Fledglings measured after Day 20 which were caught and sexed the following season, were used to test for sex differences in fledgling size. Male fledglings were larger except for inner tail, but the sample size was small (males: n=8; females: n=3) and the differences were not significant.

4.3.9 RELATIONSHIP OF YEARLING SIZE TO YEAR AND DATE OF HATCH

Yearling body-size (sexes combined or males separate) did not differ between years (Table 4.13a). Outer and inner tail-length of males were longer and wing- and keel-length shorter in 1987 whereas all female measures, except inner tail-length, were larger in 1987, significantly so for wing-length and almost significantly for outer tail-length (Table 4.13a).

There was no significant relationship in body size of "Known one year-old" to date of hatch the previous year (Table 4.13b, Fig 4.6a to d). Closer inspection revealed that trends differed within the season so first and second broods were analysed separately. Yearling outer tail-length tended to decrease with later hatching in first broods (Table 4.13b). Male yearling keel-length decreased with later hatching in second broods ($r=-0.68$, $p < 0.05$, Table 4.13b).

4.3.10 RELATIONSHIP OF "NESTLING" TO ADULT SIZE

"Nestling" size (wing, outer tail, head-to-bill and keel-length) was plotted against its' size the following year (Fig 4.7 a to d). All four parameters were positively correlated with adult size but only for outer tail-length was the relationship almost significant (Fig 4.7c). Parameters were also standardised (Section 4.2.8) and using this method "nestling" size was positively correlated with yearling size despite greater growth of small nestlings (all tests $p<0.05$; Fig 4.8a,b,c).

Table 4.13b Correlation of date of hatch (yr n) with yearling, (n+1) body size, pooled or divided by sex and brood number (coefficients and significance)

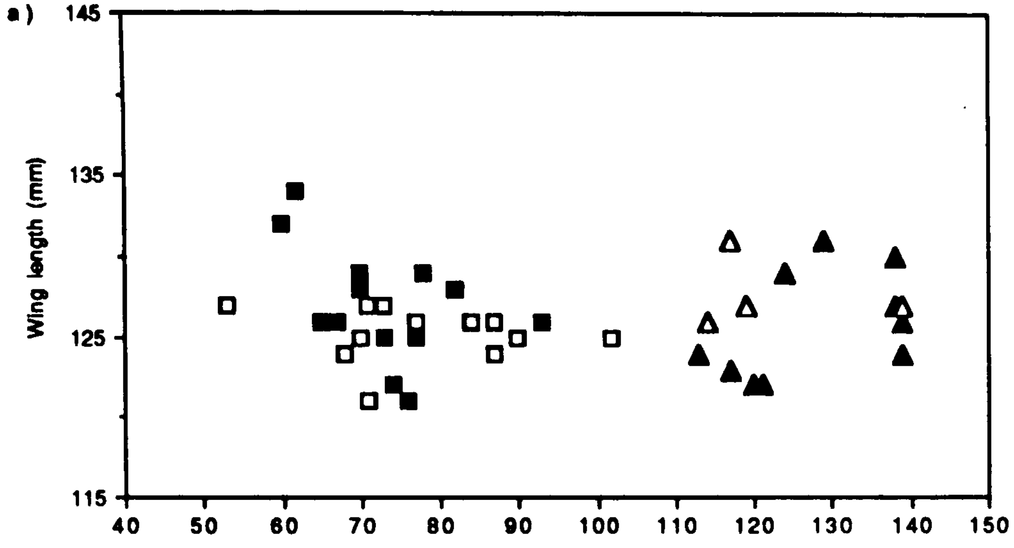
Brood	Sex	n	Wing	Outer tail	Head-to-bill	Keel
First	Male	15	-0.38	-0.42	-0.22	-0.04
			ns	ns	ns	ns
	Female	12	-0.12	-0.15	-0.07	0.08
			ns	ns	ns	ns
	Both	29	-0.27	-0.34	-0.10	-0.13
			ns	0.067	ns	ns
Second	Male	11	0.46	-0.05	-0.21	-0.68
			ns	ns	ns	*
	Both[a]	17	0.25	-0.11	-0.20	-0.57
			ns	ns	ns	*
All	Male	27	-0.15	0.19	0.04	-0.36
			ns	ns	ns	0.063
	Female	17	0.41	0.1	-0.21	0.27
			ns	ns	ns	ns
	Both	46	-0.13	0.16	-0.04	-0.15
			ns	ns	ns	ns

a - sample not big enough to analyse females separately

Table 4.14a Comparison of Swallow growth increments (mean (se))between years: 1987/1988 and 1988/1989 for each sex: t and p are for Students t-test

Growth increments	Sex	1987/88[a]		1988/89		t	p
		mean	se	mean	se		
Wing	Male	0.58	0.11	0.28	0.12	1.9	0.066
	Female	0.45	0.11	0.14	0.15	1.7	0.090
Outer tail	Male	4.89	0.52	3.91	0.54	1.31	0.194
	Female	2.37	0.31	2.73	0.41	-0.72	0.477
Inner tail	Male	0.11	0.13	0.00	0.14	0.58	0.563
	Female	0.00	0.16	0.31	0.13	-1.45	0.151
Keel	Male	-0.04	0.04	0.02	0.03	-1.42	0.158
	Female	-0.07	0.05	0.05	0.05	-1.78	0.080

a - sample sizes were 1987/88= 50, 42 and 1988/89= 46, 38 for males and females respectively



note: symbols are the same as Fig 4.6b

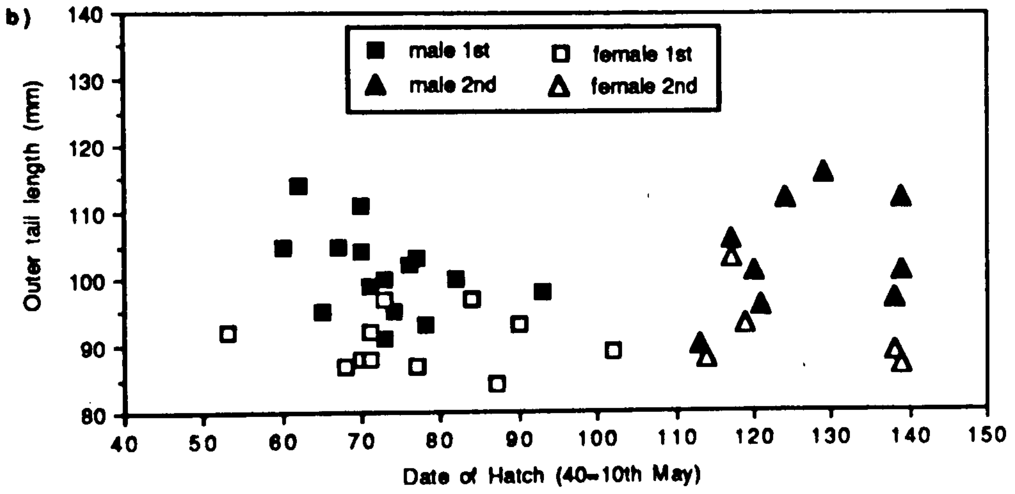
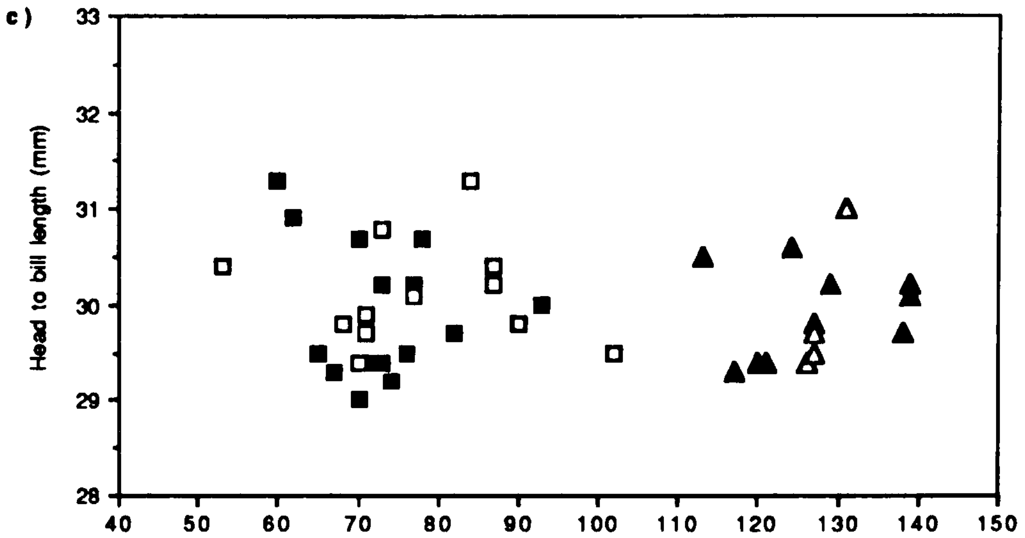


Fig 4.6 Relationship between the date that an individual hatched and: a) wing and b) outer tail length in the following year (i.e as a yearling)

note: correlation coefficients for the four sub-sets of data are given in Table 4.13b



note: symbols are the same as Fig 4.6d

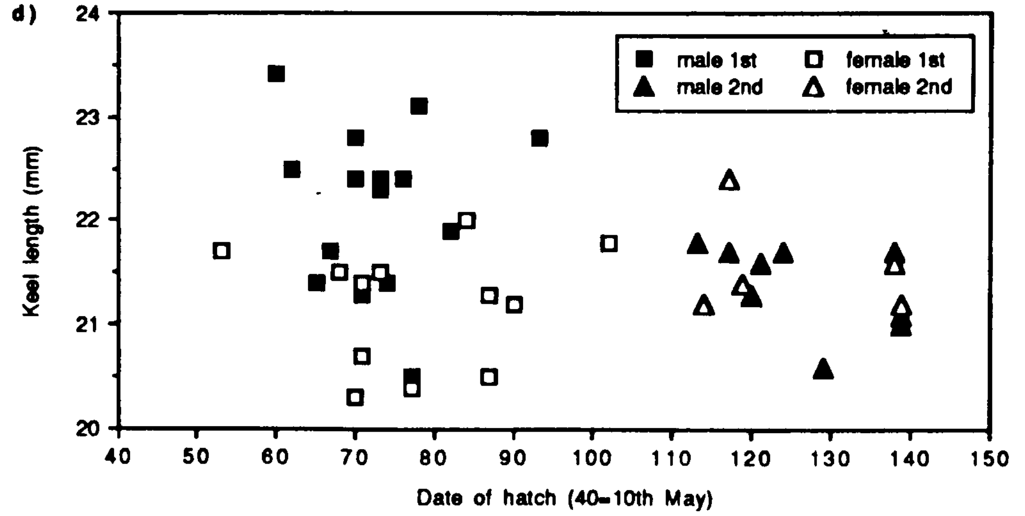


Fig 4.6 Relationship between the date that an individual hatched and: c) head-to-bill and d) keel length in the following year (i.e as a yearling)

Correlation coefficients for the four sub-sets of data are given in Table 4.13b

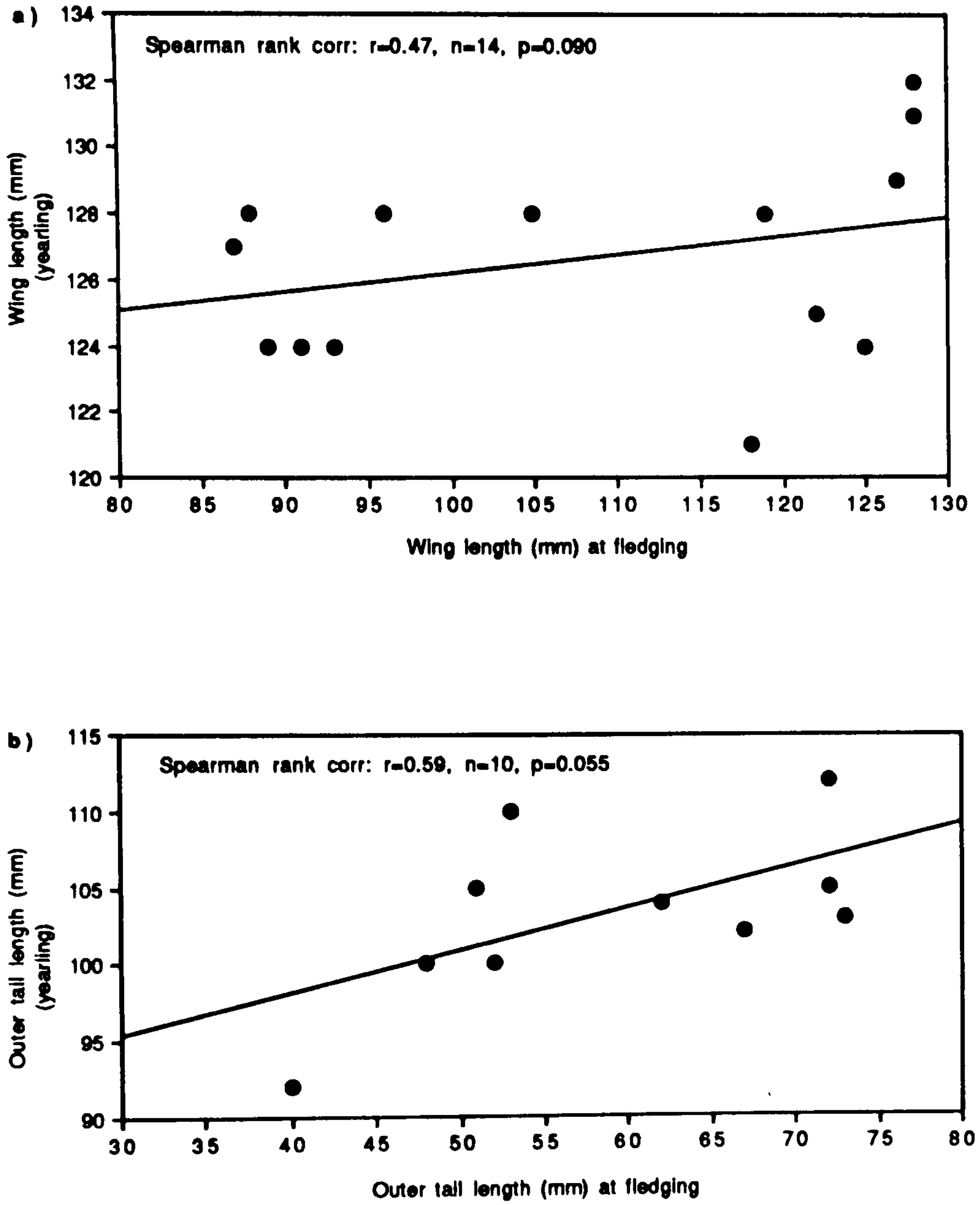


Fig 4.7 Plot of: a) wing and b) outer tail length for individuals which were measured at (or after) fledging and again in the following season

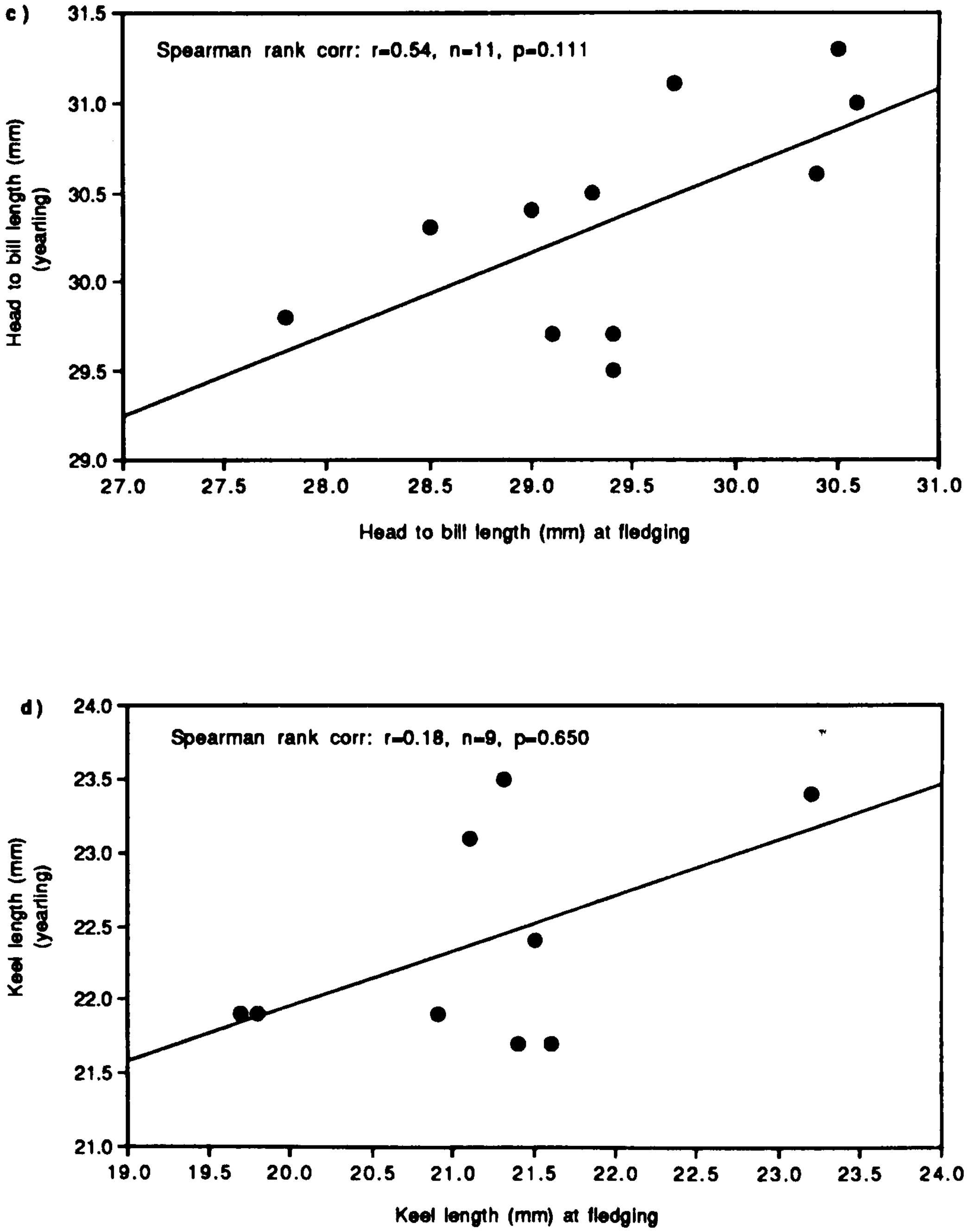


Fig 4.7 Plot of: c) head to bill and d) keel length for individuals which were measured at (or after) fledging and again in the following season

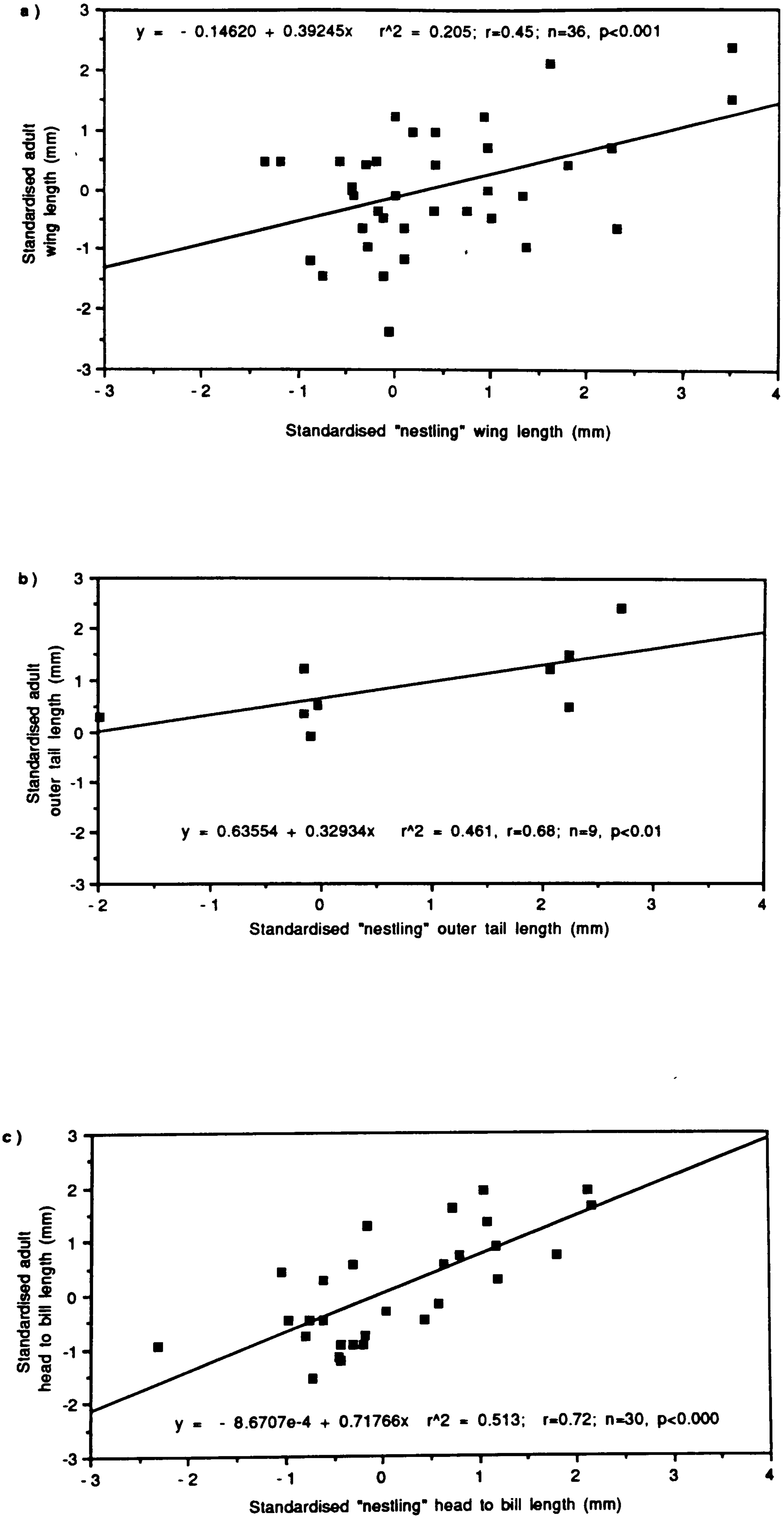


Fig 4.8 **Relationship between standardised: a) wing, b) outer tail and c) head to bill length of "nestlings" and their size in the following season**

note: a standardised "nestling" and adult size has been calculated for each individual. See text for details

4.3.11 COMPARISON OF GROWTH INCREMENTS IN ADULT SWALLOWS

The changes in size, termed growth increments here, were analysed in relation to year, sex, age and initial size.

Male and female wing-length tended to increase more from 1987 to 1988 than from 1988 to 1989 (both tests, $p<0.09$, Table 4.14a). There were no other obvious trends though female keel-length tended to increase more from 1988 to 1989. Relative growth or percentage size comparisons did not alter results (Tables 4.14b). Males increased in size more than females, significantly so for outer tail-length (Table 4.14c). Percentage size increase was also compared to control for body size effects (Section 4.2.5) but the outer tail-length trend was still significant (Table 4.14c). Only outer tail growth increment differed significantly between age classes, for both males and females, with yearlings growing 2.5 and 3 times more than older birds over the same period (Table 4.14d).

4.3.12 CORRELATION OF MALE WITH FEMALE BODY SIZE

Both sexes were identified in 45, 94 and 87 pairs in 1987, 1988 and 1989 respectively. Only outer tail-length and head-to-bill length were correlated between mates: ($r=0.13$ and $r=0.17$, both $p<0.05$; for outer tail and head-to-bill respectively). Within each age class only outer tail-length of adult pairs (≥ 2) was correlated between mates ($r=0.30$, $n=51$; $p=0.032$; *cf.* yearlings: $r=0.14$, $n=52$, ns). Females paired with "large" (≥118mm, n=37) males in adult pairs had significantly longer outer tail-lengths than those paired with "small" (≤ 99mm, n=30) males (95mm vs 90mm, $p<0.05$). The trend was similar, but insignificant, for yearling pairs (Table 4.15a,b).

4.3.13 ADULT SURVIVAL

Survival trends for 1987/1988 and 1988/1989 were similar so data were pooled for analysis. There were no differences in male or female body size when age classes were pooled except head-to-bill length of surviving double-brooded females which was smaller than that of double-brooded females not recaptured the following season ($p<0.005$; Table 4.16). Overall, smaller birds tended to survive better (Table 4.16). Within age classes (1 and ≥ 2), there were no significant differences for females or for yearling males (Table 4.17), but surviving ≥ 2 years old males were bigger than those which died, significantly so for outer tail-length($p=0.032$; Table 4.17). A two-way ANOVA showed that the relationship of outer tail-length with survival was influenced by age (age: $p=0.020$; survival: $p=0.132$; Table 4.18). Moreover, when breeding date (date of first egg laid by partner) was included as a covariate ($p=0.013$), the effect of age was no longer significant ($p=0.147$, Table 4.18).

Table 4.14b **Comparison of growth increments (mean (se)) for the same Swallows measured in successive years. d,t and p are for a paired t-test**

Growth increments	Sex	1987/1988 mean	se	1988/1989 mean	se	d	t	p	p[a]
Wing	M[b]	0.63	0.14	0.37	0.22	0.26	0.9	ns	ns
	F	0.31	0.15	0.06	0.19	0.25	0.9	ns	ns
Outer tail	M	4.28	0.92	2.67	0.74	1.61	1.1	ns	ns
	F	2.33	0.51	1.27	0.21	1.07	1.8	ns	0.07
Inner tail	M	-0.11	0.20	0.11	0.20	-0.22	-0.78	ns	ns
	F	-0.20	0.22	0.13	0.17	-0.33	-1.32	ns	ns
Keel	M	-0.02	0.05	0.06	0.05	-0.07	-0.83	ns	ns
	F	-0.09	0.10	0.03	0.06	-0.11	-0.90	ns	ns

a - Wilcoxon matched-pairs test

b - sample sizes were 19 males and 16 females

Table 4.14c **Comparison of annual growth increments (mean (se)) of male and female Swallows, by year**

Growth increments	Year	Males mean	se	Females mean	se	t	t-test sig	sig[a]	sig[b]
Wing	87	0.58	0.11	0.45	0.11	0.83	ns		
	88	0.28	0.12	0.14	0.15	0.78	ns	ns	ns
Outer tail	87	4.89	0.52	2.37	0.31	4.14	* * *		
	88	3.91	0.54	2.73	0.41	1.69	ns	* * *	*
Inner tail	87	0.11	0.13	0.00	0.016	0.54	ns		
	88	0.00	0.14	0.31	0.13	-1.57	ns	ns	ns
Keel	87	-0.04	0.04	-0.07	0.05	0.48	ns		
	88	0.02	0.03	0.05	0.05	-0.69	ns	ns	ns

a - comparison based on data for: 1987/88 and 1988/89 combined

b - Mann-Whitney U-test

sample sizes are given in Table 4.14a

Table 4.14d Comparison of Swallow growth increments (mean (se)) between different age classes, by sex

Growth		1** to 2		≥2 to ≥ 3				t-test	
increments	Sex	mean	se	mean	se	||	t	sig	sig^a
Wing	M	0.37	0.14	0.45	0.21	||	-0.34	ns	ns
	F	0.09	0.29	0.11	0.17	||	-0.05	ns	ns
Outer tail	M	6.05	0.71	2.33	0.66	||	3.86	* * *	* * *
	F	4.00	0.60	1.16	0.25	||	5.10	* * *	* * *
Inner tail	M	-0.22	0.26	0.00	0.18	||	-0.71	ns	ns
	F	0.45	0.21	0.00	0.22	||	1.39	ns	ns
Keel	M	0.01	0.01	0.05	0.05	||	-0.76	ns	ns
	F	0.13	0.10	-0.01	0.06	||	1.30	ns	ns

a - Mann-Whitney U-test

Table 4.15 Comparison of female Swallow body size paired with small, medium or large males^a, separated by age of pair^b, using Kruskal-Wallis (K-W) one-way ANOVA

(a) Yearling/Yearling

	Male size classes								
Female body	"Large"		"Medium"		"Small"			K-W	
size parameters	mean	se	mean	se	mean	se	||	X	p
n =	7		25		22				
Wing	125.2	0.49	125.1	0.62	125.1	0.56	||	0.33	0.848
Outer tail	90.6	2.02	90.6	0.88	89.0	1.25	||	1.02	0.602
Head-to-bill	29.6	0.30	29.9	0.11	29.8	0.20	||	0.54	0.764
Keel	21.2	0.52	21.2	0.11	21.0	0.15	||	1.34	0.510

a - based on outer tail-size, categories were :
"Large" = ≥ 115mm;"Medium" = 100 to 114mm and "Small" = ≤ 99mm
b - see text for definitions of pair-age combinations

(b) Adult /Adult

n =	10		26		15				
Wing	125.6	0.92	125.8	0.47	124.9	0.86	||	1.60	0.450
Outer tail	94.7	1.27	92.6	1.17	90.4	0.86	||	3.97	0.140
Head-to-bill	30.0	0.14	29.8	0.09	29.7	0.13	||	3.66	0.161
Keel	20.9	0.22	21.2	0.09	21.3	0.16	||	1.34	0.512

Table 4.16 Comparison of body size of double-brooded Swallows which Died and Survived by sex

Measures of body size	Sex	Died mean se	Survived mean se	one-way ANOVA F	p
Wing	Male[a]	127.7 (.4)	127.5 (.4)	0.08	0.776
	Female[b]	125.9 (.3)	125.5 (.3)	0.71	0.401
Outer tail	Male	107.1 (1.3)	109.5 (1.3)	1.86	0.175
	Female	90.5 (.6)	90.9 (.9)	0.12	0.732
Head-to-bill	Male	29.9 (.1)	29.9 (.1)	0.00	0.953
	Female	29.9 (.1)	29.6 (.1)	5.80	0.017
Keel	Male	21.8 (.10	21.8 (.10	0.08	0.773
	Female	21.2 (.08	21.1 (.08	0.06	0.809

a - 54 males died and 51 survived; df= 1,103

b - 73 females died and 70 survived; df= 1,141

Table 4.17 Comparison[a] of body size of non-surviving (died) and surviving (survived) double-brooded adult Swallows, by age class and sex; using one-way ANOVA[b]

Measures of body size	Sex	Age class	Died mean (se)	Survived mean (se)	One-way ANOVA F	p
Wing	Male	1	127.1 (.8)	126.3 (1.0)	0.42	0.524
		≥ 2	127.3 (.6)	128.2 (.7)	0.94	0.340
	Female	1	125.3 (.4)	124.6 (.7)	0.65	0.428
		≥ 2	127.1 (.6)	125.2 (.8)	3.44	0.073
Outer tail	Male	1	104.9 (3.2)	104.8 (2.1)	0.00	0.983
		≥ 2	108.4 (1.6)	114.5 (2.2)	5.05	0.032
	Female	1	88.9 (.8)	88.7 (2.6)	0.01	0.917
		≥ 2	94.1 (1.6)	91.0 (1.6)	1.88	0.180
Head-to-bill	Male	1	30.1 (.14)	30.2 (.18)	0.28	0.605
		≥ 2	29.7 (.18)	30.1 (.17)	2.17	0.151
	Female	1	30.0 (.13)	29.8 (.29)	0.26	0.615
		≥ 2	29.9 (.14)	29.8 (.13)	0.16	0.691

a - data are for the period 1988/89; birds were not aged in 1987

b - sample sizes were:

males: age class 1 died = 13; survived = 8; df= 1,19
age class ≥ 2 died = 21; survived = 13; df= 1,31
females: age class 1 died = 26; survived = 7; df= 1,31
age class ≥ 2 died = 14; survived = 18; df= 1,30

Table 4.18 Two-way ANOVA of age and survival differences in male outer tail-length in 1988/1989 for double-brooded Swallows

Sources of Variation	Sum of squares	Two-way ANOVA df	F	p
Main effects	597.10	2	4.059	0.023
Survival	172.89	1	2.351	0.132
Age	427.46	1	5.812	0.020
Age * Survival	120.13	1	1.633	0.207
Explained	717.23	3	239.08	0.030
Residual	3603.94	49		
Total	4321.17	52		
Date of first egg[a]	503.06	1	6.675	0.013
Main effects	218.79	2	1.452	0.245
Survival	82.12	1	1.090	0.302
Age	163.78	1	2.173	0.147
Age * Survival	119.34	1	1.584	0.215
Explained	841.19	4	2.790	0.037
Residual	3391.29	45		
Total	4232.48	49		

a - covariate; including other covariates such as clutch size or number fledged yielded non-significant results

4.4 DISCUSSION

Adult morphometrics may be directly or indirectly related to many aspects of an individuals' ecology and life history. Quantifying its variability and understanding the consequences of this variation are, therefore, of clear importance. Many early studies relied on museum specimen data, where relevant information such as age, population density or environmental conditions were not available. Morphometric data from a wild population, however, may permit further insight into the mechanisms of selection for both the individual and the population, which in turn may enable predictions of optimum body size to be made.

4.4.1 VARIATION IN ADULT BODY SIZE ASSOCIATED WITH AGE

Age-related changes in body size were indirectly examined by comparing the mean parameter values of age classes. "Known one year-old" and "assumed one year-old" birds did not differ in size, allowing them to be pooled. All feather measurements (except inner tail-length) increased from one to two years old, significantly so for wing- and outer tail-length. From "at least two years old" to "at least three years old", males increased but females decreased in size. Swallow wing-length did not differ between age classes in Poland and outer tail increased only after first moult (Banbura 1986). Møller (1988a) found a correlation coefficient of 0.51 of outer tail-length with age, slightly higher than in this study. Tail-length also increases with age in other species (Cherry 1991). A more precise test of age-related trends is to compare the size of individual birds in successive seasons (Turner 1980; Møller 1989a). In this study, three measures exhibited continued growth (wing, outer tail and head-to-bill); outer tail showing the greatest increase for both sexes (x=4.4mm and x=2.5mm, for males and females respectively). A slightly higher figure was reported for males (x=4.8mm) by Møller (1989).

It is generally considered that adult Swallow age cannot be determined from morphological features (Svensson 1975) even though it is known to be possible for Tree Swallows (Kuerzi 1941; De Steven 1978) where yearlings retain brown juvenile-like feathers distinguishing them from the blue-green of adults. There were no obvious cues for ageing Swallows in this study because the morphometric characters which varied with age (wing, outer tail, "second" tail and plumage) overlapped between age classes. A combination of these measures, however, correctly assigned 80-90% of known-aged males to their age class, though this analysis was based on only a small sample of yearlings. More reliable discrimination requires a larger sample. Inclusion of breeding parameters which vary with age, such as laying date (Banbura 1986), may further improve the precision of discrimination and provide a valid alternative to intensive ringing and measuring (Chapter 2).

4.4.2 RELATIONSHIP OF "NESTLING" SIZE TO ADULT SIZE

Skeletal parameters (head-to-bill, keel and tarsus-length) and inner tail-length were almost fully grown by the end of the nestling period whereas the wing was four-fifths developed and the outer tail just over half grown. Twenty days after fledging the wing was 95% of adult size but outer tail had still only two thirds of it's yearling size. Similar patterns were found in other hirundine studies (Turner & Bryant 1979; Turner 1980; Bryant &Westerterp 1982 Jones 1985). More interesting was the between- and within-brood variation in nestling growth in this study. Brood size explained much of this variation (see Chapter 6) as found through brood-size manipulations (Hussell 1972; Askenmo 1977; Crossner 1977; Schifferli 1978; Cronmiller & Thompson 1980; Nur 1984a; Hegner & Wingfield 1987; but see Högstedt 1980; Loman 1980; Finke *et al.* 1987; Smith *et al.* 1988) and in other hirundine studies (De Steven 1980; Bryant & Westerterp 1983b; Jones 1985). The ecological significance of this trend is that smaller size or poorer condition at fledging may decrease post-fledging survival. Both Swallows (this study) and House Martins (Bryant & Gardiner 1979) grow after fledging so it is possible that smaller fledglings exhibit compensatory growth, perhaps through additional parental care, which reduces yearling size differences relative to fledging size differences. Such compensatory growth has been found for tarsus-length in Great Tits (Lindén 1988) and there was some evidence for its existence in this study. Only 5% of the 1500 or so "nestling" Swallows which fledged returned (Chapter 3), however, making interpretation of data difficult. Nevertheless, there was some evidence that fledgling and adult size (wing and head-to-bill) were correlated. Moreover, smaller (standardised size) nestlings tended to be smaller (standardised size) yearlings, significantly so for wing-length and head-to-bill length.

4.4.2.1 Nestling size and environmental factors

Environmental conditions influence nestling growth, directly or indirectly. Hirundine nestling growth has been shown to increase with natural food availability in the House Martin (Bryant 1978a; Johnston 1990), the Tree Swallow (Blancher & Robertson 1987; Wiggins 1990) and the Swallow (Turner 1980; Jones 1985). Brood-size variation in nestling growth provides indirect evidence supporting this trend (Chapters 5 & 6 this study, for review see Martin 1987).

Brood number (first or second) and individual date of hatch were related to yearling size. Food abundance and weather conditions varied considerably with season and date (Chapter 5) so the effect of brood number and hatching date may only reflect the environmental conditions during the nestling and fledging periods. This possibility has been proposed for House Martins where nestlings grew faster when they received more of insects until Day 16 of the nestling period though it is not known if the effect persisted to adult size (Johnston 1990). A long term study (Bryant 1989a) found that House Martin yearling wing-length increased significantly with greater insect abundance in the year of hatch indicating that the environment can have a long term effect (see Chapter 5).

Wing length was not significantly correlated to components of annual or life time reproductive success, however, and so the significance of such a result is unclear (Bryant 1989a).

In the present analyses tests of the effect of annual insect abundance on adult size were inconclusive. Trends differed between sexes and between size parameters. Females tended to be bigger in 1987 (significantly so for wing-length), but there were no significant differences in male size between years. The extremely small sample sizes restrict interpretation and this relationship requires further investigation. Body-size heritability is also important in explaining variation in body size but this factor was not investigated here.

4.4.3 ADULT GROWTH

Growth increments were not affected by season but were influenced by age, sex and initial size. Male yearling wing-length and outer tail increased by the greatest absolute and relative amounts. Size increase of both sexes was negatively correlated with original size, even controlling for age. This result conflicts with Møller's (1989a) finding that long-tailed males increased in tail length more than short-tailed males but is consistent with the observation that male Swallows with experimentally elongated tails decreased in tail-length relative to their pre-manipulation size, whereas those with un-manipulated or experimentally reduced tails, increased in tail length the following season.

Feather development requires considerable deposition of protein (Murphy & King 1984) and dietary protein is known to influence nestling growth (Street 1978; Woodward *et al.* 1977). Adult growth could, therefore, be influenced by nutritional factors during the moulting period (Watt 1990) or the general conditions experienced during breeding. Poor nutrition is known to cause various feathers abnormalities, termed fault bars, which are prone to breakage (Harrison 1985). It is not known, however, if such a condition affects feather growth and therefore the length of feathers the following year. In this study, fault bars were found in adult wing and tail feathers but were not quantified, so possible causal factors were not investigated. Five percent of male Swallows possessed fault bars in Møller's (1989a) study. Most of these were short-tailed males or males which had experimentally enlarged tails the previous year (Møller 1988a, also see below).

Andersson (1989) proposed that tail-length might serve as an indication of male viability and investigated the relationship of body condition to tail-length. Smith & Montgomerie (1991) suggested that a positive relationship between the two, controlling for confounding influences such as seasonal variation, would indicate that only birds in good condition can support a longer tail.

4.4.4 ASSORTATIVE MATING IN RELATION TO BODY SIZE

Male and female outer tail and head-to-bill length were significantly correlated. Outer tail-length was also significantly correlated with age in both sexes so the correlation between sexes may just reflect assortative pairing by age. Controlling for age, only adult pairs showed a significant correlation in tail-length between mates. Reproductive performance improves with age (Chapter 5) so males with longer tails may improve their reproductive success by pairing with older females. Banbura (1986) also reported significant correlations of the tail-lengths of mates in for all pairs and for all pairs where mates were at least two years old; but not between wing-lengths of mates. Similarly, Barn Swallows females paired with males with experimentally enlarged tails had significantly longer streamers (but not wing-lengths) than those paired with males with shortened tails (Smith & Montgomerie 1991).

4.4.5 SEXUAL DIMORPHISM AND VARIABILITY IN BODY SIZE

Little sexual size dimorphism has been found in the Swallow except for the outermost tail feathers and wing-length (Vietinghoff-Riesch 1955; Banbura 1986; Møller 1988a, 1990a; Turner and Rose 1989). Dimorphism was most extreme for the outer tail feathers (mean: 108 vs 91mm, males vs females) in this study. Males also had significantly longer wing-, "second" tail-, head-to-bill and keel-length and significantly smaller inner tail-length. Similar differences in outer tail-length have been found in other studies (105mm vs 91mm, Møller 1990a; 91mm vs 78mm, Smith & Montgomerie 1991) but the wing , inner tail and tarsus-length differences found in this study were not present. Inner tail was longer in males in Denmark (Møller 1990a, Table I, p460; *cf.* this study). Coefficients of variation (cv) in Swallows were small (2-5%) for all traits except outer tail where males were more variable (8.4%) than females (6.7%) (also see Møller 1990a; and Smith & Montgomerie 1990). Similar findings have been described for a wide range of other species (Andersson 1982; Alatalo *et al.* 1988; Cherry 1990). Differences in measuring techniques preclude direct comparisons but comparisons of the sex differences should still be valid (Appendix 4.1).

Sexual dimorphism is commonly associated with polygynous birds but some monogamous birds are also sexually dimorphic (Lack 1968). Three main hypotheses have been proposed to explain the evolution of sexual dimorphism in body size (Selander 1972; Banbura 1986). These are discussed in relation to Swallows in Chapter 8.

4.4.6 ADULT BODY SIZE AND SURVIVAL

Head-to-bill length of both sexes and the outer tail-length of males increased significantly in each year of the study. Female outer tail-length showed an opposite trend to that of males, though this difference was not significant. It is possible that a change in selection pressure increased mortality of smaller females and larger males birds during 1987/ 88 relative to 1988/89 (Jones 1987c). The mean body size of those birds which died was compared with those which were recaptured in the following season. If significant differences were evident for head-to-bill length and outer tail-length but absent in other parameters, it would increase the evidence for selection during the study. There was no difference in male outer tail-length between survivors and dead birds but there was for female head-to-bill length (Table 4.16) with bigger birds less likely to survive (Table 4.16). This trend was in the opposite direction to that shown in Table 4.10.

A Sand Martin study found that a decline in keel-length between years was due to selection in favour of small body size (Jones 1987c) and numerous other studies (Andersson 1982; Fleischer & Johnston 1982, 1984; Lehikoinen 1986a; Monaghan & Metcalfe 1986; Møller 1989a; Schantz *et al.* 1989; Bryant 1989a; Wiggins 1991) have found selective size advantages, of both small and large individuals. These trends often varied with sex, environmental conditions and the exact trait under consideration and could be observed for reasons other than selection (Jones 1987c):

i) Body size differences between years could be a product of random fluctuations but trends were similar 1987/88 and 1988/89, and other traits differed in the same direction. Sand Martin and House Martin biometric data were collected by other researchers working concurrently in the same study area and if similar changes in direction are present for head-to-bill length it would further weigh against random fluctuations as an explanation of body size differences (Jones 1987c). This is currently being investigated.

ii) Phenotypic factors can influence nestling and fledgling body-size and these effects can persist into adulthood (Bryant 1989a). The differences in adult size between years may reflect differences in fledgling size between years. Yearling size varied with year of hatch (1987 vs 1988) with female wing-length significantly longer for birds hatched in 1987 (see Bryant 1989a). Other parameters showed a similar trend but the small sample size precludes firm conclusions. Jones (1987c) compared the mean keel-length of fledgling Sand Martins between years and reported no significant differences. Swallows are sexually dimorphic and since fledglings could not be sexed, this analysis was inappropriate here.

iii) Outer tail length increased significantly with age so changes in the mean size of this traits may result from shifts in the mean age of the population, such as would occur if mortality was age-related in the study population. If older females and younger males had higher overwinter mortality then the breeding population the following summer would contain more older males and younger females and result in the observed mean size differences between years. Age-related survival is considered in Chapter 5.

Chapter five
(pp 47 - 66)

Variation in Seasonal Reproductive Performance

5 VARIATION IN SEASONAL REPRODUCTIVE PERFORMANCE

5.1 INTRODUCTION

Individuals vary in their reproductive "performance" both within a season and over a lifetime. Much of this variation has been attributed to properties of the environment, to characteristics of individuals as well as other chance factors (Clutton-Brock 1988; Newton I, 1989 and references therein).

5.1.1 ENVIRONMENTAL FACTORS

Birds can increase the number and quality of young raised each season by breeding in more favourable habitats (Perrins 1965; Newton 1976; Crawford 1977; Högstedt 1980, 1981a; Reese & Kadlec 1985; Gauthier 1989; Martin 1987; Korpimaki 1988a) or at the best time of year (Perrins 1970; Klomp 1970; Daan & Dijkstra 1988; Perrins & McCleery 1989), which probably increase food availability (see Martin 1987). The timing of breeding at the same location varies between years. Spring temperature has been proposed as a factor with birds breeding later in colder springs (Kluijver 1951, 1952; Cavé 1968; Van Balen 1973) perhaps as a result of additional thermoregulatory costs (Farner & King 1978) or decreased food availability (Coulson & Thomas 1985; Boekelheide & Ainley 1989). Timing of breeding and natural food availability have been shown, directly and indirectly, to influence both clutch size and the number of broods attempted (reviewed by Davies & Lundberg 1985; Martin 1987).

5.1.2 INDIVIDUAL CHARACTERISTICS

Laying date and clutch size may also be constrained by hereditary factors so that within a species some birds may be genetically predisposed to lay earlier than others (Findlay & Cooke 1982) or to lay a particular clutch size (Coulson & Thomas 1985, reviewed by Clutton-Brock 1988). There is also much evidence to suggest that phenotypic variation (Chapter 4) is important in shaping reproductive success of birds (Downhower 1976; Dunn 1976; Perrins 1979, 1980; Bryant & Westerterp 1982; Jones 1985; Banbura 1986; Murphy 1986; Møller 1988a, 1990a; Bryant 1988b, 1989a; Langston *et al.* 1990). Relationships have not always proven to be straight forward, however, often differing between species, sexes and years.

Perhaps the most widely studied factor influencing reproductive performance has been that of parental age. Although much of the literature concerns non-passerines studies have also been made on over twenty passerine species (for recent review see Sæther 1990). Hirundine studies have collected data on the Swallow (Jarry 1982; Banbura 1986; Languy &Vansteenwegen 1989; Møller 1990a; Ward 1992); the House Martin (Bryant 1979, Bryant 1988b) and the Tree Swallow (De Steven 1978, 1980).

Studies of both non-passerine and passerine species have consistently found that breeding performance increases with age, experience and duration of the pair bond. Young birds often failed to breed or bred less well (later, smaller clutches or fewer young per brood or per season) than older birds (Sæther 1990). The increase in performance levelled off among the oldest individuals in some species (Coulson 1966; Mills 1973; Coulson & Horobin 1976; Ollason & Dunnet 1978; Findlay & Cooke 1978) but in others it declined (Perrins 1979; Newton *et al.* 1981, but see Clutton-Brock 1988). Where breeding experience is closely associated with age it is difficult to distinguish between the two (Harvey *et al.* 1979, 1985) but they may differ if individuals within the population don't all start to breed at the same age. Four, not mutually-exclusive, hypotheses have been proposed to explain the higher reproductive success of older birds (reviewed by Curio 1983; Nol & Smith 1987; Pugesek & Diem 1990; Desrochers 1992).

5.1.3 AIMS

The aim of this chapter was to identify possible causes and correlates of seasonal reproductive performance, considering both environmental factors and individual characteristics. Seasonal reproductive success is probably related to the number of broods attempted so the incidence and determinants of double-brooding were also investigated. The effects of timing, age and body size on seasonal reproductive success were examined. The reproductive performance of known individuals in successive seasons was analysed to distinguish genuine age-related trends from age effects due to selective mortality.

5.2 METHODS

Methods follow procedures outlined in Chapter 2. Total seasonal reproductive performance was calculated by combining first- and second-brood data. Three different totals were calculated, including or excluding re-lays and where "natural" or "other" failures were distinguished. The probability of a pair attempting a second brood was significantly related to the number of young reared from the first brood (Chapter 6) so only pairs which did not have their first broods manipulated were included in analyses of seasonal reproductive performance in relation to the number of broods attempted.

5.2.1 STANDARDISING MEASURES OF BREEDING PERFORMANCE BETWEEN YEARS

Laying and hatching dates differed significantly between 1988 and 1989 so direct comparisons of years could not be made (Table 5.4). To pool data a standardised laying date was calculated (McLeery & Perrins 1988) relative to the mean of each season: $\text{Standard}=[X_p-X_i) / sd_p]$ where

X_p	Mean date of laying of the population in a given year
sd_p	Standard deviation of date of laying of the population in a given year
X_i	Date of laying of a given individual

Laying earlier than the mean produces a positive score, and later a negative score. Other measures of breeding performance did not generally differ between years (Table 5.4), but as they declined through the season, standardised values were calculated for consistency.

q1

5.2.2 FOOD RESOURCES

The suction trap volume corresponding to various days in the nestling period was calculated where date of hatch was known. Catches on Days 9 (F9) to 13 (F13) were included in the data set because these five days lead up to and normally include peak nestling mass. The following volumes were also calculated: Total volume on Days 9-11; 10-12; 11-13; 9-13, (FT1, FT2, FT3 and FT4 respectively) and total volume from Days 1-7 (FMN1), 8-14 (FMN2), 15-21 (FMN3) and 1 -21 (FMNA).

5.2.3 BODY SIZE AND SURVIVAL

Body size measures and adult survival are described in Chapter 4 (Section 4.2).

5.3 RESULTS

5.3.1 SEASONAL VARIATION IN ENVIRONMENTAL CONDITIONS

5.3.1.1 Insect abundance

There was considerable daily variation in insect abundance (cm^3), particularly during the early and late stages of the breeding season (Fig 5.1). Insect abundance was positively correlated with date in 1988 and 1989 (Table 5.1) but not in 1987 when there were unusually high catches in April and May. Excluding these two months produced a significant correlation ($r=0.40$, $p<0.000$). The highest number of days in a month with < $5cm^3$ was during April and May (1988 &1989), and June and July (1987).

5.3.1.2 Maximum temperature

Temperature (^{o}C) generally increased through the season (Fig 5.2; Table 5.1) then from

Table 5.1 Pearson correlation coefficient matrix of date[a], suction trap catch and weather data, analysed by year (coefficients and significance level)

Variables	Year	Ln (Vol(ml) +1)	Temperature Maximum	Temperature Minimum	Rainfall
Day	1987	-0.04[b] ns	0.48***	0.48***	0.12 ns
	1988	0.82***	0.37***	0.44***	0.13 ns
	1989	0.61***	0.36***	0.54***	0.28***
Ln (Vol+1)	1987	-	-0.08 ns	0.08 ns	-0.02 ns
	1988	-	0.33***	0.32***	0.11 ns
	1989	-	0.35***	0.54***	0.23**
Max Temp[c]	1987	-	-	0.68***	0.00 ns
	1988	-	-	0.54***	0.00 ns
	1989	-	-	0.61***	-0.09 ns
Min Temp	1987	-	-	-	0.18 ns
	1988	-	-	-	0.17 ns
	1989	-	-	-	0.17 ns

a - data from April to September (n=183); April 1st =1

b - correlation between days 0 to 59: r=0.40; p<0.05; days 60+: r=0.40; p<0.000

c - correlation from 120 onwards: r=-0.74; -0.52 and -0.53 for,1987, 1988 and 1989 respectively (all p<0.000)

Table 5.2 Comparison of mean monthly suction trap catch, maximum temperature and rainfall between years, using t-tests

Variables	Years	April	May	June	July	August	September
Ln (Vol+1)	1987 v 1988	**	***	ns	ns	***	***
	1987 v 1989	**	**	ns	ns	**	ns
	1988 v 1989	ns	ns	ns	ns	**	***
MAX Temp	1987 v 1988	ns	**	***	***	ns	ns
	1987 v 1989	ns	***	**	**	ns	ns
	1988 v 1989	ns	**	ns	***	ns	ns
Rainfall	1987 v 1988	ns	ns	*	**	ns	ns
	1987 v 1989	ns	ns	ns	ns	ns	ns
	1988 v 1989	ns	ns	ns	***	ns	ns

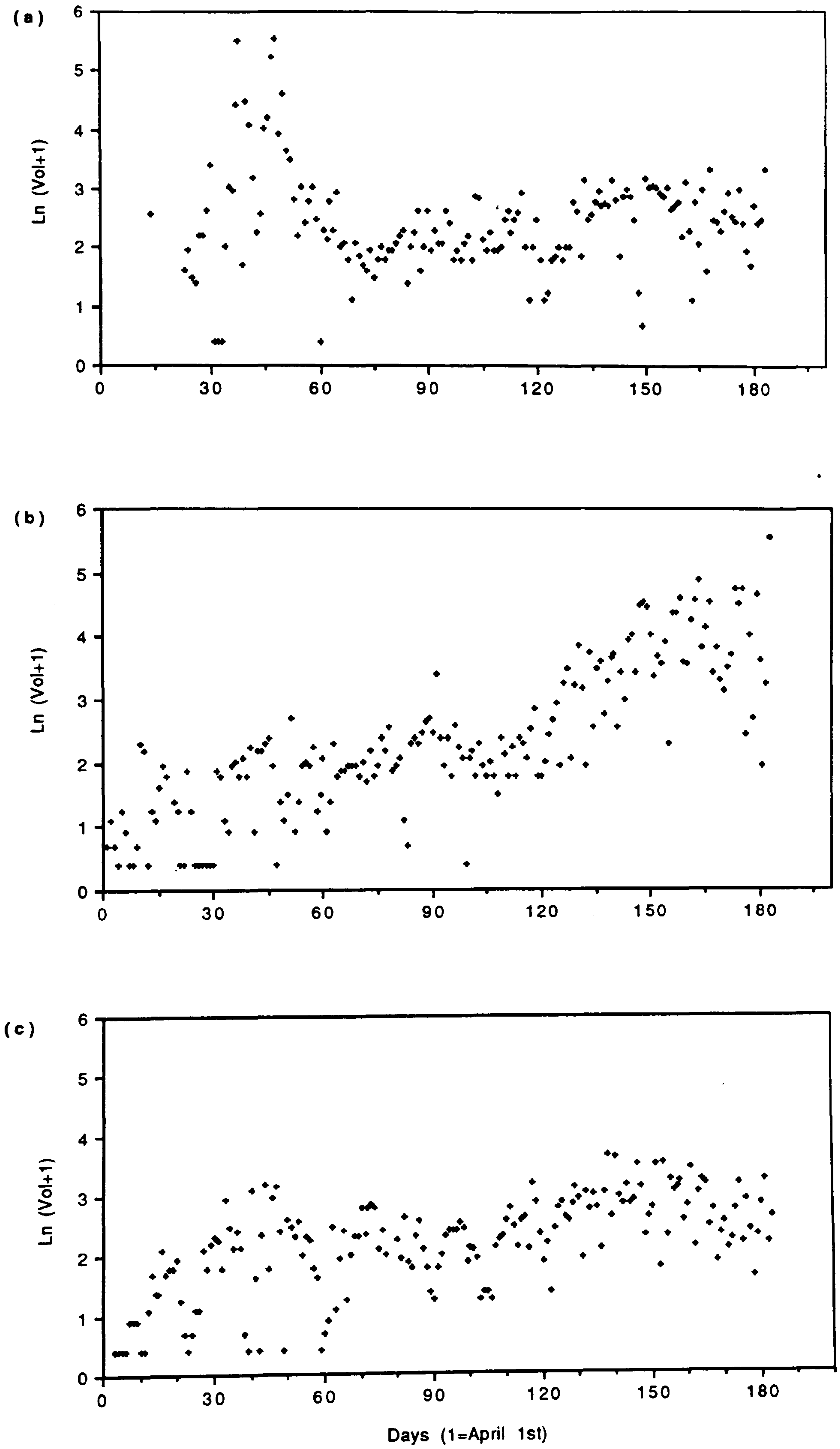


Fig 5.1 Seasonal variation in Suction trap catch (cm^3). Daily catches in: (a) 1987, (b) 1988 and (c) 1989

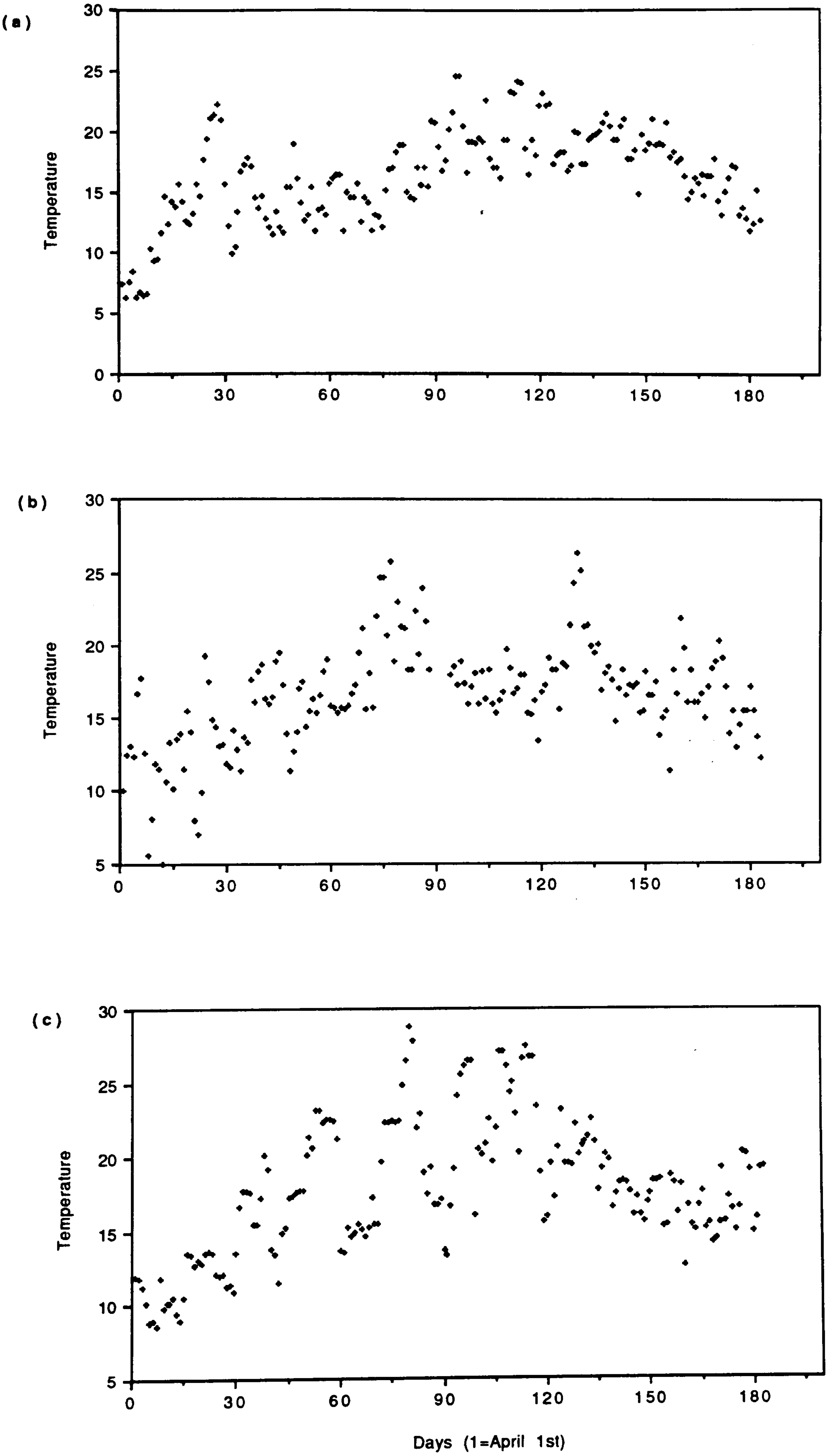


Fig 5.2 Seasonal variation in 1989 in maximum temperature (°C.), 24h maxima in: (a) 1987, (b) 1988 and (c) 1989

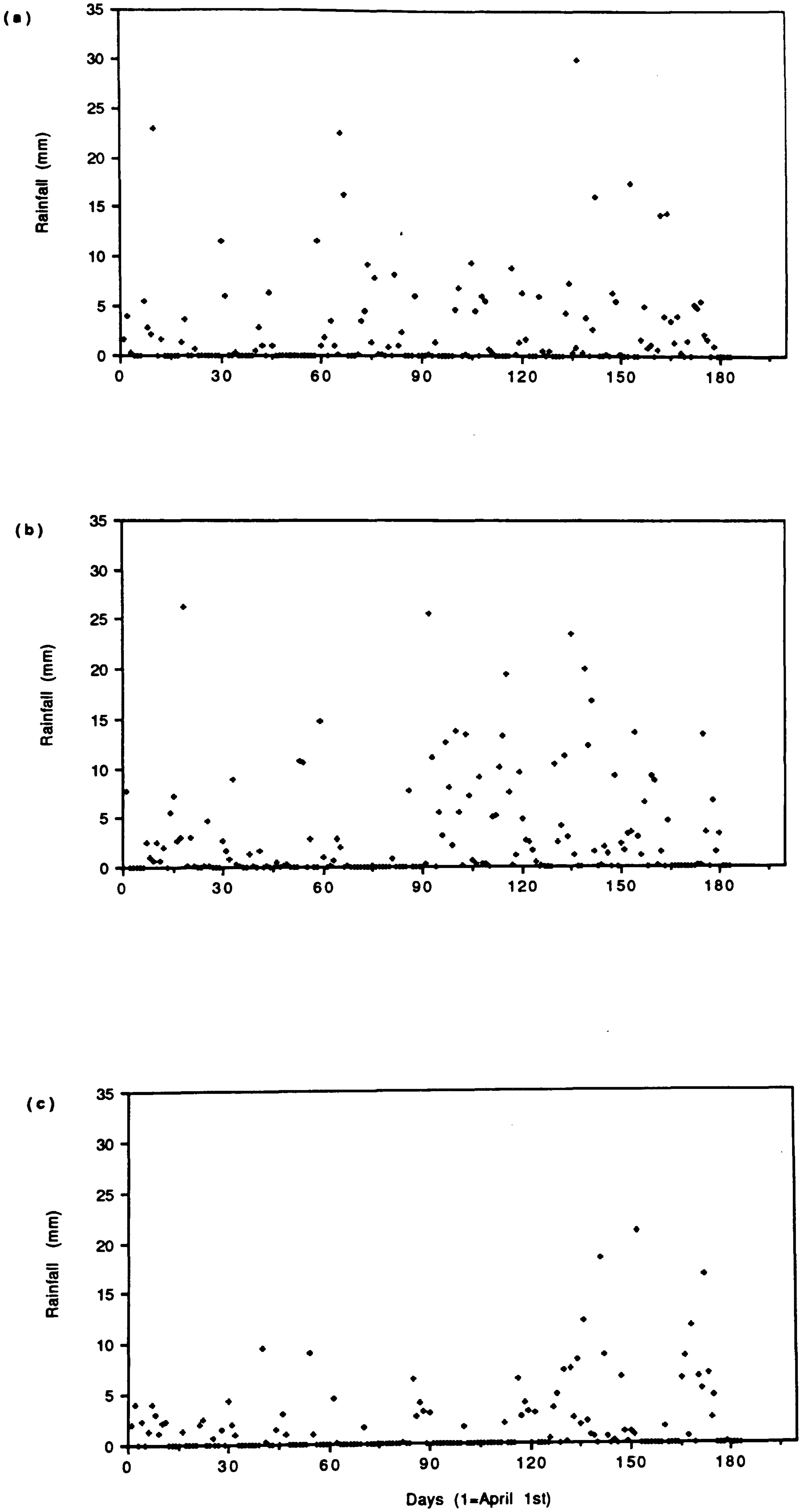


Fig 5.3 Seasonal variation in rainfall (mm), 24h totals in:
(a) 1987, (b) 1988 and (c) 1989

approximately day 120 onwards (i.e ≥ August) decreased ($r=-0.74$; $r=-0.52$; $r=-0.53$, 1987, 1988 and 1989 respectively). Trends were similar for minimum temperature.

5.3.1.3 Rainfall

There was no seasonal trends in rainfall (Fig 5.3) though slightly more fell later in the season (July, August and September) than earlier (April, May, June).

5.3.2 ANNUAL VARIATION IN ENVIRONMENTAL CONDITIONS

Mean monthly insect abundance, maximum temperature and rainfall were calculated for each year (Appendix 5.1). Comparisons were made of the same months between years (Table 5.2).

5.3.2.1 Insect abundance

Insect abundance was highest in 1988 but although in total it was twice that of 1989 (20.3 vs 10.4), in four of the six months the catch was higher in 1989. April and May insect abundance was significantly higher in 1987 (Table 5.2). Only August and September insect abundances were higher in 1988.

5.3.2.2 Maximum temperature

Maximum temperatures in 1988 were on average 0.5 $^{\circ}$C and 1 $^{\circ}$C higher than in 1987 or 1989. Peak monthly temperature was recorded in July (1987 & 1989) and June (1988). May and July maximum temperatures differed significantly between all three years being highest in 1989. June maximum temperature was significantly lower in 1987. There were no significant differences in April, August or September (Table 5.2).

5.3.2.3 Rainfall

Total monthly rainfall did not differ between 1987 and 1989 (Table 5.2). It rained more in 1988 overall (Table 5.4) but the difference was only significant for July. More rain fell in June 1987 than in June 1988 ($p<0.05$). Most rain fell in August (1987 and 1989) and July (1988). May, June and July had most rainy days in 1987, 1988 and 1989 respectively.

5.3.3 FACTORS AFFECTING FOOD ABUNDANCE

Aerial insect abundance increased during the season and with temperature in 1988 &1989, and with rainfall in 1989 (Table 5.1). Temperature (all years) and rainfall (1989) also varied with date in the season. Step-down multiple regression analyses were used to examine the independent effect of these factors on insect abundance (Table 5.3). Date explained 38% & 31% of total variation in insect abundance in 1988 & 1989 respectively. A further 8% of variation was explained by mean temperature in 1988. In 1987 only mean temperature entered significantly. When April and May were excluded more variation was explained by mean temperature and date (Table 5.3).

Table 5.3 **Stepwise Multiple regression analysis of factors (date, mean temperature and rainfall) influencing suction trap catches (Insect) between April and September in: a)1987, b) 1988 and c) 1989**

Dependent Variable	Variables entered[a]	r^2	B	Beta	T	Sig T
Insect 1987	Mean temp	4.8%	-2.57	-0.23	-3.01	0.003
	Constant		49.04		4.52	0.000
Insect 1987[c]	Date	19.4%	0.07	0.45	5.59	0.000
	Mean temp	21.5%	0.36	0.16	2.06	0.041
	Constant		-3.29		-1.17	0.243
Insect 1988	Date	37.5%	0.46	0.75	11.89	0.000
	Mean temp	44.4%	-3.36	-0.30	-4.76	0.000
	Constant		19.41		2.44	0.016
Insect 1989	Date	30.9%	0.08	0.52	7.87	0.000
	Rainfall	33.0%	0.24	0.14	2.07	0.040
	Constant		3.04		3.08	0.002
Insect (1987-89)	Date	11.7%	0.17	0.50	6.36	0.000
	Mean temp	22.6%	-2.68	0.57	-4.69	0.000
	Constant		34.8		5.11	0.000
Insect[b]	Date	45.0%	0.25	0.64	8.94	0.000
	Mean temp	46.7%	-1.17	-0.15	-2.11	0.037
	Constant		2.08		0.23	0.821

a - variables included in final regression in order of entry

b- only data from day 60 onwards included in this analyses

5.3.4 COMPARISON OF ANNUAL VARIATION IN REPRODUCTIVE PERFORMANCE

5.3.4.1 Timing of breeding

Laying started on the 4, 10 and 9th of May in 1987, 1988 and 1989 respectively and was spread over 17, 16 and 14 weeks (Fig 5.4a). The period between the first and last egg laid, was 20 days longer in 1987 (122 days) than in 1988 and 1989. A marked peak in laying occurred during first broods in Weeks 7 and 8 (77%), and 8 and 9 (60%), in 1988 and 1989 respectively (Fig 5.4b). A greater spread was evident in 1987. The onset of laying of second broods peaked in Weeks 15 and 16 in 1988 and 1989, while in 1987 it commenced one week later (Fig 5.4c). Although the onset of laying was earlier in 1987, on average laying date was later than in 1988 and 1989 for both first and second broods (Table 5.4).

5.3.4.2 Clutch size, number of young fledged and peak nestling mass

Mean clutch size did not differ between years (Table 5.4) but the frequency of first-brood clutch sizes differed (Fig 5.5a). More females laid clutches of six or seven eggs in 1989 than in 1987 and there were more clutches of five in 1988 than in 1987 or 1989. There were no such differences for second broods (Fig 5.5b). More young fledged from second broods in 1987 than in 1988 (p= 0.114, Table 5.4). Nestlings from control first broods in 1989 were an average of 1g lighter than in 1987 and 1988 (Table 5.4). There was no significant difference between years for second broods.

5.3.4.3 Relationship of peak nestling mass to brood size

Peak nestling mass declined with brood size (first) in 1987 and 1989 but not in 1988 (Fig 5.6, Table 5.5). In 1988, broods of six had unexpectedly high mass but there was no reason to exclude them from analyses. Second broods showed a similar trend to first broods (All years: r= -0.35 vs -0.36, first and second broods respectively). Correlations were only slightly weaker using brood size at Day 13 (B13) instead of at hatch (BRS) (Table 5.5).

5.3.4.4 Number of broods attempted

The percentage of pairs which were double-brooded decreased each year of the study: 90%, 83% and 75% in 1987, 1988 and 1989 respectively (Table 5.4).

5.3.5 COMPARISON OF REPRODUCTIVE PERFORMANCE OF FIRST AND SECOND BROODS

For all birds (single- and double-brooded combined) clutch size, brood size (at hatch), brood size at Day 13 and the number of fledged young were all smaller for second broods (all tests p<0.001, Table 5.6). The 0.4 more eggs laid in first broods (4.9 vs 4.5) was maintained until the number of fledged young (4.2 vs 3.8). Peak nestling mass was slightly higher in second broods (23.2g vs 22.9g, Table 5.6). The pattern for double-brooded birds was similar; second-broods had lower reproductive performance (all tests p<0.000, except peak nestling mass; Table 5.6). Productivity (number fledged/clutch

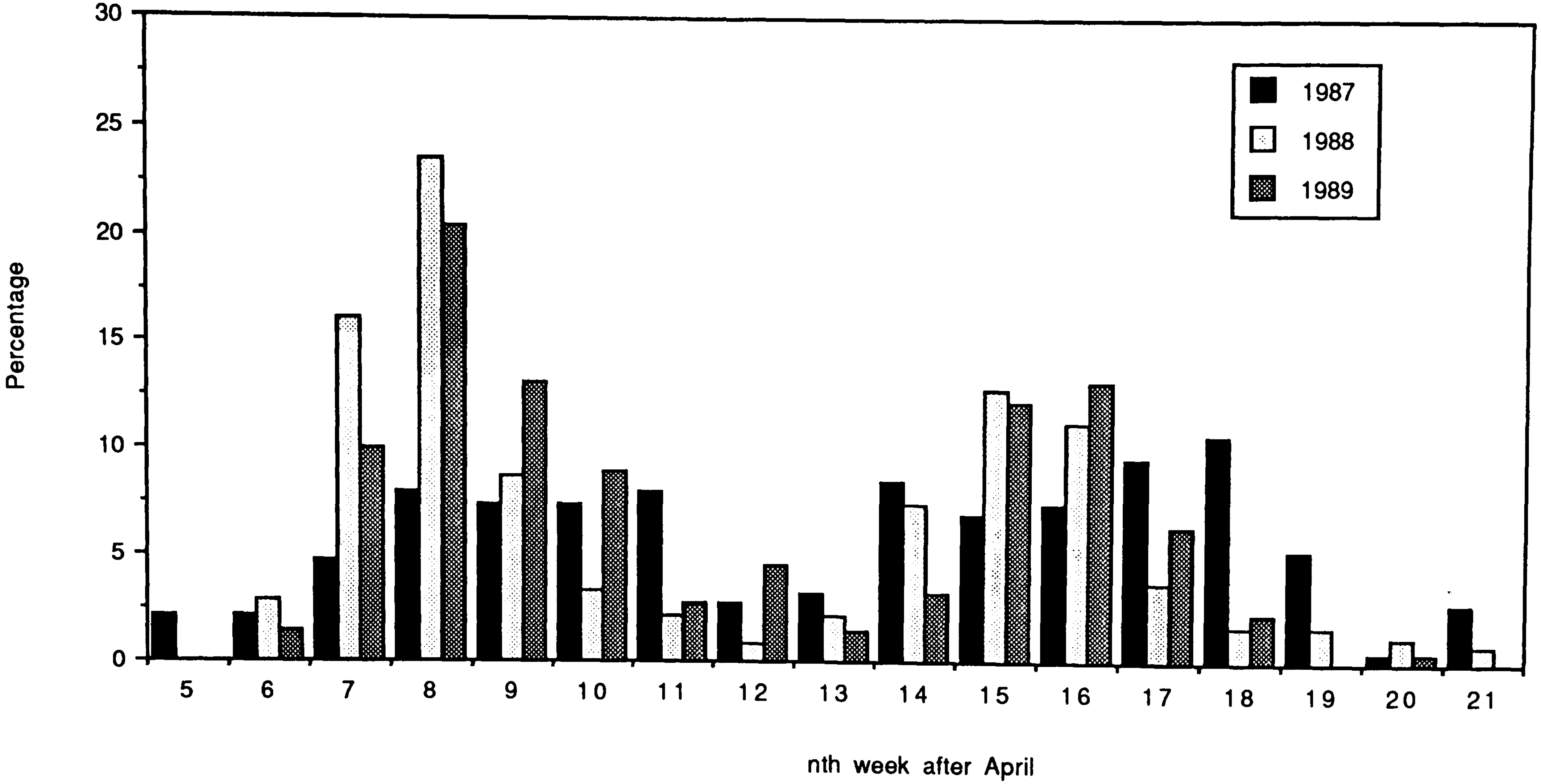


Fig 5.4a **Percentage of pairs commencing clutches in each week during: 1987 (n=133), 1988 (n=177) and 1989 (n=147)**

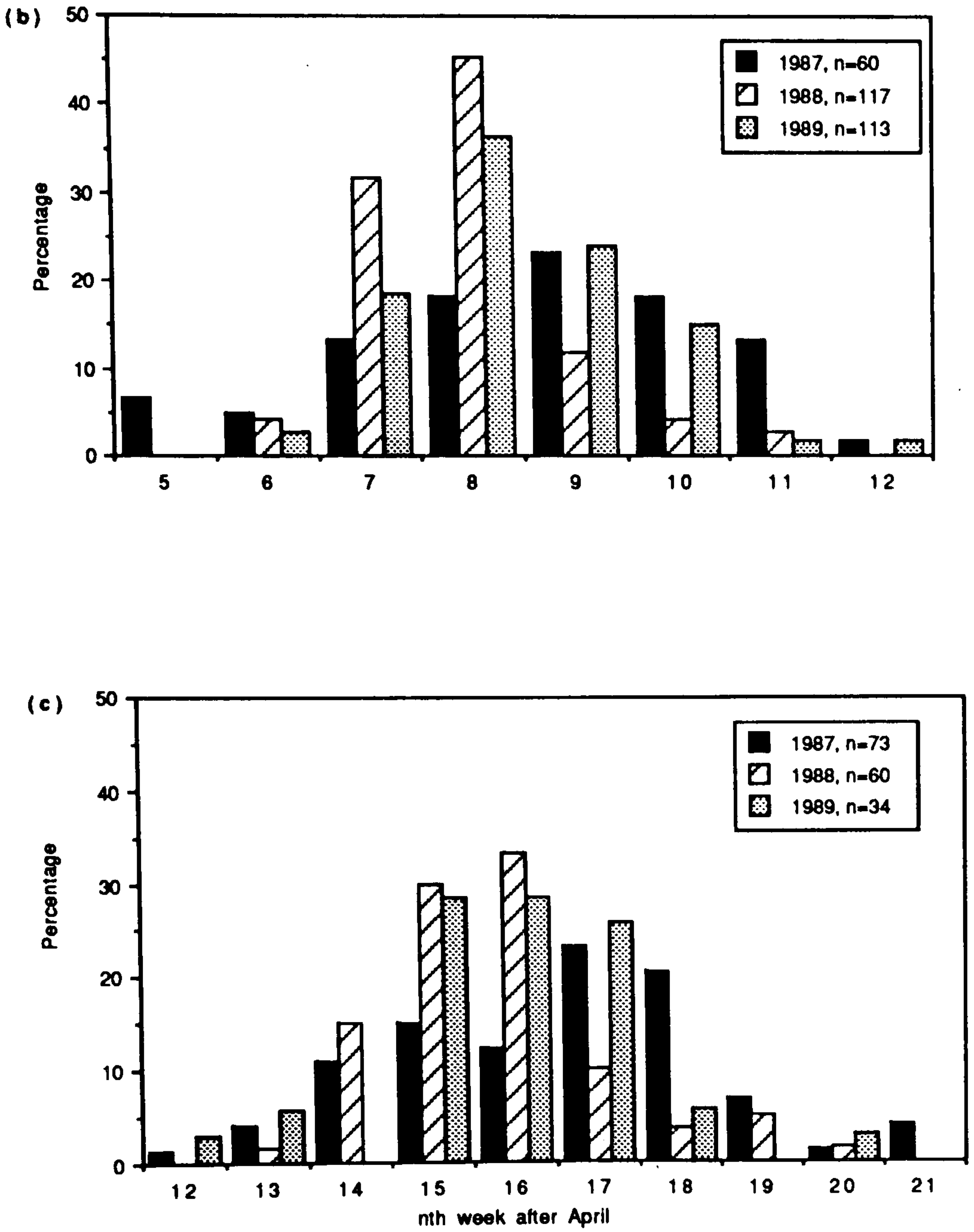


Fig 5.4 Percentage of pairs commencing clutches in each week, by year: (b) First and (c) Second clutches

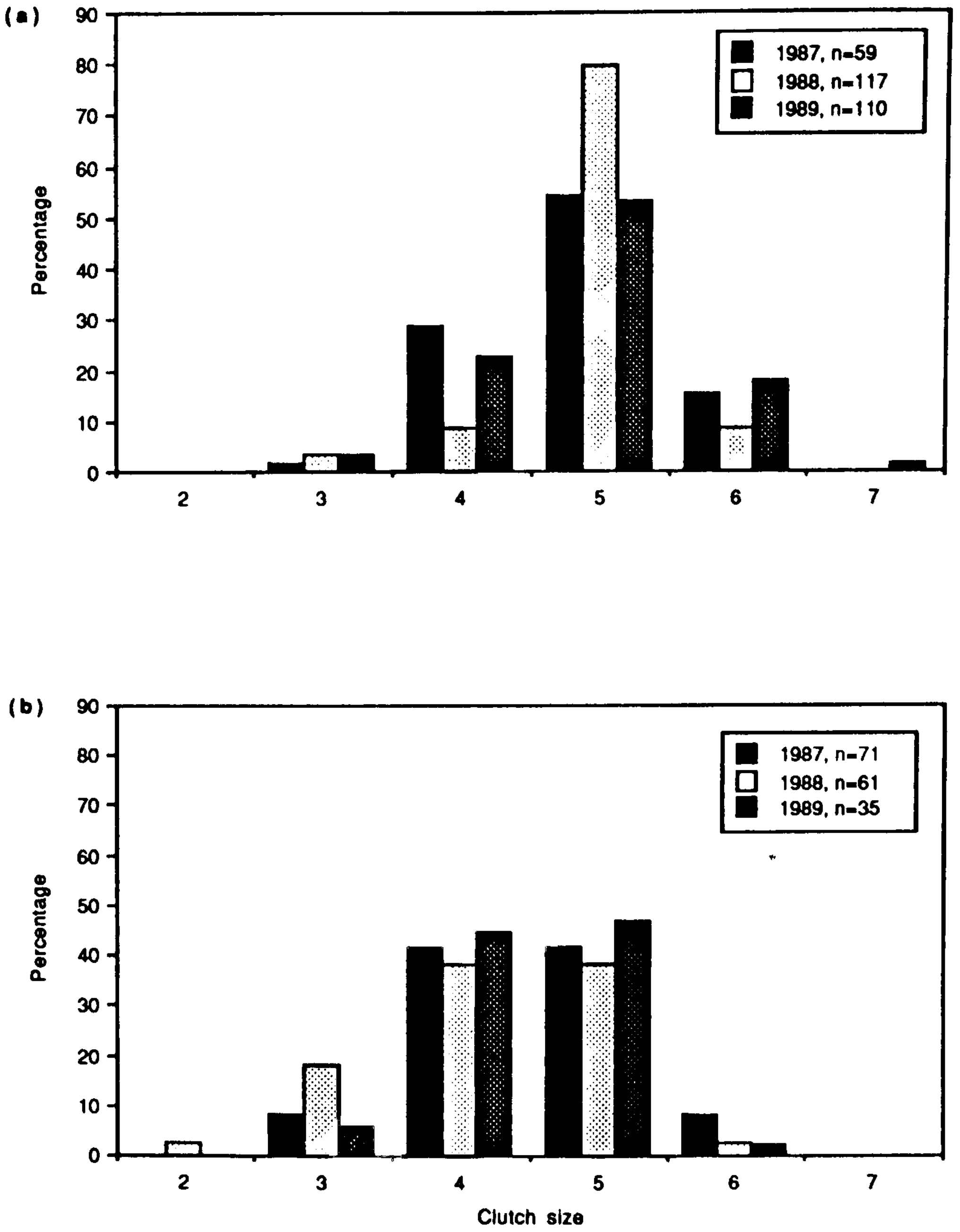


Fig 5.5 Frequency (%) of clutch sizes by year: (a) First and (b) Second clutches

Table 5.4 Comparison of Swallow breeding performance (Mean (se)) between years (1987, 1988 and 1989), by brood number. Using the Students t-test

Measures of		1987		1988		1989		87 v 88		87 v 89		88 v 89	
performance	Br[a]	x (se)	n	x (se)	n	x (se)	n	t	p	t	p	t	p
Date of[b]	F	58 (2)	(60)	52 (1)	(117)	56 (1)	(113)	3.20	0.002	0.91	0.368	-3.84	0.000
first egg	S	113 (2)	(73)	107 (1)	(60)	108 (2)	(34)	2.88	0.005	1.77	0.080	-0.56	0.578
Clutch	F	4.8 (.1)	(59)	4.9 (.1)	(117)	4.9 (.1)	(110)	-0.97	0.335	-0.71	0.476	0.15	0.883
Size	S	4.5 (.1)	(71)	4.4 (.1)	(61)	4.4 (.1)	(35)	0.61	0.546	0.61	0.542	0.06	0.953
Brood	F	4.3 (.2)	(57)	4.6 (.1)	(112)	4.6 (.1)	(102)	-1.74	0.085	-1.63	0.105	-0.01	0.990
Size	S	4.2 (.1)	(62)	4.1 (.1)	(59)	4.1 (.2)	(30)	0.24	0.812	0.65	0.518	0.43	0.671
Number	F	4.2 (.2)	(58)	4.3 (.1)	(66)	4.2 (.2)	(43)	0.15	0.880	0.36	0.718	0.21	0.830
Fledged	S	3.9 (.2)	(45)	2.8 (.3)	(37)	3.4 (.3)	(23)	3.52	0.002	1.60	0.114	-1.43	0.157
Peak	F	23.4 (.2)	(33)	23.3 (.2)	(47)	22.1 (.3)	(47)	0.34	0.809	3.33	0.001	3.51	0.001
mass (g)	S	22.7 (.5)	(17)	23.6 (.3)	(34)	22.7 (.6)	(12)	1.72	0.123	0.10	0.990	1.62	0.186
Double Brooded		88.9%		82.7%		75%							

a - Brood number; F = first and S = second

b - 1 = April 1st

Table 5.5 Pearson correlation of peak nestling mass and brood size (Day 0 and 13), by year and brood number (coefficient, (n), significance level)

Brood size/age	Year	All broods	Brood number First	First[a]	Second[a]
Brood size[b] at Day 0 (BRS)	1987	-0.31 (53) *	-0.58 (27) **	-0.46 (31) *	-0.00 (16) ns
	1988	-0.14 (77) ns	0.02 (43) ns	-0.01 (46) ns	-0.25 (31) ns
	1989	-0.58 (60) ***	-0.56 (41) ***	-0.58 (46) ***	-0.63 (12) *
	All years	-0.30 (197) ***	-0.35 (111) ***	-0.36 (123) ***	-0.36 (58) **
Brood size[b] at Day 13 (B13)	1987	-0.25 (55) ns	-0.49 (27) *	-0.42 (31) *	-0.14 (16) ns
	1988	-0.16 (79) ns	-0.06 (44) ns	-0.07 (46) ns	-0.20 (31) ns
	1989	-0.47 (61) ***	-0.51 (41) ***	-0.55 (46) ***	-0.23 (12) ns
	All years	-0.27 (196) ***	-0.33 (112) ***	-0.35 (124) ***	-0.16 (58) ns

a - includes relay attempts

b - only successful broods were included (i.e fledged at least one young); including all broods had the effect of slightly weakening the relationship though in general the level of significance did not alter.

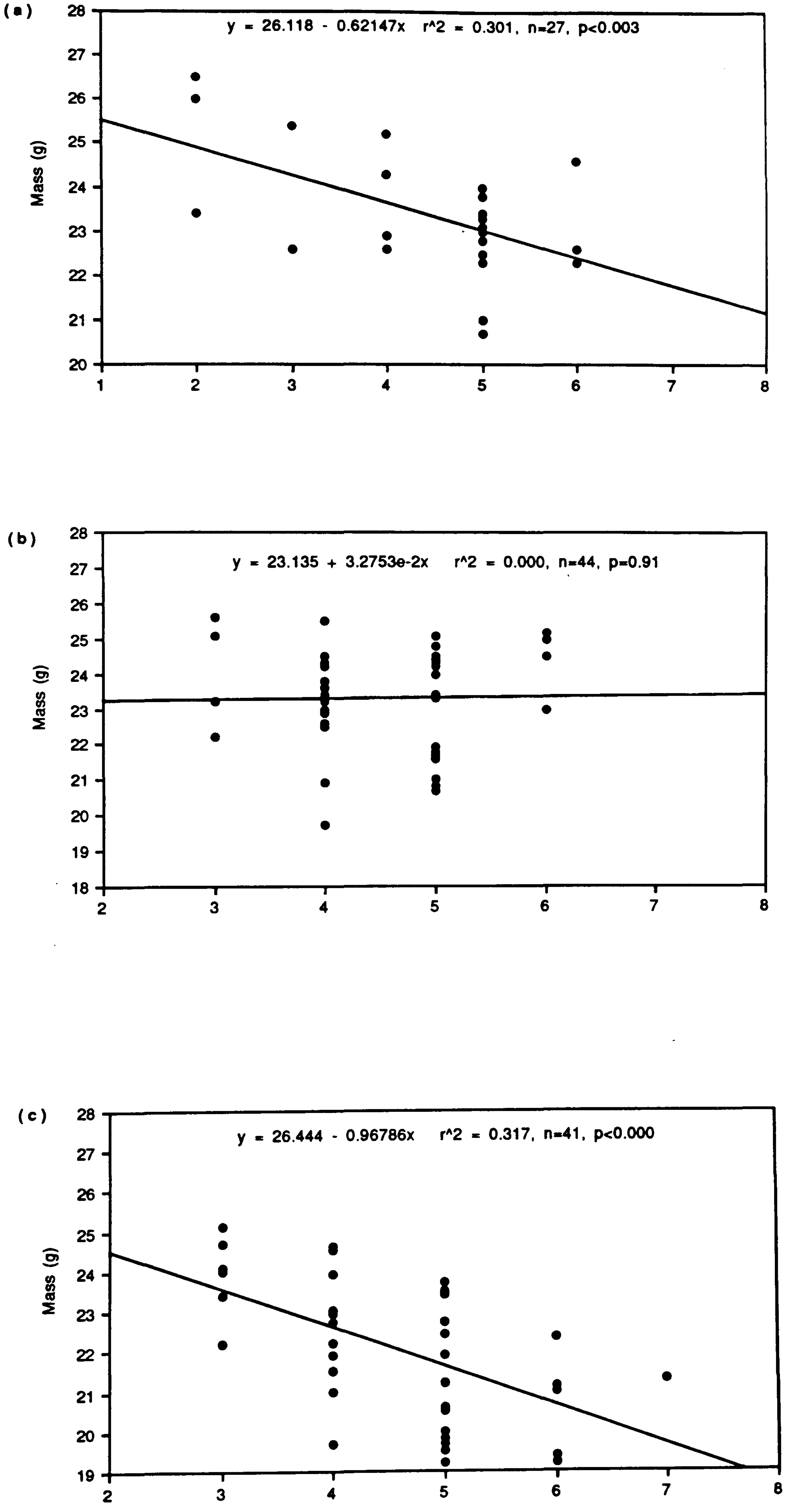


Fig 5.6 **Relationship between peak nestling mass and size of first brood: (a) 1987, (b) 1988 and (c) 1989**

size) was also higher in first broods (0.92±0.02 vs 0.78±0.03, $p<0.003$) indicating that the larger number of fledglings was not just a factor of larger clutch size in first broods. Almost half of double-brooded females laid the same clutch size for first and second broods; fourty-four percent laid smaller second clutches and eight percent larger.

5.3.5.1 Single- versus double-brooded birds

First brood clutch size, brood size and number of young fledged was greater in double-brooded than single-brooded birds, raising 0.6 more young than single-brooded birds. Differences were significant for all three measures in 1989 (all $p<0.001$).

5.3.6 SEASONAL TRENDS IN REPRODUCTIVE PERFORMANCE

Clutch size declined with laying date in all years (Table 5.7a; Fig 5.7a-c for 1987, 1988 & 1989 respectively). Only in 1989 was there a greater decline for first broods than second broods. A similar trend was observed for brood size (data not presented). Monthly clutch size decreased from May to August with about one more egg laid in May than in August (5.0 vs 3.9). No clutches were laid in April and only two were started in September (both in 1987) (Table 5.7b).

The number of young fledged from first broods declined as the season advanced in all years. In second broods this trend was only significant in 1987 (Table 5.7a).

Only all-year data showed a significant decline in first-brood peak nestling mass (PNM) with hatching date (Table 5.7a). Individual year data showed no significant trends (Table 5.7a). Only food abundance on Days 12 (F12) and 13 (F13) was correlated with date of hatch and PNM of first broods (Table 5.8). PNM was negatively correlated with date of hatch (first broods) when brood size (BRS) was included as a partial correlate (Table 5.8). The trend was similar in each year, but only significant in 1989. When first broods were split by size (≤ 3, =4 and ≥ 5), PNM decreased with laying date when at least five young were reared (Fig 5.8c); no trends were apparent for the other two brood size classes (Fig 5.8a,b).

Brood size explained most variation in PNM: 27% and 24% for 1987 and 1989 respectively in multiple regression analyses (Table 5.9). Food abundance on Day 10 (F10) and the number of young fledged explained a further 24% and 11% respectively, in 1989. PNM was not significantly correlated with date of hatch or brood size in 1988; nor was brood size significantly correlated with date of hatch in the same year.

5.3.7 JUVENILE RECRUITMENT

'Recruit' is usually taken to mean an offspring which survived to breed but here the term

Table 5.6 Comparison[a] of first- and second-brood Swallow breeding data (mean (se)) for 1987, 1988 and 1989 combined

Breeding variables	Breeding Attempts	Brood number First	Second	n	t	df	p
Clutch size	All[b]	4.9 (.1)	4.5 (.1)	182,160	6.51	340	0.000
	DB[c]	4.9 (.1)	4.5 (.1)	133	6.44	132	0.000
Brood size	All	4.5 (.1)	4.2 (.1)	181,145	3.19	324	0.002
at hatch	DB	4.5 (.1)	4.1 (.1)	118	3.87	117	0.000
Brood size	All	4.3 (.1)	3.9 (.1)	179,144	4.01	321	0.000
at day 13	DB	4.5 (.1)	3.6 (.3)	77	5.10	76	0.000
Number	All	4.2 (.1)	3.8 (.1)	175,134	3.67	305	0.000
fledged	DB	4.4 (.1)	3.5 (.2)	80	5.42	79	0.000
Peak nestling	All	22.9 (.2)	23.2 (.2)	127,63	-1.09	188	ns
mass	DB	22.9 (.3)	23.0 (.3)	27	-0.17	26	ns

---

a - only control broods included in analyses

b - all first vs all second broods, students t-test

c - first- and second-broods of double-brooded pairs only, paired t-test

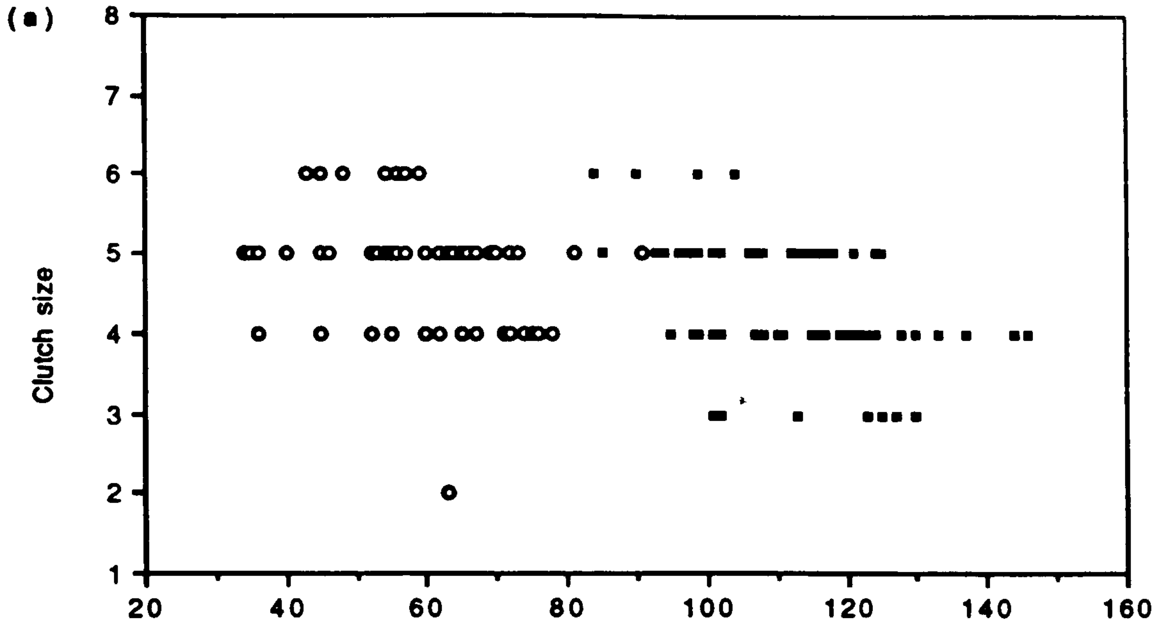
Table 5.7a Pearson correlation coefficients^a of clutch size, number fledged and peak nestling mass with date of hatch, by year and brood number (coefficient, (n^b) , p)

Breeding variables	Year	All broods	Brood number		
			First^c	First	Second^c
Clutch size	1987	-0.42 (182) 0.000	-0.37 (74) 0.001	-0.30 (66) 0.015	-0.45 (80) 0.000
	1988	-0.36 (240) 0.000	-0.17 (136) 0.049	-0.16 (125) 0.048	-0.31 (95) 0.000
	1989	-0.29 (219) 0.000	-0.32 (130) 0.000	-0.43 (120) 0.000	-0.41 (75) 0.000
Number fledged	1987	-0.19 (113) 0.049	-0.28 (59 0.030	-0.31 (54) 0.023	-0.43 (41) 0.005
	1988	-0.38 (115) 0.000	-0.16 (69) 0.183	-0.26 (63) 0.041	-0.21 (46) 0.158
	1989	-0.23 (100) 0.018	-0.36 (49) 0.011	-0.36 (42) 0.020	-0.17 (49) 0.255
Peak nestling mass	1987	-0.03 (56) 0.868	-0.12 (31) 0.532	0.14 (27) 0.503	0.41 (16) 0.117
	1988	0.13 (81) 0.237	-0.16 (47) 0.292	-0.21 (44) 0.174	0.02 (33) 0.823
	1989	0.16 (55) 0.252	0.15 (45) 0.339	-0.14 (40) 0.383	-0.68 (7) 0.093

a - only control broods

b - includes second brood relays plus third broods; significance levels did not alter when these were excluded

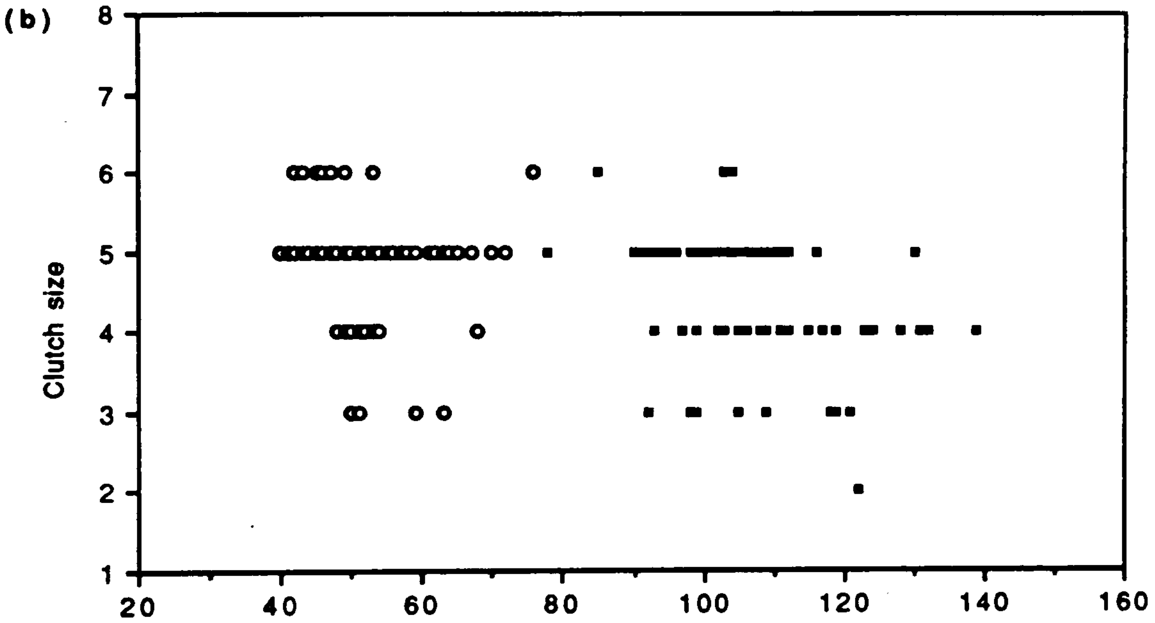
c- includes re-lays



First: Y = 5.83 - 1.6790e-2x r^2 = 0.089 r=-0.30: n=66, p<0.015

Second:Y = 7.53 - 2.7505e-2x r^2 = 0.206 r=-0.45: n=80, p<0.000

note: symbols are the same as Fig 5.7c



First: Y = 5.63 - 1.3939e-2x r^2 = 0.026 r=-0.16: n=125, p<0.048

Second:Y = 6.83 - 2.2812e-2x r^2 = 0.095 r=-0.31: n=95, p<0.002

note: symbols are the same as Fig 5.7c

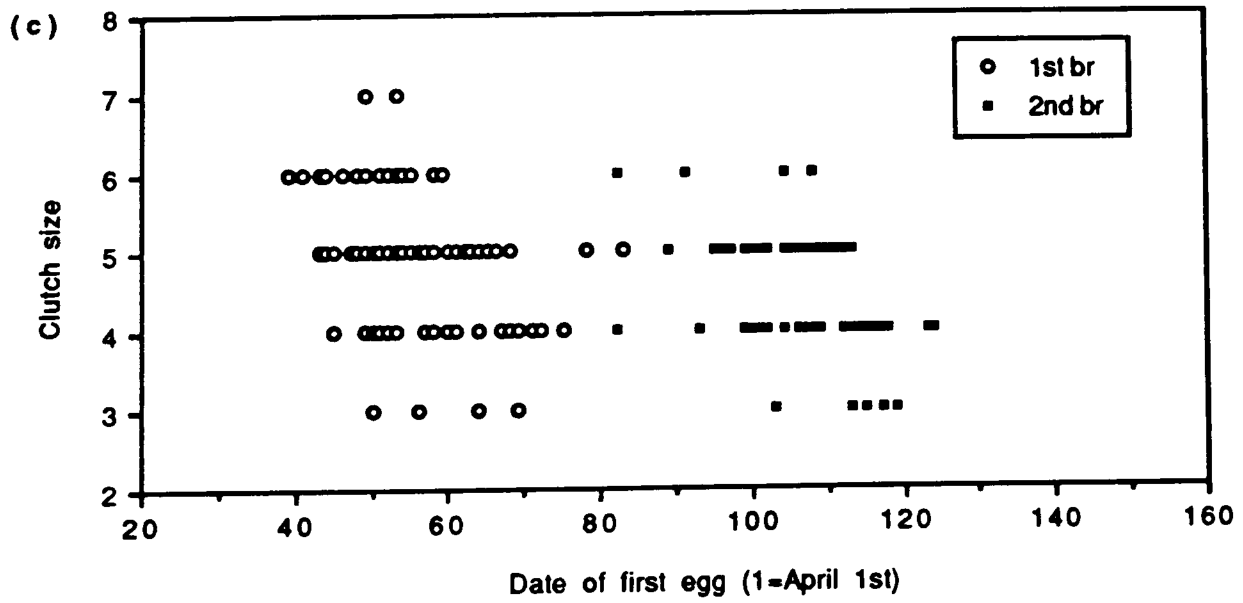


Fig 5.7 Clutch size in relation to date of laying, analysed by brood number (1st and 2nd): (a) 1987, (b) 1988 and (c) 1989

First: Y = 7.15 - 3.9755e-2x r^2 = 0.182 r=-0.43: n=120, p<0.000

Second: Y = 8.18 - 3.4814e-2x r^2 = 0.169 r=-0.41: n=75, p<0.000

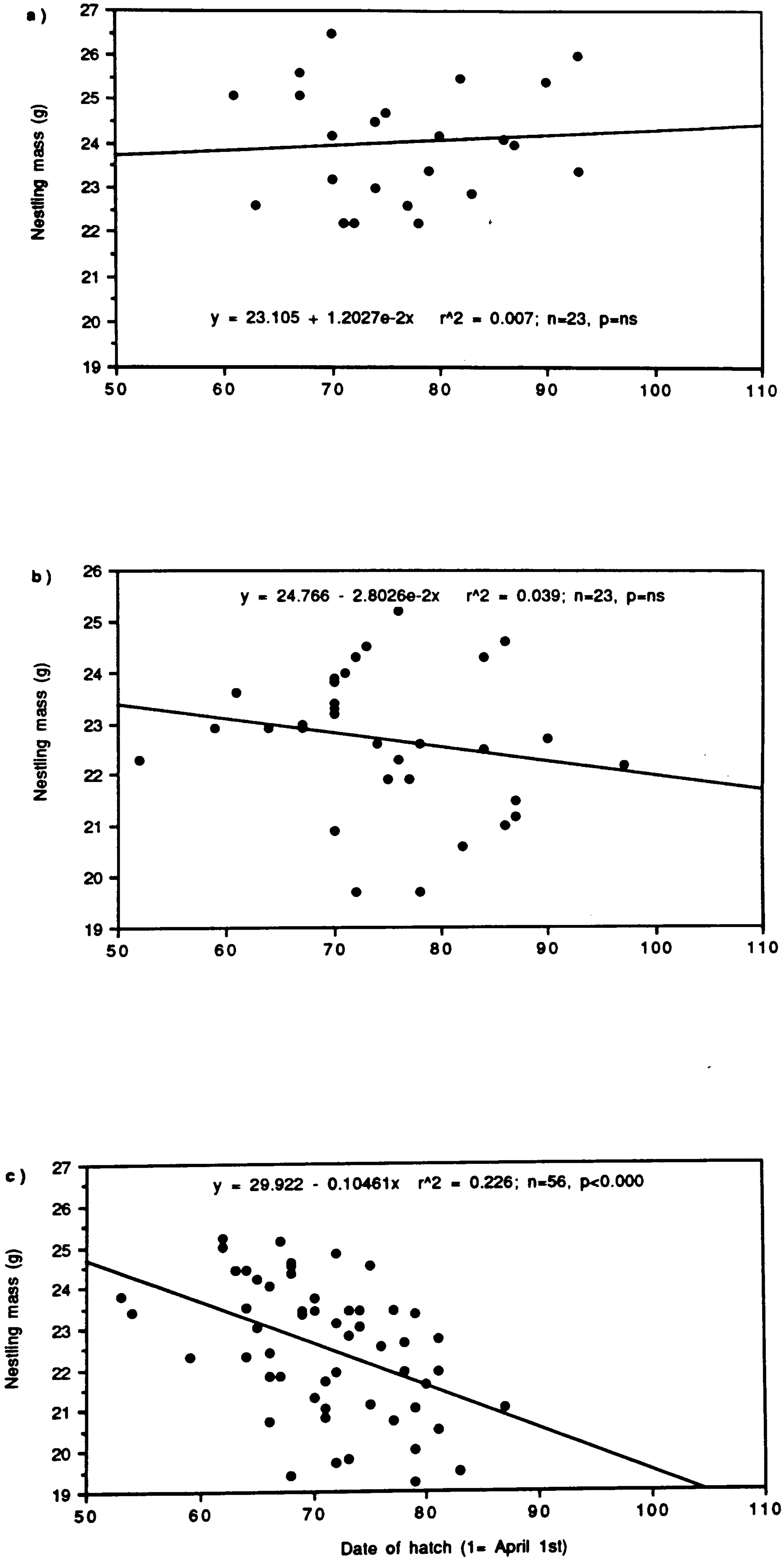


Fig 5.8 Relationship between date of hatch and nestling mass on day 13, analysed by size of first brood: (a) ≤ 3, (b) =4 and (c) ≥ 5. Data are for 1987 to 1989

Table 5.7b Mean (se) and range (n) of Swallow clutch size each month, analysed by year, first- and second-broods combined, all females (All) and double-brooded females (DB)

Year	Breeding attempts	May	June	July	August
1987	All	5.1 (.1) 4-6 (37)	4.6 (.1) 2-6 (45)	4.5 (.1) 3-6 (70)	3.9 (.1) 3-5 (29)
	DB	5.1 (.1) 4-6 (28)	4.7 (.2) 2-6 (28)	4.6 (.1) 3-6 (54)	3.8 (.1) 3-5 (17)
1988	All	4.9 (.1) 3-6 (116)	4.9 (.1) 3-6 (123)	4.4 (.1) 2-6 (85)	3.9 (.2) 3-5 (11)
	DB	5.0 (.1) 3-6 (91)	4.9 (.2) 4-6 (13)	4.4 (.1) 2-6 (84)	3.9 (.2) 3-5 (11)
1989	All	5.1 (.1) 3-7 (86)	4.6 (.1) 3-6 (49)	4.5 (.1) 3-6 (77)	3.8 (.2) 3-4 (5)
	DB	5.2 (.1) 3-7 (65)	4.7 (.2) 3-6 (21)	4.5 (.1) 3-6 (69)	3.8 (.3) 3-4 (4)
All years	All	5.0 (.0) 3-7 (239)	4.7 (.1) 2-6 (120)	4.5 (.1) 2-6 (232)	3.9 (.1) 3-5 (45)
	DB	5.1 (.1) 3-7 (184)	4.7 (.1) 2-6 (62)	4.5 (.1) 2-6 (207)	3.8 (.1) 3-5 (32)

Table 5.8 **Pearson correlation coefficients of food abundance with date of hatch and peak nestling mass during first broods, analysed by year (coefficient, significance level)**

		Measures of food abundance[a]												
	Year	F9	F10	F11	F12	F13	FT1	FT2	FT3	FT4	FMN1	FMN2	FMN3	FA
Date of hatch	1987	-0.13 ns	0.07 ns	0.11 ns	0.33 *	0.36 * *	0.34 *	0.44 *	0.29 *	0.01 ns	-0.47 * * *	0.14 ns	0.74 * * *	-0.31 *
	1988	0.17 ns	0.22 ns	0.27 *	0.16 ns	0.10 *	0.30 *	0.24 *	0.29 *	0.32 *	0.67 * * *	0.34 * *	0.09 ns	0.72 * * *
	1989	-0.19 ns	-0.42 * *	-0.23 ns	-0.01 ns	-0.15 ns	-0.34 *	-0.20 ns	-0.35 *	-0.40 *	-0.33 *	-0.17 ns	-0.03 ns	-0.48 * *
	All years	-0.00 ns	0.03 ns	0.11 ns	0.16 *	0.05 ns	0.12 ns	0.13 ns	0.14 ns	0.06 ns	-0.11 ns	0.12 ns	0.10 ns	-0.02 ns
Peak nestling mass	1987	0.25 ns	0.03 ns	-0.11 ns	0.17 ns	0.07 ns	0.24 ns	0.06 ns	0.05 ns	0.14 ns	-0.11 ns	0.005 ns	-0.11 ns	-0.08 ns
	1988	0.04 ns	-0.19 ns	-0.12 ns	0.00 ns	-0.14 ns	-0.14 ns	-0.12 ns	-0.15 ns	-0.12 ns	0.02 ns	-0.10 ns	-0.05 ns	-0.08 ns
	1989	0.20 ns	0.46 * *	0.05 ns	-0.26 ns	-0.18 ns	-0.03 ns	-0.19 ns	0.12 ns	0.33 *	0.09 ns	0.26 ns	-0.16 ns	0.26 ns
	All years	0.15 ns	0.07 ns	-0.05 ns	-0.02 ns	-0.20 *	-0.05 ns	-0.157 ns	0.00 ns	0.09 ns	-0.06 ns	0.11 ns	0.05 ns	0.01 ns

a - abbreviations: F9 to FA are described in Section 5.2

Table 5.9 Stepwise multiple regression of date of hatch,brood size[a] and food abundance[b] on peak nestling mass, by year

Analysis	Variables entered	r^2 (%)	B	Beta	T	Sig
First brood 1987-1989	Brs(0)	10.1	-1.19	-0.65	-5.48	* * *
	Date	19.6	-0.05	-0.26	-2.88	* *
	Brs(18)	24.3	0.48	0.34	2.76	* *
	Constant		30.1		17.4	* * *
First brood[c] 1987-1989	Brs(0)	10.1	-0.76	-0.42	-4.64	* * *
	Date	19.6	-0.07	-0.33	-3.68	* * *
	F13	22.2	-0.05	-0.18	-2.14	*
	Constant		31.5		18.5	* * *
1987	Brs(0)	26.9	-0.65	-0.54	-3.31	* *
	Constant		26.3		29.2	* * *
1989	Brs(0)	24.2	-1.51	-0.76	-6.00	* * *
	F10	47.7	0.22	0.38	3.23	* *
	Brs(18)	58.2	0.59	0.41	3.09	* *
	Constant		24.7		23.1	* * *
1989[c]	Brs(0)	24.2	-1.22	-0.62	-5.17	* * *
	F10	47.7	0.25	0.43	3.56	* *
	Date	52.1	-0.06	-0.25	-2.04	* * *
	Constant		30.3		10.0	* * *

a - three measures of brood size were included: Day 0, 13 and 18 (BRS, B13 and NYF)

b - all measures of food abundance (Table 5.8) were included

c - all variables included except brood size at Day 18 is used for offspring which survived to the year following hatch. Forty-seven offspring were recaptured within the study area one or two years after fledging; 60% (n=28) were male, 38% (n=17) female. Sex was not determined for the remaining two recruits (see Table 3.9). Males or females were equally likely to be recruited from first or second broods There was no significant difference in hatching date so both sexes were pooled.

5.3.7.1 Brood number

The majority of recruits came from first broods but the pattern varied with year of hatch (Table 5.10a). Only half of recruits were reared from first broods in 1987, compared to over four fifths in 1988 but this difference was not significant after controlling for the number of nests (first and second broods) from which young were known to fledge (Table 5.10b). In 1987, four pairs produced two recruits each (29%); three produced one from both their first and their second brood whilst the fourth produced two from their first brood. No individual was known to produce recruits in successive years.

5.3.7.2 Date of hatch

Offspring were recruited from throughout the season. Recruits came mostly from peak dates of hatch. The earliest hatching dates of a recruit were the 22nd May and 1st June and the latest were the 18th and 16th August, in 1987 and 1988 respectively. No young hatched after Week 20 in 1987 and Week 19 in 1988 were known to be recruited. Nests with recruits hatched on average ten days (ns) before other nests (Table 5.11a). There were no significant differences analysing first and second broods separately.

5.3.7.3 Brood size

The relationship of brood size (control) to recruitment was investigated by calculating:

No_x = Actual number recruited per brood size x, where x=2 to 6
Mean_x = (Total No. recruited from brood size x)/(Total number of nests of brood size x)

For example, if six nestlings were recruited from brood sizes of five and 200 nests had a brood size of five, then

Mean_x: =6/200 = 0.03, where x=5

Nestlings were recruited from control broods but the pattern differed between years: 1987=3, 4 and 5; 1988= 2, 3, 4, 5 and 6 (Fig 5.9a). Only two nestlings were recruited from broods of six (both in 1988). Analysing year data showed that only in 1987 did the number of recruits increase with brood size to a brood size of five, however, no recruits were produced from broods of six. Mean_x (see above) also increased with brood size. Brood sizes of two and six yielded most recruits in 1988 and, unlike 1987, there was little difference between broods of three, four and five. For pooled data, broods of five had the highest, and broods of three the lowest Mean_x. The main difference between years was the lower recruitment from broods of four and five (6/88=0.02; *cf.* 26/87) and higher recruitment from broods of six in 1988.

Table 5.10a Number of offspring recruited from first and second broods, by year of hatch

Brood No.	Year of hatch 1987[a]	1988	Both years
First	12	12	24
First Relay	1	2	3
Second	12	3	15
Second Relay	-	-	-
Third	-	-	-
Unknown	5[b]	-	5
All First	13	14[b]	27
All Second	12	3	15
All unknown	5	-	5
Total[c]	30	17	47

a - includes data from ≤ 1986
b - includes two which were ringed for the first time as fledglings (> 30 days)
c - includes five nestlings which were recruited from manipulated broods

Table 5.10b Comparison of the number and percentage of offspring recruited from first and second broods, by year. Using Chi-Square analysis (X^2, df, p)

Year of hatch	Brood number	No. and (%) of nests producing recruits No	Yes	Total	Chi-square X^2	df	p
1987	First	47 (78.3)	13 (21.7)	60			
	Second	34 (81.0)	8 (19.0)	42	0.104	1	0.748
1988	First	61 (85.9)	10 (14.1)	71			
	Second	43 (95.6)	2 (4.4)	45	2.760	1	0.097
Both years	First	108 (82.4)	23 (17.6)	131			
	Second	77 (88.5)	10 (11.5)	87	1.500	1	0.222

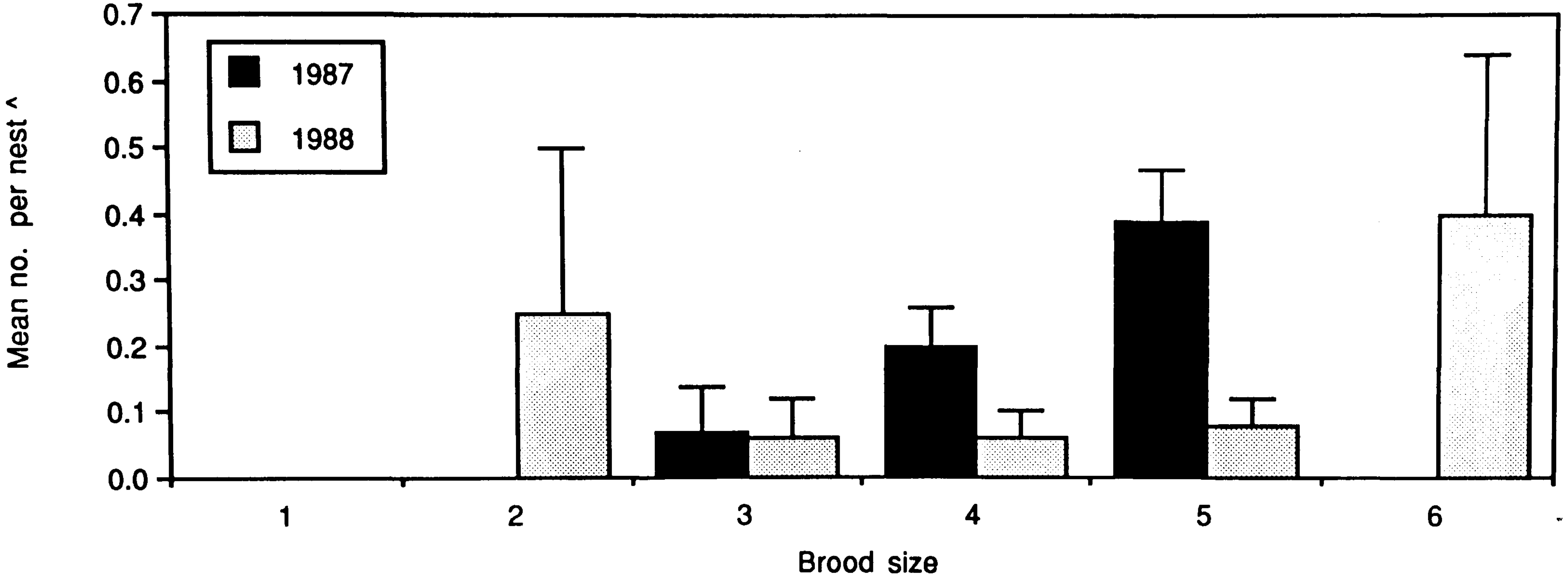
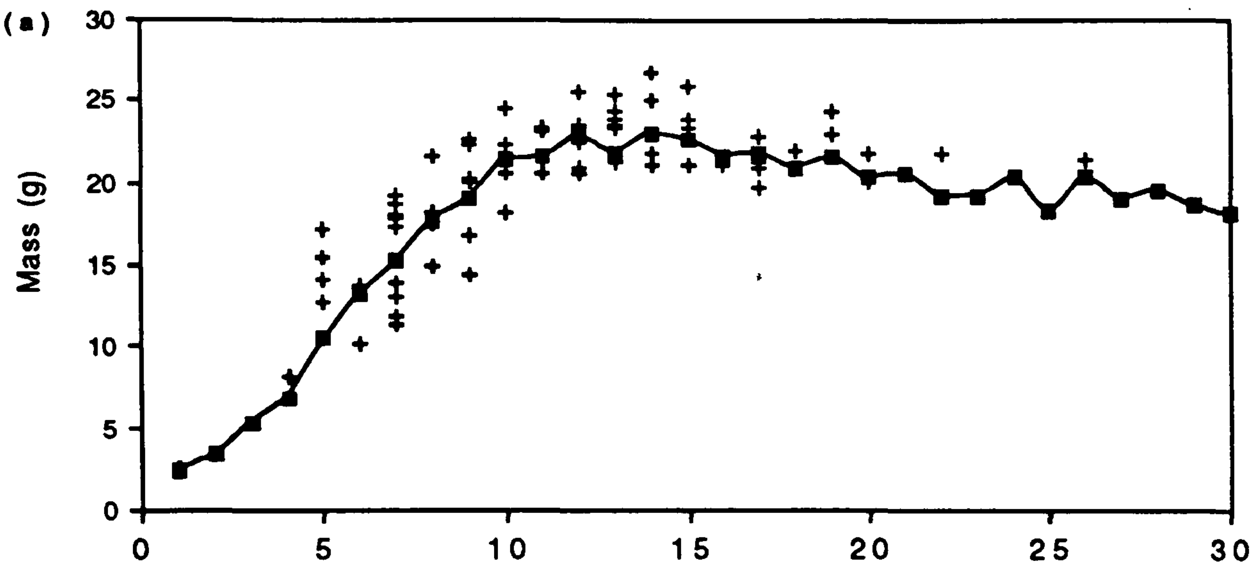
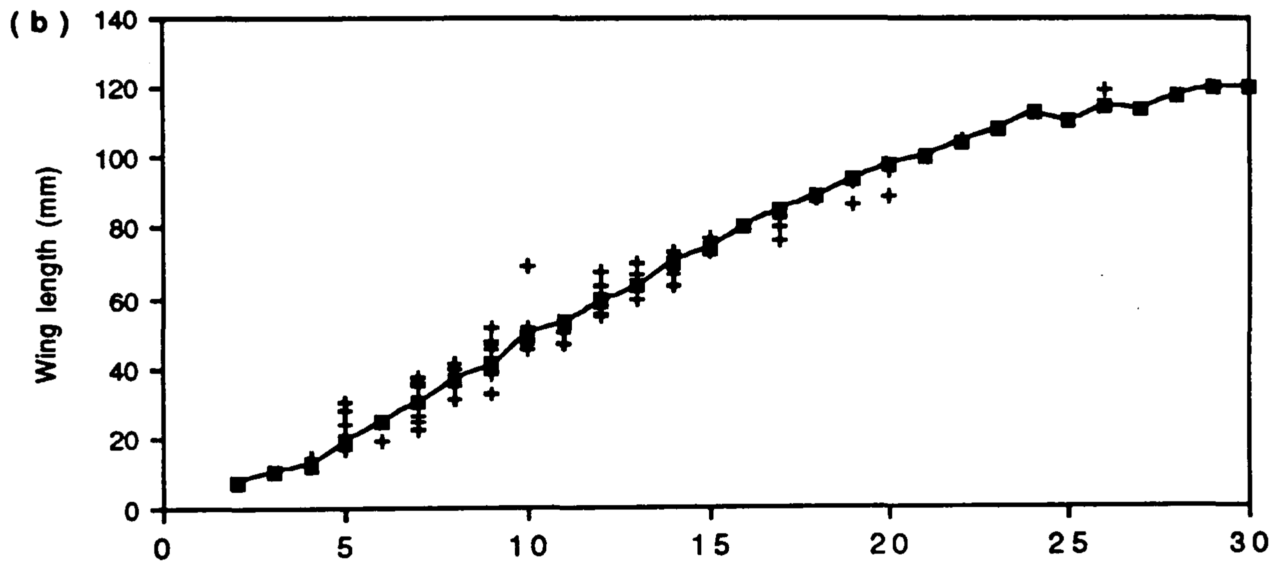


Fig 5.9 **Number of recruits (+se) produced per brood size (un-manipulated), expressed as a proportion of the total number of nests which contained each brood size, analysed by year of hatch**

note: ^ eg In 1988 four broods of two were found and one young was known to be recruited: average= 1/4=0.25



note: symbols are the same as Fig 5.10c



note: symbols are the same as Fig 5.10c

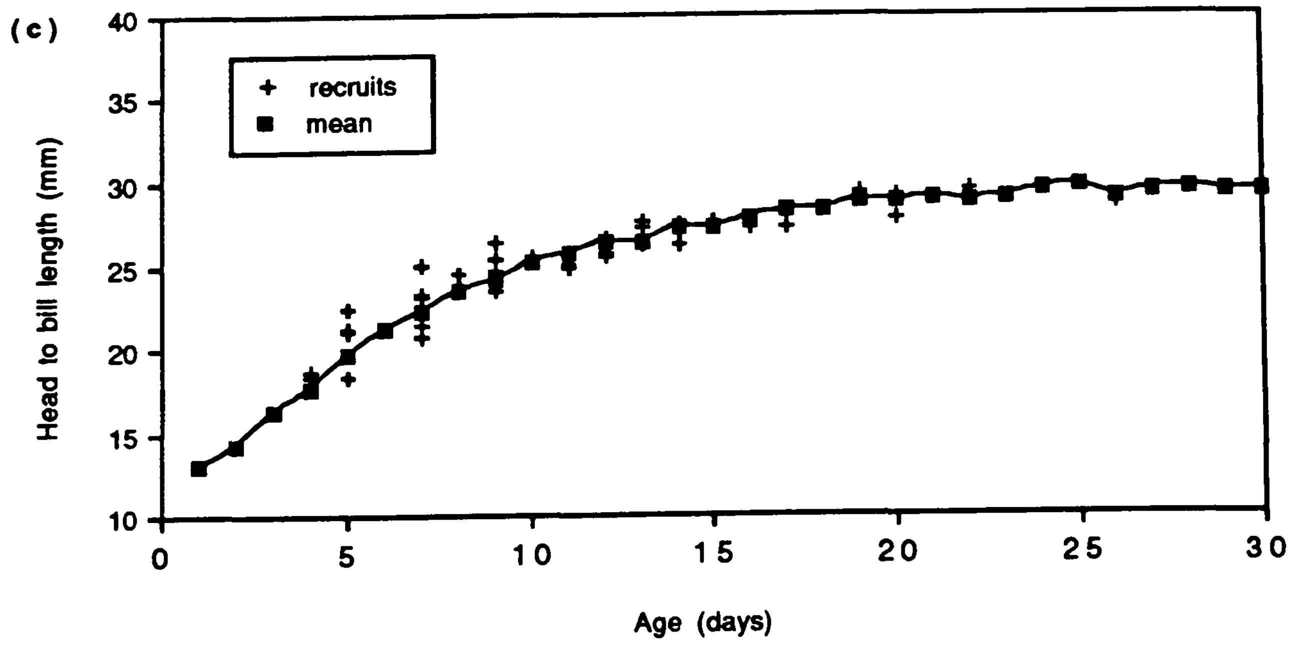


Fig 5.10 Comparison of mean nestling size per age with size of nestlings which were recruited: (a) mass; (b) wing and (c) head to bill length

5.3.7.4 Peak nestling mass

Recruits were marginally heavier but the difference was not significant (Table 5.11b).

5.3.7.5 Comparison of mean mass of all nestlings vs mean of known recruits

Recruited nestlings were only slightly heavier than those not recaptured the following season (Fig 5.10a). Wing- and head-to-bill length of recruits were measured as both bigger and smaller than the average at different ages (Days 1-30) but overall differences were not significant (Fig 5.10b,c).

5.3.7.6 Comparison of within-brood rank

Recruited nestlings were ranked from heaviest (1) to lightest (rank=brood size) nestlings within their brood. Only brood sizes of three to six were analysed. In 1987, eight broods were weighed and measured daily from Day 9 to 19. Body mass rank changed more frequently after Day 14 so only broods weighed between Days 9 and 14 were used to analyse rank. Wing-length ranks were more consistent; at only two nests did an individual alter its' rank position.

a) Body mass

Recruits came from all ranks with no significant difference between broods in the mean position of the rank from which nestlings were recruited (Table 5.11c). Within the same nest, however, there was a trend for recruits to come from higher ranks ($X^2_4=8.3$, $p=0.082$). Approximately one third were recruited from ranks one or two; two thirds (70%) from ranks one to three.

b) Wing-length

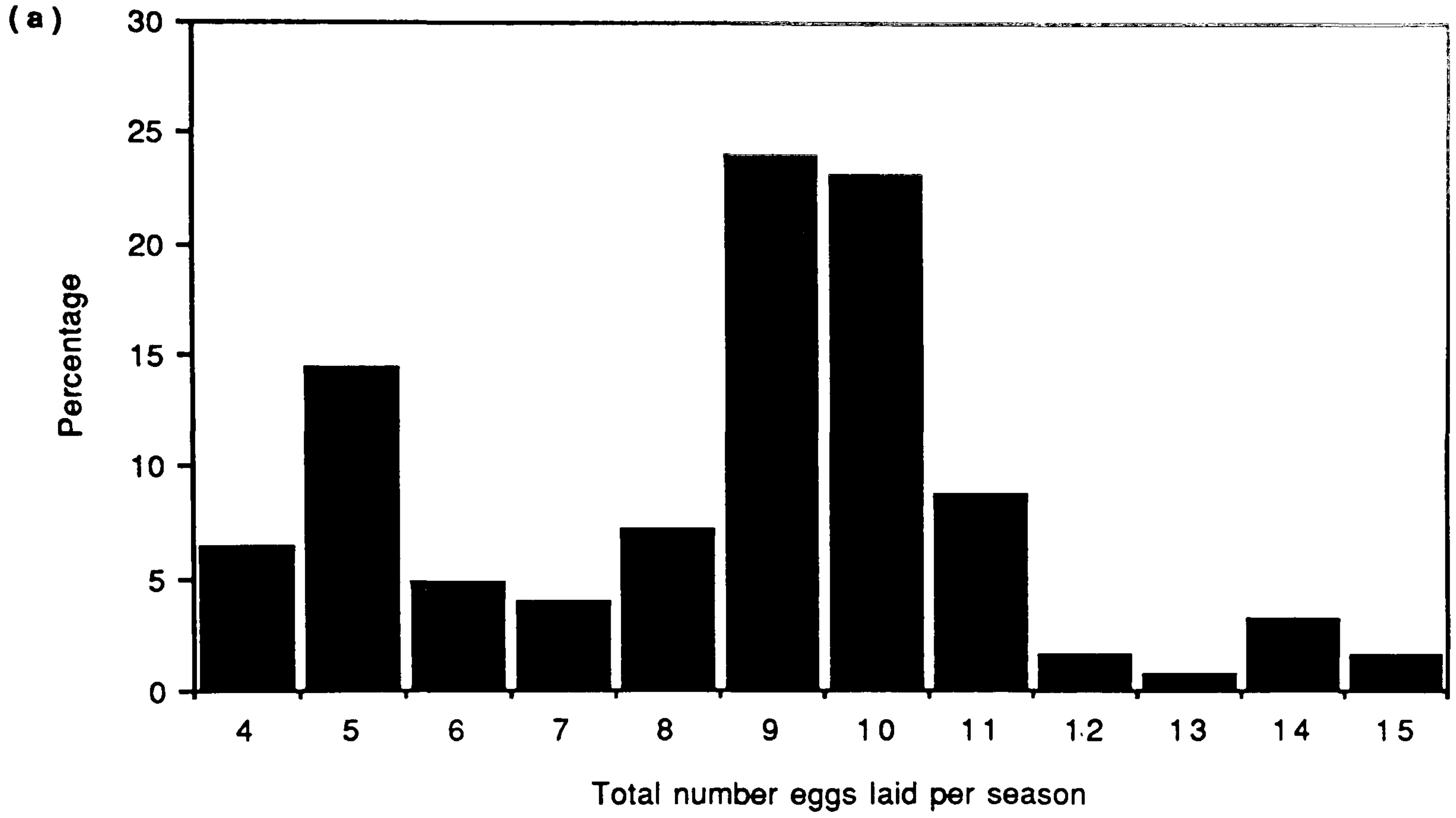
Higher wing-length ranks tended to be recruited; less than one fifth (18%) were recruited from the lowest ranks (four or five, Table 5.11c). Head-to-bill length ranks produced similar results.

5.3.7.7 Parental age

Older males or females were no more likely to rear recruits than yearlings and in fact an opposite trend was apparent: (males: 17.1% vs 13.8% and females: 16.7% vs 15.6%. Sample sizes were small reducing statistical power and the differences were not significant ($X^2=0.14$ and 0.01, for males and females respectively).

5.3.7.8 Single- or double-brooded parents

Most recruits (92%) were raised by double-brooded parents but most parents reared two broods in a season. The difference was not significant when recruits were expressed as a proportion of the total number of double- or single-broods attempted. Thirteen percent of all double-brooded parents reared recruits compared to 12% of single-brooded parents.



note: Total includes 1st + 2nd broods plus any relay attempts which occurred as a result of natural causes

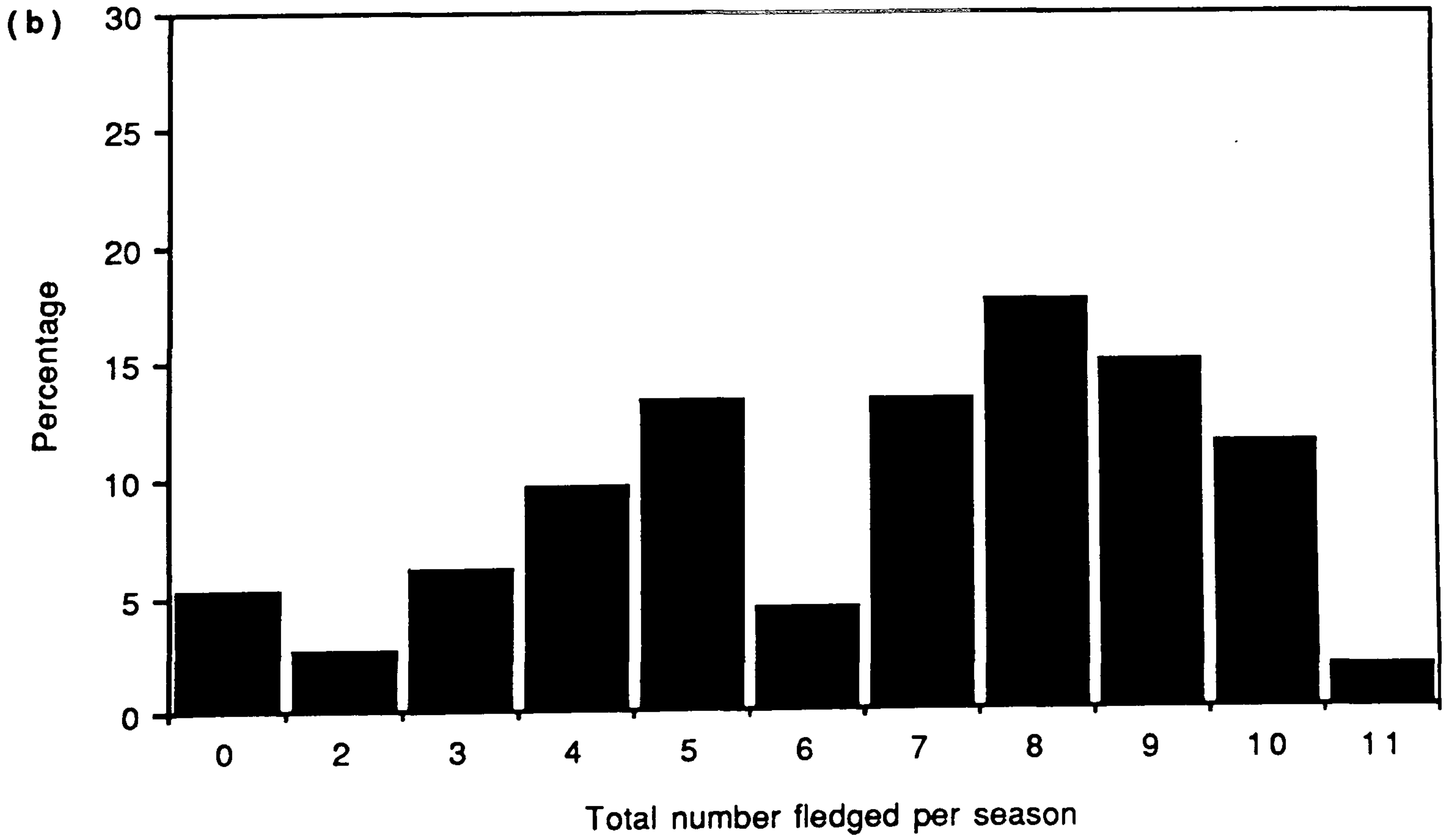


Fig 5.11 **Frequency (%) of total number of: (a) eggs laid and (b) young fledged per season (n=126). Data are for 1987 to 1989 combined**

Table 5.11 Recruitment in relation to: a) Date of hatch and b) Peak nestling mass, by year of hatch. Using Students t-test (t,df, p and sig):

a) Date of hatch

Brood Number	Year ringed	Recruits produced No	Yes	t-test t	df	p	sig
All broods	1987[a]	102.4 (2.9) (94)	96.6 (5.6) (26)	0.92	118	0.362	ns
	1988[b]	94.5 (2.8) (105)	82.5 (7.8) (10)	1.27	113	0.205	ns
First	1987	80.3 (2.2) (48)	73.4 (3.2) (13)	1.51	59	0.137	ns
	1988	71.7 (1.1) (61)	71.6 (2.7) (8)	0.01	67	0.992	ns
Second	1987	131.3 (2.4) (34)	131.4 (3.6) (8)	-0.02	40	0.983	ns

a - nestling survival over the period 1987/1988
b - nestling survival over the period 1988/1989

b) Peak nestling mass

Brood Number	Year ringed	Recruits produced No	Yes	t-test t	df	p	sig
All broods	Both[a]	23.3 (0.14 (123)	23.4 (0.31 (18)	-0.27	139	0.789	ns
First	Both	23.4 (0.17 (72)	23.1 (0.42 (11)	0.73	77	0.471	ns
Second	Both	23.2 (0.29 (44)	23.5 (0.45 (5)	-0.25	47	0.805	ns

a - nestling survival over the period 1987/1988 and 1988/1989 combined

Table 5.11c Recruitment in relation to rank position in brood, based on mass and wing length

Recruited	Rank position in brood[a] 1	2	3	4	5	Total[b]
Mass						
No	23	28	22	16	14	103
Yes	8	3	10	8	1	30
Wing length						
No	18	17	10	18	5	68
Yes	8	7	3	2	2	22

a- ranking was based on measurements taken on Day 13
b -summary results from Chi-square analysis were:

Mass: $\chi^2 = 8.3$, df=4; p = 0.082; $\chi^2 = 9.7$, df=4; p = 0.046, for one and two way respectively

Wing: $\chi^2 = 3.2$, df=4; p = 0.527; $\chi^2 = 7.5$, df= 4; p = 0.110, for one and two way respectively

Table 5.12 Swallow clutch size (mean (se) & range), by year

Breeding Variables	1987	1988	1989	All years
n	40	45	41	126
Clutch size	8.9 (.4) (4-15)	8.2 (.4) (4-14)	8.6 (.4) (4-15)	8.6 (.2) (4-15)
Brood size	7.9 (.4) (0-11)	7.4 (.3) (4-11)	8.6 (.4) (0-11)	8.6 (.2) (0-11)
No Fledged	7.3 (.4) (0-11)	6.0 (.4) (0-10)	6.2 (.5) (0-11)	6.5 (.2) (0-1

Table 5.13 Male and female Swallows present in each age class for birds 1988 and 1989

Age classes	Age code	Females 1988	Females 1989	Males 1988	Males 1989
" Known one year" old	1	7	6	6	6
"Assumed one year" old	1 *	48	50	37	20
"Known+assumed one year-old" (yearlings)	1 * *	55	56	43	26
"Known two year-old"	2	-	3	2	6
"Equal to or older than two year-old"	≥2	32	21	37	21
"Equal to or older than three year-old"	≥3	2	17	4	23
"Equal to or older than two year-old" + "equal to or older than three year-old" (adults)	≥≥2	34	41	43	50
Unknown		46	28	49	49

5.3.8 SEASONAL REPRODUCTIVE PERFORMANCE

Three females on four occasions attempted three broods in a single season . These birds were involved in a brood size manipulation experiment during the third brood so they were excluded from analyses and so the natural variation in seasonal reproductive output of Swallows was not fully reflected here. On average female Swallows laid and incubated 8.6±0.2 eggs (range 4-15, Fig. 5.11a, Table 5.12) and reared 6.5 ±0.3 (range 0-11, Fig 5.11b) young to independence in a season. Excluding pairs which re-laid because of natural desertions made little difference to the mean seasonal total clutch and brood size (figures not presented). The most productive season was 1987, when 7.3±0.4 offspring per pair were reared (*cf.* 1988: 6.0±0.4; 1989: 6.2±0.5).

5.3.9 AGE-RELATED DIFFERENCES IN REPRODUCTIVE PERFORMANCE

Only few data were available for "known one year-old" birds (n=25; males=12 and females=13, Table 5.13) so their reproductive performance was compared with individuals which were categorised as "assumed one year-old" (1*) to see if these two age classes could be grouped. There was no difference in first egg, clutch size, brood size or the number fledged (Table 5.14a,b). Yearling females, however, differed significantly in all measures from "at least two year-old" females (≥2) (Table 5.15b) and in the timing of laying, number fledged and clutch size (p=0.068) of the partners of "assumed one year-old" males (Table 5.14b). "Known" and "assumed one year-old" data were therefore pooled, confirming the conclusions of Chapter 4. Breeding parameters of unknown age birds fell between "known" and "assumed one year-old" birds further indicating that these comprised a mixed age group.

5.3.9.1 Males

Partners of at least four years old males laid earlier and had larger clutches than the partners of three, two and one year-old males in 1989 (Table 5.14a,b). Partners of older males breeding a week earlier than yearlings, had a larger clutch size and reared almost one more young to fledging (Table 15a,b). Correction for year differences did not alter results. Partners of three year-old males laid larger clutches slightly earlier than females partnered by males which were at least two years old but these differences were not significant and both groups produced 4.4 fledged young.

Partners of older males laid more eggs during a season and fledged more young than the partners of yearlings (Table 5.16a,b). Similar differences were apparent for 1989 data analysed separately. Analysis of double-brooded birds showed that males which were "at least two years old" tended to fledge more young than yearlings (p=0.056, Table 5.16a,b). Partners of males older than three years of age showed a weak tendency to lay more eggs than those partnered by two year-old females though they reared fewer to independence (Table 5.16a,b).

Table 5.14a Male measures of reproductive performance for different age classes (Mean (se)), actual and standardised

Breeding variables	Year	Males age classes[a] 1 x (se)	 1 * x (se)	 1 * * x (se)	 ≥ 2[b] x (se)	 ≥ 3[b] x (se)	 ≥ ≥ 2 x (se)	 ? ? x (se)
Date of first egg	Actual[c]	57 (2)	57 (1)	57 (1)	52 (1.2)	52 (1.5)	50 (.6)	56 (1)
	Standard[d]	.4 (.2)	.5 (.1)	.5 (.1)	e	e	-.5 (.8)	.3 (.1)
Clutch size	Actual	4.6 (.2)	4.9 (.1)	4.8 (.1)	5.1 (.1)	5.2 (.1)	5.1 (.1)	4.9 (.1)
	Standard	-.5 (.4)	-.1 (.1)	-.2 (.1)	e	e	.2 (.1)	-.1 (.2)
Brood size	Actual	4.1 (.4)	4.4 (.2)	4.4 (.2)	4.3 (.4)	4.7 (.4)	4.6 (.2)	4.5 (.2)
	Standard	-.6 (.5)	-.3 (.2)	0.0 (.2)	e	e	-0.0 (.2)	-0.2 (.2)
Number fledged	Actual	3.5 (.9)	3.7 (.3)	3.7 (.3)	4.4 (.5)	4.4 (.4)	4.6 (.2)	3.9 (.2)
	Standard	-.6 (.6)	-.4 (.2)	-.5 (.2)	e	e	0.3 (.1)	-0.2 (.2)

a - description of age codes and sample sizes are given in Table 5.13
b - data are for 1989 only; too few birds were known to be "equal to or older than three year old" in 1988 (n=4)
c - April 1st = 1
d - calculation of standardised values are given in section 5.2
e - not applicable as data are for 1989 only
1 - comparison between age classes are given in Table 5.14b
2 - data are for 1988 and 1989 combined unless otherwise stated

Table 5.14b Comparison of actual and standardised male reproductive performance between different male age classes using the Students t-Test

		Male age classes being compared									
Breeding		1 vs 1*		1 vs ≥≥2		1* vs ≥≥2		≥2 vs ≥3^		1** vs ≥≥2	
parameters		t	p	t	p	t	p	t	p	t	p
Date of	Actual	-0.02	0.988	3.52	0.001	5.87	0.000	0.25	0.806	6.30	0.000
first egg	Standard	-0.35	0.731	3.67	0.000	6.20	0.000	a	a	6.75	0.000
Clutch size	Actual	-1.16	0.252	-1.83	0.070	-1.84	0.068	-0.66	0.514	-2.15	0.033
	Standard	-1.20	0.234	-2.00	0.048	-1.74	0.085	a	a	-2.19	0.030
Brood size	Actual	-0.63	0.529	-1.01	0.317	-0.93	0.353	-0.55	0.587	-1.15	0.250
	Standard	-0.55	0.584	-1.13	0.262	-1.12	0.650	a	a	-1.34	0.181
Number	Actual	-0.30	0.764	-2.09	0.044	-2.81	0.008	0.00	1.000	-3.03	0.004
Fledged	Standard	-0.32	0.753	-2.35	0.024	-2.74	0.009	a	a	-3.04	0.004

a - comparisons not applicable as data are for 1989 only

Table 5.15a Female reproductive performance for different age classes[a], actual and standardised (Mean (se))

Breeding variables	Year	1 x (se)	1 * x (se)	1 * * x (se)	≥ 2[b] x (se)	≥ 3[b] x (se)	≥ ≥ 2 x (se)	?? x (se)
Date of first egg	Actual[c]	59 (3)	57 (1)	58 (1)	52 (1)	50 (1)	50 (1)	55 (1)
	Standard[d]	.6 (.3)	.4 (.1)	.5 (.2)	e	e	-.6 (0)	.2 (.1)
Clutch size	Actual	5.1 (.1)	4.8 (.1)	4.8 (.1)	5.0 (.1)	5.6 (.1)	5.2 (.1)	4.9 (.1)
	Standard	.2 (.1)	-.3 (.1)	-.2 (.3)	e	e	.3 (.1)	0 (.1)
Brood size	Actual	4.5 (.5)	4.2 (.1)	4.2 (.1)	4.8 (.1)	5.2 (.2)	4.9 (.1)	4.6 (.1)
	Standard	-.2 (.5)	-.4 (.2)	-.4 (.2)	e	e	.3 (.1)	0 (.1)
Number fledged	Actual	3.8 (.2)	3.8 (.2)	3.8 (.2)	4.7 (.2)	4.3 (.5)	4.7 (.2)	4.0 (.2)
	Standard	-.3 (.1)	-.4 (.2)	4.7 (.2)	e	e	0.3 (.1)	-.2 (.1)

a - description of age codes and sample sizes are given in Table 5.13

b - data are for 1989 only; too few birds were known to be "equal to or older than three year old" in 1988 (n=2)

c - nth day after April 1st

d - calculation of standardised values are given in section 5.2

e - not applicable as data are for 1989 only

Table 5.15b **Comparison of actual and standardised female reproductive performance between age classes, using the Students t-Test**

Breeding parameters		Female age class 1 vs 1* t	1 vs 1* p	1 vs ≥≥2 t	1 vs ≥≥2 p	1* vs ≥≥2 t	1* vs ≥≥2 p	≥2^ vs ≥3 t	≥2^ vs ≥3 p	1** vs ≥≥2 t	1** vs ≥≥2 p
Date of first egg	Actual	0.46	0.643	3.24	0.007	7.36	0.000	-1.16	0.252	7.67	0.000
	Standard	0.61	0.544	5.11	0.000	7.79	0.000	a	a	8.23	0.000
Clutch size	Actual	2.93	0.006	-0.57	0.569	-3.49	0.001	-1.09	0.300	-3.33	0.001
	Standard	3.10	0.003	-0.53	0.599	-3.35	0.001	a	a	-3.18	0.001
Brood size	Actual	0.56	0.576	-0.87	0.402	-3.69	0.000	-0.81	0.463	-3.62	0.000
	Standard	0.60	0.552	-0.83	0.424	-3.43	0.001	a	a	-3.37	0.001
Number Fledged	Actual	0.13	0.895	-2.04	0.049	-3.26	0.002	0.48	0.668	-3.42	0.001
	Standard	0.51	0.616	-3.28	0.005	-3.32	0.001	a	a	-3.49	0.001

a - comparisons not applicable as data are for 1989 only

Table 5.16a Seasonal male reproductive performance of different age classes, by number of breeding attempts made in a season (Mean (se))

		1988 and 1989			1989 only			
Seasonal measures	Br att	1 * * x (se)	≥≥2 x (se)	‖	1 * * x (se)	≥ 2 x (se)	≥ 3 x (se)	≥ ≥ 2 x (se)
Clutch size	All[a]	7.5 (.3)	9.6 (.3)	‖	7.1 (.5)	8.4 (.6)	10.0 (.8)	9.4 (.3)
	All[b]	7.4 (.3)	9.0 (.3)	‖	7.5 (.5)	8.3 (.6)	9.8 (.8)	9.3 (.4)
	DB[c]	9.0 (.2)	9.9 (.2)	‖	9.2 (.5)	9.8 (.2)	10.9 (.7)	10.4 (.5)
Brood at Day 13	All	5.3 (.5)	6.9 (.6)	‖	5.6 (.8)	7.6 (.8)	4.5 (1.8)	6.2 (1)
	All	5.7 (.6)	7.8 (.5)	‖	6.9 (.9)	8.2 (.8)	8.0 (1.5)	8.1 (.7)
	DB	7.6 (.6)	8.4 (.5)	‖	9.0 (.6)	8.8 (.8)	8.0 (1.5)	8.4 (.7)
Number fledged	All	4.6 (.5)	6.9 (.5)	‖	5.0 (.8)	7.5 (1)	5.2 (1.5)	6.3 (.9)
	All	4.7 (.6)	7.8 (.5)	‖	5.9 (.9)	8.2 (.8)	8.0 (1.5)	8.1 (.7)
	DB	6.8 (.6)	8.3 (.5)	‖	7.3 (1.1)	8.8 (.8)	8.0 (1.3)	8.4 (.7)

a - includes all breeding attempts (re-lays etc)

b - relay attempts excluded

c - double brooded birds only

Table 5.16b Comparison of seasonal male reproductive performance of different age classes, by number of breeding attempts made in a season. Using the Students t-test

		1988 and 1989			1989 only							
Seasonal	Br	1** vs ≥≥2			1** vs ≥2		1** vs ≥3		≥2 vs ≥3		1** vs ≥≥2	
measures	att	t	p	‖	t	p	t	p	t	p	t	p
Clutch	All[a]	-4.61	0.000	‖	-1.80	0.078	-3.45	0.001	-1.74	0.090	-5.61	0.000
size	All[b]	-3.80	0.000	‖	-1.14	0.261	-2.60	0.013	-1.57	0.125	-3.11	0.004
	DB[c]	-3.03	0.003	‖	-1.80	0.083	-2.36	0.032	-1.55	0.141	-2.76	0.011
Brood	All	-2.11	0.039	‖	-1.60	0.126	0.71	0.486	1.66	0.124	-0.42	0.680
size at	All	-2.80	0.008	‖	-0.98	0.349	-	d	-	d	-1.08	0.299
day 13	DB	-1.18	0.249	‖	-	d	-	d	-	d	-	d
Number	All	-3.15	0.003	‖	-1.86	0.082	-0.11	0.914	1.29	0.226	-1.12	0.272
fledged	All^	-3.74	0.001	‖	-1.68	0.118	-	d	-	d	-1.92	0.073
	DB	-2.00	0.056	‖	-	d	-	d	-	d	-	d

a - includes all breeding attempts (re-lays etc)
b - relay attempts excluded
c - double brooded birds only
d - sample too small for comparisons: n=9,6 and 3; 1**, ≥2 and ≥3 respectively

5.3.9.2 Females

Older females started laying a week earlier than yearlings, laid larger clutches and successfully fledged more young (all tests p <0.001, Table 5.15a,b). Females of "at least three years old" laid larger clutches earlier than females of "at least two years old" but reared fewer young to independence (differences were not significant).

Older females laid and hatched larger clutches and fledged more young than yearlings across a season (Table 5.17b). The result was not altered by excluding birds which had either a first or a second brood relay. Three year-old females laid more eggs than two year-old birds but they hatched one fewer egg and fledged fewer young though differences were not significant (Table 5.17b).

5.3.10 CORRELATION OF REPRODUCTIVE PERFORMANCE WITH PARENTAL AGE

Spearman rank correlations of female age with reproductive performance were stronger than for males. For both sexes associations were stronger for seasonal as opposed to first brood measures of reproductive performance (Table 5.18). Female age was correlated with all measures but was strongest for date of laying and the total number of eggs laid during the season. For males, only the date that partner started laying and the total number of eggs laid were significantly correlated with age. For double-brooded pairs, the total number of eggs laid during the season was still significantly correlated with male and female age, but the correlation with the total number of young fledged was considerably weaker and in the case of females no longer significant (Table 5.18).

5.3.11 EFFECT OF AGE AND SEASON ON REPRODUCTIVE PERFORMANCE

Clutch size declined with laying date for one year-old (1**), three year-old (≥ 3) and and all birds of at least two years old (≥ 2) (Table 5.19). Trends were usually stronger for males (Figs 5.12 & 5.13). When age class (1, ≥2 and ≥ 3) was included as a partial correlate clutch size decreased as the season advanced for both sexes (Table 5.19).

5.3.12 BREEDING VERSUS NON-BREEDING YEARLINGS

All birds captured during a season were categorised as having bred (breeding), not having bred (non-breeding) or undetermined (Table 5.20). Nearly all birds at least two years of age attempted to breed whereas a third of yearlings failed to breed. If birds first caught aged two (n=6) had not bred the previous year then the proportion of yearlings failing to breed increased further. Two-thirds of sexed non-breeders were male. There was no difference between breeding and non-breeding yearlings in brood number or date of hatch.

Table 5.17a **Seasonal female reproductive performance for different age classes, by number of broods attempted in a season (mean (se)).**

		1988 and 1989			1989 only			
Seasonal measures	Br att	1 * * x (se)	≥≥2 x (se)	‖	1 * * x (se)	≥ 2 x (se)	≥ 3 x (se)	≥ ≥ 2 x (se)
Clutch size	All[a]	7.5 (.3)	10.2 (.3)	‖	7.0 (.4)	9.3 (.5)	10.5 (.8)	9.8 (.5)
	All[b]	7.2 (.3)	9.9 (.3)	‖	6.9 (.4)	9.1 (.6)	10.7 (.7)	9.7 (.4)
	DB[c]	8.9 (.2)	10.3 (.2)	‖	8.9 (.2)	10.1 (.3)	11.1 (.6)	10.6 (.3)
Brood at Day <u>13</u>	All	5.3 (.4)	7.8 (.5)	‖	5.2 (.5)	8.6 (.9)	7.2 (1.4)	8.1 (.7)
	All	5.7 (.4)	8.3 (.5)	‖	5.9 (.6)	8.6 (.9)	7.7 (1.3)	8.4 (.7)
	DB	7.5 (.3)	8.8 (.4)	‖	7.8 (.3)	9.8 (.4)	7.7 (.3)	9.1 (.6)
Number fledged	All	4.7 (.4)	7.6 (.5)	‖	4.7 (.6)	8.5 (1)	6.3 (1.4	7.8 (.8)
	All	5.1 (.5)	8.2 (.5)	‖	5.4 (.6)	8.5 (1)	7.3 (1.2)	8.2 (.8)
	DB	7.0 (.4)	8.7 (.4)	‖	7.1 (.6)	9.8 (.4)	7.3 (1.2)	9.0 (.6)

a - includes all breeding attempts (relays etc)
b - relay attempts excluded
c - double brooded birds only

Table 5.17b Comparison of seasonal female reproductive performance of different age classes by number of breeding attempts in a season, using the Students t-test

		1988 and 1989			1989 only							
Seasonal *	Br	1 vs ≥≥2			1** vs ≥2		1** vs ≥3		≥2 vs ≥3		1** vs ≥≥2	
measures	att	t	p	‖	t	p	t	p	t	p	t	p
Clutch size	All	-6.48	0.000	‖	-3.15	0.002	-4.12	0.000	-1.39	0.171	-4.52	0.000
	All	-6.73	0.000	‖	-3.09	0.003	-4.84	0.000	-1.95	0.059	-4.73	0.000
	DB	-5.61	0.000	‖	-3.65	0.001	-3.77	0.002	-1.64	0.117	-4.41	0.000
Brood size at day 13	All	-4.73	0.000	‖	-3.29	0.003	-1.54	0.135	0.93	0.370	-3.21	0.003
	All^	-4.04	0.000	‖	-2.51	0.020	-1.11	0.281	0.59	0.572	-2.55	0.017
	DB	-3.75	0.000	‖	-4.36	0.001	-	a	-	a	-2.05	0.064
Number fledged	All	-4.14	0.000	‖	-3.41	0.002	-1.05	0.302	1.34	0.209	-3.11	0.004
	All^	-3.96	0.000	‖	-2.71	0.013	-1.20	0.245	0.66	0.523	-2.76	0.011
	DB	-2.59	0.014	‖	-3.42	0.005	-	a	-	a	-2.25	0.039

a - sample too small: n=9,6 and 3; 1**, ≥2 and ≥3 respectively

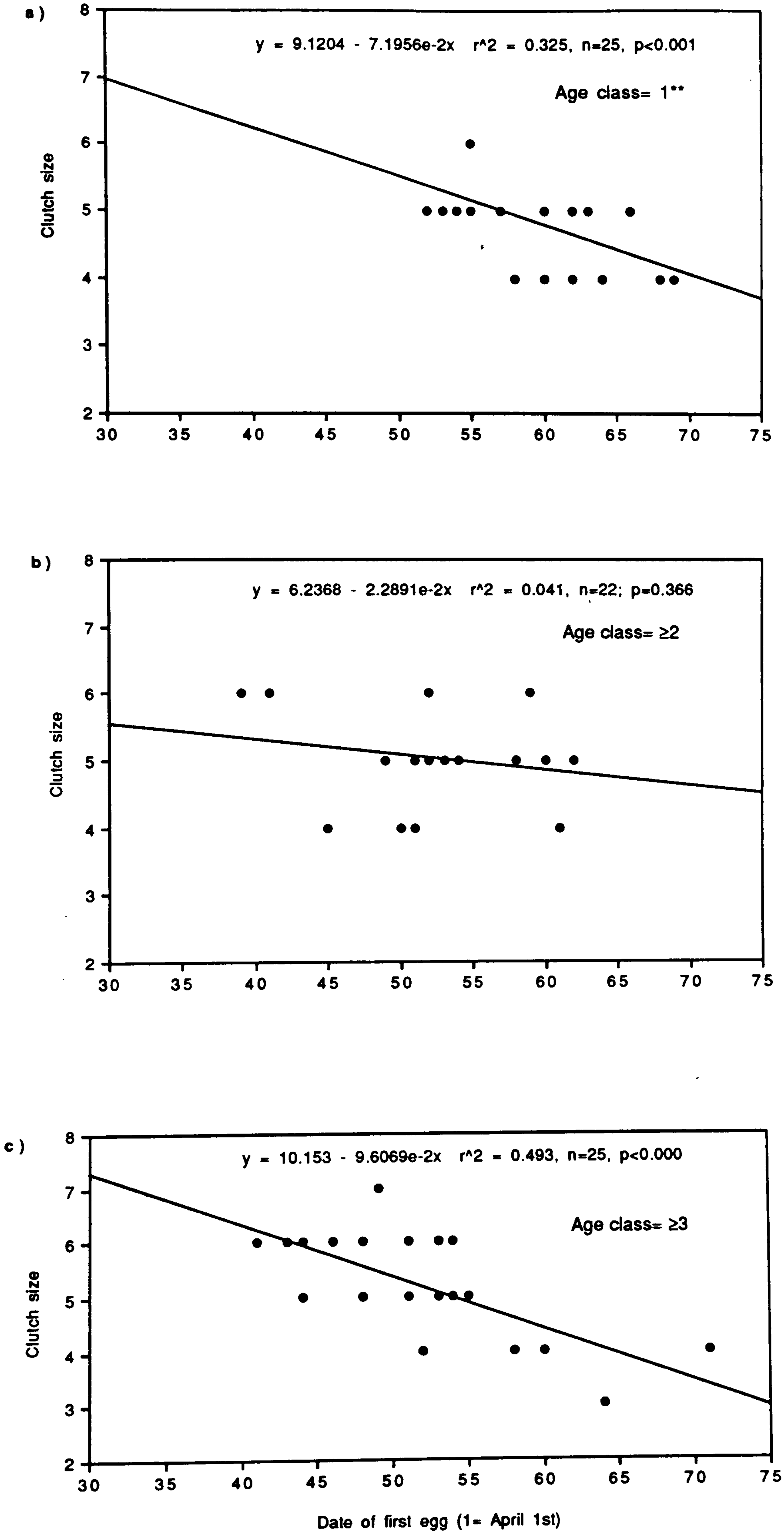


Fig 5.12 Relationship between laying date and clutch size, analysed by male age class in 1989: (a) 1** ; (b) ≥2 and (c) ≥3

Table 5.18 Spearman rank correlations of first brood seasonal reproductive performance and age class (1,≥2,≥3) in 1989, by sex (coefficient, (n), significance)

	First brood				Seasonal[a]			
Sex	Date	Cls[b]	Brs[c]	Nyf[d]	Cls	Cls[e]	Nyf	Nyf[e]
Male	-0.46	0.19	0.16	0.17	0.39	0.49	0.41	0.17
	(74)	(72)	(67)	(27)	(61)	(43)	(18)	(13)
	* * *	ns	ns	ns	* *	* *	ns	ns
Female	-0.50	0.36	0.39	0.42	0.58	0.65	0.46	0.39
	(96)	(94)	(85)	(36)	(82)	(58)	(27)	(18)
	* * *	* * *	* * *	*	* * *	* * *	* * *	ns

a - excludes re-lay attempts, b - clutch size, c - brood size, d - number of fledged young, e - only double-brooded birds

Table 5.19 Pearson correlation of date of first egg to clutch size, by male and female age class (1, ≥2 and ≥3), in 1989 (coefficient, (n), significance)**

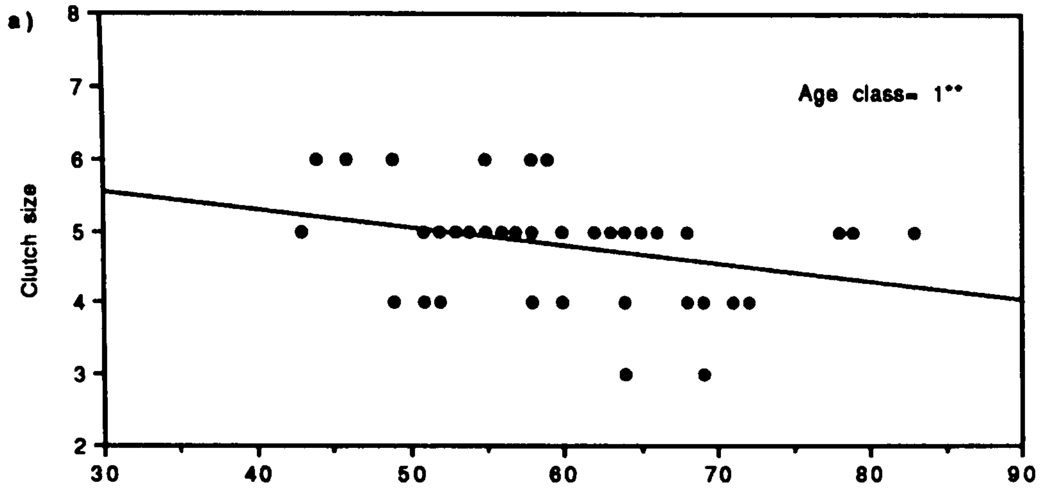
	Age classes				Partial
Sex	1	≥2	≥3	≥≥2	correlation[a]
Male	-0.57	-0.20	-0.71	-0.54	-0.46
	(25)	(22)	(25)	47	(69)
	* *	ns	* * *	* * *	* * *
Female	-0.35	-0.24	-0.54	-0.34	-0.28
	(53)	(24)	(17)	(41)	(91)
	*	ns	*	*	* *

a - partial correlation of male age: r=-0.184, ns; female age: r=-0.154, n=24,ns

Table 5.20 Breeding status of yearling Swallows, by year of hatch

Breeding Status	Year ringed 1986	1987	1988	All years
Single brooded	-	5	6	11
Double brooded	-	9	7	16
Breeding	-	14	13	27
Non-breeding	3	7	4	14
Non-breeding[a]	4	12	4	20
Total	4	26	17	47
Total[b]	3	21	17	41

a - includes first recaptured in year (n+2), b - excludes recaptures outside of the study area



$y = 6.2882 - 2.4762e{-2}x$ $r^2 = 0.093$, n=53, $p<0.01$

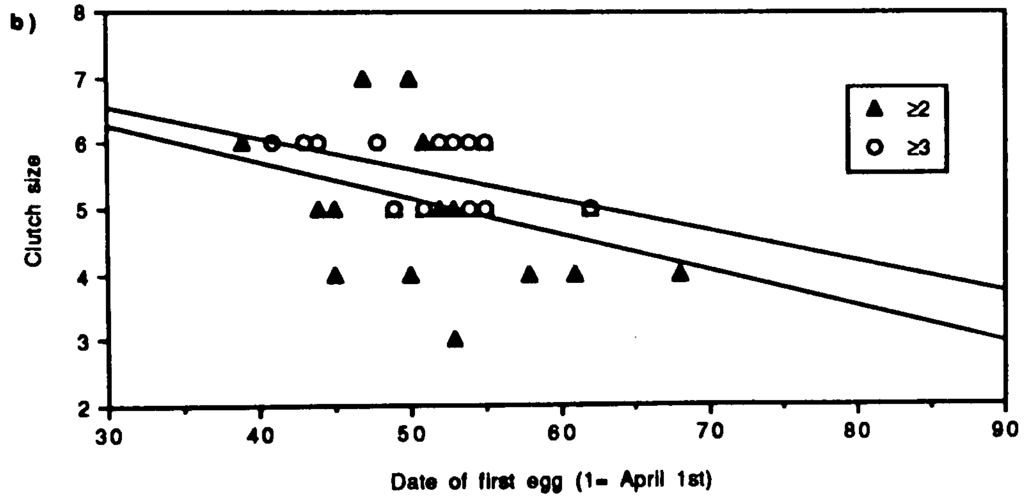


Fig 5.13 Relationship between laying date and clutch size, analysed by female age class in 1989: (a) 1**; (b) ≥2 and ≥3

≥2: $y = 7.8884 - 5.4877e{-2}x$ $r^2 = 0.128$, n=24, $p<0.01$

≥3: $y = 7.9388 - 4.6956e{-2}x$ $r^2 = 0.292$, n=17, $p<0.01$

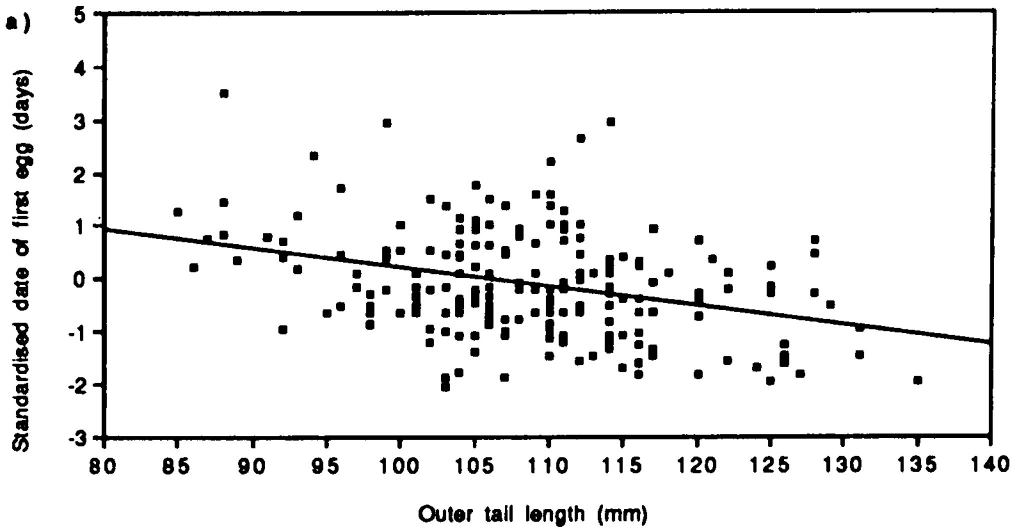


Fig 5.14a Relationship between male outer tail length and date of first egg (standardised). Data are for 1987 to 1989

$y = 3.8064 - 3.6135e{-2}x$ $r^2 = 0.116$;   r=-0.34, n=198, $p<0.000$

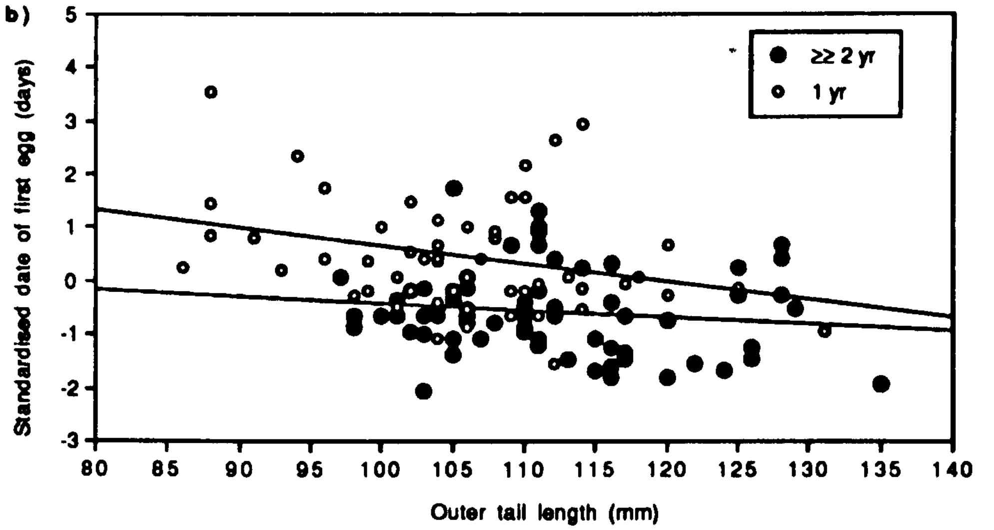


Fig 5.14b Relationship between male outer tail length and date of first egg (standardised), analysed by male age. Data are for 1988 and 1989.

1 yr: $y = 4.0456 - 3.4069e{-2}x$ $r^2 = 0.101$;   r=-0.32, n=54, $p<0.01$

≥≥ 2 yr: $y = 0.8012 - 1.2337e{-2}x$ $r^2 = 0.019$;   r=-0.14, n=72, p=0.254

5.3.13 ASSORTATIVE MATING WITH RESPECT TO AGE

Birds of a similar age tended to pair together (72%, Table 5.21). In mixed-age pairs older males were more likely to pair with yearling females (79%) than *vise versa* (21%).

5.3.14 REPRODUCTIVE PERFORMANCE IN RELATION TO AGE OF THE PAIR

Older pairs (OF/OM) laid ten days earlier than yearling pairs and six days earlier than mixed-age pairs; females in mixed-age pairs laid four days earlier than yearlings (all tests $p < 0.001$, Table 5.22a,b). Mixed-age pairs (YF/OM vs OF/YM) did not differ significantly (Table 5.22a,b). Where both sexes were "at least three years old", laying was than yearling pairs (or pairs where the male or the female was a yearling).

Pairs which had an older female laid the largest clutches (Table 5.22a,b). Yearling females laid similar clutch sizes when paired with either a yearling or an older male. In 1989, clutch size was smaller for pairs containing yearlings than all other pair age combinations such as three year-old pairings which laid clutch sizes of six. Older pairs fledged more young than any other pair-age combination, significantly so in comparison to yearling pairs (Table 5.22a.b). In mixed-age pairs, males partnered by an older female fledged more young, than those with a yearling female.

The relative importance of male and female age in relation to the reproductive performance of a pair was investigated using two-way analysis of variance. Male and female age combined (main effects) had a significant effect on the date of first egg, clutch size, brood size and the number fledged (Table 5.24). Female age had a significant independent effect on all measures but male age only had an independent effect on the number fledged. The above relationships were insignificant, however, when date was included as a covariate.

5.3.15 BODY SIZE AND REPRODUCTIVE PERFORMANCE

5.3.15.1 Males

Laying date was earlier with an increase in male outer and "second" tail-lengths (Table 5.25a), such that partners of males with longer tails laid earliest (Fig 5.14a). The relationship was similar for standardised laying date (Fig 5.14b). The earlier laying associated with longer tail-length did not always confer obvious advantages. While males with the longest outer tails fledged more young during the first brood ($r=0.22$, $p<0.05$) they did not fledge significantly more during the season. Other measures of male body size were only weakly associated with seasonal reproductive performance. Correlations were generally slightly stronger for yearlings than older birds (Table 5.25b).

Table 5.21 Summary of known-age pairing records

Female	Male age classes/ Year					
	1988			1989		
Age class	1 * *	≥ 2	≥ 3	1 * *	≥ 2	≥ 3
1 * *	37	13	-	24	11	10
≥2	4	26	-	3	8	5
≥3	-	-	-	2	6	6
≥2 + ≥ 3	4	26	-	5	14	11

Age class Female	Male	Code	Year 1988	1989	Both
Yearling	Yearling	Y/Y	37	24	61
Yearling	Old	Y/O	13	21	34
Old	Yearling	O/Y	4	5	9
Old	Old	O/O	26	25	51
Yearling	Old	Mixed	17	26	43
Old	Yearling				
Yearling	Yearling	Same	63	49	112
Old	Old				
Total		All	80	75	155

Table 5.22a First brood reproductive performance (Mean (se)) in relation to age of the pair^a

Breeding variables		Yearlings YF/YM^b	Mixed YF/OM	Mixed OF/YM	Old OF/OM	Both mixed
Date of first egg	Actual	58.3 (1)	54.8 (1.2)	51.7 (1.6)	48.4 (.8)	54.1 (1)
	Stand^c	0.65 (.14)	0.03 (.15)	-0.38 (.19)	-0.79 (.11)	-0.06 (.12)
	n	54	32	9	48	41
Clutch size	Actual	4.8 (.1)	4.9 (.1)	5.3 (.3)	5.2 (.1)	5.0 (.1)
	Stand	-0.28 (.13)	-0.02 (.20)	0.43 (.40)	0.42 (.20)	0.07 (.18)
	n	53	31	8	48	39
Brood size	Actual	4.3 (.2)	4.3 (.3)	4.8 (.5)	5.0 (.1)	4.4 (.3)
	Stand	-0.42 (.19)	-0.28 (.32)	0.05 (.58)	0.34 (.14)	-0.21 (.28)
	n	47	27	8	43	35
Number fledged	Actual	3.4 (.3)	4.5 (.3)	4.8 (.5)	4.7 (.2)	4.6 (.3)
	Stand	-0.74 (.23)	0.21 (.23)	0.43 (.38)	0.36 (.15)	0.28 (.19)
	n	25	11	5	19	16

a - data are for 1988 and 1989 combined

b - description of age-pairing codes are given in Table 5.21

c - see text for calculation of standardised values (Stand)

Table 5.22b Comparison of reproductive performance in three pair-age combinations: Yearlings, Mixed and Old; 1988 and 1989 pooled. Students t-test (t and p)

variables		Yearlings vs Mixed		Old vs Mixed		Yearlings vs Old	
		t	p	t.	p	t	p
Date of first egg	Actual	2.92	0.004	4.44	0.000	7.73	0.000
	Stand	-3.78	0.000	4.48	0.000	8.26	0.000
Clutch size	Actual	-1.59	0.116	-1.62	0.110	-3.64	0.000
	Stand	-1.57	0.121	-1.49	0.139	-3.46	0.001
Brood size	Actual	-0.46	0.644	-3.33	0.001	-1.87	0.067
	Stand	-0.65	0.519	-3.20	0.002	-1.75	0.085
Number fledged	Actual	-3.04	0.004	-0.54	0.591	-3.87	0.000
	Stand	-3.11	0.003	-0.32	0.754	-3.94	0.000

Table 5.23 Breeding performance (Mean (se)(n)) in relation to pair-age combinations in 1989.

Summary[a] of pair-age combinations[b]	Measures of reproductive performance			
	Date of first egg	Clutch Size	Brood size	Number Fledged
ONE/ONE	60.3 (1.5) (20)	4.7 (.1) (19)	4.2 (.3) (18)	3.6 (.3) (9)
ONE/TWO	56.3 (1.3) (12)	5.1 (.2) (11)	3.9 (.7) (8)	4.2 (.7) (5)
ONE/THREE	56.8 (2.3) (13)	4.9 (.3) (12)	4.9 (.3) (11)	5.0 (.4) (3)
TWO/TWO	50.0 (2.2) (8)	4.9 (.3) (8)	4.9 (.3) (7)	5.0 (.4) (4)
TWO/THREE	50.5 (1.9) (11)	5.5 (.3) (11)	5.3 (.3) (10)	5.5 (.5) (2)
THREE/THREE	47.2 (2.2) (6)	6.0 (.0) (6)	5.3 (.5) (6)	4.0 (1) (2)

a - male/female
ONE = yearling
TWO = at least two year-old,
THREE = at least three year-old

Table 5.24 Two-way ANOVA of male and female age[a] effects on first brood breeding performance, 1988 and 1989 combined using standardised values

Sources of Variation	Sum of squares	df	F	p	sig
Date of first egg					
Main effects	2567.0	2	30.6	0.000	* * *
Female age	1129.3	1	27.0	0.000	* * *
Male age	324.7	1	7.8	0.006	* *
Female x Male	0.3	1	0.0	0.939	ns
Explained	2567.2	3	13.0	0.000	* * *
Residual	5823.6	139			
Total	8390.8	142			
Clutch size					
Main effects	6.3	2	6.8	0.001	* *
Female age	3.6	1	7.7	0.009	* *
Male age	0.3	1	0.6	0.429	ns
Female x Male	0.1	1	0.3	0.574	ns
Explained	6.4	3	4.7	0.004	* *
Residual	62.5	136			
Total	68.9	139			
Brood size					
Main effects	13.0	2	4.6	0.012	*
Female age	8.7	1	6.2	0.014	*
Male age	0.2	1	0.1	0.721	ns
Female x Male	0.1	1	0.1	0.763	ns
Explained	13.1	3	3.1	0.029	*
Residual	170.0	121			
Total	183.1	124			
Number fledged					
Main effects	21.7	2	8.3	0.001	* *
Female age	5.7	1	4.4	0.041	*
Male age	5.7	1	4.4	0.041	*
Female x Male	3.5	1	2.7	0.107	ns
Explained	25.2	3	6.4	0.001	* *
Residual	73.0	56			
Total	98.2	5			

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a - two age classes were used: 1** and ≥≥2. See Table 5.13 for description

Table 5.25a Pearson correlation coefficients of male body size with reproductive performance. Standardised results (standard[a]) are given for laying dates and clutch size. Data are for all ages and years combined (coefficient, (n), significance)

Measures of performance	Wing	Outer tail	"second" tail	Inner tail	Head to bill	Keel
Date of first egg: actual	-0.06 (200) ns	-0.31 (198) * * *	-0.19 (162) * *	0.09 (195) ns	0.00 (200) ns	0.08 (198) ns
: standard	-0.11 ns	-0.34 * * *	-0.20 * *	0.07 ns	0.0 ns	0.10 ns
Clutch size (first - actual)	0.10 (199) ns	0.10 (197) ns	0.10 (161) ns	0.09 (194) ns	0.10 (199) ns	0.04 (197) ns
Clutch size (first - standard)	0.14 0.054	0.11 ns	0.13 ns	0.11 ns	0.11 ns	0.04 ns
Number fledged (first -actual)	0.03 (139) ns	0.22 (136) *	0.11 (91) ns	-0.05 (135) ns	-0.06 (139) ns	-0.05 (136) ns
Number fledged (first + second)	0.11 (61) ns	0.06 (58) ns	0.15 (40) ns	0.17 (58) ns	-0.01 (61) ns	0.11 (59) ns

a - see text

Table 5.25b Pearson correlation coefficients of male body size with standardised reproductive performance, by male age class (1 and ≥≥ 2). Data are for 1988 and 1989 pooled (Coefficient, (n), significance)

Measures of performance	Age	Wing	Outer tail	"Second" tail	Inner tail	Head-to-bill	Keel
Laying date	1	-0.26	-0.32	-0.17	0.09	0.11	0.12
		0.059	*	ns	ns	ns	ns
	≥≥ 2	-0.11	-0.14	0.04	-0.12	0.04	-0.05
		ns	ns	ns	ns	ns	ns
Clutch size	1	0.36	0.12	0.08	0.33	0.05	-0.09
		* *	ns	ns	*	ns	ns
	≥≥ 2	0.01	0.03	0.06	0.12	0.18	0.24
		ns	ns	ns	ns	ns	*
Number fledged (1st)	1	0.14	0.23	0.37	0.10	0.00	-0.12
		ns	ns	*	ns	ns	ns
	≥≥ 2	-0.06	0.03	-0.0	-0.02	-0.03	-0.00
		ns	ns	ns	ns	ns	ns
Number fledged (total)	1	0.45	0.17	0.12	0.50	0.39	0.14
		ns	ns	ns	0.069	ns	ns
	≥≥ 2	0.09	-0.35	0.04	-0.17	-0.12	0.22
		ns	ns	ns	ns	ns	ns

5.3.15.2 Females

Laying date was earlier with larger female outer tail-length. Clutch size increased with outer tail- and tarsus-length (all tests, $p < 0.05$). There was a slight tendency for clutch size and the total number of young fledged during the season to increase with skeletal measures and inner tail-length. Controlling for female age or the age of the partner did not alter these conclusions.

5.3.16 INDIVIDUAL DIFFERENCES IN FEMALE REPRODUCTIVE PERFORMANCE

Several females bred in successive seasons (1987 /1988 or 1988/1989, n=53). Direct comparisons could not always be made, however, because some of these birds were involved in experiments. Trends were similar over both periods (except for laying date), so data were pooled. Birds monitored in all three years (n=17) were excluded to ensure independence (Table 5.26a) and analysed separately (Table 5.26b).

Each female advanced their laying date in successive seasons, markedly so when yearly differences were controlled ($p<0.001$, Table 5.26a). A slight, insignificant, improvement in performance was observed in the second of two successive seasons. Three quarters of all females advanced their laying date, half and two thirds laid the same number of eggs during first and second broods respectively and about half fledged more young during their 'second' as opposed to their 'first' season.

Seventeen females were monitored in three successive seasons (Table 5.26b). Only brood size and change in clutch size ($cls_{2nd}-cls_{1st}$) increased each season. Laying date advanced by as much as ten days from 1987 to 1988 but clutch size actually decreased over this period (*cf.* the size of the second clutch 4.2 vs 4.5). Conversely clutch size increased only slightly in 1989 relative to 1988 even though laying was slightly later. There tended to be greater improvement in reproductive performance from 1987 to 1988 than 1988 to 1989, but this was only significant for laying date (standardised $p=0.02$).

5.3.16.1 Controlling for age in Year (n)

The above results cannot be explained easily because the age of the birds was unknown in 1987. To control for this factor, the data were reanalysed including only individuals which survived from 1988 to 1989 and known to be 1 or ≥2 in 1988 (Table 5.27). One year-old females advanced their laying date (standard, $p=0.020$) but other measures (clutch and brood size) hardly changed. Two year-old birds did not show any clear trends.

5.3.16.2 Controlling for survival until Year (n+1)

To control for the selective mortality effects on age-related differences in reproductive performance, comparisons of laying dates and clutch size in 1988 were made on one and two year-old females which bred in 1989. Females at least two years old laid earlier and had a larger clutch size than yearlings (Table 5.28).

Table 5.26a **Comparison of breeding performance (Mean (se)) of female Swallows monitored in successive seasons using the Wilcoxon matched-pair test**

Breeding Variables	yr (n)	yr (n+1)	Diff	n	Wilcoxon Z	p
Date of 1st egg	53.8 (1.3)	51.1 (1.1)	2.7	32	-2.05	0.04
Std. Date of 1st Egg[a]	.06 (.17)	-.51 (.13)	.57	32	-3.37	0.00
Clutch size	4.9 (.2)	4.9 (.1)	0.0	33	-0.21	0.831
Brood size	4.6 (.2)	4.4 (.3)	.2	33	-0.28	0.780
No. fledged	4.1 (.3)	4.6 (.2)	-.5	20	-1.13	0.259
Inter-brood Interval	36.9 (1.9)	34.4 (.8)	2.5	16	-1.16	0.244
2nd Clutch	4.5 (.2)	4.6 (.2)	-.1	22	-0.59	0.554
Change in Clutch Size	-.7 (.2)	-.6 (.2)	-.1	16	-0.52	0.600
Inter-brood interval[b]	36.5 (1.3)	35.5 (.8)	1.0	23	-0.34	0.733
Second clutch size[b]	4.3 (.2)	4.5 (.2)	-.2	31	-1.12	0.260
Change in Clutch Size[b]	-.7 (.2)	-.6 (.2)	-.1	24	-0.43	0.666

a - standardised laying date
b - including reduced or control broods

Table 5.26b **Comparison[a] of breeding performance (Mean (se)) of female Swallows monitored in three successive seasons by Kruskal-Wallis one-way ANOVA**

Breeding Variables	Year 1987	1988	1989	n	K-W H	p
Date of 1st egg	57 (3.6)	47 (1.1)	50 (1.6)	13,15,15	3.44	0.179
Std.Date of 1st egg	-.1 (.0)	-.8 (.2)	-.8 (.2)	13,15,15	4.73	0.094
Clutch size	5.1 (.1)	4.8 (.3)	4.9 (.5)	14,17,17	5.66	0.059
Brood size	3.4 (.5)	3.9 (.4)	4.5 (.5)	14,17,17	4.68	0.096
Second clutch size	4.2 (.4)	4.5 (.3)	4.2 (.5)	17,16,17	0.17	0.917
Change in clutch size	-.9 (.5)	-.3 (.2)	.8 (.3)	14,16,17	1.34	0.513

a - comparison of incremental change of 1987/88 vs 1988/89:

Laying date (std)	-1.18 (0.36 vs -0.04 (0.18; (n=10): 1,9,0; Z=-2.29, p=0.02
Clutch size	0.15 (0.15 vs 0.00 (0.00; (n=13): 3,1,9; Z=-0.91, ns
Brood size	0.92 (0.58 vs 0.46 (0.33; (n=13): 5,3,5; Z=-0.70, ns

Table 5.27 Comparison of first brood breeding performance (Mean (se)) for the Swallow females monitored in both 1988 and 1989, by age class (1 vs ≥ 2). Using Wilcoxon Matched-pairs test

First brood parameters	Age class	1988	1989	Diff	n	Wilcoxon Z	p
Date of 1st egg	1	56.6 (2.1)	53.7 (2.0)	2.9	11	-1.27	0.203
	≥2	46.0 (1.1)	48.3 (1.4)	-2.3	13	-1.80	0.070
Std. Date of 1st egg[a]	1	.7 (.3)	-.3 (.2)	1.0	11	-2.31	0.020
	≥2	-1 (.2)	-1 (.6)	0	13	-0.38	0.701
Clutch size	1	4.5 (.2)	4.6 (.2)	-.1	11	-0.34	0.735
	≥2	5.2 (.2)	5.2 (.4)	0	15	-1.07	0.286
Brood size	1	4.1 (.3)	3.9 (.6)	.2	11	-0.12	0.906
	≥2	4.3 (.4)	4.8 (.4)	-.5	15	-1.61	0.110

a - standardised, see text

Table 5.28 Comparison of date of first egg and clutch size (Mean (se)) in 1988 of female Swallows which bred in 1989, by age class. Using Students t-test

Breeding Variables	Age class 1	≥ 2	n	t test t	df	p
Date of 1st egg[a]	57 (2)	48 (1)	11,28	4.41	37	0.000
Clutch size	4.5 (.2)	5 (.1)	11,29	-2.73	38	0.010

a - 1 = April 1st

5.3.17 FACTORS AFFECTING THE NUMBER OF BROODS ATTEMPTED EACH SEASON

5.3.17.1 Timing of breeding

The latest dates that a first brood commenced followed by a fledged second brood were the 17th June in 1987 and the 20th June in 1988 and 1989. Triple-brooded pairs (or those which laid a replacement second clutch) which subsequently fledged young, however, laid until the 3rd, 13th and 24th July in 1987,1988 and 1989 respectively. Double-brooded pairs started laying earlier than single-brooded pairs with the difference varying between years. This trend was also significant within each age class (Table 5.29a).

5.3.17.2 Male, female and pair age

Older females attempted two broods more often than yearlings (X^2=9.0, $p<0.001$). A similar pattern was evident for males but the difference was not significant. The percentage of single- or double-brooded pairs also differed between pair ages (X^2=7.32, $p<0.03$). Almost all adult pairs (O/O) pairs were double-brooded, whereas just over two thirds of yearling pairs (Y/Y) were (X^2=5.65, p=0.018). Mixed-age pairs were intermediate (85%), but did not differ significantly from either yearlings or adult pairs.

5.3.17.3 Body size

Larger males (wings, outer tail and keel-length) were more likely to be double-brooded than smaller males (Table 5.29b). Single- and double-brooded females did not differ significantly in any size parameter taken. Controlling for age effects also failed to yield significant differences (data not presented).

5.3.17.4 Individual differences

Only 70% of males attempted the same number of broods in successive seasons (the majority from 1987 to 1988). This difference may be an artifact related to fewer brood manipulations in 1987 but a comparison of males rearing broods manipulated in the same direction in successive seasons did not alter the finding with all males observed in 1987 and 1988 (12) double-brooded whereas only half had two broods from 1988 to 1989 (5/9).

All females (27) monitored in 1987 which survived to 1988, were double-brooded and from 1988 to 1989, 91% (30/33) of all females attempted the same number of broods in each year. When nests with experimentally manipulated first broods were excluded all females attempted the same number of broods in successive years of which one was single-brooded. Furthermore, 13 of 14 females were double-brooded in three consecutive years.

A change of partner was not important in maintaining double-broodedness of females, whereas males which changed partner between seasons more frequently altered the number of broods they attempted (36%, n=9). The pattern varied slightly between years.

5.3.17.5 Number of broods attempted by parents and their offspring

Yearlings were categorised as double-brooded or not, sexes pooled. Yearlings reared by single-brooded parents were all double-brooded whereas less than one third (12/39) of all double-brooded parents reared offspring which were double-brooded the following season (X^2_1= 6.3; p=0.01). Exclusion of non-breeding yearlings (including those re-captured for the first time as two year-olds) showed that half of the breeding yearlings reared by double-brooded parents were also double-brooded but it did not alter the findings for single-brooded parents (X^2=2.45, df=1, p=0.117).

5.3.18 ADULT SURVIVAL IN RELATION TO AGE AND FECUNDITY

5.3.18.1 Age

From 1988 to 1989 yearlings survived better than older birds (≥2) (57% v 48%, $p<0.05$). The trend was similar for both sexes but was not significant for males.

5.3.18.2 Fecundity

There was no difference in the survival of single- and double-brooded males (9/21=42.9% and 43/81=53.1% X^2=0.70, p=0.403), whereas double-brooded females survived better than single-brooded (54.3% vs 20.8%, X^2=8.76 $p<0.001$). When split by year, differences were significant for females in 1987/1988 (67.4% vs 0%, X^2=13.7, $p<0.000$) but not in 1988/89 (45.2% vs 42%, X^2=0.69, p=0.406).

Surviving double-brooded males had larger clutches and broods than non-survivors but these differences were small and only significant in two cases; surviving males had one more young in the nest at Day 13 and reared one more young to independence in a season (both $p<0.05$, Table 5.30). There were no significant differences for females (Table 5.30).

Table 5.29a Comparison of date of hatch[a] (mean (se)) of single- and double-brooded Swallow pairs, by year and age class, using the Students t-test

Year	Number of broods Single	 Double	n	t	t test df	 p
1987	75 (6)	57 (2)	19,52	3.03	21.4	0.006
1988	62 (4)	50 (1)	15,54	2.90	15.0	0.011
1989	70 (4)	55 (1)	21,36	-3.46	23.9	0.001
All years	70 (3)	54 (1)	55,143	5.53	63.1	0.000
	8 (2)[b]	-.6 (.4)	55,143	3.70	57.8	0.000
1988-89	67 (3)	52 (1)	36,91	4.96	39.2	0.000
	11 (3.2)[b]	-1 (.6)	36,91	3.65	37.8	0.001
Yearlings	67 (4)	55 (1)	21,31	3.36	23.6	0.003
(Females)	12 (4.3)[b]	1 (.9)	21,31	2.63	21.8	0.015
Yearlings	73 (5)	55 (1)	12,22	3.37	11.9	0.006
(Males)	18 (7)[b]	1 (.6)	12,22	2.53	11.2	0.028

a -1 = April 1st

b - standardised values calculated when data for years were combined

2 - sample size for two year old males and females (≥≥2) which were single-brooded was too small to carry out analyses (n=3 and n=4, males and females respectively). In both cases, however, the trend was the same as to that observed for yearlings:

Females: Actual = 71 (20) vs 49 (1), n=3,33;
Standard = 19 (25) vs -4 (1);
Males : Actual = 57 (7) vs 49 (1), n=4,34;
Standard = 2 (9) vs -3 (1)

Table 5.29b Comparison of male Swallow size (Mean (se) for single- and double-brooded birds. Data are 1987, 1988 and 1989 combined, using Students t-test

Male measures of body size	No of broods Single	 Double	t	df	sig[a]	sig[b]
Wing	126.8 (.4)	127.8 (.2)	-0.20	180	*	ns
Outer tail	104.8 (1.4)	109.4 (.7)	-2.91	178	* *	* *
Second tail	64.5 (.5)	65.1 (.3)	-0.99	130	ns	ns
Inner tail	45.3 (.2)	45.3 (.1)	-0.13	176	ns	ns
Head to bill	30.1 (.1)	30.0 (.1)	0.79	181	ns	ns
Keel	21.6 (.1)	21.9 (.1)	-2.05	177	*	ns

a - excludes first broods which were enlarged: single=34, double=148

b - includes only control first broods: single=30, double=115

Table 5.30 Comparison of reproductive performance (mean (se), (n)) of non-survivors (Died) and survivor (Survived) Swallows, by sex. Data are for all years pooled but includes double-brooded birds only, using One-way ANOVA

Breeding Variables	Sex	Died	Survived	one-way ANOVA		
				df	F	p
Clutch size - 1st	M	4.9 (.1) (17)	5.0 (.2) (22)	1,37	0.00	0.947
	F	4.8 (.1) (30)	4.9 (.2) (25)	1,53	0.08	0.785
Clutch size - 2nd	M	4.3 (.2) (23)	4.7 (.2) (24)	1,45	2.43	0.126
	F	4.4 (.2) (33)	4.4 (.1) (33)	1,63	0.06	0.812
Clutch size - tot	M	9.1 (.3) (17)	9.7 (.3) (22)	1,37	2.07	0.159
	F	9.3 (.2) (29)	9.4 (.3) (25)	1,52	0.06	0.804
Brood size[a] - 1st	M	3.3 (.4) (22)	4.7 (.2) (22)	1,37	0.69	0.412
	F	4.5 (.2) (30)	4.4 (.2) (25)	1,53	0.07	0.791
Brood size[a] - 2nd	M	3.3 (.4) (22)	3.8 (.2) (25)	1,45	1.62	0.210
	F	3.4 (.3) (33)	3.9 (.2) (25)	1,64	2.11	0.151
Brood size[a] - tot	M	7.4 (.5) (16)	8.5 (.3) (22)	1,36	4.17	0.049
	F	8.0 (.3) (28)	8.2 (.4) (25)	1,51	0.25	0.618
No. fledged - 1st	M	4.4 (.2) (18)	4.7 (.2) (23)	1,39	1.16	0.288
	F	4.3 (.2) (32)	4.3 (.2) (29)	1,59	0.02	0.894
No. fledged - 2nd	M	3.2 (.4) (22)	3.8 (.3) (25)	1,45	1.62	0.210
	F	3.4 (.3) (33)	3.8 (.2) (32)	1,63	1.74	0.192
No. fledged - tot	M	7.3 (.4) (17)	8.4 (.3) (23)	1,38	4.54	0.040
	F	7.7 (.3) (30)	8.1 (.3) (28)	1,56	0.72	0.400

a - brood size at day 13

1 - attempts which failed as a result of disturbance have been excluded from the above figures though in fact this did not alter the significance level of any of the above results

2 - there was no significant differences when each year was considered separately or when only successful double-brooded pairs were included in the analyses

5.4 DISCUSSION

The seasonal reproductive performance of Swallows varied between individuals and years. Similar variation between seasons and across lifespans has been found for a wide variety of species (reviews in Clutton-Brock (1988) and Newton (1989)). Time of breeding and breeding site have been identified as particularly important in shaping reproductive success (Perrins & Birkhead 1983; Clutton-Brock 1988), both of which are related to food availability, itself an important determinant of reproductive success (Martin 1987). Habitat quality can be ignored because Swallows feed communally, defend only a small area around the nest and there is little evidence of important habitat variation. The importance of timing of breeding and food availability to reproductive performance should, therefore, be determined more accurately.

5.4.1 THE ROLE OF FOOD AVAILABILITY AND ENVIRONMENTAL CONDITIONS IN SHAPING ANNUAL AND SEASONAL REPRODUCTIVE PERFORMANCE

Swallows feed solely on aerial insects which can be easily quantified by means of a suction trap (Section 2.6). Insect abundance showed considerable daily, seasonal and annual variation which was particularly marked during the early and latter parts of the breeding season. In two out of the three years the volume of catch increased monthly; unseasonably high catches during April and May explained the lack of a comparable trend in 1987. Insect abundance also increased with temperature but multiple regressions confirmed season as the best predictor. Environmental factors were less important and also varied between years (also see Jones 1985).

There was little correlation of peak nestling mass with food abundance. This was surprising as nestlings were often seen to be in poor condition during cold rainy weather, sometimes resulting in death (Chapter 3). Furthermore, suction trap catches were positively correlated with House Martin nestling growth (Bryant 1989a; Johnston 1990). The suction trap estimates resources available for those species which forage at a similar height to the trap. Swallows commonly feed at a lower level but House Martins at a higher level (Waugh 1978), so the suction trap data may be more accurate for House Martins. In other studies of the Swallow, however, low level hand net sampling at specific study sites was significantly correlated with the suction trap catch (Turner 1980; Jones 1985). The lack of a relationship of nestling quality with food abundance as reported here might, therefore, be explained by variation in food abundance between sites or by the generally plentiful food supply for breeding Swallows. A failure to identify critical periods of the nestling period (to correlate measures of food abundance and nestling quality) would also obscure a positive relationship, if present.

Both egg size and egg quality of Swallows were correlated with insect abundance, temperature (positive) and rainfall (negative) during albumen formation indicating that eggs are primarily formed from daily food intake and not from previously accumulated reserves (Ward 1992). The relationship of clutch size with environmental factors, however, was generally weak and inconsistent (Ward 1992). These findings support the idea that while Swallow egg synthesis is under mostly energetic constraints clutch size is also genetically constrained. Notably over eighty percent of clutch size variation in Tree Swallows was attributed to food abundance during the egg laying period (Hussell & Quinney 1987).

5.4.1.1 Variation in annual reproductive performance

First-brood breeding performance did not differ between years apart from significantly earlier laying in 1988. Second-brood laying dates showed a similar pattern but significantly fewer young were reared to independence in 1988 than in 1987 and the frequency distribution of clutch size differed between years. More detailed analysis is required to identify the factors responsible for this increase. Indeed, in 1988 (i) seasonal decline in breeding performance was weaker; (ii) peak nestling mass was not significantly correlated with brood size and (iii) there were no brood sizes of two and brood sizes of six had a higher than expected peak nestling mass; contrasting with 1987 and 1989. Also the population was 25% larger in 1988 and adult and juvenile survival was lower over the period 1988/89 (*cf.* 1987/88). The explanation for these results was not clear but they there were no obvious differences between years in environmental conditions.

5.4.1.2 Variation in seasonal reproductive performance

The number of eggs laid, nestlings hatched and fledged young decreased with later date. One less egg was laid in August than in May. Similar differences occur in South-west Scotland (McGinn & Clark 1978) and in Germany (Vietinghoff-Riesch 1955). The breeding performance of double-brooded Swallows was lower for second- than first-broods. Seasonal trends in clutch size have been reported in the House Martin (Bryant 1979), the Tree Swallow (De Steven 1978; Hussell & Quinney, *unpubl.* in Hussell & Quinney 1987) and in other passerine species (Klomp 1970; Perrins 1970; Daan & Dijkstra 1988). The decline in Swallow breeding performance with date was not only caused by the lower breeding success of second broods as a decline was still present controlling for brood number. Insect abundance and temperature increased during the breeding season so the decline seems unlikely to be explained by energetic constraints upon egg production (see Ward 1992). Possible explanations for the seasonal decline in clutch size have been proposed by several authors (Lack 1954, 1966; Askenmo 1982; Murphy 1986; Verhulst & Tinbergen 1991; Ward 1992) and are further discussed in Chapter 8.

5.4.2 TIMING OF BREEDING AND BROOD NUMBER EFFECTS ON ANNUAL REPRODUCTIVE PERFORMANCE

Some Swallows successfully reared two broods in a season whilst others made only a single attempt. The number of broods attempted during a season varied with laying date such that in each season double-brooded pairs started their first broods significantly earlier than single-brooded pairs. House Martins show a similar pattern (Riley 1992). For both species the date at which breeding starts is,therefore, a major influence on annual reproductive success.

Over eighty percent of the study population here were double-brooded but this percentage decreased each year of the study. Ball (1983b) also found annual variation in the proportion of Barn Swallows which were double-brooded and the percentage of House Martins in Central Scotland which were double-brooded decreased from about 80% in 1972 to 20% in 1989 (Riley 1992). The percentage of double-brooded House Martin pairs was negatively correlated with the mean date of first egg but positively correlated with total food abundance in June and July (Bryant 1989a; Riley 1992) but these factors could not fully explain the trends observed in this study. Swallows started breeding earlier and finished later in 1987 (*cf.* 1988 and 1989) but mean monthly food abundance did not explain these annual differences in breeding span. Moreover, the probability of a second brood was not explained by the food abundance during the first-brood nestling period or post-fledging period, further indicating that the suction trap is either less appropriate for breeding Swallows or that food availability was not important in determining second brood attempts. Only an increase in laying spread across a season coincided with an increase in the percentage of Swallows which attempted two broods. Possible reasons associated with why some individuals are single-, yet other double-brooded, is discussed in Chapter 8.

5.4.3 THE ROLE OF BODY SIZE IN SHAPING REPRODUCTIVE PERFORMANCE OVER A SEASON IN ADULT MALE AND FEMALE SWALLOWS

Male body size, except for outer tail-length was only weakly correlated with breeding performance. Partners of males with longer outer tails laid earlier and fledged more young during their first brood. Banbura (1986) also found significant relationships of wing and outer tail-length with date of laying. Males with experimentally elongated outer tails attempted more EPCs, acquired mates more easily and their partners commenced laying earlier than males with shortened tails (Møller 1988a,1989a,1990a; Smith & Montgomerie 1991). As already discussed, birds which start their first broods earliest are probably more successful. Thus tail-length may be an indicator of male viability (Møller 1989a, 1990e). The exact influence of age in this relationship is unknown. The significant correlation of tail-length with laying date was only present for yearlings in this study, whereas Banbura (1986) only found a significant correlation for two year-old birds. The functional significance of the positive correlation of male keel length with clutch size laid and the number of young fledged was also unclear. In House Martins, male keel length (and wing length) is also positively correlated with annual and lifetime egg production as well as life span (Bryant & Westerterp 1982;

Bryant 1988b). Double-brooded male Swallows (wing, outer tail and keel length) and House Martins (wing and keel length) are bigger than single-brooded birds.

Female body size was generally unrelated to reproductive performance but the onset of laying advanced with increasing female outer tail-length. This relationship was not significant after controlling for age (also see Banbura 1986). Single- and double-brooded female Swallows did not differ in body size. In House Martins female keel length was positively correlated with the frequency of double brooding (Bryant 1988b) and annual (Bryant & Westerterp 1982, Table 2) and lifetime egg production (Bryant 1988b) but these trends were not present for Swallows where only female tarsus-length was significantly correlated with clutch size. Similarly, Ward (1992) found that body size was not significantly correlated with clutch size or mean egg size of Swallows.

5.4.4 THE ROLE OF AGE IN SHAPING ANNUAL REPRODUCTIVE PERFORMANCE

Swallow breeding performance improved with age class. Yearling females laid fewer eggs later, raised fewer young to independence and were less likely to be double-brooded than older birds (also see Ward 1992). The lower number of young fledged in a season by yearlings was also caused by lower fledging success. Comparisons of only double-brooded birds yielded similar results. Trends were similar but slightly weaker for male age classes possibly because non-breeding of yearling males caused an underestimate of age class differences. Although performance differences were most pronounced between yearlings and birds of "at least two years" old, females which were three years old or older (≤3) had earlier laying dates and larger clutches than birds categorised as "at least two years" old (≤2), however, they raised fewer young to independence. This decline may be an artifact of a small sample but the possibility of senescence cannot be discounted (Perrins & Moss 1974; Dhondt 1985, 1987).

Age-related trends in breeding performance observed during this study is consistent with results reported in other studies of hirundines (De Steven 1978; Bryant 1979, 1988b; Jarry 1982; Vansteenwegen 1987) and in general with other passerines and non-passerines (for review see Sæther 1990) but see (Geupel & De Sante 1989; Nol & Smith 1987; Bédard & LaPointe 1985). Breeding performance declines seasonally so the smaller clutches of younger birds may simply reflect later laying but age differences were still present after controlling for laying date in this study as well as for Tree Swallows (De Steven 1978, but see Perrins & Moss 1974; Lessells & Krebs 1989).

Although results from a wide variety of species seem to provide clear evidence supporting an increase in reproductive performance with age the above analyses do not control for differences in individual quality (Bryant 1979; Smith 1981; Clutton-Brock 1988; Perrins & McCleery 1989). If better quality birds laid earlier, had a larger clutch size and were more likely to survive until the following breeding season then the birds for which breeding performance was determined at an older age would be of higher quality than yearlings. True age effects are only demonstrated if the same individual improves it's performance each season. A number of hypotheses have been proposed to explain apparent age-related trends (for reviews see Curio 1983; Nol & Smith 1987; Pugesek & Diem 1990; Desrochers 1992; Sæther 1990 and references therein) and these are discussed in relation to data collected here in Chapter 8.

5.4.5 PARENTAL SURVIVAL AND FECUNDITY

If high fecundity reduced the probability of parental survival then individuals would benefit by foregoing maximisation of annual fecundity. An increase in adult mortality of breeders relative to non-breeders (Clutton-Brock *et al.* 1983; Ekman & Askenmo 1986) as well as a positive association with increased fecundity, which has been observed in some animals (for review see Reznick 1985) support this conclusion. Yet in studies of birds the relationship of parental survival and brood size have yielded conflicting results (Lack 1966; Högstedt 1981; Smith 1981). Although Bryant (1979) reported significant differences in survival of single- and double-brooded House Martins this was unrelated to brood size. Similarly there was no evidence from the present study to support a positive association of brood size with parental survival and in fact an opposite trend was observe. Double-brooded females were more than twice as likely to survive until the following breeding season than single-brooded birds (also see Boer-Hazewinkel 1987; Geupel & DeSante 1990). Although male survival was not significantly affected by the number of brood attempts (though the trend was in the same direction) males which raised more young in a season had a significantly higher probability of survival. It was, concluded, therefore, that unlike House martins (Bryant 1979), there appeared to be no cost of being double-brooded for Swallows.

Number of offspring may be a poor measure of reproductive effort. If individuals adjust clutch size to their own ability (or circumstances), then fecundity would not relate to survival. Higher quality individuals, or those with better territories, might rear more youngsters yet incur less breeding 'stress' (Perrins & Moss 1975; Drent & Daan 1980; Högstedt 1980, 1981; Smith 1981; Askenmo 1982; Reznick 1985; Noordwijk & De Jong 1986; Nur 1988b). There was evidence from this study that double-brooded Swallows were higher quality individuals so a positive relationship of fecundity with survival would be expected. Effects of individual differences, fecundity and possible trade-offs can be disentangled by experimentally manipulating reproductive effort. This was attempted in the present study by manipulating brood size and the results from these experiments are presented in Chapters 6 and 7.

5.4.7 RECRUITMENT

In two out of three years peak nestling mass declined with increasing brood size (control) as has been found in other studies (Perrins 1965; Crossner 1977; Bryant 1978b; Bryant & Gardiner 1979; Ross 1980a, but see McGillvray 1983). This negative relationship is perhaps surprising if individuals are able to adjust clutch size to their own ability. In Swallows, bigger broods occurred earlier in the season so there may be more time for parental care and therefore compensatory growth to improve the probability of recruitment of nestlings from large broods.

Return rate of Swallows to their natal area was very low and varied between years. Moreover, recruitment also differed markedly between years. Over four fifths were recruited from first broods in 1988 compared to only half in 1987. Significantly fewer fledged from second broods in 1988 (*cf.* 1987) which may partly explain the low recruitment from second broods that year. It is difficult to explain the low recruitment from first broods (*cf.* second broods) in 1987 but it did not appear to be caused by conditions during the nestling period because: a) more young fledged during first broods (4.2 vs 3.9) and b) peak nestling mass was higher (23.4 vs 22.7) in 1987. Post-fledging conditions may be important (review by Clutton-Brock 1988). Recruitment differences between years and broods were not matched by differences in peak nestling mass, as found for some other species including the Tree Swallow (De Steven 1980) although positive relationships have been found as well (reviewed in Magrath 1991). These interspecific differences may be caused by differences in measurement. For example, mean nestling mass on Day 13 which was used here, may be an inadequate measure of nestling 'quality'. Similarly, variation within a brood with a tendency for the heaviest or biggest to survive would invalidate comparisons of means. Nestling mass at fledging or actual growth rates may be more important because in Swallows: (i) there was an overall tendency for recruits to be heavier than non recruits and, (ii) nestlings ranked one or two were more likely to survive than those occupying lower ranks.

Offspring were recruited from throughout the season, from first and second broods but they were more likely to have hatched from first broods and in general, those which hatched earliest were more likely to be recruited. Similar results have been reported for the Tree Swallow (De Steven 1980) and the Great Tit (Kluyver 1951; Perrins 1965; Perrins & McLeery 1989). Later nestlings might recruit poorly because nestling quality declines with season and survival is positively correlated with nestling quality (Magrath 1991). Seasonal decline in recruitment was still weak after controlling for brood size. The weaker trends for second broods may be explained by the higher food abundance during the second half of the season, by greater parental investment or by higher 'quality' of double-brooded birds. The relationship of offspring survival with brood size (control) varied annually but there was a general tendency for the number of recruits to increase with brood size. Brood size and the number of offspring surviving to maturity have also been shown to be positively correlated in other studies (Perrins 1965; De Steven 1980; Ross & McLaren 1981; Nur 1984a).

Chapter six
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Inter - and Intra-Seasonal Costs of Manipulated Brood Sizes

6 INTER-AND INTRA-SEASONAL COSTS OF MANIPULATED BROOD SIZES

6.1 INTRODUCTION

David Lack (1947, 1948a, 1948b, 1954; 1968) suggested that clutch size in nidicolous species evolved through natural selection to match the maximum number of young which parents could raise. Central to Lack's hypothesis are two important propositions: (i) the average clutch size corresponds to the most productive and, (ii) the ultimate factor limiting clutch size is the ability of the parents to feed their young adequately. Since Lack's pioneering work, however, other studies have found that the clutch size producing most fledglings is often larger than the modal clutch size (Murphy & Haukioja 1986; Lessells 1986). It is possible that if reproduction is "costly" individuals need to "decide" the allocation of resources to either current or future fecundity. This is the "trade-off" or "costs of reproduction" hypothesis (see General Introduction). The idea of a trade-off was first proposed by Williams (1966) and is now a fundamental assumption of much life history theory (Charnov & Krebs 1974; Stearns 1976; Calow 1979). If high fecundity reduces nestling (Smith *et al.* 1987, 1989b and references therein) or parental "condition", so reducing their probability of survival or future fecundity (reviewed by Dijkstra *et al.* 1990; Partridge 1989) then individuals might benefit by foregoing maximisation of annual fecundity.

6.1.1 THE PROBLEM OF PHENOTYPIC PLASTICITY

Over the last thirty years or so studies have been made to identify costs of reproduction in natural avian populations (Kluyver 1963, 1971; Perrins 1965; Lack 1966; Bryant 1979; Hogstedt 1981; Smith 1981; Tinbergen *et al.* 1985; Ekman & Askenmo 1986; Orell & Ojanen 1986; Boer-Hazewinkel 1987; Korpimaki 1988a) and although some data are convincing (Bryant 1979; Ekman & Askenmo 1986; Boer-Hazewinkel 1987), no general patterns have emerged. Number of offspring may be a poor measure of reproductive effort. If individuals adjust their clutch size to their own ability (or circumstances), then fecundity (eg. clutch size) would not be expected to be related to survival; higher quality individuals, or those with better territories might rear more youngsters yet incur less breeding "stress" than those of poorer quality rearing fewer offspring (Drent & Daan 1980; Hogstedt 1980, 1981; Smith 1981; Askenmo 1982; Reznick 1985; van Noordwijk & De Jong 1986; Nur 1988). A more rigorous test of "the trade-off" hypothesis, therefore, is to experimentally manipulate reproductive effort (but see Reznick 1992a,b; Partridge 1992).

6.1.2 EFFECTS OF MANIPULATION OF BROOD SIZE ON COSTS OF REPRODUCTION

Manipulation of reproductive "effort" has been attempted through altering brood size and in most such studies of passerines inter- and intra-seasonal reproductive costs have been demonstrated for both nestlings and parents (reviewed by Dijkstra *et al.* 1989).

6.1.2.1 Intra-seasonal costs

In multi-brooded species, an effect on fecundity has been detected within the same season in both natural (Nice 1937; Pinowski 1977; Kluyver *et al.* 1977; Smith & Roff 1980; Stamps *et al.* 1985; McGillivray 1983) and experimental (Finke *et al.* 1987; Slagsvold 1984; Tinbergen & Albers 1984; Smith *et al.* 1987, 1989a,b; Tinbergen 1987; Hegner & Wingfield 1987; Lindén 1988; DeLaet & Dhondt 1989) studies. Rearing an enlarged first brood increased the duration of the inter-brood interval (Nice 1937; Pinowski 1977; Smith & Roff 1980; McGillivray 1983; Stamps *et al.* 1985; Slagsvold 1984; Smith *et al.* 1987, 1989; Tinbergen 1987; Linden 1988) and/or reduced the frequency (Kluyver 1963; Pinowski 1977; Tinbergen & Albers 1984; Tinbergen 1987; Smith *et al.* 1987; Linden 1988), size (Smith *et al.* 1987; Hegner & Wingfield 1987; Pinowski 1977) and success (Slagsvold 1984; Smith *et al.* 1987; McGillivray 1983) of subsequent broods. Only two studies failed to identify intra-seasonal costs of any kind (Finke *et al.* 1987; Pettifor *et al.* 1988).

6.1.2.2 Nestlings

Nestlings from experimentally enlarged broods tended to be lighter and show reduced survival until fledging compared to those from control or reduced broods (Lindén & Møller 1988; Dijkstra *et al.* 1989). Moreover, Great Tits and Collared Flycatchers from enlarged broods had lower recruitment into the breeding population than those from control broods (Pettifor *et al.* 1988; Gustafsson & Sutherland 1988).

6.1.2.3 Parents

Studies of the relationship of manipulated brood size to parental survival have yielded inconclusive results. Female Blue Tits (Nur 1984a) and male Pied Flycatchers (Askenmo 1979) that reared enlarged broods were less likely to return the following season, but female Tree Swallows and male Rooks, Collared Flycatchers, Great Tits and Tengmalms Owls did not show this effect (De Steven 1980; Røskaft 1985a; Gustafsson & Sutherland 1988; Pettifor *et al.* 1988 and Korpimaki 1988a respectively).

6.1.4 AIMS

The effect of manipulating brood size on parents and their offspring was examined. Nestling mass and survival to the next year; the occurrence, timing, size and success of second broods in relation to the size of first brood reared were measured and the relationship of brood size to parental survival were all examined. For double-brooded parents, their response to manipulation of first or second broods was investigated.

6.2 METHODS

6.2.1 MANIPULATION OF BROOD SIZE: EXPERIMENTAL PROCEDURES

Brood size was manipulated when nestlings were four days old (± 1 day) in three nests of a similar hatch date (± 1 day). If there was a difference in the age of donor and recipient broods then younger nestlings were never transplanted into older broods. Preliminary studies in 1987 revealed that the maximum number of young which could be raised in a natural nest was eight and that reducing broods to one could cause immediate desertion so broods were almost always manipulated within the range of two to eight. Nestlings were usually swapped between nests at the same site or were transferred in a cloth bag to a neighbouring site. They were never out of the nest for longer than fifteen minutes. Brood size prior to manipulation did not always match original clutch size because of hatching failure.

One, two or three young were removed from one nest (Reduced) and added to another (Enlarged); control nests were unaltered (Control). Parents may be able to distinguish between their own and transplanted nestlings so young of the same age were also swapped between nests (1989 only). Parents in other species do not discriminate between their own and foster young (Hegner & Wingfield 1987; Korpimaki 1988a; Pettifor *et al.* 1988). Most nests were randomly allocated to the treatments described above, however, where fertile eggs were damaged or a nestling died shortly after hatch as a result of interference, broods were considered as being reduced (n <10 during the study). Only nestlings added before Day 6 were included in analyses. The change in brood size after manipulation (DBR) was calculated by subtracting original brood size (BRS) from brood size after manipulation (BAM).

6.2.2 BREEDING PERFORMANCE AFTER MANIPULATION OF BROOD SIZE

After manipulation, the number of young in the nest was counted on Day 13 (±1) and at fledging. Where at least one young from a nest fledged, the pair was considered "successful". Broods which failed shortly after manipulation, were predated, or did not fledge, were excluded from analyses. Second broods which failed but re-laid, were assessed on their re-laid brood which may or may not have been manipulated.

6.2.3 NESTLING "QUALITY"

On Day 13 (±1 day), nestlings were ringed and weighed (to the nearest 0.1g). Wing- (nearest 1mm), head-to-bill (nearest 0.1mm) and tarsus-length (nearest 0.1mm) were also measured. Some broods were measured at fledging. Brood means were used in analyses.

6.2.4 INTER-BROOD INTERVAL (IBI)

The time from the date of hatch of the first brood to the date that the first egg of the second brood was laid was used as the IBI in this study. Where one member of a pair was predated or a change in site or partner occurred, the IBI was not included in analyses. The time from the date when a nest failed to the date when the first egg of a replacement clutch was laid was called the re-lay interval.

6.3 RESULTS

6.3.1 MANIPULATION OF BROOD SIZE

Brood sizes of Swallows were experimentally manipulated in three successive years: 1987, 1988 and 1989. First broods were manipulated in 1988 and 1989 and second broods in 1987 and 1988 (Table 6.1a). In 1987 and 1989, first and second broods respectively were not systematically altered but were manipulated in conjunction with other experiments. The direction of second brood manipulation in relation to the first brood manipulation, and the mean number of nestlings added or removed from each brood is summarised in Table 6.1b (also see Appendix 6.1).

6.3.2 ANNUAL VARIABILITY IN BREEDING PERFORMANCE

Breeding performance (clutch size, brood size and the number fledged) did not differ significantly between years (1988 and 1989), except for a later date of hatch in 1989 (73 (1) vs 82 (2), $p<0.001$). Peak nestling mass of Enlarged and Reduced broods did not differ between years ($p=0.60$) but Control broods were 1g lighter in 1989 than in 1987 ($p<0.002$) and 1988 ($p<0.000$), (23.2 (.2), 23.3 (.2) and 22.1 (.3), for 1987, 1988 and 1989 respectively). Fewer second broods were manipulated so the data are not presented separately for 1987 and 1988.

6.3.2 ANNUAL VARIABILITY IN BROOD SIZE MANIPULATION

First broods tended to be reduced (-2.6 (.1) vs -2.1 (.2), $p=0.075$) and enlarged (2.7 (.2) vs 2.4 (.1), $p=0.069$) less in 1989 than in 1988. Second broods were reduced similarly in 1987 and 1988 (-2.6 (.3) vs -2.4 (.2)) but enlarged more in 1988 (3.3 (.2) vs 2.7 (.2), $p <0.05$).

6.3.3 BREEDING PERFORMANCE PRIOR TO MANIPULATION OF BROOD SIZE

Breeding performance (clutch size, brood size and date of hatch) did not differ between

Table 6.1a First and second brood treatments[a] in 1987, 1988 and 1989

Year	Brood No.	Reduced	Control	Enlarged
1987	First	1	82	3
	Second	8	44	8
1988	First	30	77	26
	Second	19	58	15
1989	First	35	58	24
	Second	6	73	2
All years	First	60	217	53
	Second	33	175	25

a- nests which failed during Days 1-7 of the nestling period (NP1) have been excluded. For pairs which failed but which relayed; only the relay attempt has been counted in the above figures.

Table 6.1b Manipulation protocols for double-brooded birds: second brood manipulation in relation to first brood manipulation, in 1987,1988 and 1989

	First brood	Second brood treatment		
Year	treatment	Reduced	Control	Enlarged
1987	Reduced	-	-	-
	Control	8	43	8
	Enlarged	-	1	0
1988	Reduced	4	14	3
	Control	13	39	8
	Enlarged	2	5	4
1989	Reduced	2	24	1
	Control	3	33	1
	Enlarged	1	15	0
All years	Reduced	6	38	4
	Control	24	115	17
	Enlarged	3	21	4

treatments prior to manipulation of first broods, except that in 1989 Reduced and Enlarged broods which were experimentally manipulated hatched earlier than Control broods, significantly so for Reduced broods (Table 6.2a). There were no differences when 1988 and 1989 were pooled so any differences in breeding performance measured after manipulation were attributed to effects of the manipulation itself.

Reduced and Enlarged second broods did not differ significantly in any measure of breeding performance prior to manipulation but Control second broods had smaller clutches and broods than Enlarged broods and smaller broods and later hatching than Reduced broods.

6.3.4 BREEDING PERFORMANCE AFTER BROOD SIZE MANIPULATION

The change in brood size (DBR) and the brood size after manipulation (BAM) differed significantly between treatments until at least Day 13 of the nestling period ($p<0.000$, Table 6.3a). More young tended to be reared to independence in Enlarged broods than in Control broods ($p=0.074$, Table 6.3a) and exclusion of broods which failed completely produced significant differences between all three treatments (2.1 vs 4.1 vs 5.4; Reduced, Control and Enlarged, respectively). The pattern varied slightly between years. In 1988 Enlarged broods fledged 1.3 more young than Control broods whereas in 1989 only 0.2 more were fledged. This was partly because broods were enlarged less in this year and partly because of higher nestling mortality in the late nestling period.

Degree of manipulation (SDBR), brood size after manipulation (SBAM) and the number reared to independence (SNYF) during second broods were all significantly different between treatments ($p<0.000$, Table 6.3b). Enlarged second broods produced almost twice as many fledglings than Control broods (6.1 vs 3.8).

6.3.5 NESTLING MORTALITY IN RELATION TO MANIPULATION OF BROOD SIZE

Nestling mortality varied between treatments (1st brood). From manipulation to peak nestling mass at Day 13 ± 1, more nestlings died (10% more in terms of % of brood size after manipulation) in Enlarged than in Control or Reduced broods ($p<0.000$, Table 6.4a). Differences were even greater when mortality over the entire nestling period was compared. One third of Enlarged nestlings failed to reach independence whereas only eleven and nine percent of Control and Reduced broods respectively, failed to fledge. Nestling mortality was lower in Reduced broods than in Control broods ($p<0.01$, Table 6.4a). Complete nest failures were more common in Enlarged broods and this accounted for a large proportion of their total casualties.

A similar pattern of nestling mortality was found for second broods. All four mortality

Table 6.2 **Comparison[a] of reproductive performance (Mean (se)) prior to brood manipulation, by year. Using one-way ANOVA (significance):**

a) First broods

Breeding parameters	Year	Reduced	Control	Enlarged	One-way ANOVA R v C	C v E	R v E
Clutch size	1988	5.0 (.1)	4.9 (.1)	5.0 (.1)	ns	ns	ns
	1989	5.1 (.1)	4.8 (.1)	5.0 (.2)	ns	ns	ns
	Both	5.0 (.1)	4.9 (.1)	5.0 (.1)	ns	ns	ns
Date of hatch[b]	1988	73.1 (1.8)	73.4 (1.3)	74.7 (2.0)	ns	ns	ns
	1989	76.0 (1.5)	81.9 (2.2)	76.6 (2.0)	*	0.077	ns
	Both	74.7 (1.2)	77.1 (1.2)	75.6 (1.4)	ns	ns	ns
Brood size	1988	4.6 (.2)	4.6 (.1)	4.9 (.1)	ns	0.060	ns
	1989	4.7 (.2)	4.5 (.1)	4.4 (.3)	ns	ns	ns
	Both	4.7 (.1)	4.5 (.1)	4.7 (.2)	ns	ns	ns

a - comparisons between years within each manipulation category are given in the text
a - nth day after April 1st

b) Second broods

Breeding parameters	Reduced	Control	Enlarged	One-way ANOVA R v C	C v E	R v E
Clutch size	4.6 (.2)	4.3 (.1)	4.8 (.1)	ns	* *	ns
Date of hatch	123.5 (2.0)	129.2 (1.3)	124.6 (1.9)	0.057	ns	ns
Brood size	4.5 (.2)	3.9 (.1)	4.5 (.1)	*	* *	ns

Table 6.3 Comparison[a] of reproductive performance (Mean (se)) after manipulation of brood size, by year, using one-way ANOVA (significance):

a) First brood size

First brood sizes at different ages after manip	Year	Reduced	Control	Enlarged	One-way ANOVA R v C	One-way ANOVA C v E	One-way ANOVA R v E
Brood size	1988	2.1 (.1)	4.6 (.1)	7.6 (.1)	* * *	* * *	* * *
on Day 5	1989	2.5 (.1)	4.5 (.1)	6.8 (.3)	* * *	* * *	* * *
(BAM)	Both	2.3 (.1)	4.5 (.1)	7.2 (.2)	* * *	* * *	* * *
Brood size	1988	2.0 (.1)	4.4 (.1)	6.7 (.3)	* * *	* * *	* * *
on Day 13	1989	2.5 (.1)	4.2 (.2)	5.5 (.4)	* * *	* *	* * *
(B13)	Both	2.3 (.1)	4.3 (.1)	6.1 (.2)	* * *	* * *	* * *
Number	1988	1.9 (.1)	4.1 (.2)	5.4 (.5)	* * *	*	* * *
fledged	1989	2.2 (.1)	3.7 (.2)	3.9 (.5)	* * *	ns	* * *
(NYF)	Both	2.1 (.1)	3.9 (.1)	4.7 (.6)	* * *	0.074	* * *
Number	1988	1.9 (.1)	4.3 (.1)	5.8 (.5)	* * *	* *	* * *
fledged	1989	2.3 (.1)	4.0 (.2)	4.9 (.4)	* * *	*	* * *
	Both	2.1 (.1)	4.1 (.1)	5.4 (.3)	* * *	* * *	* * *

a - excluding complete nest failures (i.e no young fledged from nest)

b) Second brood size

Second brood sizes at different ages after manip	Reduced	Control	Enlarged	One-way ANOVA R v C	One-way ANOVA C v E	One-way ANOVA R v E
Brood size on Day 5 (SBAM)	2.1 (.2)	3.9 (.1)	7.5 (.2)	* * *	* * *	* * *
Brood size on Day 13 (SB13)	1.9 (.2)	3.5 (.1)	6.3 (.2)	* * *	* * *	* * *
Number fledged (SNYF)	1.8 (.2)	3.4 (.2)	6.3 (.2)	* * *	* * *	* * *
Number fledged	2.0 (.2)	3.8 (.1)	6.1 (.2)	* * *	* * *	* * *

Table 6.4 **Comparison of nestling mortality (Mean (se and %)) between treatments, by year, using one-way ANOVA:**

a) First brood treatments

Mortality Category[a]	Year	Reduced	Control	Enlarged	||	One-way ANOVA R v C	 C v E	 R v E
A1	1988	-0.07 (.05) 3.3%	-0.10 (.04) 2.5%	-0.88 (.24) 11.6%	||	ns	* *	* *
	1989	-0.06 (.04) 2.4%	-0.26 (.10) 5.6%	-1.28 (.40) 17.2%	||	0.063	*	* *
	Both	-0.06 (.03) 2.8%	-0.17 (.05) 3.9%	-1.08 (.23) 14.4%	||	0.056	* * *	* * *
A2	Both	-0.06 (.03) 2.9%	-0.12 (.03 2.8%	-0.80 (.19) 10.6%	||	ns	* *	* * *
B1	1988	-0.13 (.08) 6.7%	-0.32 (.13) 6.8%	-2.23 (.48) 30.0%	||	ns	* *	* * *
	1989	-0.31 (.13) 11.2%	-0.73 (.18) 16.0%	-2.88 (.64) 37.9%	||	0.063	* *	* *
	Both	-0.23 (.08) 9.0%	-0.50 (.11) 10.9%	-2.54 (.39) 33.1%	||	*	* * *	* * *
B2	Both	-0.19 (.07) 7.7%	-0.29 (.07) 6.4%	-1.74 (.32) 22.9%	||	ns	* * *	* * *

a - A1 - mortality = (BAM) - (B13); A2 - as A1 but excludes complete nest failures
B1 - BAM - NYF; B2 - as B1 but excludes complete nest failure

b) Second brood treatments

Mortality Category	Reduced	Control	Enlarged	||	One-way ANOVA R v C	 C v E	 R v E
A1	0.00 (.0)	-0.16 (.1)	-1.32 (.3)	||	ns	* * *	* * *
A2	0.00 (.0)	-0.13 (.0)	-1.13 (.3)	||	ns	* *	* * *
B1	-0.21 (.2)	-0.51 (.1)	-1.61 (.4)	||	ns	*	* * *
B2	-0.11 (.1)	-0.44 (.1)	-1.13 (.3)	||	*	*	* *

measures were significantly higher in Enlarged than Reduced broods ($p<0.000$, Table 6.4b). Few nestlings died in Reduced broods but there was no significant difference from Control broods. Three times as many died in Enlarged broods than Control broods ($p<0.000$). Excluding broods where all nestlings died did not affect these results.

6.3.6 EFFECT OF MANIPULATION OF BROOD SIZE ON BREEDING SUCCESS

The "success" (Section 6.2.2) of nestlings from each treatment during first broods was analysed. More Enlarged pairs were unsuccessful than Control or Reduced pairs (all tests $p<0.05$, Table 6.5). The strikingly high success of Reduced pairs is, however, an artefact of excluding pairs from analyses which deserted but which immediately re-laid from (Section 6.2.2). Altering the criterion so that only pairs which fledged at least two young were considered as "successful", further enhanced the differences between treatments ($p<0.001$; Table 6.5).

6.3.7 EFFECT OF BROOD SIZE ON NESTLING MASS

6.3.7.1 Comparison of treatments:

Enlarged peak nestling mass was about 2.5g less than for Control nestlings and 3.4 g less than for Reduced nestlings (1st broods: all tests $p<0.000$; Table 6.6a). Reduced nestlings were significantly heavier than Control nestlings ($p<0.001$) in 1989 but not in 1988 (Table 6.6a). There were no differences in fledgling mass between treatments but fewer nestlings were measured at this stage (Table 6.6a).

Reduced second-brood nestlings were heavier than Control nestlings ($p<0.05$; Table 6.6b) whereas Enlarged nestlings were 3g lighter than Control nestlings ($p<0.000$; Table 6.6b). Unlike first broods, these differences were still present in fledging mass where Enlarged fledglings were lighter than fledglings from other treatments ($p<0.05$, Table 6.6b).

6.3.7.2 Relationship of peak nestling mass to manipulated brood size:

Peak nestling mass declined significantly as brood size (1st) increased (Table 6.7a). The number of young in the nest immediately after manipulation (BAM) explained 29% of the variation (Fig 6.1), 9% more than that explained by brood size on Day 13 (B13). The variation explained differed between years: BAM (18% and 45%); B13 (21% and 25%) in 1988 and 1989 respectively. Inclusion of the quadratic terms BAM^2 and $B13^2$ did not alter the percentage of variation explained for the pooled data set but in 1988, 22% and 26% was explained with the inclusion of BAM^2 and $B13^2$ respectively. The range in peak nestling mass was ~ 4.5g with brood sizes of two and eight having the highest and lowest masses respectively . Broods of one had even higher nestling mass but the sample size was only nine.

The trend was similar for second broods. Over twice as much variation was explained in

Table 6.5 Comparison[a] of the number of pairs which successfully fledged young (%) in relation to first brood manipulation, by year

Year	Outcome	Reduced	Control	Enlarged
1988[bd]	Successful	100 (30)	97.4 (74)	92.3 (24)
	Unsuccessful	0 (0)	2.6 (2)	7.7 (2)
	Total	30	76	26
1989[b]	Successful	97.1 (33)	94.5 (52)	80.0 (20)
	Unsuccessful	2.9 (1)	5.5 (3)	20.0 (5)
	Total	(34)	(55)	(25)
Both[bd]	Successful	98.4 (63)	96.2 (126)	86.3 (44)
	Unsuccessful	1.6 (1)	3.8 (5)	13.7 (7)
	Total	(64)	(131)	(51)
Both[bd]	Successful	83.1 (54)	75.4 (92)	30.0 (15)
	Unsuccessful	16.9 (11)	24.6 (30)	70.0 (35)
	Total	(65)	(122)	(50)

a - in all cases only genuine first broods have been considered (i.e those which incurred a re-lay attempt are not included

b - nest is said to have been successful only if ≥ one young was fledged

c - nest is said to have been successful only if ≥ two young were fledged

d - significant results from one-way ANOVA between treatments were as follows:

1989[a] : R vs E; $p=0.074$

Both[a] : R vs E and C vs E; both $p<0.01$

Both[b] : R vs E and C vs E; both $p<0.000$

Table 6.6 Comparison of peak nestling mass (Day 13) and fledging mass (Day 18) between manipulation treatments, by year, using one-way ANOVA:

a) First brood manipulation

Nestling mass/age	Year	Reduced	Control	Enlarged	One-way ANOVA		
					R vs C	C vs E	R vs E
Day 13 (B13)	1988	23.7 (.3) (27)	23.3 (.2) (48)	20.4 (.5) (25)	ns	* * *	* * *
	1989	23.6 (.3) (33)	22.1 (.3) (51)	20.5 (.5) (24)	* *	* *	* * *
	Both	23.6 (.2) (60)	22.7 (.2) (99)	20.2 (.3) (49)	* *	* * *	* * *
Fledging (Day 18) (NYF)	1988	20.5 (.4) (10)	20.5 (.3) (16)	19.8 (.5) (15)	ns	ns	ns
	1989	19.7 (.4) (10)	18.8 (1.2) (5)	20.2 (.5) (7)	ns	ns	ns
	Both	20.1 (.3) (20)	20.1 (.4) (21)	19.9 (.4) (22)	ns	ns	ns

b) Second brood manipulation

Nestling mass/age	Reduced	Control	Enlarged	One-way ANOVA		
				R v C	C v E	R v E
Day 13 (B13)	24.3 (.3) (17)	23.3 (.6) (50)	20.7 (.4) (20)	*	* * *	* * *
Fledging (Day 18) (NYF)	21.7 (.6) (4)	21.2 (.4) (23)	19.9 (.4) (10)	ns	*	*

1988 than in 1987 (SBAM: 42% vs 18%; Table 6.7a) largely because broods of three and four had much lower than expected mean mass in 1987. Exclusion of these two points increased the variation explained from 17% to 35%, much closer to the 1988 figure (42%). SBAM and SB13 or $SBAM^2$ and $SB13^2$ explained 45% and 50% or 35% and 38% of the variation in peak nestling mass for pooled data (Fig 6.2).

6.3.7.3 Relationship of peak nestling mass to change in brood size

Peak nestling mass declined significantly with the change in brood size (DBR) within all categories (all tests; $p<0.000$, Table 6.7b). DBR explained slightly less variation in peak nestling mass than BAM during first (23% cf. 29%, Fig 6.3) and second (32% cf. 34%, Fig 6.4) broods. Change in brood size (D13) was an even poorer predictor, explaining 15% and 22% of variation in first and second broods respectively. This again differed between years: 1988 18% and 21% and 1989: 31% and 14% of the variation was explained by DBR and D13 respectively, during first broods. Similar differences were apparent during second broods (Table 6.7b).

Nestlings from Control broods of five or six nestlings were of similar mass to nestlings from Enlarged broods of this size (22.3 (.3), $n=60$ vs 21.6 (.6), $n=9$; $p=0.427$). Reduced broods of one to four nestlings were just slightly heavier than naturally occurring broods of this size (23.3 (.2), $n=70$ vs 23.7 (.2), $n=82$; $p=0.112$). Enlarged broods of seven or eight were no different in peak nestling mass in those enlarged by two ($n=18$) than in those enlarged by three ($n=32$) nestlings. Broods reduced by three nestlings ($n=32$), however, tended to be heavier than those reduced by two nestlings ($n=21$): (23.2 (.3) vs 24.0 (.2), $t=-1.83$, $p=0.074$).

Measures of change in brood size (DBR, D13 and DNYF) were not significant factors in any of the multivariate analyses carried out (Table 6.8). In experimentally manipulated broods, 41% of the variation in peak nestling mass was explained by BAM^2 (28%), NYF (10%) and B13 (3%) (Table 6.8). The best predictor in 1988 was $B13^2$ which explained one quarter of the variation (*cf.* BAM in 1989).

6.3.8 DESERTION IN RELATION TO CLUTCH SIZE REDUCTION

6.3.8.1 Experimental reductions

In 1987 and 1988, one to three eggs were removed from a total of thirteen nests which had un-manipulated clutch sizes of three to six (Table 6.9a). All eggs were removed during the first week of incubation. At six of the thirteen nests, desertion followed egg removal (Table 6.9b) and in all but one of these cases the nest was known or thought to have been abandoned on the day of manipulation. At one nest with an electronic nest balance set up, the pattern of attendance following the removal of three eggs (at 1230h) showed that the female returned to the nest and incubated only twice (10 and 8 minutes) before abandoning the nest completely, within one hour of the manipulation. Desertion seemed

Table 6.7 Pearson correlation coefficients[a] of peak nestling mass with brood parameters after manipulation, at Day 0 (BAM) and Day 13 (B13), by year and brood number (coefficient, (n), significance):

a) Brood size

Brood size	Year	All broods	Brood number First	First[b]	Second[b]
BAM	1987	First broods not manipulated			-0.43 (25) *
	1988	-0.55 (159) ***	-0.42 (90) ***	-0.67 (98) ***	-0.65 (62) ***
	1989	-0.65 (125) ***	-0.67 (98) ***	-0.67 (104) ***	Second broods not manipulated
	All years	-0.55 (353) ***	-0.53 (217) ***	-0.55 (237) ***	-0.56 (104) ***
B13	1987	First broods not manipulated			-0.27 (26) ns
	1988	-0.5 (161) ***	-0.46 (91) ***	-0.47 (98) ***	-0.60 (62) *
	1989	-0.47 (126) ***	-0.50 (98) ***	-0.54 (104) ***	Second broods not manipulated
	All years	-0.45 (358) ***	-0.45 (218) ***	-0.46 (238) ***	-0.45 (105) ***

---

a - additional statistics were as follows:

BAM - 1987 and 1988: Second r=-0.57, n=81, p<0.000
B13 - 1987 and 1988: Second r=-0.48, n=82, p<0.000
BAM - 1988 and 1989: First r=-0.53, n=188, p<0.000
BAM - 1988 and 1989: First[b] r=-0.56, n=201, p<0.000
B13 - 1988 and 1989: First r=-0.45, n=189, p<0.000
B13 - 1988 and 1989: First[b] r=-0.46, n=202, p<0.000

b - includes re-lay attempts

b) Change in brood size[c]

Change in brood size	Year	All broods	Brood number		
			First	First[b]	Second[b]
DBR	1987	First broods not manipulated			-0.44 (23) *
	1988	-0.52 (159) * * *	-0.42 (90) * * *	-0.46 (97) * * *	-0.61 (62) * * *
	1989	-0.50 (125) * * *	-0.56 (98) * * *	-0.50 (104) ***	Second broods not manipulated
	All years	-0.49 (353) * * *	-0.46 (217) * * *	-0.48 (237) * * *	-0.52 (104) * * *
D13	1987	First broods not manipulated			-0.28 (23) ns
	1988	-0.47 (159) * * *	-0.46 (90) * * *	-0.44 (97) * * *	-0.54 (62) * * *
	1989	-0.29 (125) * * *	-0.37 (98) * * *	-0.36 (104) * * *	Second broods not manipulated
	All years	-0.37 (353) * * *	-0.37 (217) * * *	-0.37 (237) * * *	-0.39 (104) * * *

b - includes re-lay attempts

c - additional statistics were as follows:

DBR - 1987 and 1988: Second r=-0.58, n=81, p<0.000
D13 - 1987 and 1988: Second r=-0.47, n=81, p<0.000
DBR - 1988 and 1989: First r=-0.48, n=188, p<0.000
DBR - 1988 and 1989: First[r] r=-0.49, n=201, p<0.000
D13 - 1988 and 1989 First r=-0.39, n=188, p<0.000
D13 - 1988 and 1989 First[r] r=-0.39, n=202, p<0.000

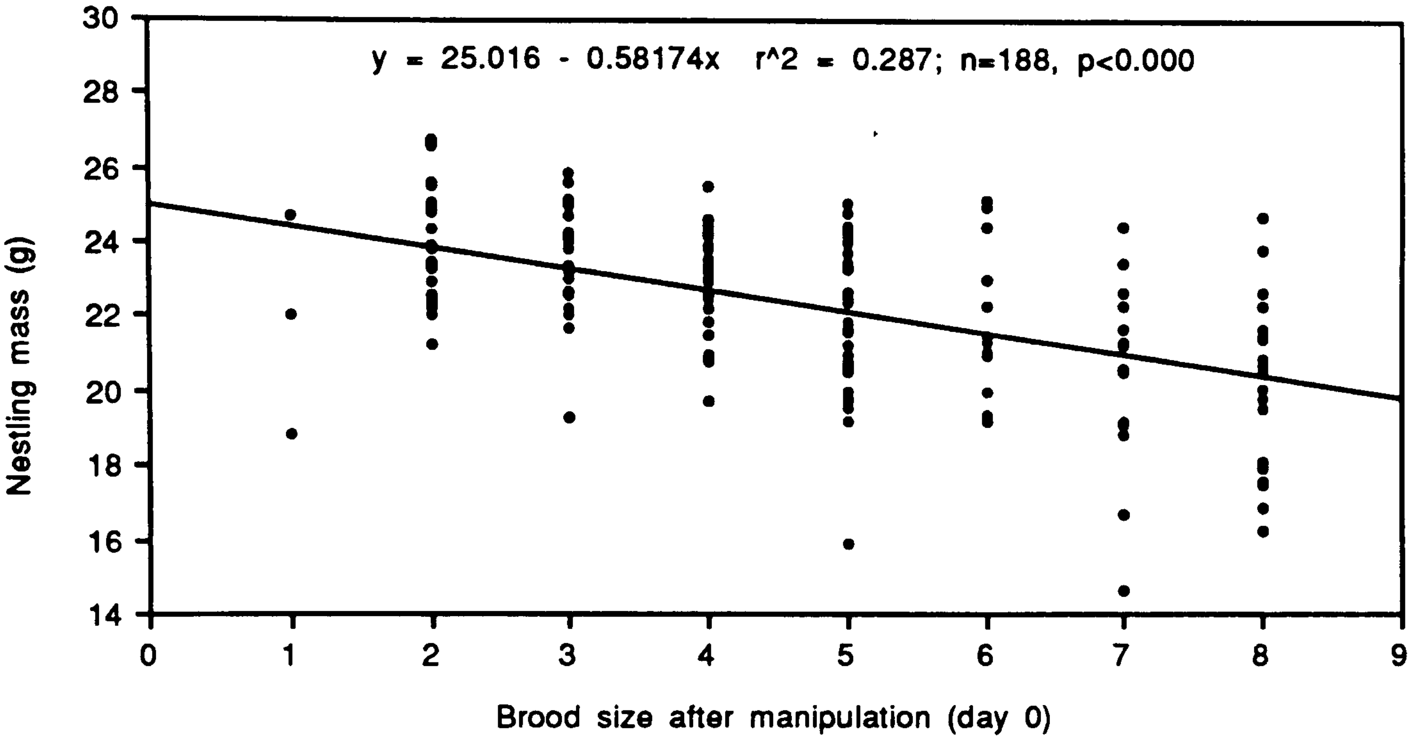


Fig 6.1 **Relationship between peak nestling mass and brood size (1st) after manipulation at day 0 (BAM). Data are for 1988 and 1989**

Regression based on brood size after manipulation on day 13 (B13) was as follows:

y = 24.652 - 0.53257x r^2 = 0.205, n=189, p<0.000

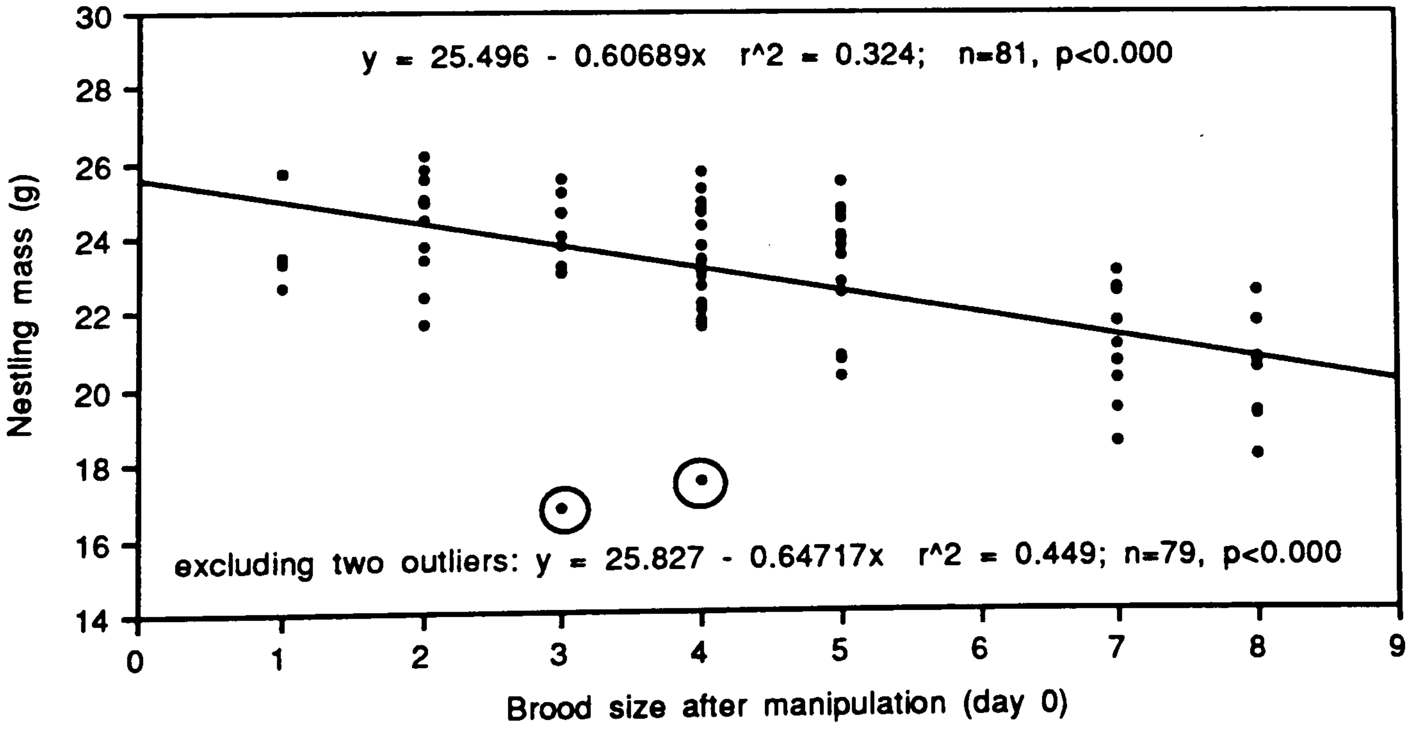


Fig 6.2 **Relationship between peak nestling mass and brood size (2nd) after manipulation at day 0 (SBAM). Data are for 1987 and 1988**

Regression based on the brood size after manipulation on day 13 (SB13) was as follows:

y = 25.247 - 0.59531x r^2 = 0.235; n=82, p<0.000

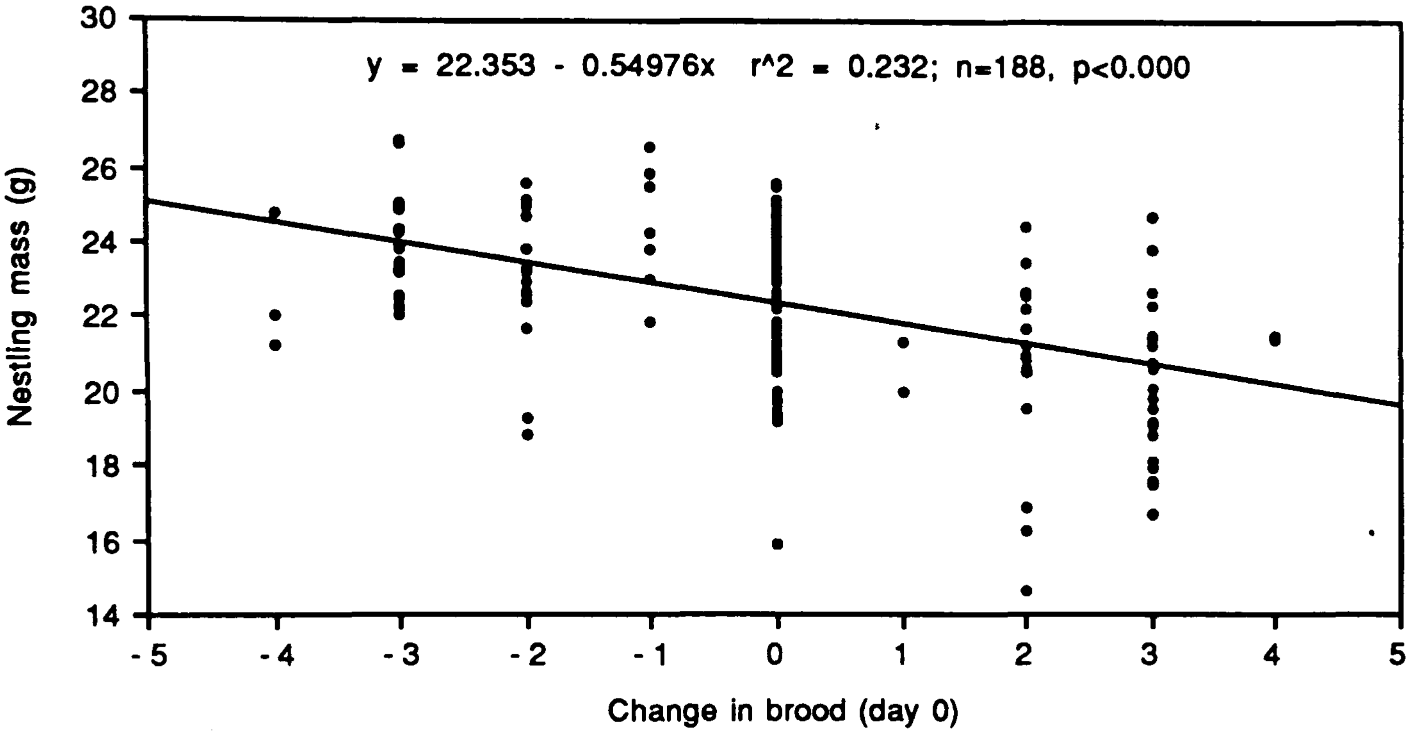


Fig 6.3 **Relationship between peak nestling mass and change in brood size (1st) after manipulation at day 0 (DBR). Data are for 1988 and 1989**

Regression based on change in brood size at day 13 (D13) was as follows:

y = 22.238 - 0.48038x r^2 = 0.150; n=202, p<0.000

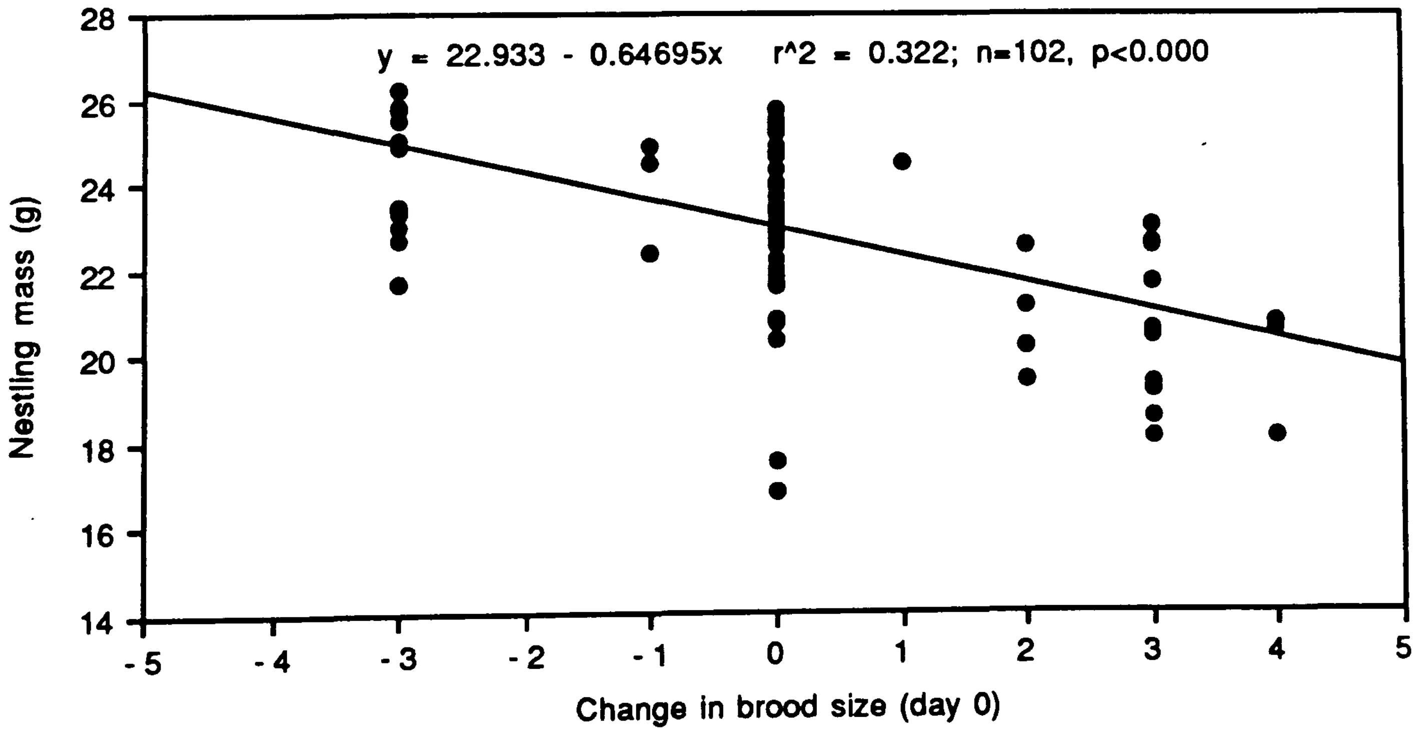


Fig 6.4 **Relationship between peak nestling mass and change in brood size (2nd) after manipulation at day 0 (SDBR). Data are for 1987 and 1988**

Regression based on change in brood size at day 13 (SD13) was as follows:

y = 22.723 - 0.60756x r^2 = 0.217; n=102, p<0.000

Table 6.8 **Stepwise[a] multiple regression analysis (MRA) of factors influencing peak nestling mass during first broods, year**

Year	Analysis[b]	Variables entered	r^2	B	Beta	T	Sig T
1988	A	$B13^2$	24.9	-0.13	-1.26	-7.6	0.000
		NYF	42.1	0.85	0.86	5.2	0.000
		Constant		22.3		54.3	
1989	A	BAM	43.7	-2.41	-1.99	-5.1	0.000
		NYF	54.9	0.63	0.47	5.7	0.000
		BAM^2	58.6	0.14	0.05	3.0	0.003
		Constant		27.4		29.1	
Both years	A	BAM^2	28.0	-0.05	-0.42	-3.24	0.001
		NYF	38.4	0.67	0.60	6.55	0.000
		B13	41.4	-0.62	-0.53	-3.24	0.001
		Constant		23.6		62.7	
Both years	B	BAM^2	27.1	-0.05	-0.42	-3.3	0.001
		NYF	38.0	0.61	0.54	5.8	0.000
		B13	41.3	-0.58	-0.48	-3.0	0.003
		DOH	43.3	-0.05	-0.17	-2.8	0.005
		F9	44.4	0.06	0.12	2.1	0.040
		Constant		26.7		19.7	

a - criteria for inclusion are described in section 6.2. The full list of independent variables included in analyses (A and B) were as follows:

b - A = BAM, B13, NYF, DBRS, D13 and DNYF. Quadratic terms were also included.

B = as above except measures of food abundance, date of hatch and original brood size prior to manipulation (BRS) were also included

A third analysis which was identical to 'B' except that measures of food abundance were not included, yielded the same results as A

Table 6.9a Experimental (Exp) and "natural" (Nat) reductions in clutch size: number of eggs removed in relation to the original clutch size. Experimental data are for 1987 and 1988 only

Original clutch size	Category Exp/Nat	Number of eggs removed				
		4	3	2	1	All
3	Exp	0	0	1	2	3
	Nat	0	0	0	0	0
4	Exp	0	1	2	0	3
	Nat	0	0	1	1	2
5	Exp	0	4	0	2	6
	Nat	0	2	2	2	6
6	Exp	0	0	1	0	1
	Nat	1	1	0	0	2
Total	Exp	0	5	4	4	13
	Nat	1	3	3	3	10
Total	Both	1	8	7	7	23

a -'natural' reductions occurred when eggs disappeared from nests due to known (i.e broken) or unknown causes but were assumed to have been be removed by parents

Table 6.9b Desertion (%) relative to the number of eggs 'naturally' or experimentally removed (n)

Number of eggs removed	Percentage deserted		
	Experimental	Natural	Exp and Nat
4	0 (0)	100 (1)	100 (1)
3	100 (5)	100 (3)	100 (8)
2	25 (4)	67 (7)	43 (7)
1	0 (4)	0 (3)	0 (7)
Total	46 (13)	60 (10)	52 (23)

to depend on both the number of eggs removed and the number remaining (Table 6.9b). All nests deserted when three eggs were removed but only one female deserted after two eggs had been removed and no female deserted after removal of one egg. Both nests left with only a single egg, half of nests left with two eggs and none left with three eggs deserted.

6.3.8.2 "Natural" reductions

It was noted that cracked eggs within a clutch usually disappeared and it was assumed that these eggs were removed by the parents (probably the female). This "natural" reduction of clutch size was observed to occur at 14 different nests. Where removal of at least three eggs occurred the nests were deserted; two thirds deserted when two eggs were removed but no parents abandoned when only a single egg was removed (Table 6.9b). After experimental manipulation, all nests which had two eggs removed "naturally" were subsequently deserted (*cf.* 50% for experimental) (Table 6.9c). None of those with four eggs remaining, and only half those left with three eggs, deserted.

6.3.9 DESERTION IN RELATION TO EXPERIMENTAL REDUCTION OF BROOD SIZE

The probability of nest desertion following removal of young was lower and less consistent than that observed for egg removal. One fifth of broods which had two or three nestlings removed were subsequently deserted, whereas only 7% deserted when one chick was removed. Almost half (43%) the broods left with a single nestling deserted whereas only 14% of those left with two or three young in the nest deserted. Parents were slightly more likely to desert a first brood than a second brood (19% vs 14%) even after controlling for the number of young removed and remaining (Table 6.10b).

6.3.10 RECRUITMENT IN RELATION TO MANIPULATION OF BROOD SIZE

Nestlings were recruited from Control broods of 2, 3, 4, 5 & 6 (Chapter 5) and from manipulated broods of two (Reduced) and eight (Enlarged) (n=5). Broods of one and seven (n= 23, only 2 Control) failed to produce any recruits. The number of nestlings recruited increased with brood size (one to five) but decreased from six to eight. Control nestlings were significantly more likely to be recruited than nestlings from manipulated broods (p=0.015, Table 6.11). The probability of recruitment was the same for Reduced and Enlarged (p=0.600, Table 6.11).

6.3.11 FACTORS AFFECTING THE INTER-BROOD INTERVAL (IBI):

6.3.11.1 Year

The inter-brood interval (IBI) for Control broods was shorter in 1987 than in 1988 (p= 0.040) but not 1989 (p=0.434). There was no difference between 1988 and 1989.

Table 6.9c **Desertion (%) during incubation relative to the the number of eggs remaining in the nest following 'natural' or experimental removal of eggs**

Number of eggs remaining	Percentage deserted Experimental	 Natural	 Exp and Nat
4	0 (3)	0 (2)	0 (5)
3	0 (0)	33 (3)	33 (3)
2	50 (8)	100 (4)	67 (12)
1	100 (2)	100 (1)	100 (3)

Table 6.10a **Brood desertion (n & %) relative to the number of nestlings experimentally removed**

Chicks removed or remaining	Number of young removed/remaining 4	 3	 2	 1
Removed	-	9/49 (19.6%)	7/34 20.6%)	1/14 (7.1%)
Remaining	0/4 (0)	3/22 (13.6%)	8/57 (14%)	6/14 (42.9%)

Table 6.10b **Brood desertion relative to the number of nestlings removed or remaining in the nest, following experimental reduction of brood size, by brood number**

Number of	chicks	Number deserted Brood number	
Removed	Remaining	First	Second
-4	2	1/6	0/2
-3	2	4/25	1/7
-3	1	2/4	1/5
-2	3 or 4	2/11	0/2
-2	2	2/12	1/5
-2	1	1/1	1/3
-1	all	1/10	0/4
Total		13/69 18.8%	4/28 14.0%

Table 6.11 Offspring recruited (n & (%)) from Reduced, Control and Enlarged broods, by year in which nestlings were reared

Year ringed	Brood number	Produced Recruits	Reduced	Control	Enlarged
1987-88	All broods	Yes	3 (6.3%)	41 (17.0%)	2 (4.0%)
		NO	45 (93.7%)	200 (83.0%)	48 (96.0%)
1988	First broods	Yes	2 (5.3%)	12 (10.3%)	3 (7.0%)
		NO	36 (94.7%)	105 (89.7%)	40 (93.0%)

a - summary of results from one-way Chi-Square analysis between treatments:

1987/88 : R vs C vs E : $X^2_2=8.39$; p=0.015; R vs E : $X^2_1 = 0.26$, ns
R vs C : $X^2_1 = 3.43$, p=0.064; C vs E : $X^2_1 = 5.57$, $p<0.05$

1988: R vs C vs E : $X^2_2 = 1.09$, p=0.579;
pair-wise comparisons were all non-significant

Table 6.12 Comparison[a] of inter-brood interval between treatments, using one-way ANOVA (mean,(se),(n))

	First brood treatments				one-way ANOVA		
Year	Reduced	Control	Enlarged	||	R v C	C v E	R v E
1988	29.7 (1.0) (23)	35.6 (.5) (57)	36.4 (1.0) (17)	||	***	ns	***
1989	30.9 (1.1) (28)	34.4 (1.0) (34)	34.5 (1.3) (16)	||	*	ns	*
1988/89	30.3 (.8) (51)	35.2 (.5) (91)	35.4 (.8) (33)	||	***	ns	***

a - comparison of IBI per manipulation categories between years were as follows:
1988 vs 1989 : all ns; Control: 1987 vs 1988 : $p<0.05$; 1987 vs 1989 : ns
Brood were not manipulated in 1987 (IBI : 33.3 (1.0) (n=61).

6.3.11.2 Manipulation of the first brood

Control broods had an IBI of about five weeks (34 (1), n=152; range=23-42) whereas the IBI of manipulated broods ranged from 17-48 days. On three occasions' the first egg of the second clutch was laid while nestlings of the first brood were still in the nest (just prior to fledging) after the pair had raised a Reduced first brood. Pairs which reared Reduced broods had a shorter IBI than those which reared Control broods (30 (1) (n=51) vs 35 (1) (n=91), $p<0.000$) or Enlarged broods (vs 35 (1) (n=33) , $p<0.000$, 1988 and 1989 pooled). There appeared to be an upper limit to the time taken to start a second clutch as the IBI was only 0.7 days longer for broods of eight than broods of seven whereas there was a difference of 5.7 days between broods of one and two.

6.3.11.3 Measures of first-brood reproductive performance:

a) Control broods only

IBI increased significantly with original clutch size in 1987 and 1989 but not in 1988 (Table 6.13). In each year IBI increased significantly with brood size (at Days 0, 13 & 18; for Day 13 see Figs 6.5a,b,c). IBI decreased with later first-brood date of hatch in 1989 ($p<0.05$; Table 6.13, Fig 6.6c) but there was no such trend in 1987 or 1988 (Fig 6.6a,b). Similarly, IBI only decreased with increasing first-brood peak nestling mass in 1989 ($r=-0.69$, $p<0.000$, Table 6.13, Fig 6.7c) with no discernible trend in the other two years (Fig 6.7a,b). IBI still increased with brood size after controlling for date of hatch but controlling for peak nestling mass removed the brood size effect (Table 6.13).

b) All brood sizes

Neither the size of first broods prior to manipulation (BRS) nor date of hatch (DOH) were significantly related to the IBI (Table 6.14). Brood size manipulation increased the range of inter-brood intervals (Control: 19 days; Experimental: 31 days). In both years, IBI increased with brood size (BAM, B13 & NYF) but was best predicted by B13 (Table 6.14; Fig 6.8). Change in brood size at Day 13 (D13) explained about a third of the variation in IBI in both 1988 and 1989 ($p<0.000$, Table 6.14, Fig 6,10). IBI decreased with increasing peak nestling mass (Fig 6.9). Partialling out date of hatch yielded a similar result (1988 and 1989 pooled: $r=-0.31$, $p<0.000$) but the relationship was not significant after partialling out B13 ($r_{B13\ (partial)}=0.02$, n=130, $p=0.02$).

6.3.11.4 Multiple regression of factors affecting the inter-brood interval

In 1989, almost half (46%) of the variation in IBI of Control broods was explained by peak nestling mass (Table 6.15). Including date of hatch (17%) and the number of young which fledged (8%) explained a total of 71% of the variation in IBI. Yet there were no factors entered significantly in 1987 or 1988. Peak nestling mass was measured in all 1989 nests but only in half of the nests in 1987 and 1988. A more accurate comparison of years is, therefore, to exclude peak nestling mass from the list of independent variables (Table 6.15). The number of first-brood fledged young explained a significant amount of variation in both 1987 and 1989 (Table 6.15) as did B13 and date of hatch in 1988, albeit

Table 6.13 Pearson correlation coefficientsof inter-brood interval of Control broods with first brood breeding performance, by year. Partial correlates (date,brood size and nestling mass) were included in analyses

Breeding parameters	1987	1988	1989*	1988/89	All years
Clutch size	0.37 (56) * *	0.11 (52) ns	0.44 (27) *	0.22 (79) 0.057	0.27 (135) * *
Date of hatch (DOH)	0.01 (56) ns	0.24 (54) ns	-0.44 (27) * *	-0.04 (81) ns	-0.11 (137) ns
Brood size at hatch (BRS)	0.40 (56) * *	0.31 (52) *	0.56 (27) * *	0.36 (79) * *	0.39 (135) * * *
Brood size at Day <u>13</u> (B13)	0.35 (54) * *	0.31 (52) *	0.57 (27) * *	0.37 (79) * * *	0.38 (133) * * *
Number fledged (NYF)	0.37 (55) * *	0.31 (54) *	0.64 (27) * * *	0.42 (81) * * *	0.41 (136) * * *
Peak mass (PNM)	0.00 (27) ns	0.09 (36) ns	-0.69 (26) * * *	-0.16 (62) ns	-0.12 (89) ns
$\mathrm{Brs}^{\mathrm{DOH}}$	0.40 (53) * *	0.33 (49) *	0.43 (24) * *	0.30 (73) * *	0.34 (126) * * *
$\mathrm{BRS}^{\mathrm{PNM}}$	0.21 (26) ns	0.25 (33) ns	0.12 (23) ns	0.23 (56) 0.076	0.21 (82) *
$\mathrm{Peak}^{\mathrm{BRS}}$ mass	0.04 (26) ns	0.09 (33) ns	-0.60 (23) * *	-0.07 (56) ns	-0.07 (82) ns
$\mathrm{Peak}^{\mathrm{DOH}}$ mass	-0.05 (26) ns	0.10 (33) ns	-0.77 (23) * * *	-0.17 (56) ns	-0.16 (82) ns

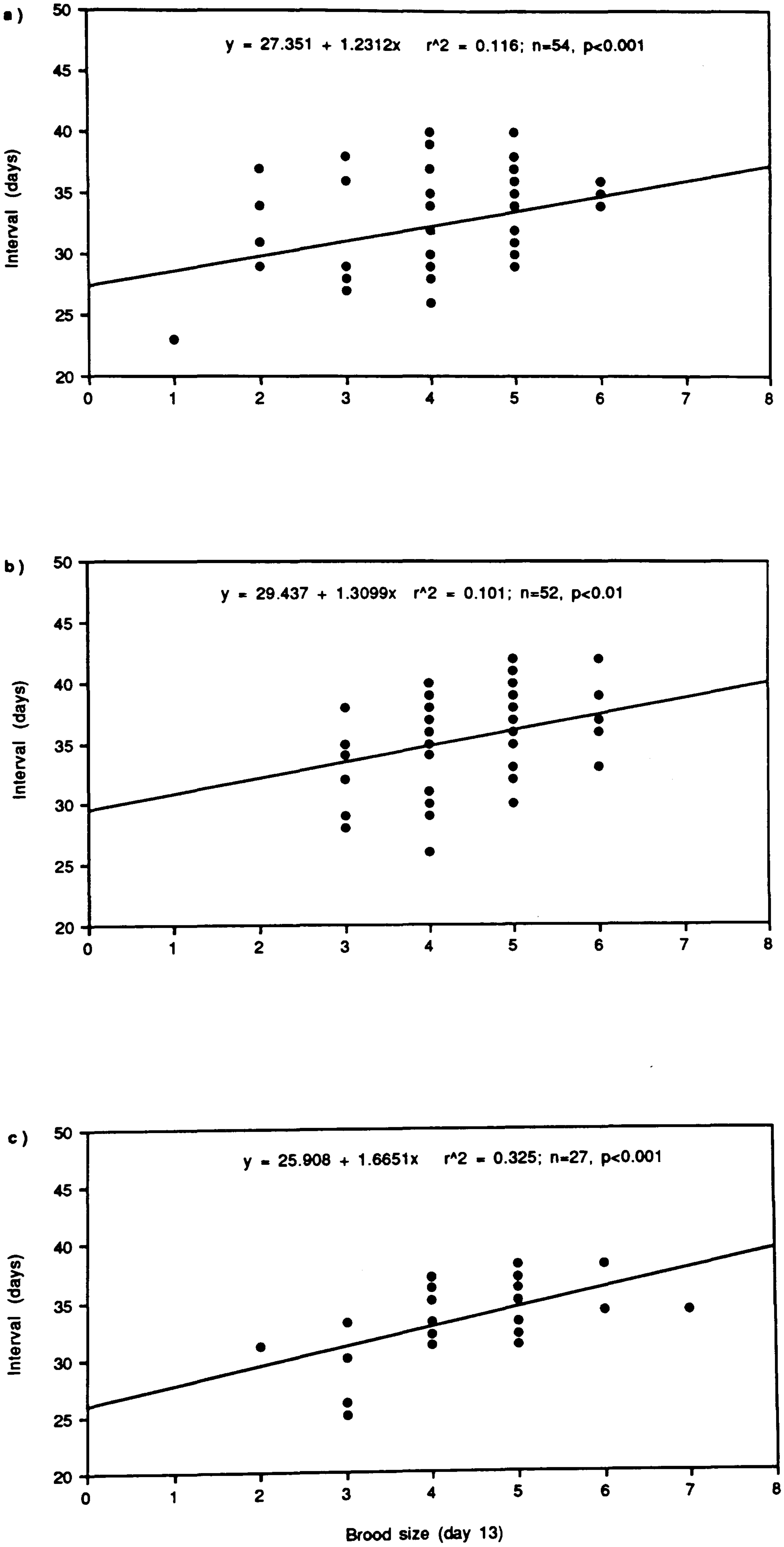


Fig 6.5 Relationship between inter-brood interval and brood size on day 13 (un-manipulated): a) 1987, b) 1988 and c) 1989

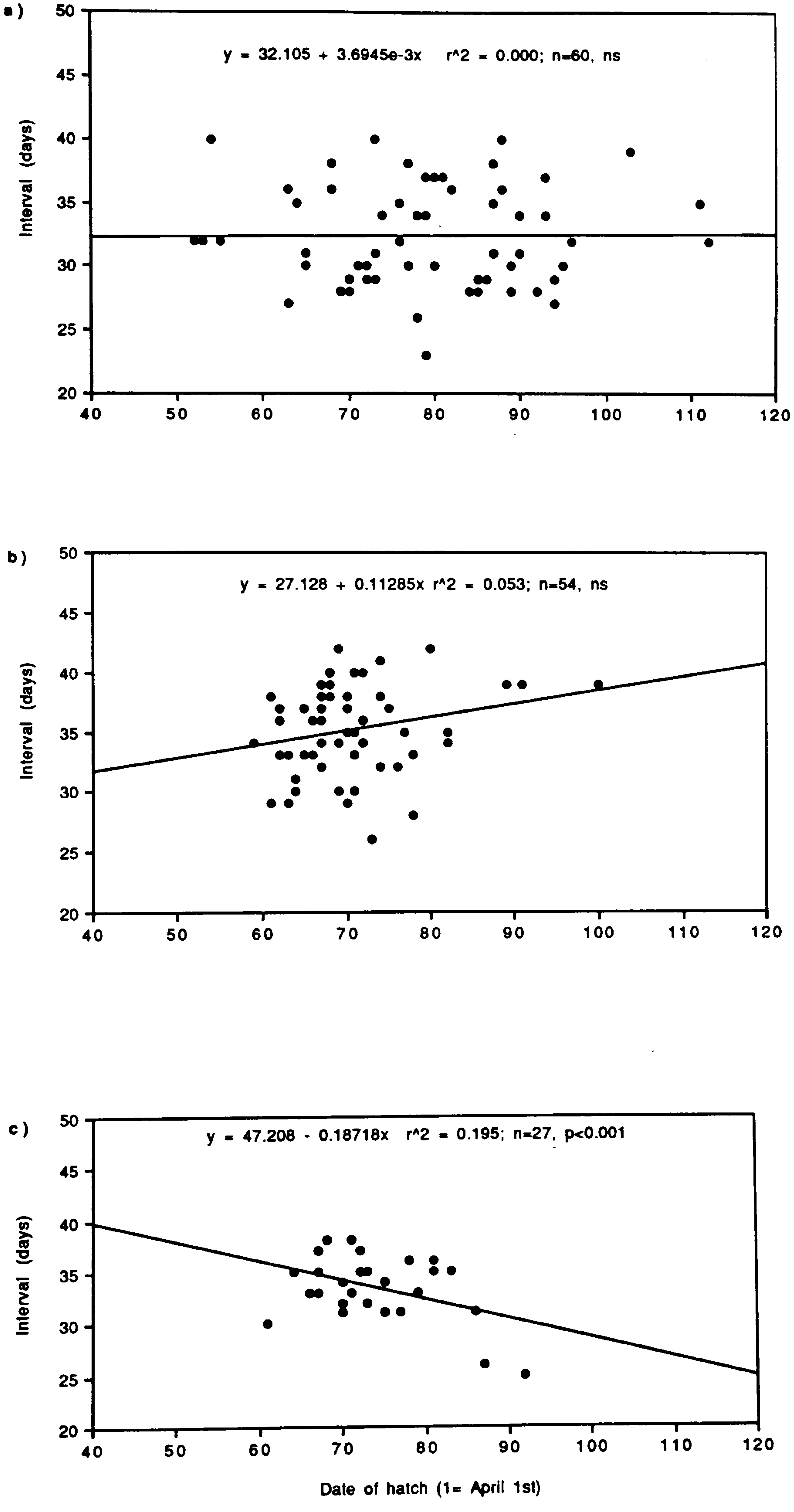


Fig 6.6 Relationship between inter-brood interval and date of hatch (un-manipulated first broods only): a) 1987, b) 1988 and c) 1989.

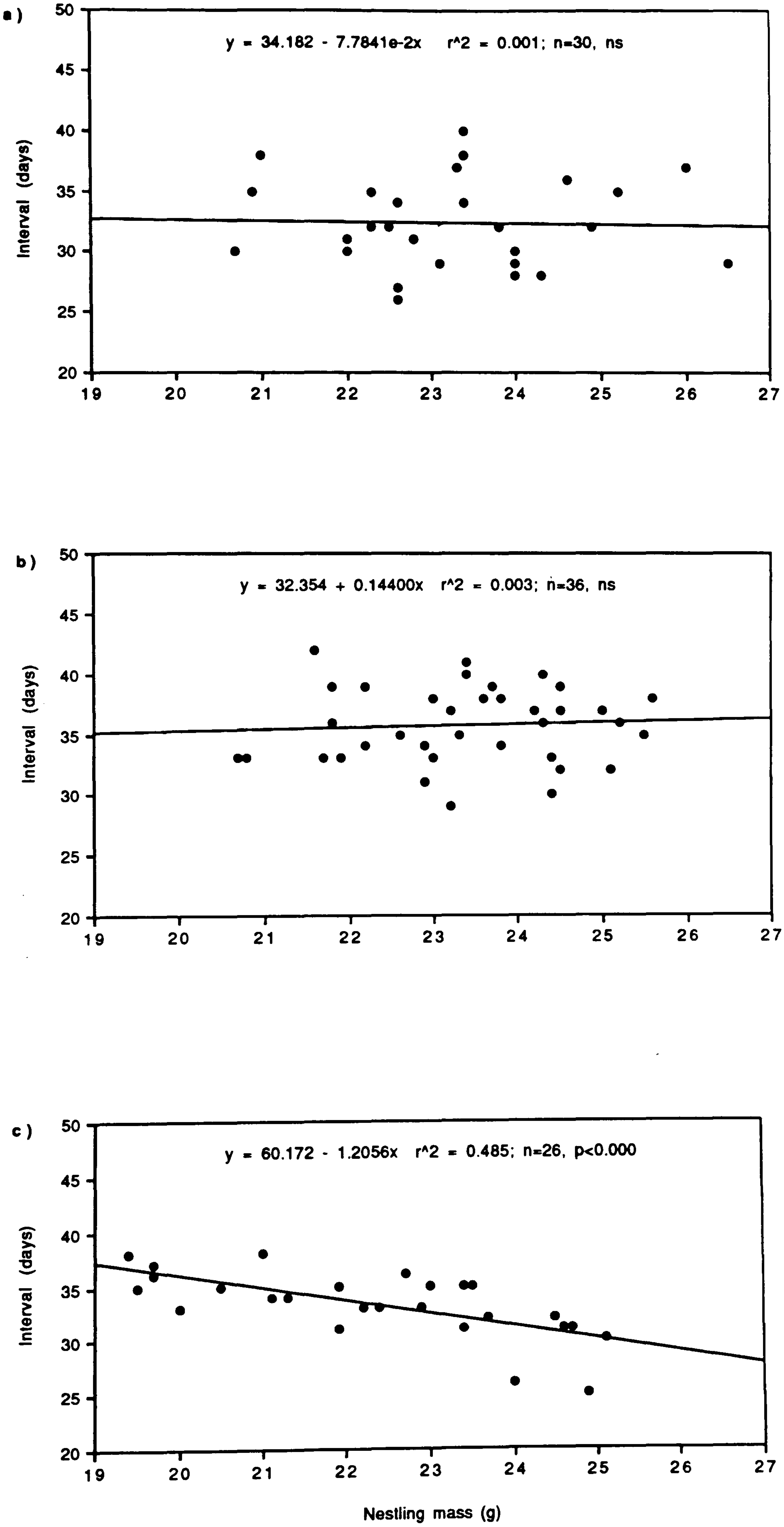


Fig 6.7 Relationship between inter-brood interval and peak nestling mass (un-manipulated first broods only): a) 1987, b) 1988 and c) 1989

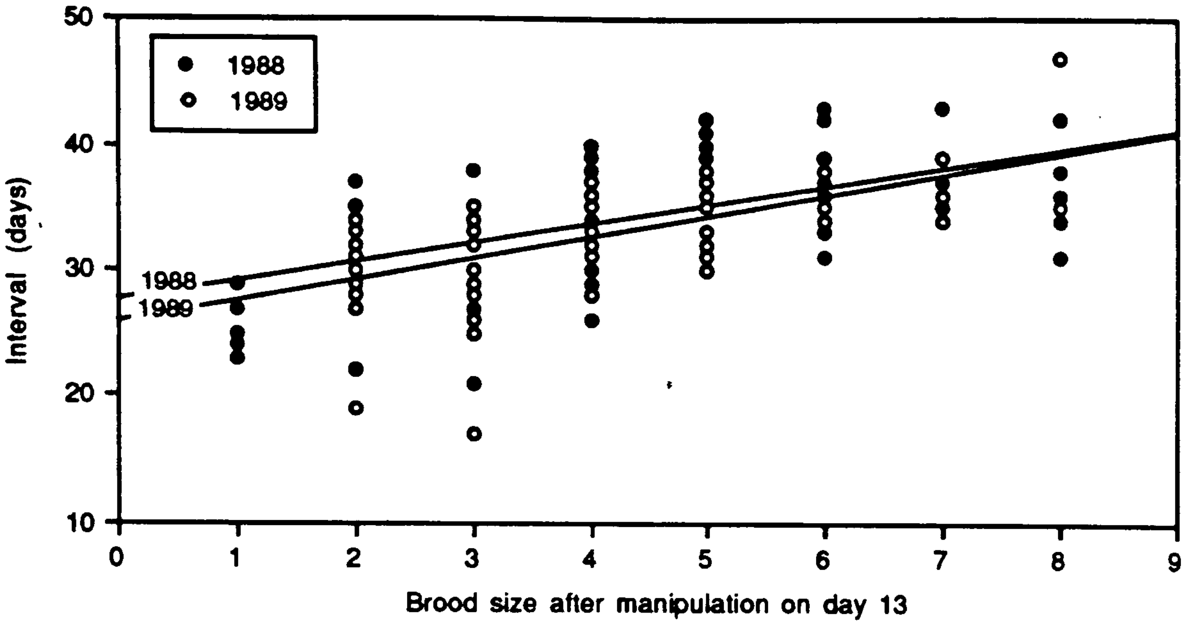


Fig 6.8 Relationship between inter-brood interval and brood size (1st) after manipulation at day 13. Data are for 1988 and 1989

1988: y = 27.683 + 1.4862x r^2 = 0.310; n=89, p<0.000
1989: y = 25.839 + 1.6665x r^2 = 0.377; n=64, p<0.000
Both: y = 26.859 + 1.5718x r^2 = 0.336; n=153, p<0.000

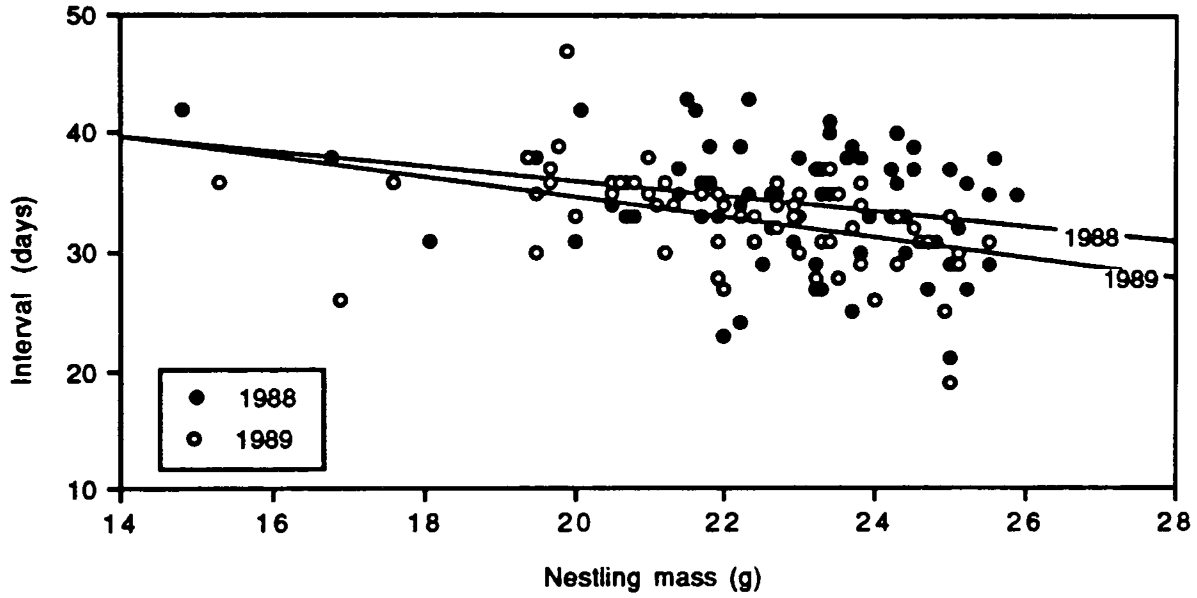


Fig 6.9 Relationship between inter-brood interval and peak nestling mass (1st). Data are for 1988 and 1989

1988: y = 48.516 - 0.62516x r^2 = 0.069; n=71, p<0.01
1989: y = 51.559 - 0.84572x r^2 = 0.189; n=64, p<0.000
Both: y = 48.329 - 0.65515x r^2 = 0.090; n=135, p<0.000

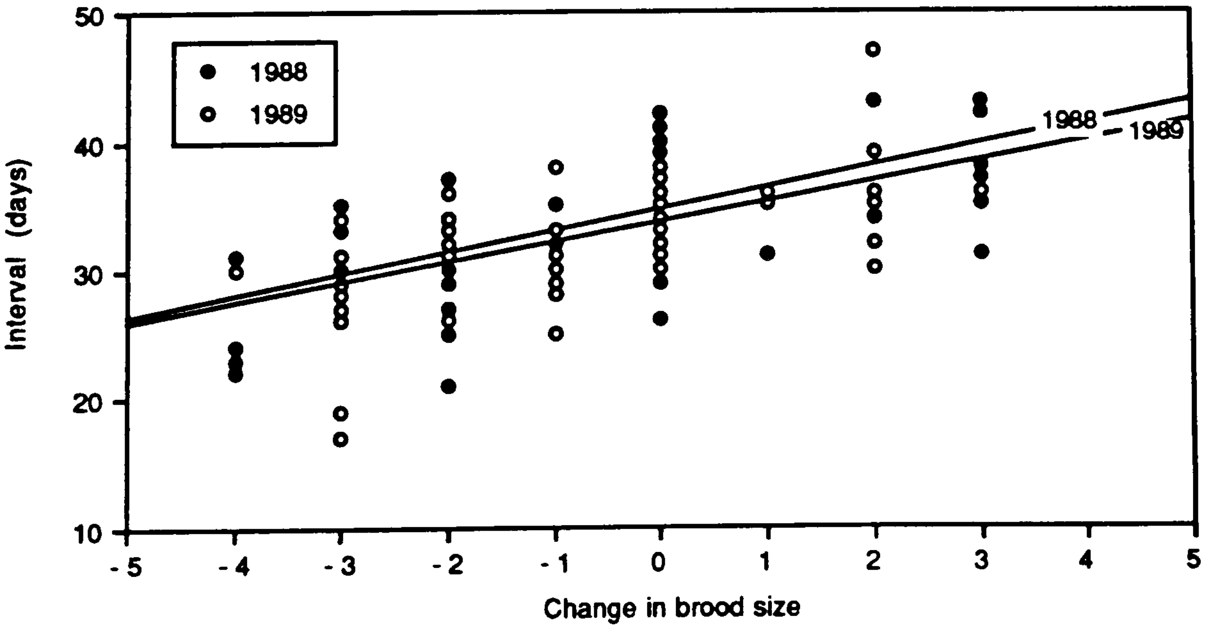


Fig 6.10 Relationship between inter-brood interval and change in brood size (1st) after manipulation at day 13 Data are for 1988 and 1989

1988: y = 34.622 + 1.6575x r^2 = 0.324; n=89, p<0.000
1989: y = 33.563 + 1.5657x r^2 = 0.347; n=64, p<0.000
Both: y = 34.195 + 1.6416x r^2 = 0.336; n=153, p<0.000

Table 6.14 Pearson correlation coefficients of inter-brood interval with first brood breeding performance: date of hatch (DOH), brood size[a] and change in brood size[b] after manipulation (Days 0, 13 and 18) and peak nestling mass for all broods (Reduced, Control and Enlarged), by year[c]

		Measures of breeding performance (First brood)									
Year		CLS	DOH	BRS	BAM	B13	NYF	DBR	D13	D18	PNM
1988	r	-0.10	0.15	0.08	0.55	0.56	0.52	0.55	0.57	0.50	-0.26
	sig	ns	ns	ns	***	***	***	***	***	***	*
1989	r	0.03	-0.18	0.05	0.53	0.61	0.54	0.50	0.56	0.046	-0.44
	sig	ns	ns	ns	***	***	***	***	***	***	***
1988/89	r	-0.05	-0.03	0.06	0.54	0.58	0.53	0.53	0.57	0.50	-0.30
	sig	ns	ns	ns	***	***	***	***	***	***	***

a - brood size after manipulation on Days: 0, 13 and 18 = BAM, B13 and NYF respectively

b - change in brood size after manipulation: 0, 13 and 18 = DBR, D13 and DNYF respectively

c- sample sizes: 1988 - n=89, except PNM=71; 1989 n=64 including only successful first broods

Table 6.15 Stepwise multiple regression of factors influencing the inter-brood interval in Control broods, by year

Year	Analyses[a]	Variables entered	r^2	B	Beta	T	Sig T
1987	A	None					
1988	A	None					
1989	A	Peak nestling mass	46.3	-0.94	-0.54	-4.47	0.000
		Date of hatch	63.1	-0.14	0.05	-0.33	0.002
		Number fledged	71.1	1.00	0.34	2.73	0.010
		Constant		60.1		8.35	
1987	B	Number fledged	13.3	1.45	0.39	3.04	0.004
		Constant		26.4		12.56	
1988	B	Brood size at Day 13	8.3	1.47	0.36	2.72	0.009
		Date of hatch	14.3	0.13	0.28	2.12	0.040
		Constant		19.31		5.35	
1989	B	Number fledged	39.2	1.93	0.64	4.22	0.000
		Constant		25.14		2.01	
1987	C	None					
1988	C	F11[b]	07.4	-0.26	-0.37	-2.88	0.006
		Date of hatch	15.4	0.15	0.32	2.43	0.000
		Constant		26.2		5.96	
1989	C	F11	30.1	0.66	0.58	3.10	0.006
		Constant		28.1		16.88	

---

a - full list of independent variables included in different analyses were as follows:
A - clutch size, date of hatch, brood size (day 0,13,18), peak nestling mass and measures of food abundance during nestling period. Full list given in Table 5.8
B - as above except peak nestling mass not included
C - only date of hatch and measures of food abundance included.
b - F11 is the food abundance on Day 11 of the nestling period

Table 6.16 Stepwise multiple regression of factors affecting the inter-brood interval in manipulated broods, by year

Year	Analysis[a]	Variables entered	r^2	B	Beta	T	Sig T
1988	A	Change in brood size (D13)	33.7	1.56	0.59	6.05	0.000
		Constant		34.7		73.5	0.000
1989	A	Brood size at Day 13 (B13)	41.5	1.57	0.65	6.57	0.000
		Constant		26.3		25.3	
Both years	A	B13	35.5	0.89	0.37	2.84	0.005
		D13	37.2	0.71	0.28	2.14	0.033
		Constant		30.1		20.3	
1988	B	D13	31.6	1.66	0.57	6.45	0.000
		Constant		34.6		79.0	
1989	B	B13	36.6	1.62	0.60	6.56	0.000
		Date of hatch	42.1	-0.22	-0.39	-4.21	0.000
		FT2[b]	52.5	-0.67	-0.33	-3.70	0.000
		BRS	55.7	-0.77	-0.21	-2.30	0.025
		Constant		51.1		10.17	
Both years	B	D13	33.2	0.89	0.32	2.65	0.009
		B13	35.7	0.85	0.31	2.64	0.009
		Constant		30.3		20.0	

a - full list of independent variables included in each of the analyses were:

A - clutch size, date of hatch, brood size (day 0,13,18), change in brood size (DBR, D13), peak nestling mass and measures of food abundance during nestling period

B - as above except peak nestling mass not included

b - FT2 is total volume on days 10 to 12 of the nestling period (see section 5.2.3)

Table 6.17 Comparison[a] of Inter-brood intervals (days) between male and female age classes, by treatment, using the Students t-test (mean, (se), (n))

		Age classes		t-test		
Treatment	Sex	1 * *	≥ 2	t	p	sig
Reduced	Male	30.0 (1.5) (11)	30.2 (1.4) (16)	0.22	0.827	ns
	Female	32.5 (.9) (12)	28.9 (1.2) (20)	2.14	0.041	*
Control	Male	34.5 (.8) (19)	34.1 (.7 (30)	-0.98	0.338	ns
	Female	34.3 (.8) (26)	34.4 (.9 (29)	-0.11	0.916	ns
Enlarged	Male	35.4 (1.9) (8)	37.3 (1.0) (16)	-0.98	0.338	ns
	Female	36.0 (1.0) (15)	37.1 (1.6) (11)	-0.61	0.549	ns

a - 1988 and 1989 combined, there was no significant difference between the two.

only 14% of the total variation. For Experimental broods about one third of the variation in IBI was explained by the number of nestlings in the nest after manipulation on Day 13 (Table 6.16; Fig 6.10).

6.3.11.5 Male and female age

IBI (Control broods) did not differ between male or female age classes: 1 vs ≥ 2 respectively (Table 6.17). Data were reanalysed controlling for date of hatch (DOH) and brood size but there were still no significant differences. Both older males and females which reared Enlarged first broods had a slightly longer IBI than yearlings (males: 35.4 vs 37.3 and females: 36.0 vs 37.1) but these differences were not significant. Conversely, older birds which reared Reduced broods had a shorter IBI, significantly so for females (29 (1) vs 33 (1), t=2.14, p=0.041). Inclusion of covariates (DOH, BAM, DBR) did not alter any of the results. Moreover, older females had a significantly shorter IBI than yearlings which reared the same number of nestlings after manipulation. Older females took five or three less days to start their second broods after rearing two or three nestlings respectively. There was hardly any difference in IBI between yearling and older birds for other brood sizes. The trends were the same when analyses were made using only Control broods (data not presented).

6.3.12 EFFECTS OF MANIPULATION ON SECOND BROODS

Pairs which reared Enlarged first broods were less likely ($p<0.05$) to attempt a second brood compared to those which reared Control or Reduced first broods (66%, 85% and 80%, Reduced, Control and Enlarged respectively, 1988 & 1989 pooled). Moreover, double-brooded pairs which successfully reared Enlarged, Reduced or Control first broods differed in the number of second-brood fledglings produced ($p<0.018$) and also tended to differ in second brood size ($p<0.094$, Table 6.18). Reduced first broods produced more fledglings during their second broods than Enlarged (Z=2.70, p=0.007) or Control (Z=-2.10, p=0.038) broods (Table 6.18). Notably, these differences were not caused by larger second-brood clutch size or higher hatching success of Reduced broods but by reduced nestling mortality.

The number of young fledged from second broods by parents which reared Enlarged, Reduced or Control first broods was adjusted to the number expected for a given date of hatch, to see if they reared more or less than expected. This residual SNYF was calculated by subtracting the expected number fledged from the observed number fledged. The expected number fledged was calculated based on linear regressions for Control broods of the number of young fledged on second-brood date of hatch:

1988: $Y_{EXPECTED} = 5.889 - 0.015X$

1989: $Y_{EXPECTED} = 11.592 - 0.061X$, where X = Date of hatch (2nd broods)

Table 6.18 Effect of first brood manipulation on second brood parameters, by year, using the Kruskal-Wallis one-way ANOVA (mean, (se), (n))

2nd brood parameters	Year	First Brood Treatment Reduced	 Control	 Enlarged	K-W one-way ANOVA df	 H	 p
Clutch size	1988	4.4 (.2) (21)	4.4 (.1) (61)	4.5 (.1) (16)	2,98	0.13	ns
	1989	4.6 (.2) (28)	4.3 (.1) (36)	4.5 (.2) (16)	2,80	1.47	ns
	Both	4.5 (.1)	4.4 (.1)	4.5 (.1)	2,178	0.73	ns
ΔClutch size[a]	1988	-0.62 (.12) (21)	-0.44 (.13) (55)	-0.63 (.20) (16)	2,92	1.48	ns
	1989	-0.54 (.14) (28)	-0.60 (.12) (35)	-0.63 (.26) (16)	2,98	0.13	ns
	Both	-0.57 (.11)	-0.50 (.09)	-0.63 (.16)	2,171	0.60	ns
Brood size	1988	4.1 (.2) (20)	4.1 (.1) (59)	2.8 (.5) (16)	2,95	5.69	0.058
	1989	4.1 (.3) (28)	3.8 (.2) (33)	3.9 (.3) (16)	2,77	1.59	ns
	Both	4.1 (.2)	4.0 (.1)	3.31 (.3)	2,172	4.73	0.090
Number[b] fledged	1988	3.7 (.4) (13)	3.1 (.3) (36)	2.2 (.9) (5)	2,54	2.68	ns
	1989	4.0 (.3) (23)	3.6 (.2) (23)	2.9 (.4) (15)	2,61	5.81	*
	Both	3.9 (.2)	3.3 (.2)	2.8 (.4)	2,115	8.05	*
Residual[c]	Both	-0.09 (.22	-0.65 (.20	-1.06 (.37	2,115	6.00	*

a -ΔClutch size =Clutch size (2nd)-Clutch size (1st)

b - excludes all second broods which were manipulated (thus reduced sample size)

c - number fledged (observed)-number fledged (expected); see text

The number fledged from second broods differed between first-brood treatments even after controlling for seasonal decline (H=6.0, p=0.05, Table 6.18). Parents rearing Reduced first broods had a higher residual value than those which reared Enlarged (-0.09 (.22) vs -1.06 (.37), Z=-2.31, p=0.021) or Control (vs -0.65 (.20), Z=-1.68, p=0.093) first broods, which themselves did not differ significantly (Z=-1.09, p=0.274).

6.3.12.1 Success of second broods

Double-brooded pairs which reared experimentally Enlarged first broods and which attempted a second brood were more likely to be unsuccessful in their second brood than pairs which reared Control or experimentally Reduced first broods (26.1%, 17.9% and 5.0% for Enlarged, Control and Reduced broods respectively, p<0.018, Fig 6.11c). The result was more marked in 1988 when 43% of all parents which reared an Enlarged first brood failed to fledge any young during their second brood; twice as many as had failed in 1989 (19%) (Fig 6.11a,b). Pairs which had Enlarged first broods were less likely to attempt a second brood so the sample size in this category was unavoidably small.

6.3.13 PARENTAL SURVIVAL AND MANIPULATION OF BROOD SIZE

6.3.13.1 Manipulation of first broods only

First-brood manipulations did not significantly affect male survival (p=0.714, Table 6.19a,b) but there was a weak tendency for males which reared Reduced broods to survive better than those which reared Control or Enlarged broods (56% vs 45% and 44%).

Females rearing Control second broods after rearing experimentally Enlarged first broods tended to have lower survival than those which reared Control or Reduced first broods (21%, 39% and 44% respectively; Table 6.19a) though this trend was not significant (X^2=2.49, p<0.288, Table 6.19b, Fig 6.12a). Trends were similar when all second broods were pooled (Table 6.19a,b).

6.3.13.2 Manipulation of second broods only

Males which reared experimentally Enlarged second broods in 1988 survived half as well as those which reared Reduced broods (22.2% vs 44.4%) but statistical power was low (n=9, for both categories) and the difference was not significant (Table 6.19a). Females which reared Reduced second broods survived better than those which reared Control or Enlarged second broods in 1988 (90% vs 34% and 50%, X^2_2=9.46, p<0.001, Table 6.19b, Fig 6.12). Pair-wise comparisons showed a significant difference with females which reared Control (X^2_1=7.35, p<0.001) but not with females that reared Enlarged (p=0.09) second broods. There was no difference between Control and Enlarged treatments in female survival (X^2_1=0.167, p=0.683). Inclusion of 1987 data did not affect results.

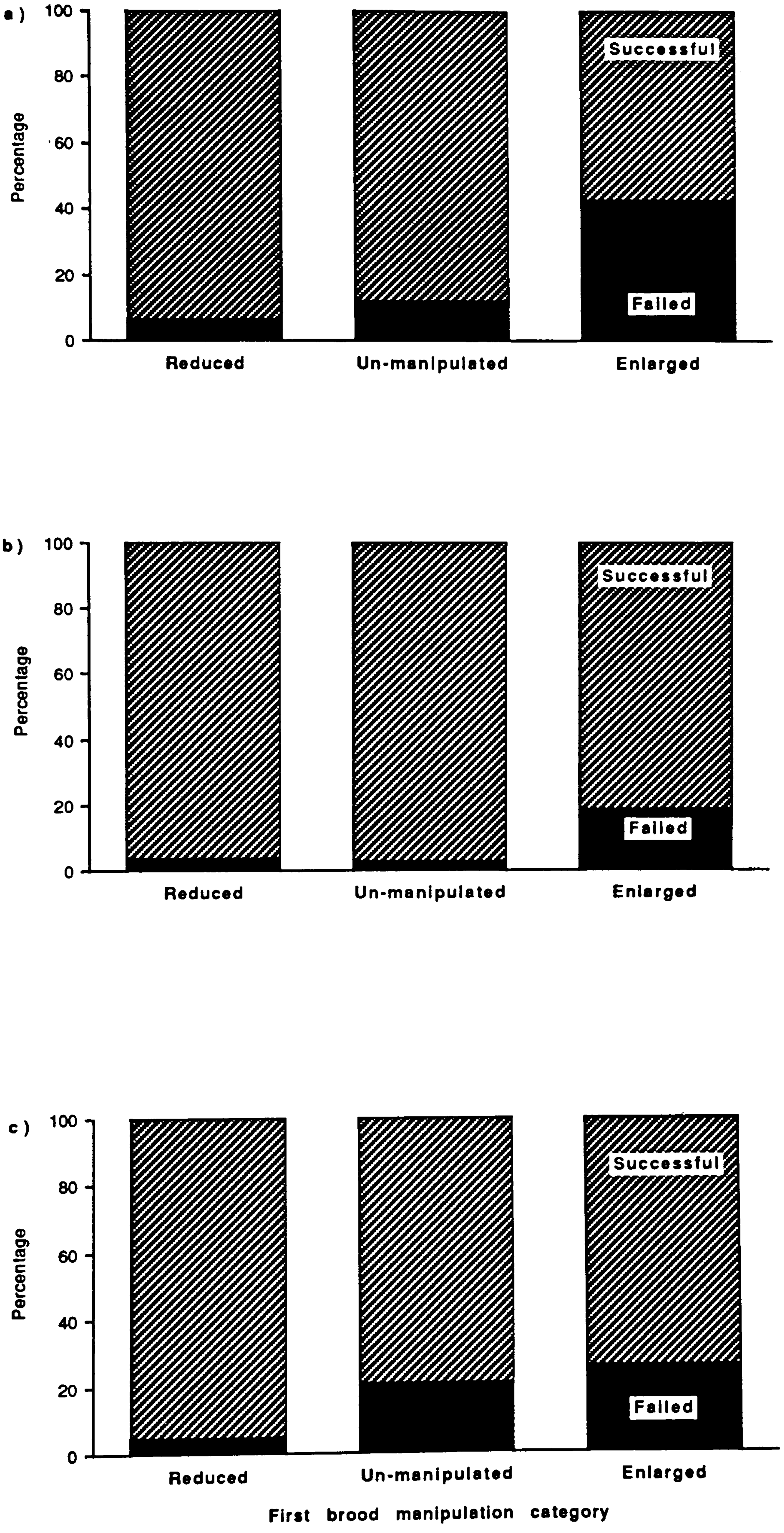


Fig 6.11 Effect of manipulation of first brood size on the successful completion of second broods: a) 1988, b) 1989 and c) 1988 and 1989

Table 6.19a Adult survival (%) in each treatment by brood number and sex

			Males			Females		
Year	Brood[a]	Surv	Reduced	Control	Enlarged	Reduced	Control	Enlarged
1988	1st	Yes	56.2	44.7	44.4	43.8	39.2	21.1
	(A)		(9)	(17)	(8)	(7)	(20)	(4)
		No	43.8	55.3	55.6	56.2	60.8	78.9
			(7)	(21)	(10)	(9)	(31)	(15)
1988	1st	Yes	52.6	43.4	40.9	50.0	55.9	75.0
	(B)		(10)	(23)	(9)	(11)	(30)	(6)
		No	47.4	56.6	59.1	50.0	44.1	25.0
			(9)	(30)	(13)	(11)	(38)	(18)
1988	2nd	Yes	44.4	57.1	22.2	90.0	34.4	50.0
	(A)		(4)	(12)	(2)	(9)	(11)	(4)
		No	55.6	42.9	77.8	10.0	65.6	50.0
			(5)	(9)	(7)	(1)	(21)	(4)
1988	2nd	Yes	44.4	50.0	28.6	78.6	39.1	40.0
	(B)		(4)	(16)	(4)	(11)	(18)	(6)
		No	55.6	50.0	71.4	21.4	60.9	6.0
			(5)	(16)	(10)	(3)	(28)	(9)
1987/88	2nd	Yes	44.4	57.1	22.2	86.7	49.2	52.9
	(A)		(4)	(12)	(2)	(13)	(31)	(9)
		No	55.6	42.9	77.8	13.3	50.8	47.1
			(5)	(9)	(7)	(2)	(32)	(8)
1987/88	2nd	Yes	41.7	54.5	37.5	83.3	48.7	43.5
	(B)		(5)	(24)	(6)	(15)	(38)	(10)
		No	58.3	45.5	62.5	16.7	51.3	56.5
			(7)	(20)	(10)	(3)	(40)	(13)

a - A - only Control second broods included

B - all second broods included regardless of whether manipulated or not

C - only Control first broods included

D - all first broods included regardless of whether manipulated or not

Table 6.19b Comparison of adult survival (%) between treatments, by sex using the Chi-Square test[a]

			Males[b]				Females[b]	
Year	Brood	X^2	p	Sig	‖	X^2	df	p
1988	1st A	0.67	0.714	ns	‖	2.49	0.288	ns
1988	1st B	0.65	0.723	ns	‖	3.54	0.170	ns
1988	2nd A	3.11	0.212	ns	‖	9.46	0.009	* *
1988	2nd B	1.82	0.440	ns	‖	7.04	0.030	*
1987/88	2nd A	3.11	0.212	ns	‖	6.96	0.031	*
1987/88	2nd B	1.64	0.440	ns	‖	8.06	0.178	ns

a - degrees of freedom are all =2

b - results from pair-wise comparisons between manipulation categories:

Males: all non-significant

Females:
a - R vs C: X = 7.34, df=1, p=0.007;
b - R vs C: X = 5.47, df=1, p= 0.019;
c - R vs E: X = 5.17, df=1, p=0.023

Including broods which had been manipulated did not alter the significance level of any of the above results nor did grouping all reduced broods with Control broods
Percentage survival and sample sizes for each treatment category are given in Table 6.19a

6.3.14 PARENTAL SURVIVAL AND BROOD SIZE

Adult survival was examined in relation to brood size after manipulation at Day 5 (BAM), on Day 13 (B13) and at fledging (NYF). Single- and double-brooded birds were analysed separately.

6.3.14.1 Single-brooded

Surviving single-brooded males had a smaller change in brood size (DBR) and reared significantly fewer young to fledging than those which died. The difference was almost significant when based on brood size at Day 13 when surviving males reared two fewer nestlings (5.4 vs 3.6, p=0.059). Surviving males had one less fledgling (4.1 vs 3.3, p=0.438, Table 6.20). Surviving females tended to have a smaller brood size after manipulation (5.3 vs 5.0), and a smaller change in brood size (DBR: 0.7 vs 0.3), than those which died, but these differences did not approach statistical significance (all p>0.100, Table 6.20).

6.3.14.2 Double-brooded

Brood size (first, second and both combined) did not differ between surviving and non-surviving double-brooded male Swallows (all p>0.05) and nor did brood manipulation affect male survival. By comparison brood reduction increased female survival (Table 6.21) as shown by the differences between survivors and non-survivors in second brood manipulation (SDBR: 0.7 vs -0.2, p=0.018), the total change in brood size (first and second broods combined) (TDBR: 0.5 vs -0.6 p<0.036) and the total number of young in the nest on Day 13 of second broods (SB13: 4.5 vs 3.8, p=0.035). During a season, surviving double-brooded females had one fewer nestling after manipulation (BAM: 9.3 vs 8.4), had 0.6 nestlings removed, raised one fewer nestling to Day 13 (8.8 vs 7.9) and fledged 0.6 fewer (8.3 vs 7.7, Table 6.21) than non-survivors. Inclusion of all second brood pairs, regardless of their success, increased the significance of the result. Comparison of the total change in brood size showed that female survivors raised 0.4 young fewer than normal whereas non-survivors raised 0.7 young more than normal (p<0.006 , Table 6.21). The number of first-brood fledglings was, however, almost identical.

6.3.14.3 Effect of first or second brood manipulation on survival

The results above show that double-brooded females which reared additional nestlings (at least until Day 13) during a season had lower survival. In an attempt to distinguish between the effects of first and second brood manipulations, data were reanalysed controlling for each. Regardless of the brood manipulated, surviving females tended to have lower BAM, B13 and NYF. Survivors also tended to have a reduced first DBR (0.3 vs -0.2) or second brood SDBR (0.5 vs -0.1) but in all cases these differences were not significant (data not presented).

Table 6.20 **Reproductive performance (Mean (se)) of non-surviving (died) and surviving[a] (Survived) single-brooded adult swallows, by sex, 1987/88 and 1988/89 combined. Both manipulated Control broods are included. One-way ANOVA was used for comparisons**

	Males[b]		One-way ANOVA		Females[b]		One-way ANOVA	
Breeding parameters of first broods	Died Mean (se)	Survived Mean (se	F	sig	Died Mean (se)	Survived Mean (se)	F	sig
Date of first egg[b] (DOE)	56.6 (2.6)	63.4 (5.1)	1.73	ns	58.0 (3.1)	61.8 (5.4)	0.42	ns
Clutch size (CLS)	5.0 (0)	4.9 (.1)	1.79	ns	4.9 (.1)	4.7 (.2)	2.55	ns
Brood size at hatch (BRS)	4.8 (.1)	4.7 (.2)	0.34	ns	4.6 (.2)	4.7 (.2)	0.05	ns
Brood size after manipulation (BAM)	5.6 (.5)	4.4 (1.2)	1.16	ns	5.3 (.5)	5.0 (.8)	0.07	ns
Change in brood size after manip (DBR)	0.8 (.5)	-0.3 (1.1)	0.90	ns	0.7 (.5)	0.3 (.8)	0.14	ns
Change in brood size at Day 13 ((1) (D13)	5.4 (.5)	3.57 (.9)	4.09	0.059	4.7 (.5)	4.5 (.6)	0.04	ns
Number fledged (NYF)	4.1 (.8)	3.3 (.7)	0.48	ns	3.80 (.6)	3.7 (.8)	0.02	ns
Peak nestling mass (PNM)	21.4 (.9)	22.6 (1.1)	0.64	ns	21.39 (.9)	22.2 (.5)	0.33	ns

a - known to survive from 1987 at least until 1988 and from 1988 until 1989

b - sample sizes were :

Males died = 7 ; survived =12; degrees of freedom = 1,17

Females: died =15 ; survived = 6; degrees of freedom = 1,19

c - April 1st = 1

Table 6.21 **Reproductive performance (Mean (se)) of non-surviving (died) and surviving (survived), double-brooded female Swallows, 1987/88 and 1988/89 combined[a]. Both manipulated and Control broods are included. One-way ANOVA was used for comparisons**

	Successful second broods only				All second broods			
Measures of brood size	Died Mean (se)	Survived Mean (se)	F	sig	Died Mean (se)	Survived Mean (se)	F	sig
First brood size after manipulation (BAM)	4.5 (.3)	4.3 (.2)	0.61	ns	4.9 (.2)	4.4 (.2)	2.19	ns
Second brood size after manipulation (SBAM)	4.8 (.3)	4.1 (.3)	3.47	0.065	2.9 (.3)	3.4 (.3)	1.21	ns
Total brood size after manipulation (TBAM)	9.3 (.4)	8.4 (.4)	3.13	0.080	7.8 (.3)	7.8 (.4)	0.00	ns
Change in first brood size after manipulation (DBR)	-0.11 (.24)	-0.36 (.17)	0.77	ns	0.32 (.19)	-0.14 (.17)	3.15	0.078
Change in second brood size after manipulation (SDBR)	0.65 (.22)	-0.19 (.27)	5.77	*	0.36 (.12)	-0.21 (.21	6.08	*
Change in total brood size after manipulation (TDBR)	0.49 (.35)	-0.55 (.34)	4.50	*	0.65 (.23)	-0.36 (.28	7.78	* *
First brood size at day 13 ((1) (B13)	4.2 (.2)	4.1 (.2)	0.19	ns	4.5 (.2)	4.2 (.2)	1.13	ns
Second brood size at day 13 ((1) (SB13)	4.5 (.2)	3.8 (.2)	4.58	*	2.6 (.3)	3.0 (.3)	1.09	ns

Table 6.21 **Contd.**

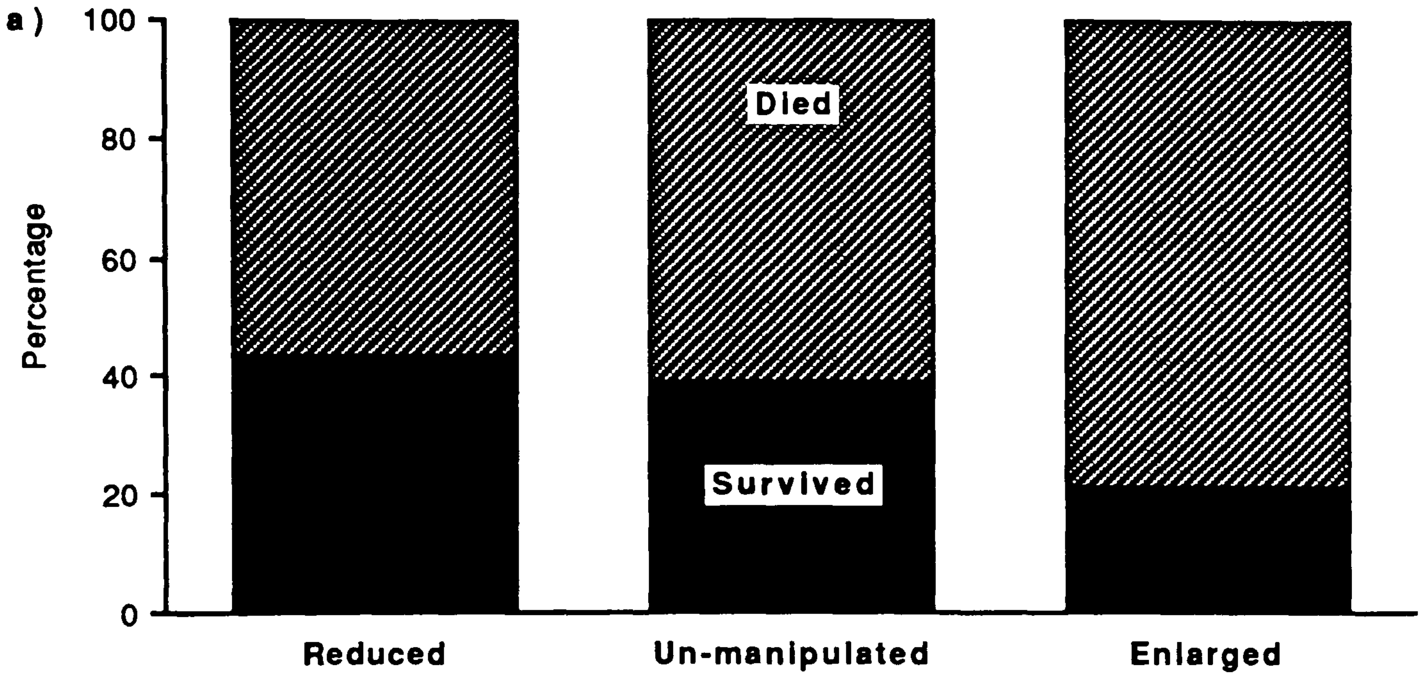
	Successful[b] second broods only				All[c] second broods			
Measures of brood size	Died Mean (se)	Survived Mean (se)	F	sig	Died Mean (se	Survived Mean (se	F	sig
Total brood size at day 13 ((1) (TB13)	8.7 (.3)	7.87 (.33	3.34	0.071	7.1 (.3)	7.2 (.3)	0.05	ns
Number fledged during first broods (NYF)	4.0 (.2)	3.9 (.2)	0.10	ns	4.1 (.2)	4.0 (.2)	0.28	ns
Number fledged during second broods (SNYF)	4.2 (.3)	3.7 (.2)	2.13	ns	2.4 (.3)	2.9 (.3)	1.66	ns
Total number fledged during first and second broods (NYF)	8.3 (.3)	7.7 (.3)	1.60	ns	6.5 (.3)	6.9 (.3)	0.56	ns

a - sample sizes were as follows: Died=48; Survived=53, df =1,99

b - All: Died = 86; Survived = 70, degrees of freedom = 1, 154

b - at least one young from both first- and second-brood

c - includes all bird, regardless of whether they reared young to independence, had re-lay attempts etc



note: only females which reared un-manipulated second broods are included in the analyses

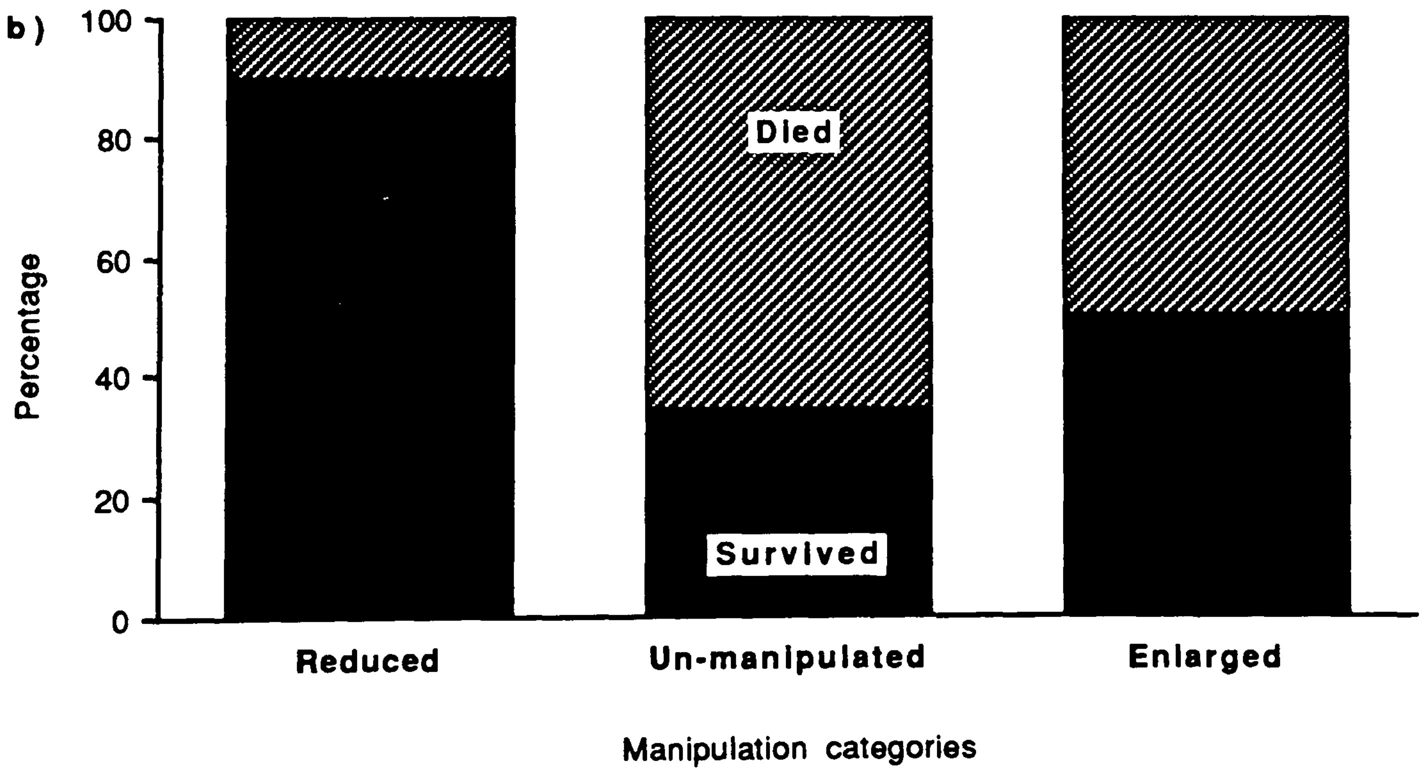


Fig 6.12 Female survival in relation to manipulation (Reduced, Un-manipulated and Enlarged) of brood size in 1988: a) First and b) Second

note: only females which reared Un-manipulated first broods are included in the analyses

6.4 DISCUSSION

Reproductive effort was manipulated by altering the brood size (first and second) of Swallows and the intra- and inter-seasonal (survival) effects on both nestlings and parents were investigated. In order to provide an accurate interpretation of these results two important assumptions are necessary. First, parents which rear manipulated brood sizes or those which were unsuccessful, defined here as a failure to rear any young to independence, are not any more likely to disperse than those with control broods. Second, juvenile dispersal is unrelated to brood size. These assumptions are necessary because if parents which reared additional nestlings were less likely to: a) be successful, b) attempt a second brood or, c) return the following year, and these results were related to dispersal then any conclusions linking brood manipulation with costs of reproduction might not be valid. It is also noted, however, that dispersal might have negative implications for reproductive success and survival. For instance in Collared Flycatchers it has been shown that low reproductive success among female and low survival among males has been associated with increased dispersal (Part 1990).

6.4.1 IMPLICATIONS OF DIFFERENTIAL DISPERSAL FOR ESTIMATING COSTS OF REPRODUCTION

A definitive demonstration of adult or juvenile survival requires analysing true instead of local survival estimates (Dijkstra *et al.* 1990), but for most studies made on wild population these data might be difficult, if not impossible to collect. Instead estimates have been based on the recapture or resighting of individuals which is widely recognised as being an imperfect measure of survival (but see Dobson 1990). If dispersers are found to be a non random sample of the population, biased with respect to aspects of breeding performance, such as brood size or breeding success (pairs which failed to rear any young to independence were more likely to disperse further between years (Harvey *et al.* 1979; Boer-Hazewinkel 1987; but see Shields 1984b) then examining the relationship of future fecundity or parental survival with brood size would cause results to be wrongly interpreted (Högstedt 1980). If assumptions one and two (above) can be fulfilled then recapture data should be a non-biased estimate of survival.

6.4.1.1 Adult dispersal

Intra- and inter-seasonal dispersal was rare in Swallows and of the few instances recorded it was unrelated to brood size or breeding success (Chapter 3). Disturbance at their former site, the loss of their partner or other chance factors largely explained the few instances noted. In any case only pairs which fledged at least one young were included in the analyses here. Data for other species further give some support to this conclusion. In studies of the Kestrel (Dijkstra *et al.* 1990), Blue Tit (Nur 1984a, 1988) and Great Tit (Slagsvold 1984) pairs which reared experimentally enlarged broods did not move further away from their nest site in successive years and in the case of Blue Tits and Kestrels there was a non significant tendency for pairs which reared smaller broods to move further away. Although dispersal had been incompletely analysed here it was concluded that recapture rate of adults should provide an unbiased estimate of overwinter survival. Any relationships between survival and brood size or breeding success identified here will not, therefore, be considered to be an artefact of dispersal.

6.4.1.2 Juvenile dispersal

Possible causes for natal dispersal include sex, population density, time of birth, dominance status and territory quality (Smith 1988; Part 1990 and references therein). The possible importance of brood size and nestling quality in influencing dispersal is less clear. Smith *et al.* (1988) found that brood size and size at fledgling (tarsus and wing length) were unrelated to dispersal in Great Tits while in a study of Collared Flycatchers brood size (natural) was found to be significantly related to local dispersal; females from small broods moved further away than large broods (Part 1990). The implication from Part's analyses, is that there could be a tendency to under estimate the probability of survival of nestlings reared in smaller broods. Data concerning overwinter survival of juveniles, therefore should be interpreted with more caution. More data are required to elucidate the factors governing juvenile dispersal.

6.4.2 EFFECT OF BROOD SIZE ON NESTLING MORTALITY AND "QUALITY"

Nestling mortality was highest for Swallows which reared experimentally Enlarged first or second broods; but they still produced as many and usually more fledglings than parents rearing Control or Reduced broods. House Martin nestling mortality is also affected by brood manipulation (Riley 1992). Swallow nestling mortality was much higher for Enlarged broods in 1989 (*cf.* 1988), probably because a prolonged spell of unseasonably cold and wet weather which caused a greater loss of complete broods during the latter half of the nestling period in this year. Other studies of passerines have also demonstrated that an increase in nestling mortality with manipulated brood size did not prevent parents from raising more young than their initial clutch size (Cronmiller & Thompson 1980; De Steven 1980; Nur 1984a; Finke *et al.* 1987; Hegner & Wingfield 1987; Tinbergen 1987; Lindén 1988; Smith *et al.* 1987, 1989b).

Why, therefore, do all pairs not attempt to raise additional nestlings ? One assumption of natural selection is that a trade-off exists between offspring number and offspring quality. A decrease in nestling "quality" associated with an increase in brood size has been demonstrated in a majority of published studies (Smith *et al.* 1988 and references therein) and was also observed here for Swallows. Peak nestling mass declined significantly with increasing manipulated brood size but the relationship differed slightly between years (also see Smith *et al.* 1988). A similar trend has been reported for the House Martin (Bryant & Westerterp 1983), House Wren (Cronmiller & Thompson 1980), Pied Flycatcher (Askenmo 1977), Collared Flycatcher (Gustafsson & Sutherland

1988), Great Tit (Slagsvold 1984, Tinbergen 1987, Lindén 1988), Blue Tit (Nur 1984b, Orell & Koivula 1988), House Sparrow (Schifferli 1978, Hegner & Wingfield 1987), Starling (Crossner 1977), Kestrel (Dijkstra *et al.* 1990) and Song Sparrow (Smith *et al.* 1989) but see (Ward 1965; Hussell 1972; Loman 1980; Hogstedt 1980; Finke *et al.* 1987, for review see Dijkstra *et al.* 1990).

Both BAM and DBR were important in predicting the peak nestling mass of Swallows, however, the effect was asymmetrical during first broods; nestlings from Enlarged were significantly lighter, while those from Reduced broods did not differ from Control broods. Differences between treatments were more marked during second broods. The absence of a significant difference between Reduced and Control first broods might be explained by one or more of the following : (i) treatment differences would be underestimated if nestlings in Reduced broods peaked in mass earlier, (ii) increased food intake per nestling in reduced broods might be off-set by increased thermoregulatory costs and, (iii) differences might only become evident during periods of food shortage since presumably there is an upper ceiling beyond which additional reserves are not beneficial or cannot be utilised by a nestling. There was no difference in fledging mass between first brood treatments. This could be because of compensatory growth in Enlarged broods. Other parameters or overall growth should, therefore, also be used for treatment comparisons (Smith *et al.* (1988).

6.4.2.1 Intra-brood variation

Intra-brood variation in nestling size also increased with brood size (Smith *et al.* 1988). The smallest nestlings were those which usually perished (Clark & Wilson 1981; Smith *et al.* 1988; Riley 1992; this study). In other studies this trend held true only during unfavourable conditions (Nur 1984a) or did not exist at all (De Steven 1980; Finke *et al.* 1987; Hegner & Wingfield 1987). Nestling mortality of Swallows was highest during the mid- nestling period (this study). Nestling size hierarchies were not induced by manipulation, however, since only nestlings of the same age were transplanted. Moreover, a spread in nestling size was apparent even within Control broods though less pronounced than that observed within artificially Enlarged broods (see Chapter 5). Increased mortality within broods might be due to: (i) unequal competitive ability of nestlings (Rydén & Bengtsson 1980) or, (ii) a selective tendency of the parents to to allocate less resources to the smallest nestlings (Wittenberger 1982).

These theories were not tested here but it is suggested that starvation could have both directly and indirectly increased nestling mortality. Indirectly, undernourishment could have caused over-begging so that nestlings fell, or were pushed out of the nest, by bigger siblings. There was some evidence for this possibility but chicks found on boards below the nests (Section 7.2) were not always the 'weakest'. It could be that there is just not enough room in the nest to raise additional nestlings with a higher probability of each nestling falling out of the nest. In preliminary trials, there were no casualties through falls when nestlings from Enlarged broods were placed in an artificial nest bigger than the normal nest. Thus, the validity of artificial nests in studies of reproductive costs is questioned (Chapter 8). A third possibility, that Enlarged broods might be more vulnerable to predation through being more conspicuous, was not supported here as predation of nests was negligible. Post-fledging mortality was not examined, however. For a discussion of brood reduction, intra-brood variation in nestling size and it's possible adaptiveness see O'Connor (1978c).

6.4.3 RECRUITMENT IN RELATION TO BROOD SIZE

If more nestlings were reared to fledging but were of poorer quality, post-fledgling mortality might be higher. The number of offspring recruited into the breeding population is, therefore, a more appropriate measure of reproductive success than the number of fledglings. Offspring were more likely to be recruited from Control broods than from manipulated broods; fewest from Enlarged broods. Moreover, the total number, mean and proportion recruited from broods of eight was lower than for any other brood size, indicating that there was higher overwinter mortality from larger broods. Despite the fact that nestlings reared in Reduced broods were significantly heavier than those from Control brood sizes, fewer were recruited than those reared in Control broods (see Part 1990 and above).

Brood size manipulation has been shown to affect recruitment in other species: the Kestrel (Dijkstra *et al.* 1990), Great Tit (Tinbergen 1987, *unpubl.* in Dijkstra *et al.* 1990; Pettifor *et al.* 1988; Smith *et al.* 1989b), Collared Flycatcher (Gustafsson & Sutherland 1988) and Bullfinch (Newton in Lack 1966). Gustafsson & Sutherland (1988) and Pettifor *et al.* (1988) also showed that brood size manipulation, Enlarged or Reduced, lowered the number of offspring recruited and concluded that the most recruits were produced by pairs rearing their own clutch size. In other studies no effect of brood size on offspring survival was detected (Murton *et al.* 1974; De Steven 1980; Nur 1984b respectively).

6.4.4 DESERTION IN ASSOCIATION WITH CLUTCH AND BROOD SIZE

No pair ever abandoned their nest following the addition of eggs or nestlings, but desertion sometimes occurred following their removal and was related to both the severity of the reduction as well as the number of eggs or chicks remaining. Since there was no experiment specifically designed to look at this phenomenon here, it was not possible to test the outcome of, for instance, removing three eggs from a clutch of six or one egg from a clutch of two. In a well designed study of the Tree Swallow Winkler (1991), found that all pairs (n=19) which had their original clutch size reduced from five or six eggs to a single egg deserted, whereas only 21% of those faced with a 50% reduction abandoned their clutches. Similar results have been reported in several other species of passerines (Rothstein 1982). Two explanations have been proposed for these findings

(Winkler 1991 and references therein).

Firstly, parents might abandon their nests if they associate the disappearance of eggs with disturbance or a predator. Three observations suggested that this was unlikely to be the correct explanation: a) "natural" (i.e removal of contents by parents themselves) disappearance of eggs resulted in desertion; b) there was no desertion following short term enlargement of clutch size and, c) data collected via electronic nest balances demonstrated females returned to the nest several times after the eggs had been removed.

A second idea comes from the theory that reproductive decisions are influenced by expected benefits accruing to a behavioural option as opposed to past reproductive investments (*sensu* Dawkins & Carlisle 1976). This is the so-called "Concorde Fallacy" which asserts that in a system where there is seasonal decline in breeding performance or where time is otherwise a limiting resource, an individual can increase its' seasonal reproductive success by abandoning a depleted clutch or brood. A decision to desert could, therefore, be influenced by several factors: (i) stage in the nesting cycle; (ii) stage in the season, (iii) contents "lost" or "missing" (i.e by parents or through disturbance) and, (iv) contents remaining. Several testable predictions can be made. Firstly, the more eggs removed the higher the probability of abandonment. Secondly, desertion is likely to be negatively correlated with the days after laying so that the later on in incubation that eggs are removed the less likely desertion. Thirdly, it follows that desertion should be less frequent when young are removed rather than eggs. Fourthly, desertion should be higher during first broods than during second broods. Finally, after the removal of eggs (or chicks) a replacement clutch should be laid as soon as possible. To this end , other factors being equal, re-using an old nest would save more time.

Most pairs of Swallows abandoned their nest almost immediately and the propensity to abandon increased with the degree of reduction. Desertion was more frequent when eggs as opposed to nestlings were removed and there was indeed a higher probability of desertion for first than second broods. A fresh clutch was always re-laid within ten days at deserted nests. Similarly, Tree Swallows re-nested almost immediately. Thus both Winkler's' experiment on Tree Swallows and the data collected here support the suggestion that the number of eggs in the nest is used as a cue to assess seasonal offspring production when deciding to desert a depleted clutch or brood. A notable difference between the species, however, was that Swallows nearly always occupied a new nest for their replacement clutch whereas Tree Swallows usually laid in the same nest-box. Although this could have been due to a lack of alternative nests sites for Tree Swallows this this did not appear to be the case (Winkler 1991). Other possible mechanisms relate to the differential costs associated with nest re-use but the available data do not allow accurate assessment of these possibilities (also see Chapter 8). Moreover, since Tree Swallows occupied nest boxes whereas Swallows used natural nests, the consequences of nest re-use are likely to differ between species so results are not strictly comparable.

6.4.5 FACTORS AFFECTING THE TIMING OF SECOND BROODS

The duration of the inter-brood interval for parents rearing Control broods differed significantly between years. During 1987, when the IBI was short, there were more double-brooded pairs, the breeding season was longer and the date of hatch was significantly later than in both 1988 and 1989. It appears that in seasons where breeding started earlier, the IBI was longer. This could be because earlier breeding allowed more time in which to attempt a second brood which by implication, suggests that a longer IBI is preferred. Other studies have reported that the IBI was shorter in optimal habitats (Kluyver *et al.* 1977) or when birds which were given extra food during the nestling period (Kluyver *et al.* 1977; Eden *et al.* 1989). Both suggest that the onset and/or the finish of breeding is, at least in part, shaped by environmental conditions. Although annual differences in the IBI were closely related to the timing of breeding a similar trend was not consistently present for individuals within a season. Only in 1989 was there a negative correlation between date of hatch and IBI. Smith *et al.* (1987) also reported that the IBI of Great Tits decreased with later date of hatch.

A consistent finding across years was that both natural and manipulated brood size had a significant effect on the timing of second broods; brood size was negatively and significantly correlated with the inter brood interval. These results were consistent with findings reported in other studies of both natural (Kluyver 1963; Kluyver *et al.* 1977; Pinowski 1977; Smith & Roff 1980; McGillivray 1983; Stamps *et al.* 1985; Riley 1992) and experimental (Kluyver *et al.* 1977; Slagsvold 1984; Tinbergen 1987; Smith *et al.* 1987; Finke *et al.* 1987; Hegner & Wingfield 1987; Lindén 1988; Riley 1992) variation in brood size (reviewed by Lindén & Møller 1988). Swallows which reared Reduced broods started their second brood five days earlier than those which reared Control broods; parents which reared an Enlarged first broods did not take significantly longer than Control broods to start their second brood. This contrasts with the House Martin (Riley 1992) and the Great Tit (Tinbergen 1987; Smith *et al.* 1988) where rearing additional young had the effect of delaying a second brood.

Why then does the IBI increase with brood size? If larger broods are in poorer condition (see above) then parents could compensate for this by extending the period that nestlings remain within the nest or by providing additional care during the post-fledging period, both of which could delay the onset of laying of a second brood (Tinbergen 1987; Lindén 1988). In the present study, however, parents which reared additional nestlings did not have a longer interval between broods even though there were marked differences in peak nestling mass between Enlarged and Control broods (*cf.* Reduced vs Control). There are several explanations for these findings.

Firstly, if an an upper limit to the IBI existed, such that any delay (above a certain threshold) resulted in a second brood not being attempted would explain the lack of an ever increasing IBI. The mean difference in the IBI of parents which reared enlarged brood sizes of seven and eight was only 0.7 days compared to about six days for broods of one and two. The idea could not be tested since brood size could not be increased beyond eight.

Secondly, experimental studies on Great Tits suggest that the number of young in the nest around the time of fledging (i.e not immediately after manipulation) was crucial in determining the delay before a second brood was started (Slagsvold 1982; Tinbergen 1987; Lindén 1988). Slagsvold manipulated the brood size of Great Tits shortly after hatch and on Day 15 removed all the nestlings from each nest. There was only a small resultant difference in the IBI 1 (< 1 day) between Enlarged and Reduced broods. Tinbergen (1987) and Lindén (1988) also reported that the development of young at fledging, mass and tarsus-length, was strongly correlated with brood size. Tinbergen (1987) argued that parents compensated for poorer development by attending larger broods for a prolonged period after fledging. This idea was supported by Lindén's study which reported that " 8 clearly underdeveloped fledglings (weight ≤ 15g and/or tarsus <21mm) recruited to breed" and also suggested that "underdeveloped young probably enjoyed an extended period of parental care to to catch up in developmental status" (Lindén 1988, p289). Brood size at Day 18 and Day 13 were the single best predictors of the IBI in Swallows, for parents of Control and manipulated brood size respectively. The difference was attributed to the higher nestling mortality in Enlarged broods as confirmed by the absence of a significant difference in brood size at fledging between Control and Enlarged treatments. Lindén (1988) pointed out that where rearing an enlarged first brood decreased the number of second broods (see below) it may only be possible to detect differences in IBI with brood size between control and reduced broods. The results from this study support this view (see 6.4.6).

6.4.6 EFFECTS OF MANIPULATED BROOD SIZES ON FUTURE FECUNDITY

An increase in the IBI associated with rearing additional first brood young cannot itself substantiate the existence of intra-seasonal costs. In species with a seasonal decline in productivity, or which have a cut-off date beyond which second broods are not attempted, a delay in starting a second brood may well impose a cost. Experimentally altering the first brood size of Swallows affected the occurrence, size and success of second broods. Parents rearing additional young were less likely and those with Reduced broods slightly more likely to produce a second clutch. Similar trends have been found in the Great Tit (Tinbergen & Albers 1984; Smith *et al.* 1987; Tinbergen 1987; Linden 1988) and the House Martin (Riley 1992; but see Finke *et al.* 1987; Hegner & Wingfield 1987). Manipulation of brood size also affected the size and success of second broods in Swallows. Parents which reared Enlarged first broods and which attempted a second brood were less likely to fledge any second brood young (*cf.* Control or Reduced). This indicates that an increase in effort had a longer term effect than just the decision to start a second brood. Moreover, parents which reared experimentally Reduced first broods fledged more second-brood young (*cf.* Control or Enlarged first broods). These effects could be explained by: a) a delayed second brood, b) an inability of parents to invest in future broods or, c) an artefact of significant differences in breeding performance prior to manipulation.

Parents which reared Reduced first broods had a significantly shorter IBI so the greater number fledged during second broods could reflect earlier laying of their second brood. This seemed not to be the case, however, because the number fledged from second broods differed between first brood manipulation treatments even after controlling for seasonal decline. Moreover, rearing an Enlarged first brood affected second brood fecundity even though these birds did not commence their second clutch significantly later than Control broods. Poorer hatching and fledging success during second broods indicates that rearing additional young during the first brood affected parental investment in a second brood. While the absence of an effect on the number of eggs laid during the second brood might mean that clutch size is generally fixed (see Chapter 5). By comparison first-brood manipulation in House Sparrows (Hegner & Wingfield 1987) and Great Tits (Smith *et al.* 1989) only affected the size of the second clutch. In Great Tits, this was attributed to a delay in the onset of the second brood. The number of young reared during the first brood, however, had no effect on the proportion which fledged during the second brood (Hegner & Wingfield 1987; Smith *et al.* 1989). Other experimental studies have shown only a tendency for pairs which reared enlarged first broods to perform less well (Slagsvold 1984; Tinbergen 1987).

It was concluded that the number of young reared during the first brood by Swallows influenced parental ability to rear a second brood, perhaps through parental condition (Chapter 7), but that within limits, second clutch size appeared to be insensitive to these effects.

6.4.7 EFFECTS OF MANIPULATED BROOD SIZES ON PARENTAL SURVIVAL

Manipulation of brood size affected parental survival in this study. This effect differed between males and females, and between first and second brood manipulations. Double-brooded males which reared a reduced first brood had a higher probability of survival than those which reared Control or Enlarged first broods. The difference was more marked for females; those which reared Reduced first broods survived twice as well as those which reared enlarged broods. The non-significant result may just reflect a small sample size (see De Steven 1980). Moreover, females appeared to respond differently to second brood manipulation, most notably for those rearing enlarged second broods which had 30% higher survival relative than females rearing Enlarged first broods. The clearest and most significant result was that males or females which reared a Reduced first or second brood survived better than those which reared Control or Enlarged broods.

Other studies have also reported that parents which reared reduced broods tended to survive better and those with additional young fared worse, than those rearing control broods (for reviews see Partridge 1989; Dijkstra *et al.* 1990; Lessells 1991). For instance the survival of Kestrels which reared Reduced broods was 10%-15% higher than those with Control or Enlarged broods (Dijkstra *et al.* 1990). Pied Flycatchers (Askenmo 1979), Glaucous-winged Gulls (Reid 1987) and Rooks (Røskaft 1985b) rearing Enlarged broods, had lower survival than those rearing Control broods; fifty per cent lower in the case of the Pied Flycatcher. A notable exception was that male Tengmalms Owls which reared Reduced broods had poorer survival than those with Control or Enlarged broods (20% vs 28% vs 25% respectively, Korpimaki 1988a). During this experiment, however, survival was much lower than was observed for other species indicating that either: a) the experimental conditions may have been uncharacteristic or, b) local dispersal was higher than in other species.

Chapter seven

(pp 88-117)

Adult Body mass and Condition during the Breeding cycle and the Implications for Future Fecundity and Survival

7 ADULT BODY MASS AND CONDITION DURING THE BREEDING CYCLE AND THE IMPLICATIONS FOR FUTURE FECUNDITY AND SURVIVAL

7.1 INTRODUCTION

Although energy is typically stored as fat (King & Farner 1966; Blem 1976), the non-fat component (mainly protein) may also act as an a energy store (Jones & Ward 1976; Fogden & Fogden 1979; Houston *et al.* 1983; Jones 1987d; Jones 1990, M). Since both these reserves may vary independently any comprehensive assessment of body condition should, therefore, attempt to reflect the status of both lipid and protein.

7.1.1 MEASURING BODY CONDITION

7.1.1.1 Dead individuals

Traditionally, body reserves have been measured by analysis of carcass composition. Lipid reserves can be measured directly involving standard procedures for lipid extraction whereas the resulting lean dry material is taken to represent total protein reserves (Dunn 1975; Evans & Smith 1975; Jones & Ward 1976; Owen & Cook 1977; Bryant & Gardiner 1978; Pienkowski *et al.* 1979; Reinecke *et al.* 1982; Bryant & Westerterp 1983a; Jones 1985, 1987d; Hails & Turner 1985; Johnson *et al.* 1985; Davidson *et al.* 1986b; Mertens 1987; Newton, S.F 1989, 1993; Morton *et al.* 1990). Results are usually expressed as lipid (Hanson 1962; Evans & Smith 1975; Houston 1977; Owen & Cook 1977; Bryant & Westerterp 1983a; Morton *et al.* 1990) or protein indices (Houston 1977; Woodall 1978; Jones, M 1990).

More specifically, the lean dry mass of the flight muscles is usually assumed to be a measure of total body protein (Kendall 1973; Jones and Ward 1976; Ward 1979). If it can be shown that an individual's: a) total lean dry mass is a reliable estimate of total body protein and that, b) pectoralis lean dry mass is related to total lean dry mass, then this assumption should be valid. Associated data from a variety of studies are consistent with this view (Hanson 1962; Schifferli 1976; Jones & Ward 1976; Ward 1977; Marcström & Kenward 1981; Brittas & Marcström 1982; Jones,M 1990).

Firstly, the flight muscles represent 20%-30% of an individual's total lean dry muscle mass (Hanson 1962; Schifferli 1976). Secondly, a direct relationship of the lean dry mass of the flight muscles with total lean dry mass (Marcström and Kenward 1981; Jones 1985,1987d; Sears 1988; Newton, S.F 1989, 1993) as well as with total protein content (Brittas and Marcström 1982) has been demonstrated. Thirdly, a reduction in the lean dry mass of pectoralis muscles during periods of high protein requirements (Ward 1969; Baggot 1975; Schifferli 1976; Jones and Ward 1976; Fogden and Fogden 1979; Houston et al. 1983) provide further indirect evidence that the pectoralis muscles can be directly related to an individual's total body protein. Finally, and most importantly the recent use of more accurate biochemical techniques showed that a loss of lean dry mass of pectoralis muscle prior to and during laying was directly related to a loss of protein (Jones, M 1990). Moreover , the amount of protein lost compared well with the associated decreases of lean dry material of pectoralis muscles (Jones, M 1990). A reduction in the lean dry mass of flight muscles should, therefore, primarily reflect a loss of protein.

7.1.1.2 Live individuals

Carcass analysis is undoubtedly accurate but it is destructive and such methods are increasingly unacceptable. In recent years, more effort has been made to find non-destructive ways of measuring body condition of live birds. The total lipid content of birds has been reliably estimated by fat-scoring (Wolfson 1954; Fry et al. 1970; Owen 1981; Bryant & Westerterp 1983a; Nolan & Ketterson 1983; Jones 1987d; Sears 1988; Rodgers & Rodgers 1990; Piper & Wiley 1990). In this method, the visible, subcutaneous fat is quantified via a system of scoring. Such a method has been applied to hirundines and checked using carcass analysis (Bryant & Westerterp 1983a; Jones 1987d).

Protein reserves of live birds have only more recently been measured with any ease and precision (Sears 1988, Newton, S.F 1989, but see Davidson 1979; Sibly *et al.* 1987). In studies of Mute Swans (Sears 1988), Dippers and Canaries (Newton 1989, 1993), an ultra-sound device was used to measure the thickness of breast muscles of live birds. The technique is based on the assumption that muscle thickness accurately reflects protein reserves and that the protein content of the flight muscles is a good indicator of an individual's overall protein content (see 7.1.1.1 above).

7.1.2 RELATIONSHIP OF BODY MASS TO BODY "CONDITION"

Both body mass (Crick & Fry 1986; Meijer *et al.* 1988) and size-corrected body mass (Bailey 1979; Wishart 1979; Iverson & Vohs 1982; Davidson 1983; Piersma 1984) have also been used as indices of body condition. Although body mass may accurately reflect condition (Jones & Ward 1976; Fogden & Fogden 1979; Ankney & MacInnes 1978), it is potentially unreliable since it may vary both within and between individuals, independently of their body reserves. Such factors as diurnal (Clark 1979; Rodgers & Rodgers 1990), seasonal (Clark 1979) and latitudinal variation in body size, age, moulting and migratory activities (reviewed by Clark 1979), atrophy of reproductive structures (Petersen 1955; Ricklefs 1974) and optimisation of wing loading (Freed 1981; Norberg 1981) could all undermine measures of body condition which rely on body mass.

7.1.3 RELATIONSHIP OF BODY "CONDITION" TO REPRODUCTIVE PERFORMANCE AND COSTS OF REPRODUCTION

Theories of the life history strategies of birds commonly make two fundamental assumptions. Firstly, that the demands on parents' time and energy are highest during breeding (Drent & Daan 1980; Bryant & Westerterp 1983a; Bryant 1988a), in particular while feeding nestlings (Drent & Daan 1980; Walsberg 1983; Wijnandts 1984; Bryant & Tatner 1988) and secondly, that reproduction is costly. Both assumptions have been challenged (see Martin 1987), but current evidence supports the existence of short and long term reproductive costs (see Chapter 6). The exact route or currency (*viz* Reid 1987) by which costs are manifest has yet to be clearly established. Body condition has been directly related to components of fitness so a causal link between condition and reproductive costs has often been sought (Harris 1970; Hussell 1972; Askenmo 1977, 1979; DeSteven 1980; Nur 1984a, 1988a,b; Røskaft 1985a; Finke *et al.* 1987; Hegner & Wingfield 1987; Reid 1987; Smith *et al.* 1987; Tinbergen 1987; Korpimaki 1988a; Gustafsson & Sutherland 1988; Orell & Koivula 1988; Pettifor *et al.* 1988; DeLaet & Dhondt 1989; Dijkstra *et al.* 1990).

In multi-brooded species variation in parental "condition" during first broods could explain why some individuals are unable, or take longer, to start a second brood than others (Chapter 6). If it is assumed that parental mass (initial, final or change) influences future fecundity then several testable predictions can be made:

i) Parents rearing enlarged broods will lose more mass than those rearing fewer young.

ii) Lower mass or an increase in rate of mass loss while rearing a first brood will result in a: (a) longer inter-brood interval, or b) reduced probability of a second brood.

(iii) Lower mass or an increase in rate of mass loss during breeding will reduce an individual's probability of survival or fecundity in the following year.

7.1.4 AIMS

The aims of this section were firstly, to derive indices of lipid and protein in dead Swallows so that the body condition of live adult birds could be accurately described. Two males which apparently starved to death were also analysed to show what happens to body components under extreme nutrient shortage. Secondly, to describe changes in adult body mass during the nesting cycle and develop quantitative methods of assessing lipid and protein reserves of live individuals in the field. These methods were validated against the data from carcass analyses. Thirdly, the relationship of body mass and other condition indices to: a) brood size , b) future fecundity, and c) the probability of parental survival until the following season, was explored.

7.2 METHODS

7.2.1 CARCASS ANALYSIS

Adult Swallows from different stages of the breeding cycle were used for carcass analysis. Six of these were killed at night by chloroform inhalation under license from the Nature Conservancy Council. Of the remaining ten birds, three were found dead within the study area (fresh and un-injured), two were injured and subsequently killed, two died through heat stress caused by handling on an exceptionally hot day (the only handling casualties during the study) and one apparently starved to death at the nest whilst brood rearing. Two fledged young were also analysed. Data for a further six adults were made available from G. Jones's study of Swallows in 1985.

7.2.1.1 Laboratory procedure

Prior to killing (or immediately after collection of a dead bird), all birds were measured, fat scored and an ultra-sound measure of pectoral muscle thickness was made. Individuals were immediately sacrificed and frozen. Before dissection they were thawed overnight at room temperature. Carcass analysis was carried out by A. Gardiner of the University of Stirling. Methods followed Jones (1987d).

Carcasses were dissected into sixteen individual components: wing and tail feathers, skin and contour feathers, legs (cut at the hip),wings (cut at the shoulder), pectoralis major and minor muscles, head, neck, oesophagus and gizzard (hereafter referred to as oesophagus), lungs, heart, liver, gut, kidneys and where discernible the gonads. The final component was the body shell which was the remainder of the body after all of the above organs and tissues had been removed. All components were freeze dried for seven days and weighed to give a dry mass (DM). Lipids were extracted from components in a soxhlet apparatus for 40 h using a mixture of 5:1 diethyl ether and chloroform as a solvent. Components were then freeze dried for a further seven days before being reweighed (all masses were measured to the nearest 0.0001g on an Oertling balance) to determine Lean (Lipid free) dry masses (LDM). Lipid indices, component lipid indices and water indices were calculated (Table 7a).

7.2.2 ASSESSING BODY RESERVES IN LIVE BIRDS

Individually marked birds of known sex and stage in the breeding cycle were caught at their breeding sites from arrival until departure.

7.2.2.1 Lipid reserves

Avian body fat is deposited at many sites (King & Farner 1965). Subcutaneous fat, particularly in the abdomen (posterior edge of the sternum) and claviculo-coracoid (inter-clavicular pit), is visible, and can thus be scored. Adults were fat scored in 1988

Table 7a **Summary of terms, abbreviations, calculations and indices associated with carcass analyses**

Term	Abb	Definition/calculation
Live mass	WM	Mass prior to killing
Dry mass	DM	Mass of all dissected components after freeze-drying
Lean dry mass	LDM	Dry mass after removal of lipid (via soxhlet)
Pectoralis dry mass	PDM	Dry mass of pectoral muscles (major+minor)
Pectoralis lean dry mass	PLDM	Dry mass of pectoral muscles (major+minor) after removal of lipid (via soxhlet)
Lipid content	LC	Dry mass-Lean dry mass
Lipid index	LI	((DM-LDM)/LDM)*100
Component LI	LI_c	$((DM_c-LDM_c)/LDM_c)*100$, where c is a component
Water content	H_2O	Wet mass-Dry mass
Water index	H_2O I	$(H_2O\ /LDM)*100$
% Water content	$\%H_2O$	$(H_2O/WM)*100$
Expected mass	$Mass_{exp}$	Mass which would be predicted for a bird of a given body size as predicted from the regression for mass as a function of body size (carcasses: section 7.3.2, Fig 7.4a) and (live birds: section 7.3.5.2).
Residual mass	Residual	$Mass_{obs} - Mass_{exp}$
Expected pectoralis lean dry mass	$PLDM_{exp}$	PLDM for a bird of a given body size as predicted from the regression for PLDM as a function of keel-length (section 7.3.4, Fig 7.4c), as follows:
	$PLDM_{exp}$	= -2.9983 + (.1880 * keel length) (r^2*100 = 48%, n=15)
Residual pectoralis lean dry mass	$PLDM_{res}$	$PLDM_{obs} - PLDM_{exp}$

and 1989, but not during the first season (1987). After a bird was caught and processed (Chapter 4), the amount of fat present at the inter-clavicular pit and the posterior edge of the sternum was estimated. Ventral feathers were blown aside so that these areas were clearly visible. The amount of fat was estimated using a ten point scale (1 and 10 represent birds of low and high fat respectively).

7.2.2.2 Protein reserves

Flight muscle thickness was measured in live birds using a portable ultrasonic flaw detector, (Krautkramer, instrument model number USK7), powered by rechargeable batteries. The principles of this technique have been described by Baldassare *et al.* (1980). The ultra-sound device was available for use in the present study between 25/7/88 and 13/9/88. All data related to second brood birds. Methods, equipment and calibration used in this study follow Newton, S.F (1989, 1993). The transducer, comprises a small cylindrical probe (diameter 9mm, height 11mm) and readings are recorded from the grid as an interval on the x-axis to the first reflection. Individual ultra-sound readings (R1 to R3 and L1 to L3) were not converted into muscle volume (*cf.* Newton 1989) and so values recorded are in arbitrary "ultra-sound units".

Birds were held in the left hand and all the feathers on the underside wiped aside using damp cotton wool. In order to obtain full contact between the probe and the body surface the face of the probe was wetted with a small amount of alcohol. The probe was placed at three standard locations on either side of the keel (R1,R2,R3 and L1, L2, L3). The probe was applied at a constant pressure and angle to the body surface. Several measurements were taken at each location until a stable reading was achieved. Birds were retained for five minutes before release to ensure complete drying of feathers.

7.2.3 BODY MASS

All captured birds were weighed using a 50g Salter spring balance (to the nearest 0.1g). The hour of weighing was also recorded. Unless otherwise stated Mass includes all data on body mass. Each weighing is treated as an independent data point. Where individuals were captured more than once but at the same stage of the nesting cycle, a mean value per stage was computed.

7.2.3.1 Automated precision electronic nest balances

Each season a small proportion of nests was selected for the electronic nest balances. This involved erecting a wooden shelf to support the balance and removing the nests from their natural situation and attaching the nest to a flat hardboard support using plaster which was then placed on the balance as close to the original position of the nests as possible (also see Jones 1985, 1987e,f; Ward 1992)

Four Mettler electronic balances, accurate to 0.01g, were placed underneath occupied

Swallow nests. Data were logged automatically, either on GA40 thermal printers (see Jones 1985) or on a BBC computer. Balances attached to printers were activated by a timing device which could log the mass at the nests at intervals of 30 seconds to 60 minutes. Two of the balances could be linked to a BBC computer. This proved more efficient because the balances were programmed to log data in response to the change in mass at the nest as well as recording the activity at a regular interval. This second method offered a number of advantages : (i) presence of birds at the nest could be accurately recorded, (ii) the male often perched at the nest during incubation so his mass could also be measured, (iii) during the early nestling period, feeding visits and mass of both sexes could be documented, (iv) data could be down-loaded directly onto a main frame computer for analyses.

7.2.4 STAGE IN THE BREEDING CYCLE

The exact date that each individual was captured (including those used in carcass analysis) was assigned to a stage in the nesting cycle. For most analyses the nesting cycle (first and second brood) was divided into the following stages: Pre-breeding; Nest building; Laying; Incubation; Nestling period I, II and III; Inter-brood and Post-fledging. For double-brooded pairs, birds caught between broods were classed as Inter-brood whereas single-brooded birds were coded as Post-fledging. Where accuracy of data permitted, the date of capture was also related to day (± 1 day) in the nesting cycle. Negative values represent Pre-laying individuals (-1 = 1 day before date of first egg, -2 two days before laying and so on), zero values are laying females (or partners of laying females, with the same value being given for 1st, 2nd, nth egg) and positive values are post-laying (1= 1st day of incubation, 2=2nd and so on).

7.3 RESULTS

BODY MASS AND CONDITION: PART I - CARCASS ANALYSIS

Carcass analysis was performed on 22 adult and five fledgling Swallows. For purposes of comparison, methodology followed that of Jones (1985, 1987d). One trivial difference, however, was that in this study tracheal lipid was combined with that from skin and contour feathers, whereas Jones analysed them separately.

7.3.1 INTER-SEXUAL COMPARISONS

The body size of the sample of birds used for carcass analyses was similar to those presented in Chapter 4, indicating that the sample was representative of the larger population. Differences in the lipid, protein and water content of sexes were summarised by calculating the total dry mass (DM) and lean dry mass (LDM) (Table 7.1a).

Table 7.1a Biometric and carcass analysis of Swallows (mean (se)) split by sex (sizes (mm), masses (g))

				Starved*	
Summary	Males	Males[a]	Females	Males	Fledglings
Wing	125.7 (1.1)	125.9 (1.4)	126.0 (.8)	126	113.4 (.1)
Outer	105.8 (2.9)	105.8 (3.8)	88.6 (1.4)	106[b]	75.0
Inner	43.8 (.5)	43.8 (.6)	45.5 (.2)	44	43.0
Head to bill	30.0 (.1)	29.9 (.2)	29.9 (.2)	30.1	29.5
Keel	21.3 (.1)	21.3 (.2)	21.2 (.2)	21.5	20.8
Tarsus	13.0 (.2)	12.9 (.2)	13.1 (.1)	13.0	13.0
Wet mass	18.8 (.3)	18.3 (.3)	20.8 (.8)	16.0 (.5)	17.6 (1.3)
DM[c]	6.71 (.25)	7.03 (.13)	7.82 (.39)	5.53 (.29)	6.49 (.53)
LDM	5.56 (.11)	5.63 (.12)	6.08 (.18)	5.30 (.25)	5.07 (.18)
PDM	0.97 (.06)	1.03 (.06)	1.10 (.05)	0.77 (.13)	0.83 (.07)
PLDM	0.86 (.05)	0.89 (.05)	0.98 (.04)	0.74 (.11)	0.74 (.06)
RDM	5.74 (.20)	6.01 (.10)	6.71 (.34)	4.76 (.16)	5.66 (.48)
RLDM	4.70 (.06)	5.10 (.15)	5.10 (.15)	4.56 (.13)	4.32 (.13)
Lipid cont	1.16 (.19)	1.37 (.10)	1.74 (.26)	0.23 (.04)	1.43 (.37)
Lipid index	20.8 (3.4)	25.1 (2.1)	28.7 (3.7)	4.4 (.6)	28.2 (7.0)
Water cont	11.1 (.3)	11.3 (.2)	13.0 (.6)	10.4 (.2)	11.1 (.8)
Water index	199.4 (4.4)	200.7 (4.4)	213.3 (2.8)	196.9 (6.1)	218.3 (11.9)
% Water	62.3 (.5)	61.6 (.5)	62.4 (.9)	65.3 (.8)	63.1 (.9)
% Pect DM[d]	14.4	14.6	14.1	14.0	12.8
% Pect LDM[e]	15.4	15.9	16.2	13.9	14.7
Sample	9	7	13	2	5

1 - includes data of 9 birds from G Jones (1985), hereafter referred to as GJ: Females (n=2): post-breeding and unknown stage; Males (n=4): nestling period II (n=2), post-fledging (n=1), unknown stage (n=1) and fledglings (n=3)

a - excluding two males which were suspected of having starved to death - see *

b - one of these birds (*) was from GJs data; only body size measures for birds measured by the author are included (i.e n=1)

c - abbreviations and derivation of terms are explained in Table 7a

RDM =(DM -PDM); RLDM= (LDM-PLDM)

d - calculated as follows: [(PDM/DM)*100]

e - calculated as follows: [(PLDM/LDM)*100]

7.3.1.1 Whole body measurements

Female wet mass ($p<0.001$), DM and LDM ($p<0.05$) were all significantly heavier than in males and the difference in pectoralis muscle LDM ($p=0.065$) was nearly significant (Table 7.1b). The overall differences between sexes were not only due to larger flight muscles of females, because their total RDM (dry mass - pectoralis dry mass) was also significantly heavier ($p=0.023$). Lipid content and lipid indices (ns), water content ($p<0.01$) and water indices (ns) were also higher in females (Table 7.1b). Two males that probably starved to death were then excluded from analyses to determine if these lower values influenced the significant differences between sexes. All measures were still higher for females but only significantly so for total LDM and RLDM (both $p<0.05$, Table 7.1b).

7.3.1.2 Component dry and lean dry masses

Mean and standard error for dry and lean dry masses and lipid indices of dissected body components for males, females, adults, fledglings and all birds combined are given in Appendices 7.1a-g

Female components were in general heavier (dry mass) than males; significantly so for the oesophagus ($p<0.05$), liver ($p<0.05$), gut and kidneys ($p<0.001$) and almost significantly for wing and tail feathers ($p=0.059$, Table 7.2). Lean dry mass of female liver, gut and kidneys ($p<0.001$) and oesophagus ($p<0.05$) were also significantly heavier than in males; pectoralis muscles also tended to be heavier in females ($p=0.065$). In contrast, the lean dry masses of the head, neck and lungs, were all heavier in males but these differences were not significant (Table 7.2).

7.3.1.3 Lipid indices (LI)

Lowest LIs (%) for both sexes were the oesophagus, lungs, pectoralis muscles and the heart; highest for males were for the gut (40.8) and legs (38.3), whereas for females it was for body shell, skin and body feathers and the legs (47.9, 42.7, 47.4 respectively). Females tended to have higher LI than males, though only for skin and body feathers and pectoralis minor muscles were the differences significant ($p<0.05$, Table 7.2, Fig 7.1a). For four components (wings, pectoralis major, pectoralis minor and gut), males had a higher LI than females (Table 7.2). Lipid indices of all components were lower for starved than healthy males (Fig 7.1b). Highest LIs for starved males were for the gut, gonads and kidneys. Skin and body feathers, pectoralis minor, neck and the oesophagus all had LIs of under three. The lipid index for healthy males was highest for legs, gut and body shell and lowest for lungs and pectoralis minor muscles.

7.3.1.4 Distribution of lipid reserves

The lipid content of each component was calculated as a percentage of the total body lipid. Overall lipid distribution was similar between sexes (Fig 7.2a,b). Pectoralis minor muscle, lungs and liver each contained <1% of total body lipid whereas skin and body feathers, legs, pectoralis muscles, wings, liver and head accounted for almost nine

Table 7.1b **Comparison of Swallow carcass analysis measurements between males and females, using the Students t-test**

Summary data	M vs F			M[a] vs F		
	t	p	Sig	t	p	Sig
Wet mass[b]	-3.18	0.009	* *	0.55	0.608	ns
Dry mass	-2.18	0.041	*	0.41	0.691	ns
Lean dry mass	-2.21	0.039	*	2.49	0.028	*
Pect DM	-1.71	0.102	ns	1.37	0.196	ns
Pect LDM	-1.95	0.065	ns	1.41	0.183	ns
RDM	-2.47	0.023	*	0.16	0.877	ns
RLDM	-2.50	0.024	*	2.95	0.012	*
Lipid content	-1.69	0.107	ns	-0.76	0.462	ns
Lipid index	-1.39	0.180	ns	-1.00	0.335	ns
Water content	-3.06	0.012	*	0.23	0.825	ns
Water index	-1.42	0.179	ns	-1.57	0.147	ns
% water content	0.15	0.882	ns	-1.74	0.113	ns

a - excluding two males which were suspected of having starved to death
b - mean and se values are given in Table 7.1a

Table 7.2 Comparison of mean dry masses (DM), lean dry masses (LDM) and lipid indices for male[a] and female body components,using the Students t-Test. Mean (se) in Appendices 7.1a-g

Components	DM		LDM		LI	
	t	p	t	p	t	p
Wing and tail feathers	2.02	0.059	-	-	-	-
Skin and body feathers	-1.92	0.073	-0.11	ns	-2.25	*
Legs	-1.42	ns	-1.80	0.087	0.13	ns
Wings	-0.67	ns	-1.19	ns	0.43	ns
Pectoralis major	-1.50	ns	-1.78	0.090	1.31	ns
Pectoralis minor	-1.05	ns	-1.30	ns	2.27	*
Pectoralis	-1.71	ns	-1.95	0.065	1.42	ns
Body shell	-1.47	ns	-1.02	ns	-0.48	ns
Head	-0.46	ns	0.47	ns	-0.16	ns
Neck	-0.55	ns	0.21	ns	-0.40	ns
Oesophagus	-2.52	*	-2.24	*	-0.55	ns
Lungs	0.28	ns	0.60	ns	-0.96	ns
Heart	-1.03	ns	-0.77	ns	-0.52	ns
Liver	-2.74	*	-3.31	* *	-0.72	ns
Gut	-3.26	* *	-3.12	* *	0.94	ns
Kidneys	-3.26	* *	-3.12	* *	-0.06	ns

a - excluding two males which were suspected of having starved to death a)

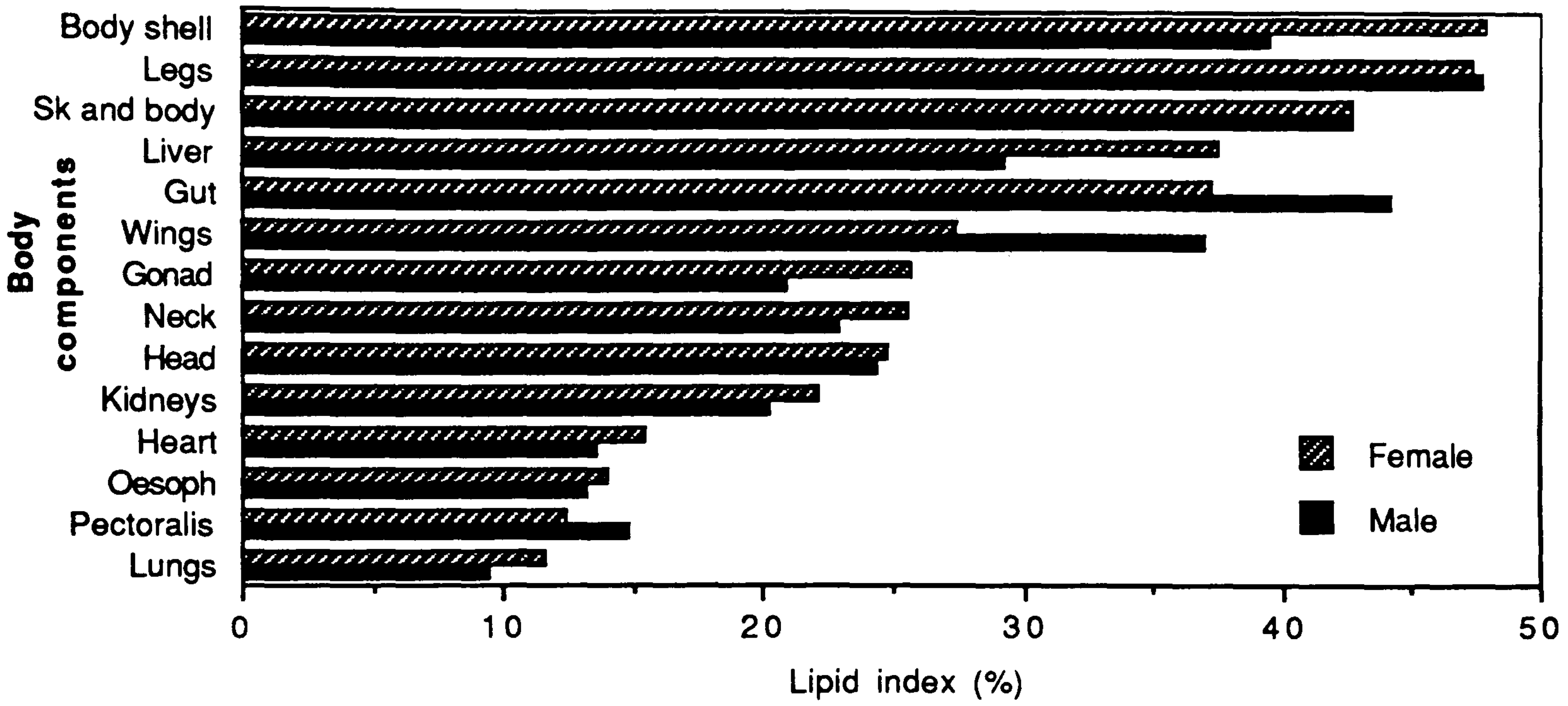


Fig 7.1a Comparison of component lipid indices between male† and female adult Swallows

† - two males which apparently died as a result of starvation are not included in the above figures. Values are given in Appendices 7.1b and 7.1g, for females and males respectively

b)

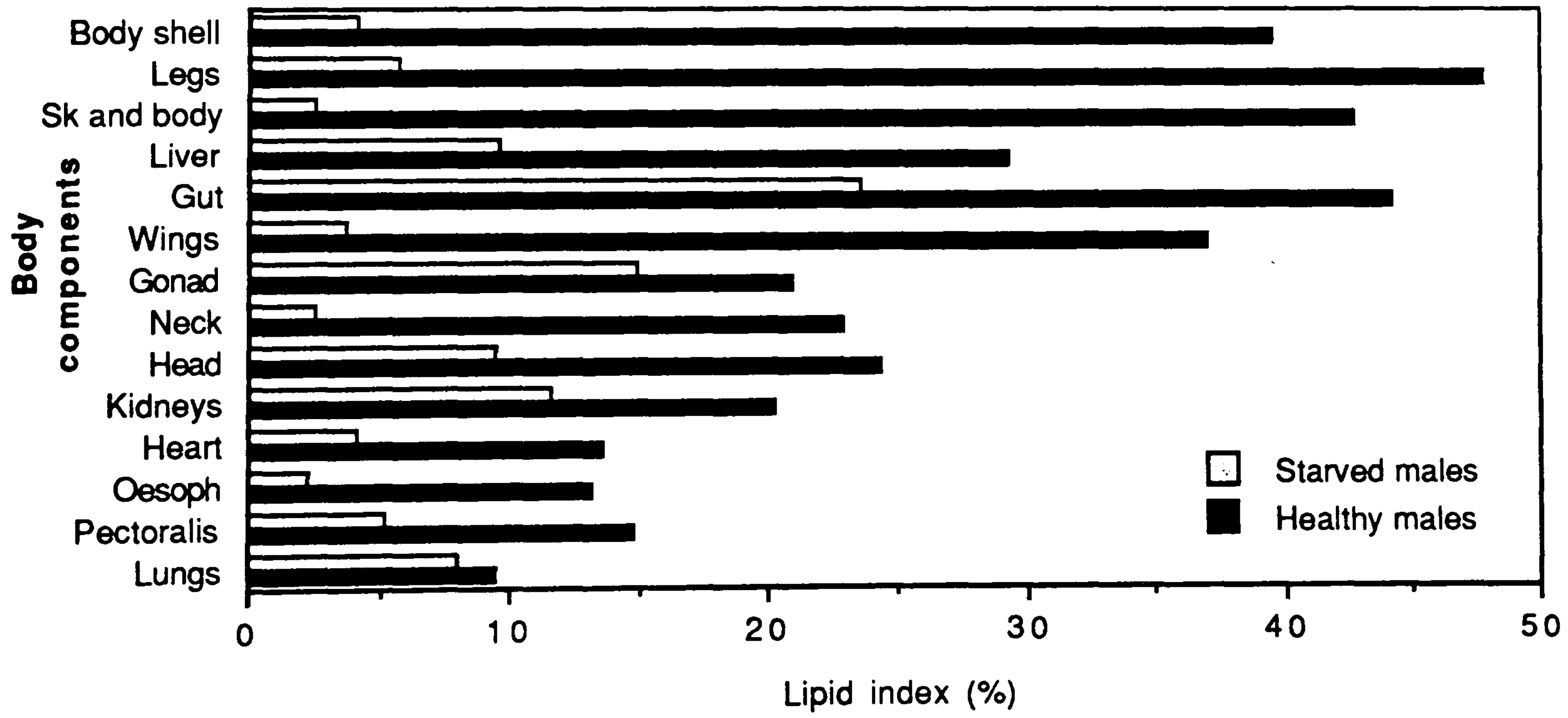


Fig 7.1b Comparison of component lipid indices between healthy and starved adult male Swallows

Values are given in Appendices 7.1f and 7.1g, for starved and healthy males respectively

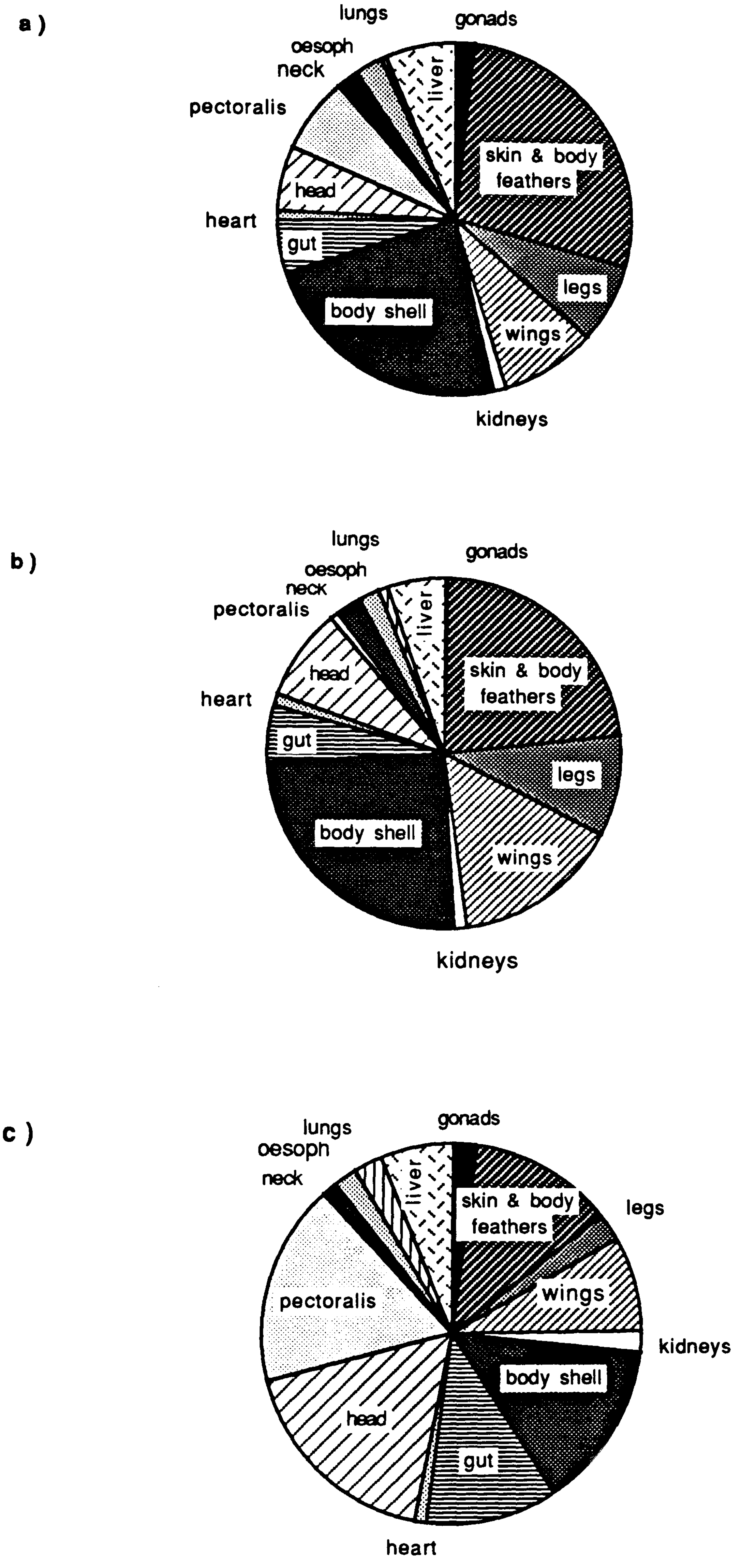


Fig 7.2 **Distribution of lipid components in adult Swallows: a) Females, b) Healthy males and c) Starved males**

tenths of total body lipids (almost half in the former two components). Males which died through starvation had almost completely depleted their lipid reserves (Table 7.1a) and approximately half their total body lipid was within the head, pectoralis muscles and body shell (17.8, 17.3 &14.2 respectively, Fig 7.2c).

7.3.1.5 Distribution of lean mass (protein reserves)

The lean dry mass of each component was expressed as a percentage of the total lean dry mass for females, "healthy" and "starved" males (Fig 7.3a-c respectively). Healthy males and females had proportionately the highest amount of lean material in the pectoralis muscles, wing and tail feathers, body shell and skin and body feathers. The percentage LDM of pectoralis muscles was highest for females and lowest for starved birds. Other components showed less difference between starved and healthy females (Fig 7.1c). The differences between starved and healthy males (Fig. 7.3d) imply that under extreme nutrient shortage, total lean mass and pectoralis lean mass are drawn upon.

7.3.2 RELATIONSHIP OF BODY SIZE TO MASS DERIVED FROM CARCASS ANALYSIS

Before analysing body condition it is necessary to standardise for variation in body size (see Chapter 4). Wet mass and dry masses (DM, LDM, PDM, PLDM) were correlated with body size (for details see Chapter 4). Keel-length was positively and significantly correlated with all masses (all $p<0.001$ level, Table 7.3; Fig 7.4a-c). All body size parameters were positively correlated except for outer tail-length (Table 7.3). Overall 'size' (PC1) did not explain as much of the variation in mass as keel-length. Moreover, keel-length was the only variable entered significantly in a multiple regression. These results obviously require confirmation for a larger sample (performed in Part II). To standardise carcass measures for body size, however, keel-length was used to calculate an expected mass. The regression equations for all adults combined were as follows:

Equation 7.1: Body mass $_{\mathrm{Exp}}$= -66.88 + 4.10*keel-length ($r2*100 = 53\%$, n=15; Fig 7.4a)

Equation 7.2: LDM $_{\mathrm{Exp}}$= -11.85 + 0.85*keel-length ($r2*100 = 57\%$, n=15; Fig 7.4b)

Equation 7.3: PLDM $_{\mathrm{Exp}}$= -3.0 + 0.19*keel-length ($r2*100 = 48\%$, n=15; Fig 7.4c)

7.3.3 ASSESSING BODY RESERVES

7.3.3.1 Lipid reserves

Lipid reserves in live adult Swallows during the breeding cycle were investigated by examining the relationship of mean fat scores (MFS) to body mass and lipid. MFS increased linearly with mass ($r=0.72$; Fig 7.5a), total lipid content ($r=0.78$; Fig 7.5b) and

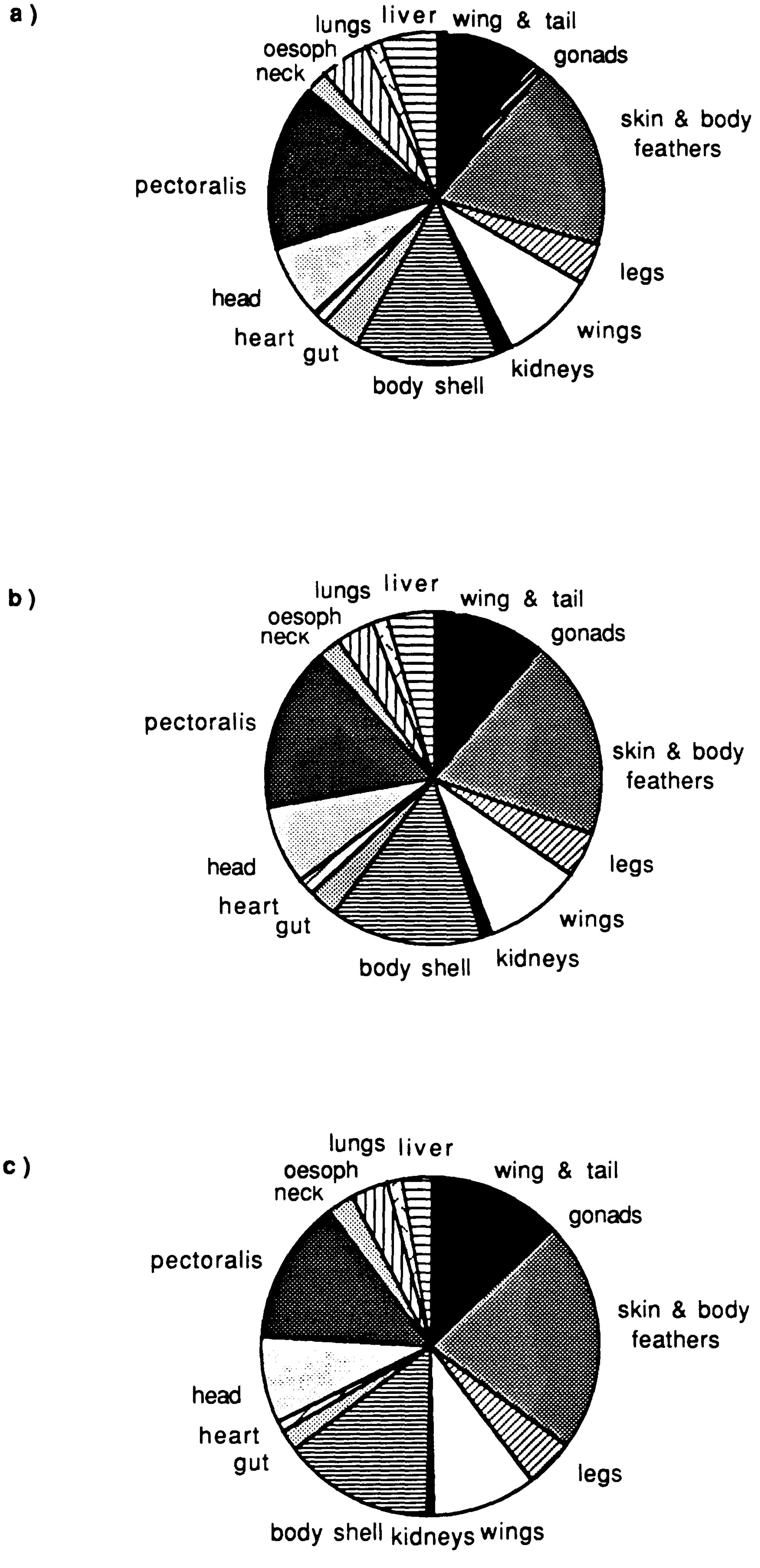


Fig 7.3 Distribution of lean components in adult Swallows: (a) Females, (b) Healthy males and (c) Starved males

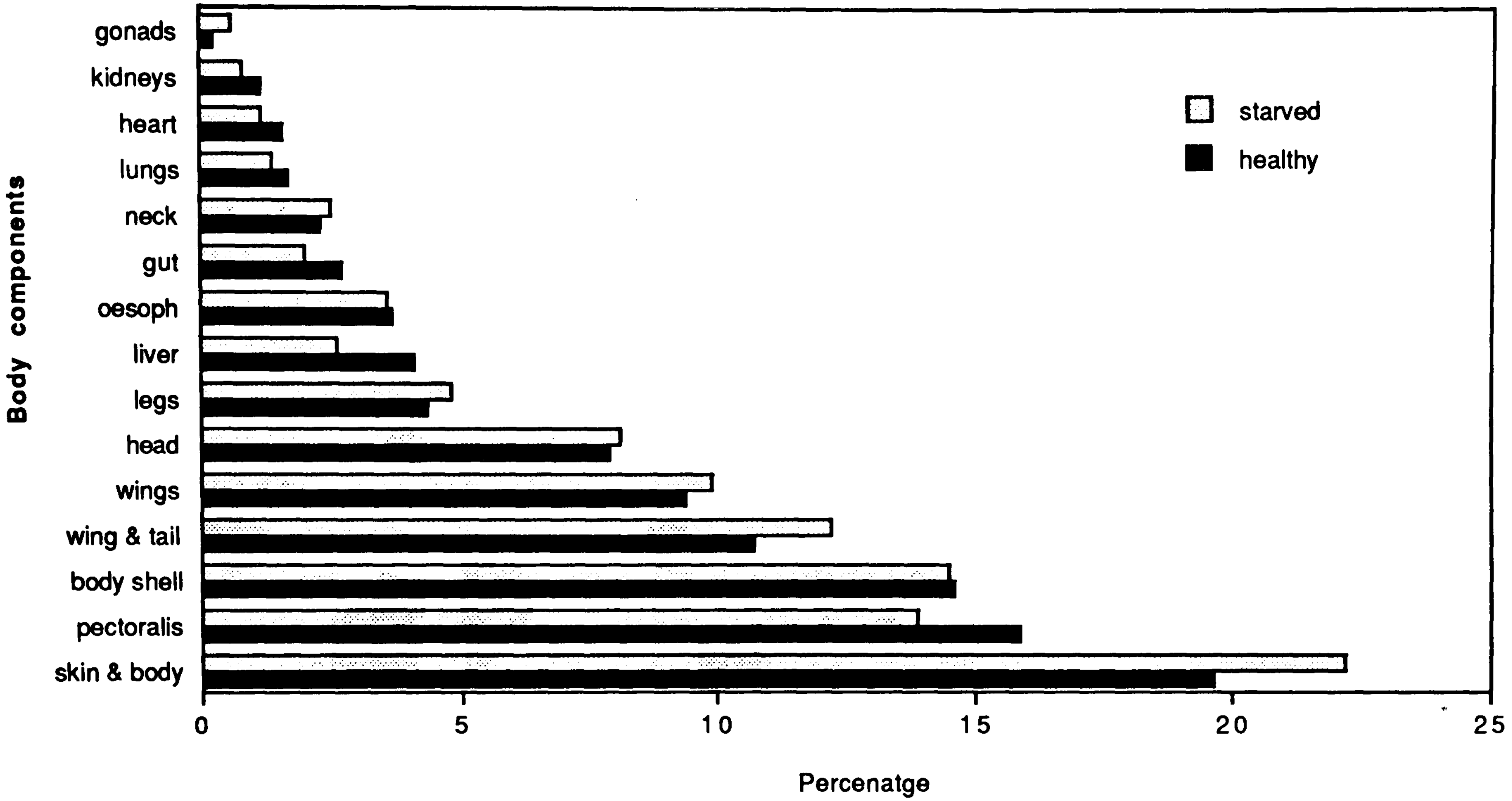


Fig 7.3d Comparison of component lean dry mass expressed as a percentage of total lean dry mass between healthy and starved adult male Swallows

Table 7.3 Pearson correlation coefficient matrix[a] of adult body size and mass with various measure of mass derived from carcass analysis (coefficient, significance)

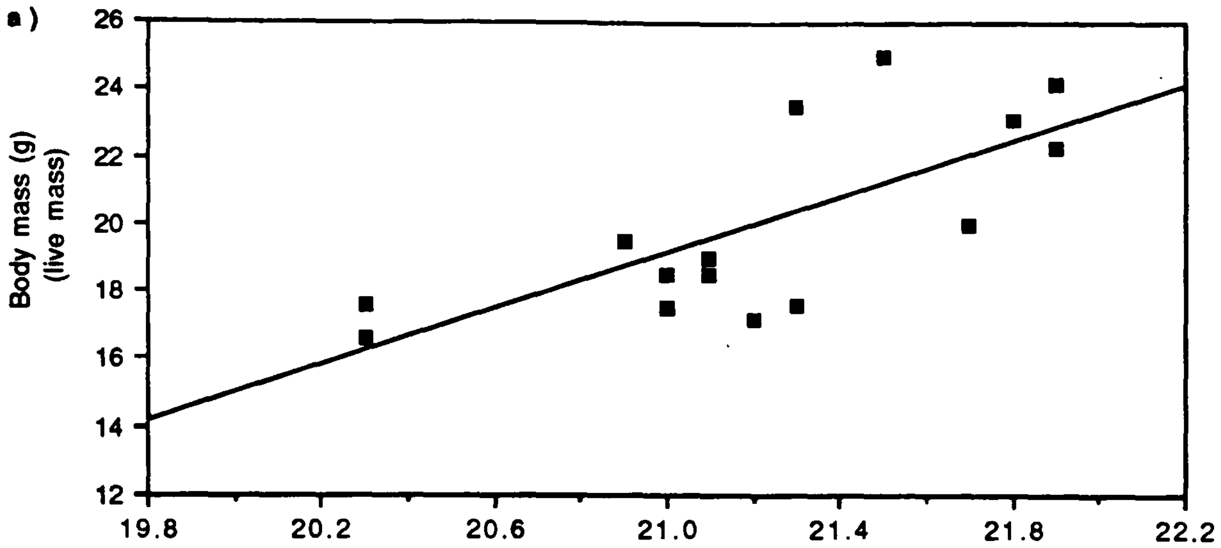
Body size measures	Measures from carcass analysis Wet mass	DM[b]	LDM[b]	Pectoralis DM	LDM
Wing	-0.04 ns	-0.08 ns	0.15 ns	0.20 ns	0.27 ns
Outer tail	-0.51 *	-0.43 ns	-0.29 ns	-0.14 ns	-0.13 ns
Inner tail	0.47 ns	0.33 ns	0.53 *	0.36 ns	0.49 ns
Head to bill	0.41 ns	0.38 ns	0.41 ns	0.21 ns	0.26 ns
Keel[c]	0.75 * *	0.78 * *	0.75 * *	0.73 *	0.69 *
PC1[d]	0.70 *	0.71 * *	0.59 *	0.42 ns	0.39 ns

a - only body size measures taken by the author are included in the analyses, sample sizes for adults are as given in Appendix 7.1a,b. Single male which was presumed to have starved to death has been excluded.

b - DM and LDM refer to total dry and lean dry masses respectively

c - only keel length was entered in a stepwise multiple regression analyses

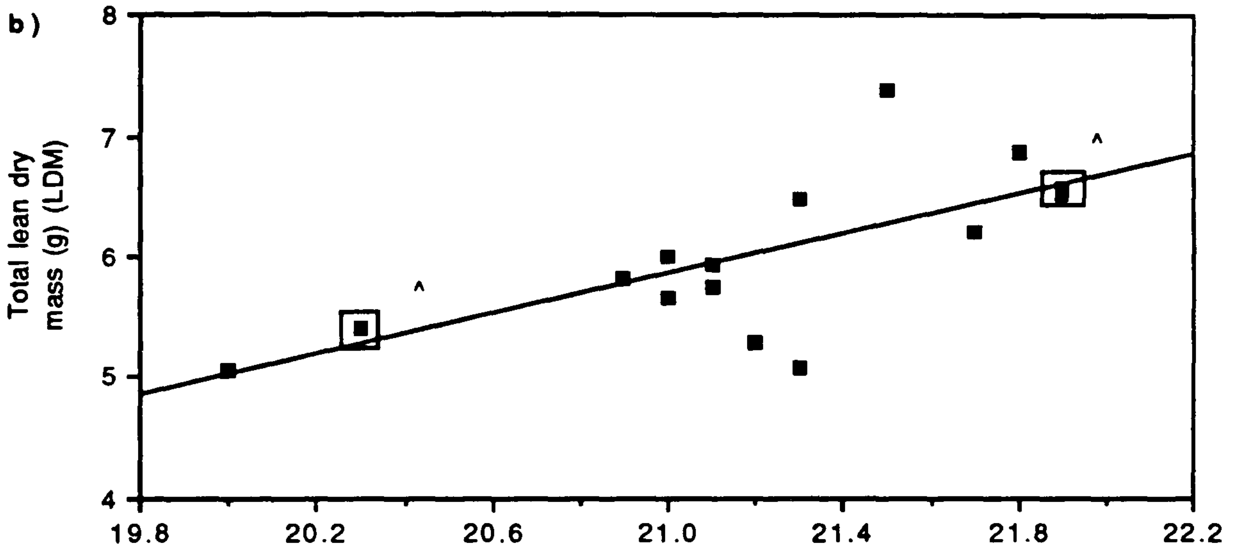
d - PC1 'size' was computed from Principal Component Analyses: using wing, outer tail, inner tail,head and bill and keel length



All: y = - 67.429 + 4.1204x r^2 = 0.528; n=15; p<0.001

Adult: y = - 66.881 + 4.1034x r^2 = 0.566; n=14, p<0.001

Female: y = - 61.614 + 3.8854x r^2 = 0.642; n=10, p<0.001



All: y = - 11.775 + 0.83912x r^2 = 0.515; n=16, p<0.001

Adult: y = - 11.853 + 0.84502x r^2 = 0.566; n=15, p<0.001

Female: y = - 12.320 + 0.87233x r^2 = 0.731; n=11, p<0.000

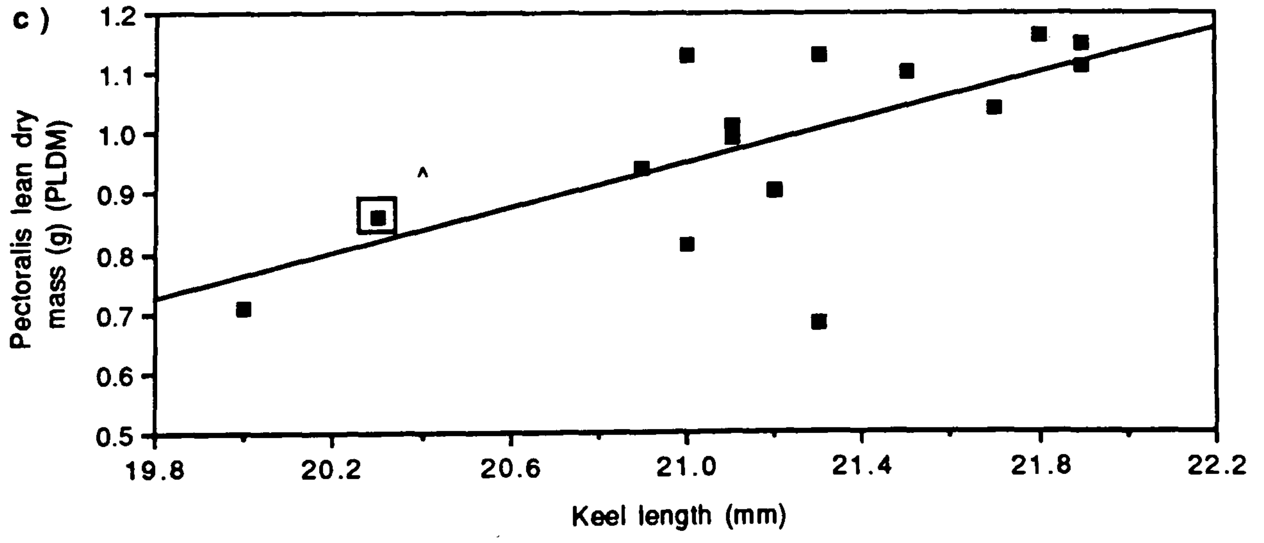
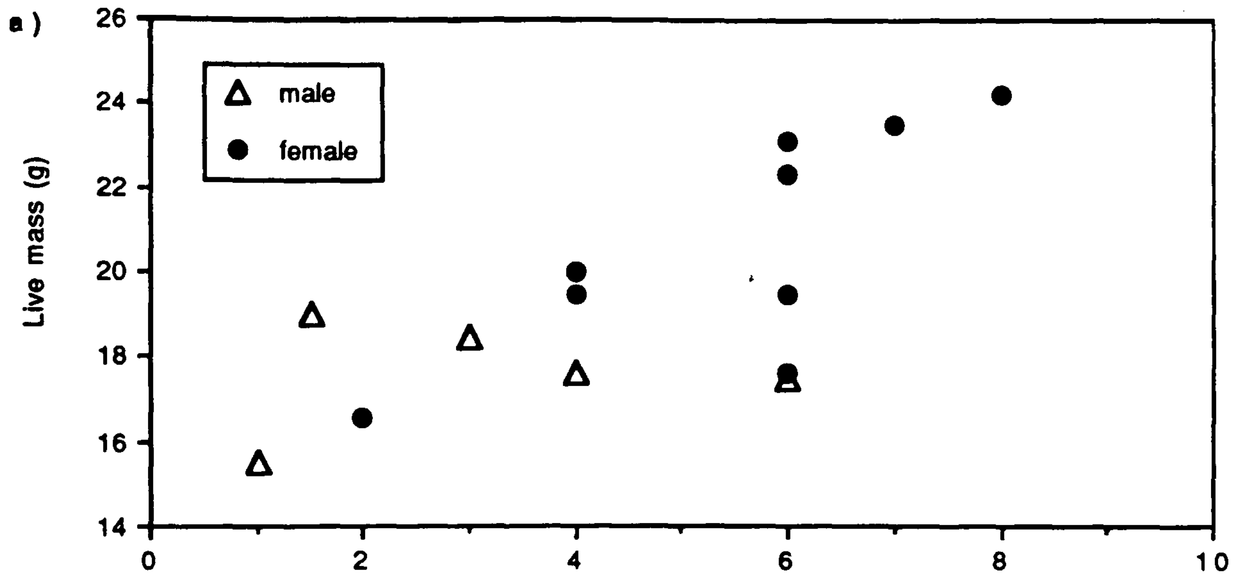


Fig 7.4 Relationship of keel length with: a) Live mass, b) LDM and c) PLDM in a sample of Swallows measured prior to carcass analysis. (^ refers to two points, female; regression lines are for all data)

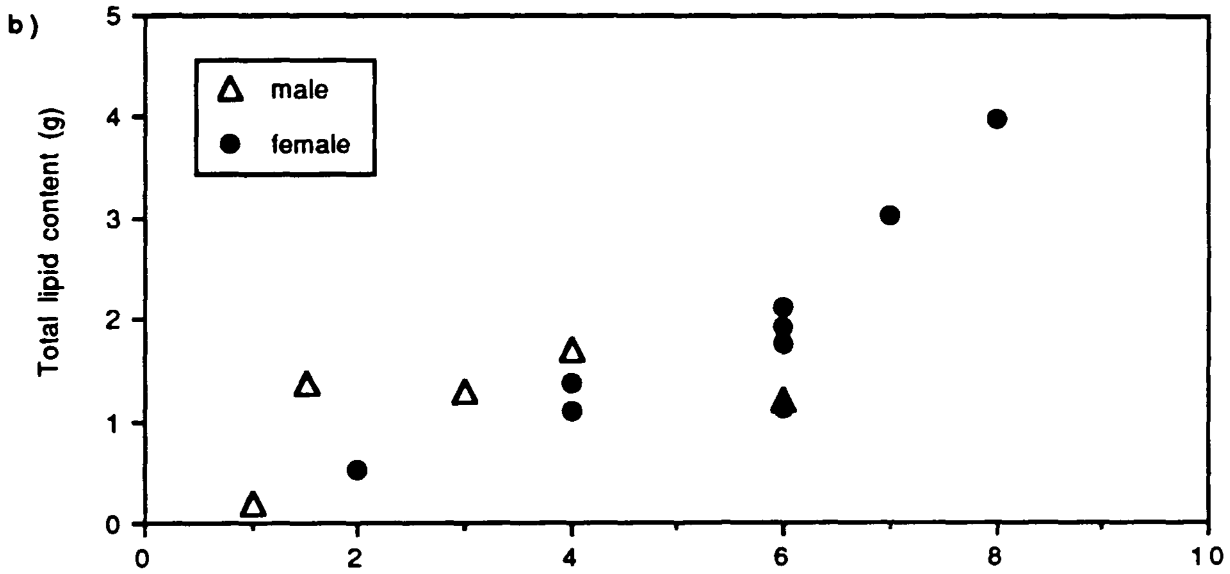
All: y = - 2.9829 + 0.18710x r^2 = 0.468; n=16, p<0.001

Adult: y = - 2.9983 + 0.18807x r^2 = 0.480; n=15, p<0.001

Female: y = - 3.2124 + 0.19934x r^2 = 0.890; n=11, p<0.000



y = 15.383 + 0.91530x r^2 = 0.525; n=14, p<0.000



y = 6.1218e-3 + 0.35061x r^2 = 0.616; n=14, p<0.001

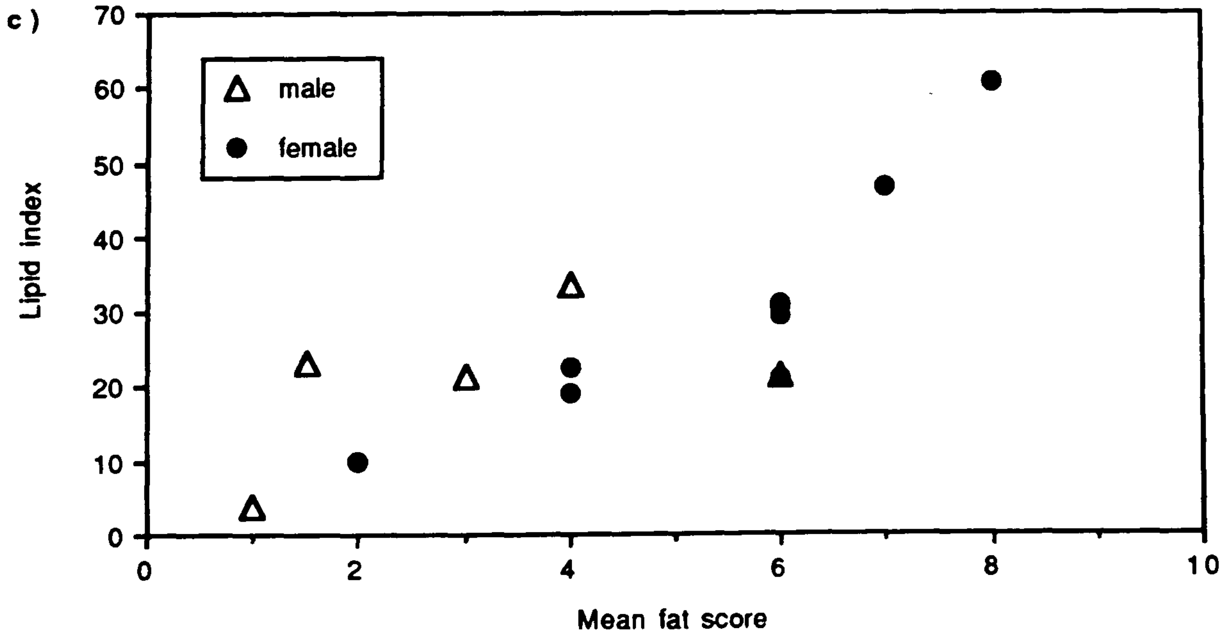


Fig 7.5 Relationship of Mean fat score and: a) Live mass, b) Lipid content and c) Lipid index in adult Swallows

y = 2.8525 + 5.1647x r^2 = 0.614; n=14, p<0.001

lipid index (r=0.79; p<0.001; Fig 7.5c; all p<0.001). Data were more scattered for males suggesting that they were scored less accurately. The use of mass as a predictor of body fat was also tested and it was found to be significantly and positively correlated with both measures (r=0.89; Fig 7.6a; r=0.83; Fig 7.6b; lipid content and lipid index respectively, both p<0.000). It was, therefore, concluded that mass was more useful to estimate lipid reserves than fat scoring.

7.3.3.2 Protein reserves

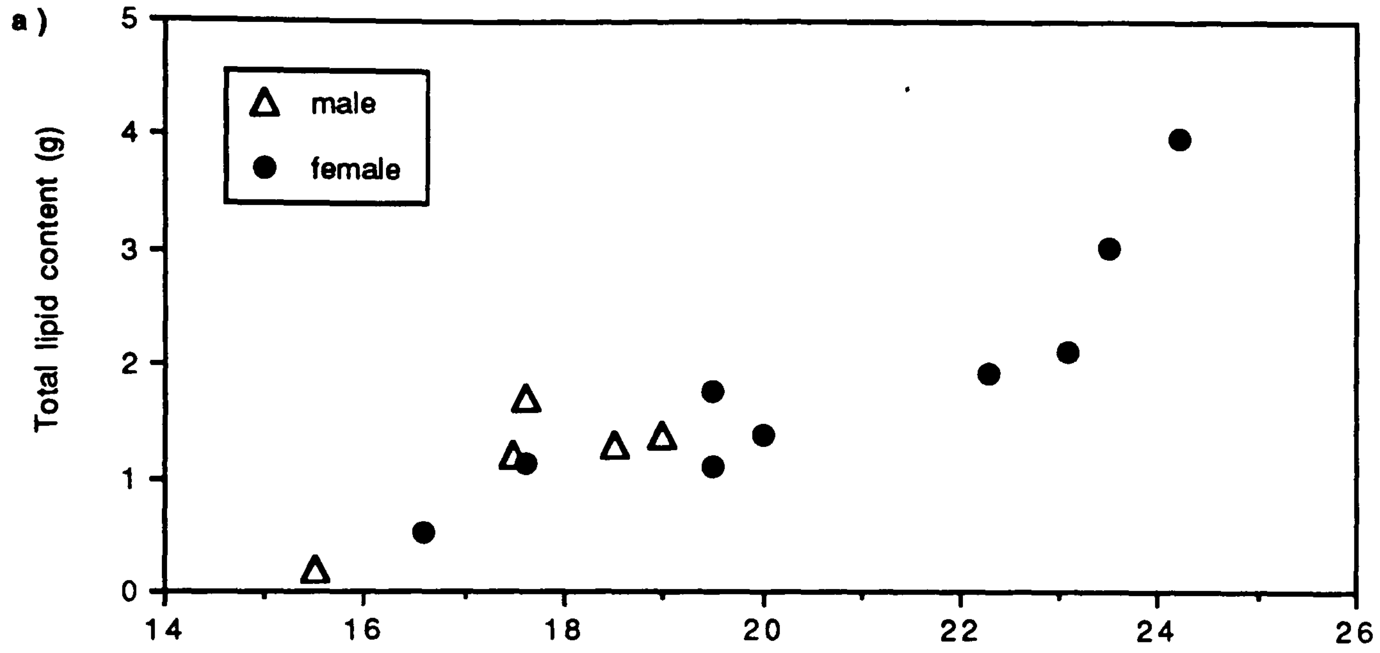
Pectoralis dry mass and lean dry mass increased significantly with total live, dry and lean dry mass (all p<0.000, Table 7.4). The relationship of total lean dry mass and PLDM to wet mass was more significant for females than males (Fig 7.7a,b). Lean dry mass of the pectoralis muscles accounted for 84% of total variation associated with total lean dry mass in adult Swallows (Fig 7.7c).

An ultra-sound device was used to measure muscle thickness as a measure of protein reserves (Section 7.1.2.2). Individual ultra-sound readings (R1 to R3 and L1 to L3; Section 7.2.2.2) were all significantly correlated with total DM, LDM and pectoralis DM and LDM. Thus, the mean ultra-sound reading (MUS) was computed and used in analyses. Other indices were calculated, based on anterior measures, middle measures, right or left only, but none altered the significance levels of the results. MUS was positively and significantly correlated with all measures of mass from carcass analysis (Table 7.5): body mass (r=0.81, p<0.001, Fig. 7.7c); dry mass (r=0.83, p<0.001); lean dry mass (r=0.77, p<0.001, Fig. 7.7d), pectoralis DM (r=0.87, p<0.000) and pectoralis LDM (r=0.81, p<0.001, Fig. 7.7e). Multiplying MUS by keel length gave an index of muscle volume and explained more variation in mass and DM & LDM, but not PDM or PLDM (Table 7.5).

Body mass was also significantly correlated with PLDM, though 11% less variation was explained (r^2= 56% vs 67%) than by MUS volume. It was assumed, therefore, that MUS was a reasonable predictor of pectoralis muscle thickness and could be used to measure potential protein reserves in adult Swallows in the field. Also, MUS explained 59% of the variation in total lipid content, increased by 7% when adjusted for keel length (Table 7.5). These results indicate that, in general, lipid and protein reserves were deposited or utilised simultaneously.

7.3.4 CHANGES IN BODY RESERVES DURING THE BREEDING CYCLE

Sample sizes for each stage in the nesting cycle were very small. The sample of two laying birds included one female which died from natural causes (the day that her third egg was laid), so data are, therefore presented separately for each bird; Laying (normal) and Laying anomaly (died during laying). Sexes could not be combined because of the different parental roles of males and females (Chapter 3). The small sample precluded statistical comparison but mean values are presented (Table 7.6a,b).



y = -4.5300 + 0.3185x r^2 = 0.787; n=14, p<0.000

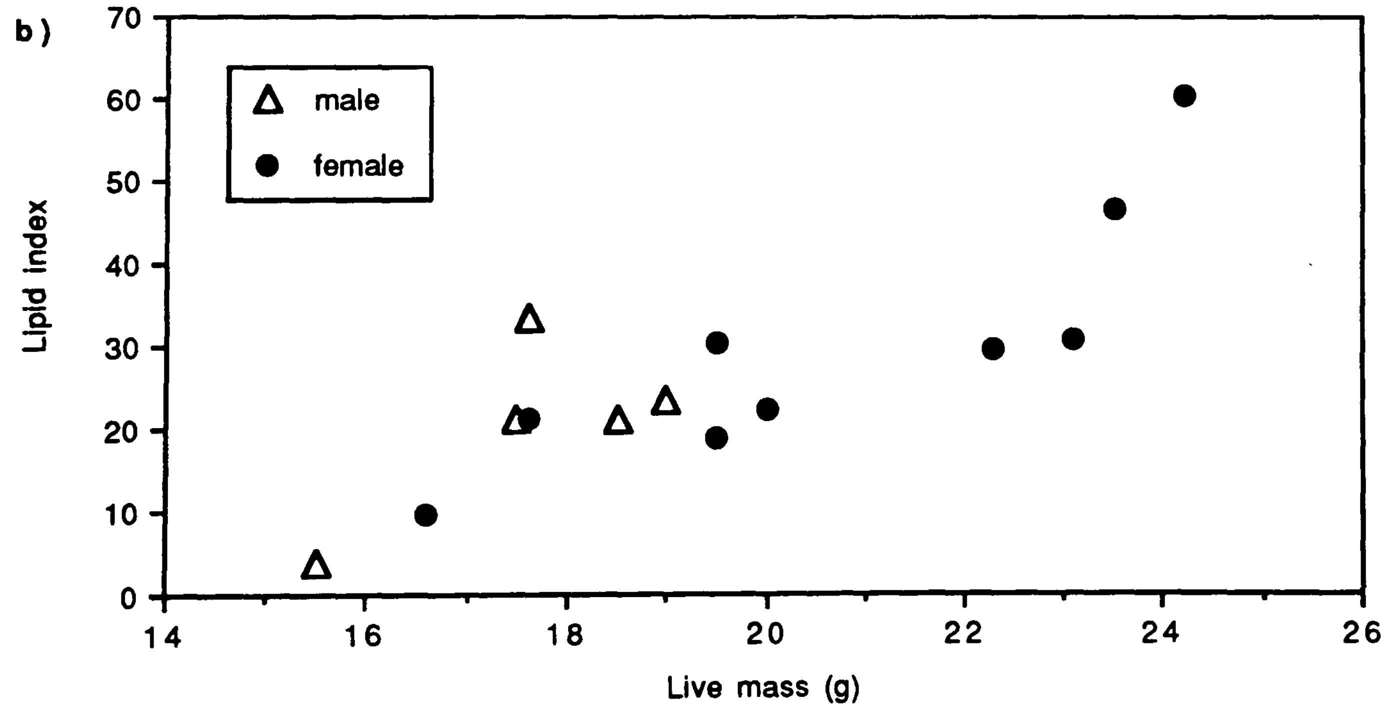
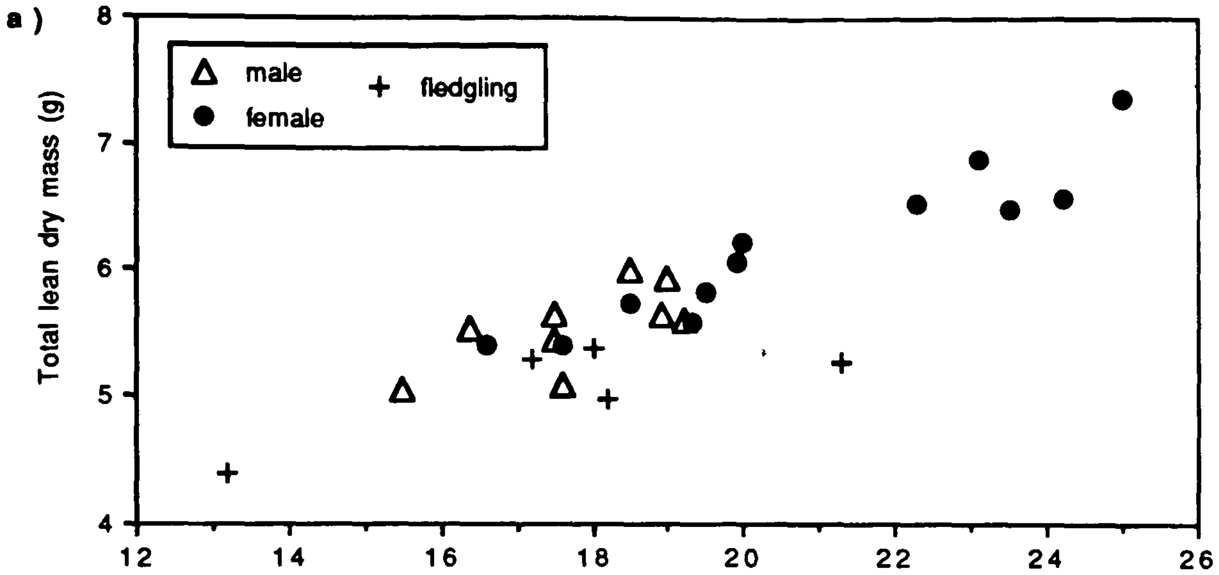


Fig 7.6 Relationship of Live body mass and: a) Total lipid and b) Lipid index in adult Swallows

y = - 58.194 + 4.3286x r^2 = 0.688; n=14, p<0.000

Table 7.4 **Correlation matrix of carcass analysis measurements of Swallows (coefficient, significance). Adults and fledglings (n=27) in plain, and adults only (n=22) in bold text**

				Measures from carcass analysis					
Measures from carcass analysis	Wet mass	DM	LDM	Pectoralis DM	Pectoralis LDM	Water (g)	Water Index	Fat (g)	Fat Index
Wet Mass	-	0.95 ***	0.88 ***	0.78 ***	0.75 ***	0.97 ***	0.41 *	0.80 ***	0.70 ***
Dry Mass (DM)	**0.95** ***	-	0.84 ***	0.86 ***	0.80 ***	0.85 ***	0.25 ns	0.91 ***	0.81 ***
Lean dry mass (LDM)	**0.93** ***	**0.85** ***	-	0.87 ***	0.90 ***	0.86 ***	0.01 ns	0.54 **	0.38 *
Pectoralis DM	**0.82** ***	**0.87** ***	**0.84** ***	-	0.98 ***	0.67 ***	-0.13 ns	0.66 ***	0.53 **
Pectoralis LDM	**0.81** ***	**0.83** ***	**0.88** ***	**0.98** ***	-	0.66 ***	-0.19 ns	0.56 **	0.41 *
Water content	**0.96** ***	**0.82** ***	**0.92** ***	**0.70** ***	**0.73** ***	-	0.51 **	0.65 ***	0.55 **
Water Index	**0.52** *	**0.36** **ns**	**0.28** **ns**	**0.10** **ns**	**0.07** **ns**	**0.61** **	-	0.39 *	0.47 *
Fat content	**0.78** ***	**0.92** ***	**0.58** **	**0.74** ***	**0.64** **	**0.60** **	**0.35** **ns**	-	0.98 ***
Fat Index	**0.69** **	**0.85** ***	**0.44** *	**0.66** **	**0.53** *	**0.48** *	**0.34** **ns**		-



All: y = 1.7755 + 0.20749x r^2 = 0.780; n=26, p<0.000

Adults: y = 1.8787 + 0.20659x r^2 = 0.865; n=21, p<0.000

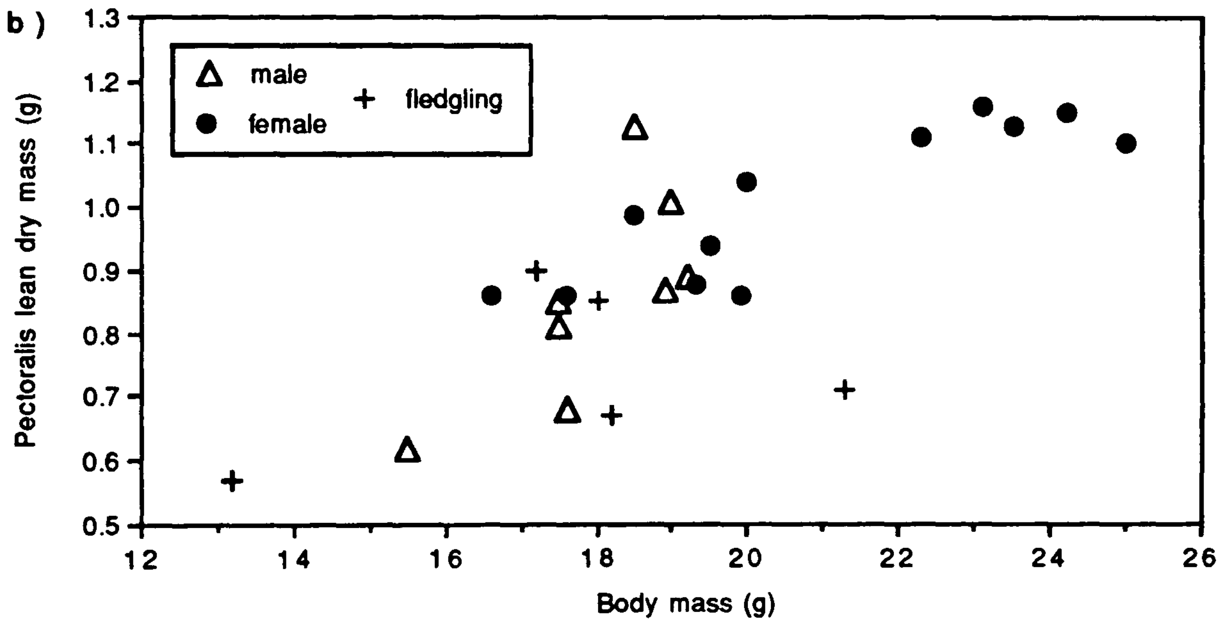


Fig 7.7 Relationship between adult body mass and: a) Total lean dry mass and, b) Pectoralis lean dry mass in Swallows

All: y = 0.0093 + 0.04660x r^2 = 0.574; n=25, p<0.000

Adults: y = 0.0148 + 0.04741x r^2 = 0.654; n=20, p<0.000

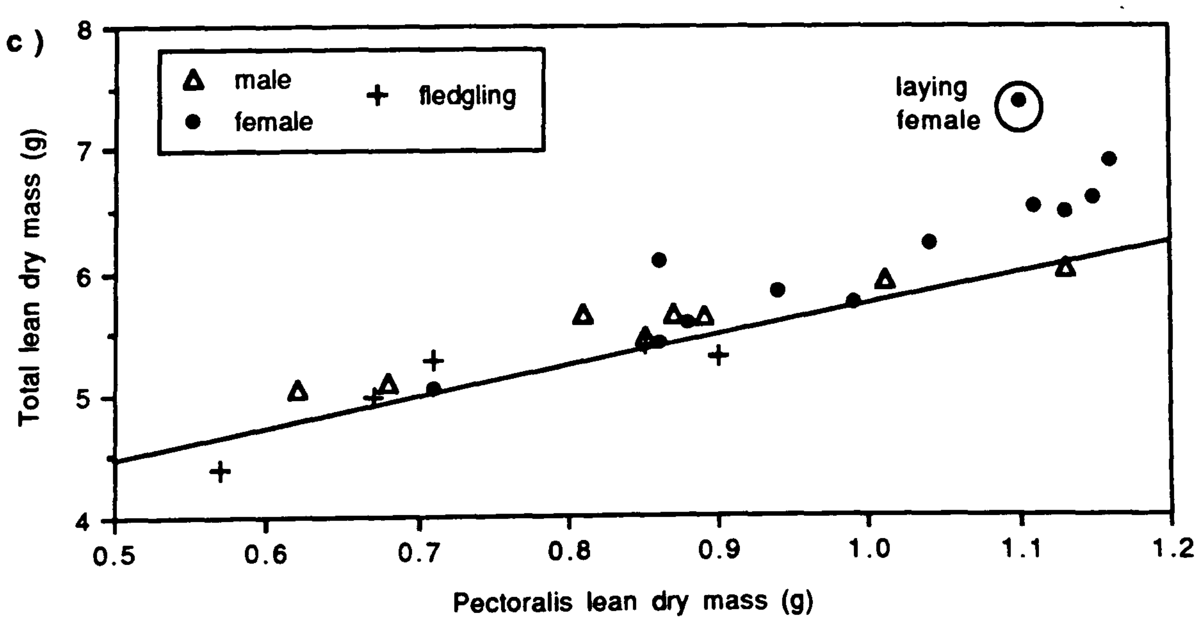
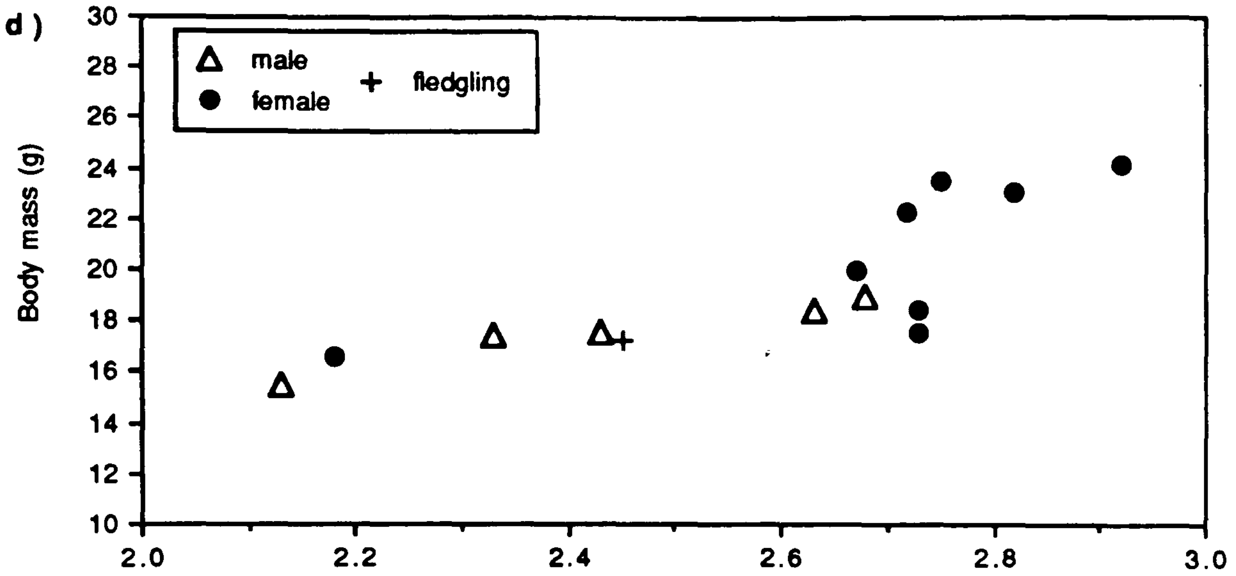


Fig 7.7c Relationship between Pectoralis lean dry mass and total lean dry mass in Swallows

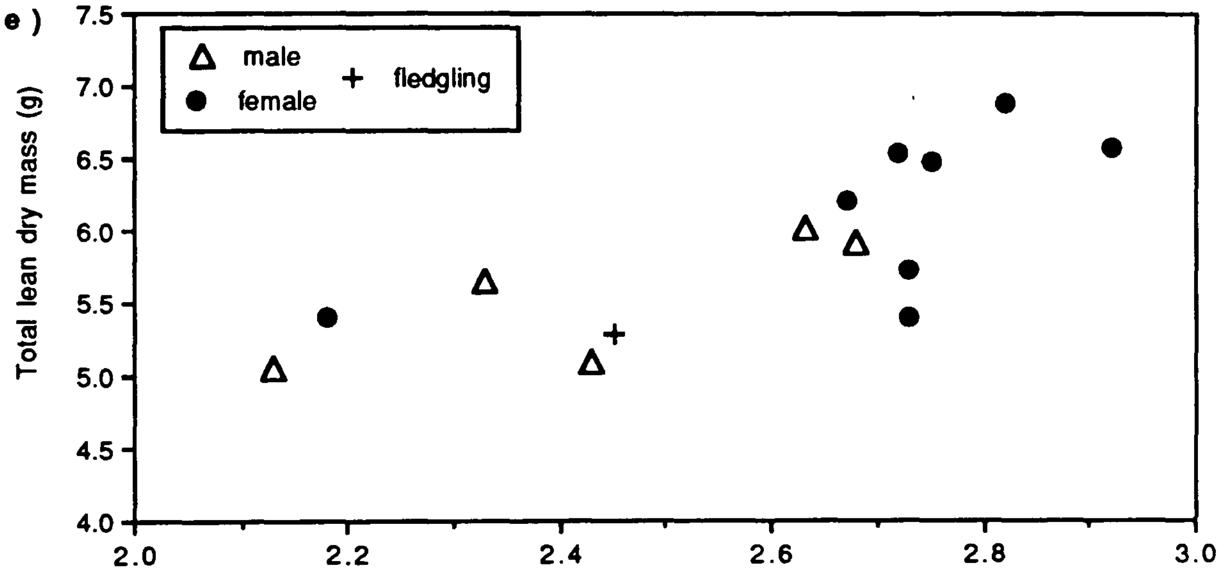
All: y = 2.8487 + 3.1601x r^2 = 0.859 || All^: y = 2.633 + 3.4447x r^2 = 0.805

Male: y = 3.8189 + 2.0261x r^2 = 0.914 || Female^: y = 2.425 + 3.6488x r^2 = 0.871

Adults^: y = 3.0135 + 3.0156x r^2 = 0.841 (^ = exlude laying female)



Adults: y = -4.54901 + 9.27976x r^2 = 0.640; n=13, p<0.001



Adults: y = 1.8787 + 0.20659x r^2 = 0.584; n=13, p<0.001

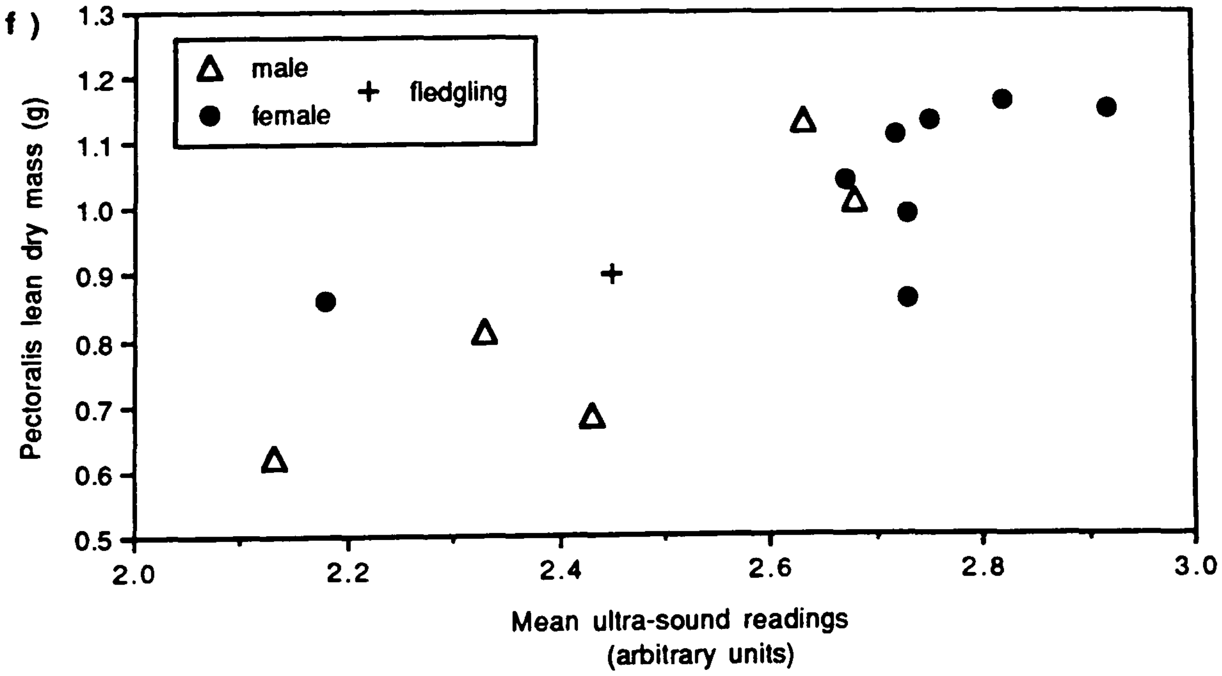


Fig 7.7 Relationship between Mean ultra-sound and: d) Body mass, e) Total lean dry mass and f) Pectoralis lean dry mass in Swallows

Adults: y = -0.59412 + 0.60078x r^2 = 0.660; n=13, p<0.000

Table 7.5 **Correlation of mean ultra-sound readings (MUS) and mass in Swallows (adults, fledglingspooled) to carcass measures (coefficient (n) significance)**

	Measures from carcass analysis						
Body size^a measures	MUS	MUS volume	DM	LDM	Pectoralis DM	Pectoralis LDM	Total Lipid
Mass	0.81 (14) **	0.87 (14) ***	0.95 (26) ***	0.88 (26) ***	0.78 (25) ***	0.76 (25) ***	0.80 (26) ***
MUS	-	-	0.83 (14) ***	0.77 (14) **	0.87 (14) ***	0.81 (14) **	0.77 (14) **
Mus volume	-	-	0.88 (14) ***	0.83 (14) ***	0.87 (14) ***	0.82 (14) ***	0.81 (14) ***

a - MUS - mean ultra-sound-readings (arbitrary units);
MUS volume -((mean ultra-sound readings * keel length)*100)

Table 7.6a **Summary of carcass analyses (Mean (se)) of adult Swallows during different stages of the breeding cycle:**

(a) Males

Summary			Stages in the nesting cycle			
data	Pre-breeding	Incubation	Rearing[a]	Rearing[b]	Starved[c]	Starved[d]
Live mass	18.0 (.5)	19.0	18.3 (.4)	18.3 (.4)	15.5	16.0 (.5)
Mass/keel	85.7 (.5)	90.1	82.6[e]	77.4 (5.3)	72.1	-
Residual mass	-1.29 (.50	-0.70	-2.92[e]	-4.38 (1.46)	-5.84	-
Dry mass	7.0693 (.223)	7.3163	6.9452 (.193)	6.6055 (.371)	5.2466	5.5343 (.288)
Lean dry mass	5.8302 (.180)	5.9333	5.4536 (.127)	5.3733 (.127)	5.0519	5.2981 (.246)
PLDM	0.9684 (.016)	1.10114	0.8255 (.048)	0.7850 (.055)	0.6228	0.7351 (.112)
PLDMK	4.61 (.75)	4.79	3.21[f]	3.00 (.10)	2.90	-
PLDMres	0.019 (.16)	0.04	-0.32[f]	-0.37 (.01)	-0.42	-
Lipid content	1.2391 (.043)	1.3830	1.4916 (.168)	1.2322 (.290)	0.1947	0.2362 (.041)
Lipid index	21.25 (.08)	23.31	27.44 (3.27)	22.72 (5.3)	3.85	4.4314 (.577)
Water content	10.9307 (.277)	11.6837	11.3548 (.332)	11.3548 (.332)	10.25	-
Water index	187.52 (1.055)	196.92	208.26 (.437	208.26 (4.37)	202.96	-
% water content	60.73 (.15)	61.49	62.04 (.75)	62.04 (.75)	66.00	
n	2	1	4	5	1	2

a - excludes, b includes a male which was presumed to have died as a result of starvation during nestling rearing
c - male which was presumed to have died as a result of starvation during nestling rearing
d - two males which were presumed to have died as a result of starvation (includes one birds from GJs data)
e - n=1, because sample included carcasses of GJs and thus keel length not included in the above sample
f - abbreviations and derivation of terms are given in Table 7a
PLDMK=(pectoralis lean dry mass / keel-length) *100

Table 7.6 (b) Females

Summary			Stages in the nesting cycle				
data	Pre-breeding	Laying	Incubation	Rearing	IBI	Post	Laying^a
Live mass	17.6	25.0	22.28 (2.01)	19.53 (2.06)	20.0	19.3	-
Mass/keel	86.7	116.3	102.90 (3.66)	93.26 (8.70)	92.17	-	-
Residual mass	1.18	3.66	0.42 (.40)	0.65 (1.23)	-2.16	-	-
Dry mass (DM)	6.5499	9.1024	8.7354 (.751)	7.6382 (1.028)	7.5763	7.3897	6.1165
Lean DM (LDM)	5.4103	7.3605	6.4515 (.224)	5.8765 (.316)	6.2124	5.5844	5.0516
PLDM	0.8550	1.0993	1.0879 (.051)	0.9944 (.077)	1.0370	0.8772	0.7056
PLDMK	4.21	5.113	5.02 (.19)	4.75 (.31)	4.78	-	3.53
PLDMres	0.04	0.06	0.02 (.01)	0.06 (.03)	-0.04	-	-
Lipid content	1.1396	1.7359	2.2839 (.607)	1.7617 (.718)	1.3827	1.8053	1.065
Lipid index	21.1	23.6	35.0 (8.91)	28.89 (10.64)	22.3	32.3	21.1
Water content	11.1	15.8976	13.5396 (.336)	11.8951 (1.06)	11.24	11.90	-
Water index	204.2	215.8	210.1 (2.11)	201.7 (7.35	200.0	213.3	-
% water content	62.8	63.6	60.1 (1.54)	61.1 (1.54)	62.1	61.7	-
n	1	2	4	3	1	1	

a - abbreviations and other notes are as in Table 7.6a and Table 7a

7.3.4.1 Lipid reserves

Total lipid content of males was lowest during the Pre-breeding period, peaked during Incubation followed by a decline during the Nestling period. Although exclusion of a male which starved while rearing nestlings made the lipid index of rearers higher than in the other two stages, since this particular male was found dead in the nest and mortality was attributed directly to feeding an enlarged brood, there is no sound reason for its exclusion (Table 7.6a).

Female lipid index was also highest during Incubation and lowest during the Pre-laying and Laying periods. Notably, the female which died during the laying period had a lipid index similar to that of a single Pre-laying female. These two birds had the lowest lipid indices of all stages compared (Table 7.6b).

7.3.4.2 Protein reserves

Live mass, DM and LDM, PDM and PLDM were all highest for males during the Incubation period and lowest during the Pre-breeding period (Table 7.6a). All dry and lean dry masses were lowest for the male suspected of dying from starvation, particularly PLDM. When adjusted for keel length, both residual live mass and PLDM were negative in nestling rearers and most extreme for the starved male. The LDM of pectoralis muscles, as a percentage of total lean dry mass, was lowest for starved birds, implying that protein reserves were also utilised during periods of nutrient stress.

Variation in female protein reserves during the nesting cycle can be summarised as follows (Table 7.6b):

DM : Laying >Incubation >Rearing >Inter-brood>Post-br >Pre-br> Laying anomaly

LDM&PLDM: Laying >Incubation >Inter-brood >Rearing >Post-br>Pre-br >Lay anomaly

PART II - LIVE BIRDS

7.3.5 VARIATION IN MEASURES OF BODY CONDITION OF ADULT SWALLOWS DURING THE BREEDING CYCLE IN RELATION TO YEAR, BODY SIZE AND AGE

Mean and standard error values of male and female body mass for each stage in the nesting cycle during 1987, 1988 & 1989 are given in Appendices 7.3a & 7.3b and fat scores Appendices 7.4a & 7.4b, for first and second broods respectively; age-related differences in mass for different stages in first brood nesting cycle are presented in Appendices 7.5a & 7.5b for males and females respectively.

7.3.5.1 Annual variation

For both sexes, and for first and second broods at each stage of the nesting cycle, there

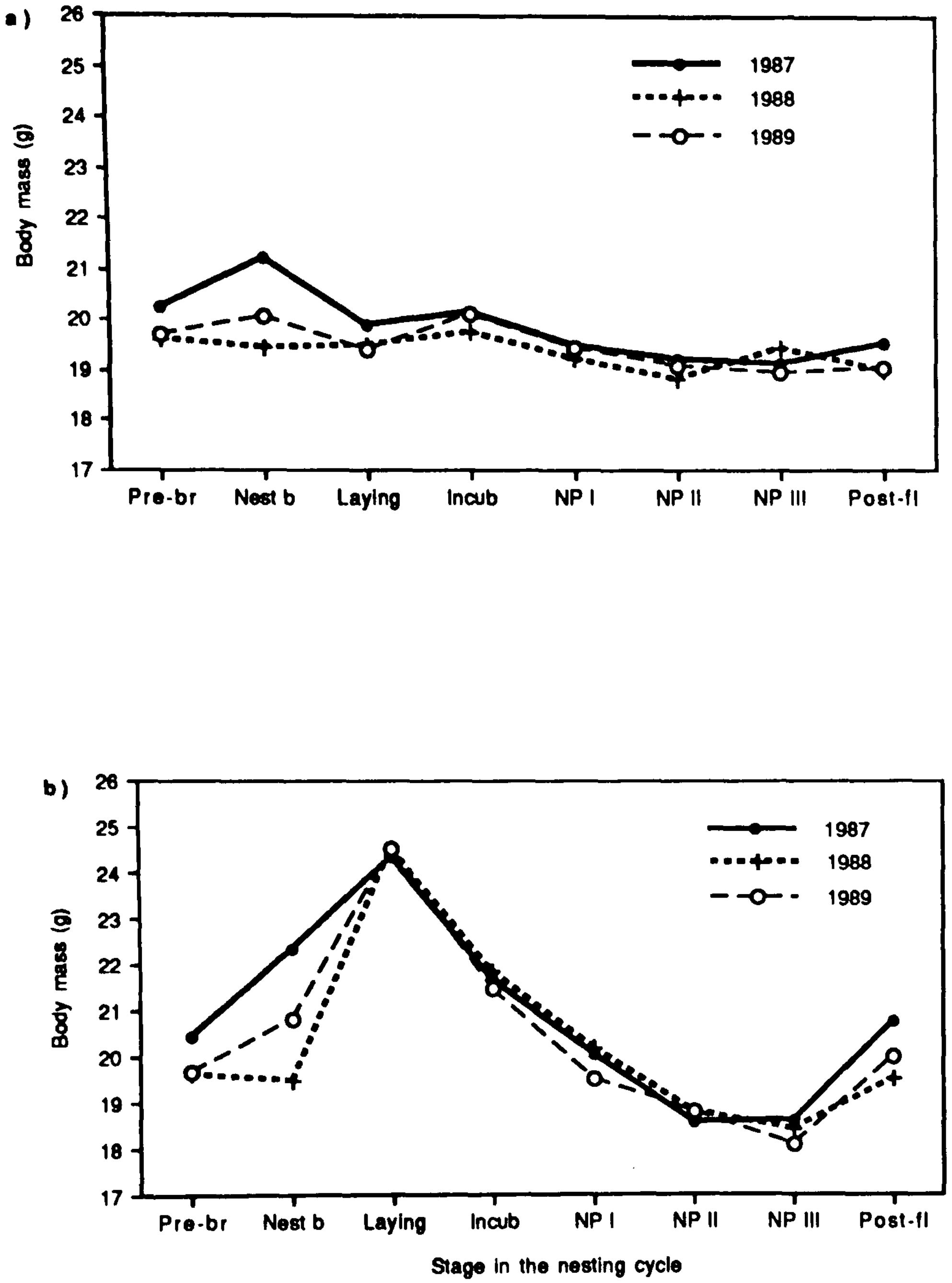


Fig 7.8 Variation in adult body mass of Swallows during the nesting cycle (1st broods), by year: a) Males and b) Females

Only mean values are plotted. Sample sizes, mean and se values are given in Appendix 7.3a

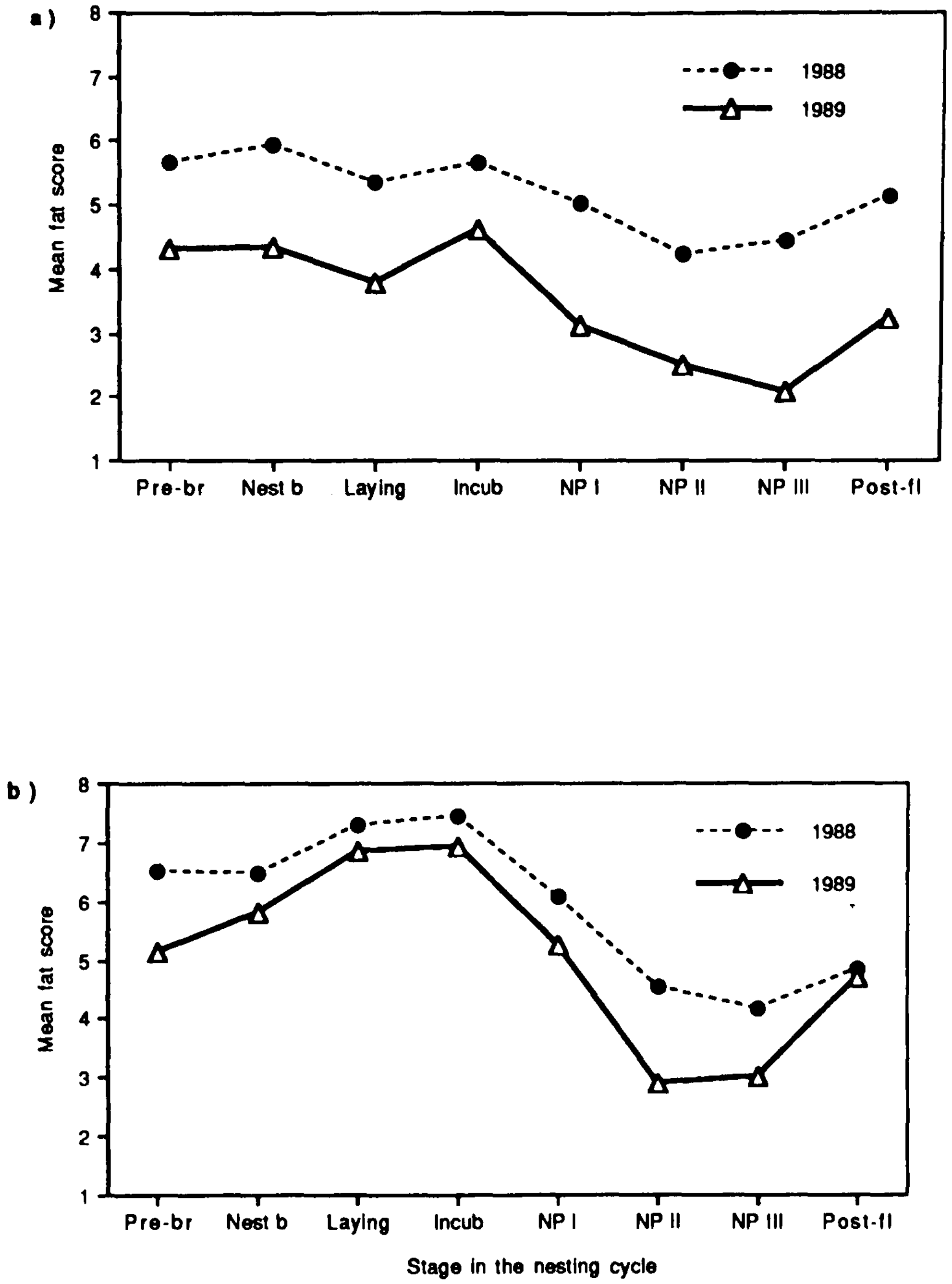


Fig 7.9 Variation in mean fat scores of adult Swallows during the nesting cycle (1st brood), by year: a) Males and b) Females

Only mean values are plotted. Sample sizes, mean and se values are given in Appendix 7.4a were only a few significant differences in body mass between years (1987, 1988 and 1989, Table 7.7a, Figs 7.8a,b): (i) first brood males during Nest building were significantly heavier in 1987 than in 1988 (21.2 vs 19.4, $p<0.001$ and 1989 vs 20.1, $p<0.05$, Table 7.7a) and, (ii) Post-fledging females in 1987 (first brood) were heavier than in both other years, significantly so for 1988 (20.8 vs 19.5, $p<0.05$; Table 7.7a). Fewer birds were captured during second broods so comparisons between years could not be made for all stages. Males during nestling rearing (NP I, II and III combined) were heavier in 1987 than in 1988 (20.0 vs 19.2, $p<0.05$ and 1989 vs 18.7, ns; Table 7.7b). There were no significant differences in female body mass during second broods between years. In view of these findings data for all years were pooled.

At all first brood stages males had a significantly lower MFS in 1989 than in 1988 (Table 7.8, Fig 7.9a). Trends were similar, though less marked, for females and significantly so during first brood Pre-breeding and NP II ($p<0.000$; Table 7.8, Fig 7.9b). The trend was similar for comparisons based on second brood data (Table 7.8). It was, therefore, concluded that an 'error' in the system of scoring resulted in birds being given higher fat scores in 1989 (*cf.* 1988) and so it was not valid to pool 1988 and 1989 data for fat scores.

7.3.5.2 Body size variation

Results in Part I from carcass analyses indicated that keel-length was the most highly correlated body size measure with body mass. The relationship of body mass to body size was further explored using the much larger data set collected on live birds between 1987 and 1989. Some birds were captured several times so a mean value was computed for each individual. Correlations of tail-length (outer and inner) with body mass were weak, non-significant and more variable between years (data not presented). Wing, head-to-bill and keel-length correlations with mass were similar between years so only pooled data are discussed below.

A linear regression model which included all data, showed that keel-length explained most variation in body mass; 13% and 11% for males and females respectively (Table 7.9a). Head-to-bill (9% & 5%) and wing length (7% & 4%) were also significantly and positively correlated with body mass in both sexes. The total variation in body mass explained increased slightly using a model which included keel-, head-to-bill, wing- and outer tail-length for males and keel- and wing-length for females (Table 7.9b). All correlations were positive except for outer tail-length. Analysing only first broods produced a similar result between mass and keel length. More variation in mass was explained by body size when only incubating birds were considered (26%, Fig 7.10a & 19%, Figs 7.10b; males and females respectively). The following equations were used to calculate an expected (Exp) mass for a bird of a given size:

Equation 7.4 Males: $Y_{Exp} = (0.368^*\text{keel}) + (0.334^*\text{head to bill}) + (0.067^*\text{wing}) - (0.013^*\text{outer tail}) - 5.6324$

Equation 7.5 Females: $Y_{Exp} = (0.0685^*\text{keel}) + (0.088^*\text{wing}) - 5.135$

Table 7.7 **Comparison of body mass at different stages of the nesting cycle between years, split by sex, using the Students t-test**

(a) **First broods**

Stage in the nesting cycle	Sex	1987 v 1988		1987 v 1989		1988 v 1989	
		t	sig	t	sig	t	sig
Pre- breeding	M	1.42	ns	1.03	ns	-0.47	ns
	F	1.33	ns	1.10	ns	0.41	ns
Nest Building	M	3.20	* *	1.99	*	-2.08	*
	F	1.60	ns	1.98	ns	0.56	ns
Laying	M	0.30	ns	0.81	ns	0.45	ns
	F	-0.21	ns	0.32	ns	0.67	ns
Incubation	M	1.06	ns	0.07	ns	-1.11	ns
	F	-0.62	ns	0.53	ns	1.40	ns
Nestling period I	M	0.62	ns	0.13	ns	-0.49	ns
	F	-0.37	ns	1.32	ns	1.81	ns
Nestling period II	M	1.02	ns	0.38	ns	-0.91	ns
	F	-0.73	ns	-0.68	ns	-0.04	ns
Nestling period III	M	-0.54	ns	0.27	ns	0.70	ns
	F	0.37	ns	1.29	ns	0.39	ns
Nestling (All)	M	1.08	ns	0.47	ns	-0.60	ns
	F	0.38	ns	0.73	ns	0.45	ns
Post fledging	M	1.01	ns	0.87	ns	-0.07	ns
	F	2.04	*	1.15	ns	-0.60	ns

a - comparisons are based on mean and se values given in Appendix 7.3a.

Table 7.7 Contd. (b) Second broods[a]

Stage in the nesting cycle	Sex	1987 v 1988		1987 v 1989		1988 v 1989	
		t	p	t	p	t	p
Pre- Laying	M	-	-	-	-	-0.15	ns
	F	-	-	-	-	0.14	ns
Laying	M	-	-	-	-	-0.62	ns
	F	-	-	-	-	-0.69	ns
Incubation	M	1.30	ns	2.06	0.062	-0.62	ns
	F	-0.22	ns	0.54	ns	1.16	ns
Nestling period I	M	1.11	ns	-	-	-	-
	F	0.54	ns	-	-	-	-
Nestling period II	M	1.20	ns	1.99	0.060	1.22	ns
	F	0.18	ns	0.48	ns	0.52	ns
Nestling period III	M	2.73	*	-	-	-	-
	F	-	-	-	-	-	-
Nestling (All)	M	2.52	*	2.58	*	1.06	ns
	F	0.96	ns	1.17	ns	0.88	ns
Post fledging	M	-0.57	ns	-	-	-	-
	F	1.50	ns	-	-	-	-

a - comparisons are based on mean and se values given in Appendix 7.3b.

Table 7.8 Comparison[a] of mean fat scores for different stages the nesting cycle between years 1988 v1989, split by sex and brood number, using the Students t-test

	Males				Females			
Stages in the nesting cycle	1st		2nd		1st		2nd	
	t	sig	t	sig	t	sig	t	sig
Pre- br	3.17	* *	-	-	-	* *	0.01	ns
Nest Build	3.58	* *	2.77	*	1.47	ns	1.03	ns
Laying	2.86	* *	0.04	ns	0.94	ns	-0.98	ns
Incubation	2.56	*	4.02	* * *	2.51	ns	-	-
NP[b] I	3.85	* * *	-	-	1.65	ns	-	-
NP II	4.92	* * *	-	-	5.81	* * *	-	-
NP III	2.70	*	-	-	0.68	ns	-	-
NP (All)	6.68	* * *	-	-	3.48	* *	-	-
Post-fledging	3.52	* *	-	-	0.18	ns	-	-

a - comparisons are based on mean (se) values in Appendix 7.4a,b, for first and second broods respectively

b - nestling period

Table 7.9a **Pearson correlation coefficient matrix[a] of adult body mass with adult body size, split by year and sex (Coefficient, (n), significance)**

Body		Males		All		Females			All
mass	size	1987	1988	1989	years	1987	1988	1989	years
All[b]	Keel	0.39 (102) * * *	0.29 (160) * * *	0.44 (118) * * *	0.36 (380) * * *	0.30 (96) * *	0.26 (163) * * *	0.42 (129) * * *	0.33 (388) * * *
	Head	0.28 * *	0.27 * *	0.48 * * *	0.30 * * *	0.18 ns	0.26 * * *	0.29 * * *	0.22 * * *
	Wing	0.28 * *	0.29 * * *	0.21 *	0.26 * * *	0.17 ns	0.30 * * *	0.15 ns	0.21 * * *
All[b] first broods	Keel	0.37 (56) * *	0.28 (109) * *	0.40 (95) * * *	0.34 (260) * * *	0.28 (68) *	0.22 (120) *	0.41 (111) * * *	0.31 (299) * * *
	Head	0.22 ns	0.35 * * *	0.43 * * *	0.32 * * *	0.15 ns	0.21 *	0.28 * *	0.18 * *
	Wing	0.32 *	0.33 * * *	0.19 ns	0.28 * * *	0.17 ns	0.18 *	0.10 ns	0.14 ns

a - for each year correlations were based on a mean measure of body size

b - all laying females have been excluded.

Table 7.9b **Stepwise Multiple regression[a] of adult Swallow body mass on body size, split by sex**

Sex	Analysis	Variables entered	Cumulative r^2	B	Beta	T	Sig T
Male	All	Keel (K)	12.2	0.37	0.24	4.56	0.000
		Head-to-bill (HB)	16.0	0.33	0.19	3.72	0.000
		Wing (W)	17.2	0.07	0.17	3.16	0.001
		Outer tail (OT)	18.1	-0.01	-0.11	-2.17	0.010
		Constant	-5.63	-	-	-1.82	0.069
Female	All	Keel	11.5	0.68	0.31	6.43	0.000
		Wing	13.4	0.09	0.16	3.28	0.001
		Constant	-5.13	-	-	-1.40	0.164
Male	Incubation	Keel	26.0	0.79	0.50	5.65	0.000
		Constant	2.70	-	-	1.033	0.304
Female	Incubation	Keel	19.1	0.95	0.39	5.99	0.000
		Head-to-bill	20.6	0.36	0.15	2.29	0.010
		Constant	-9.39	-	-	-1.97	0.010

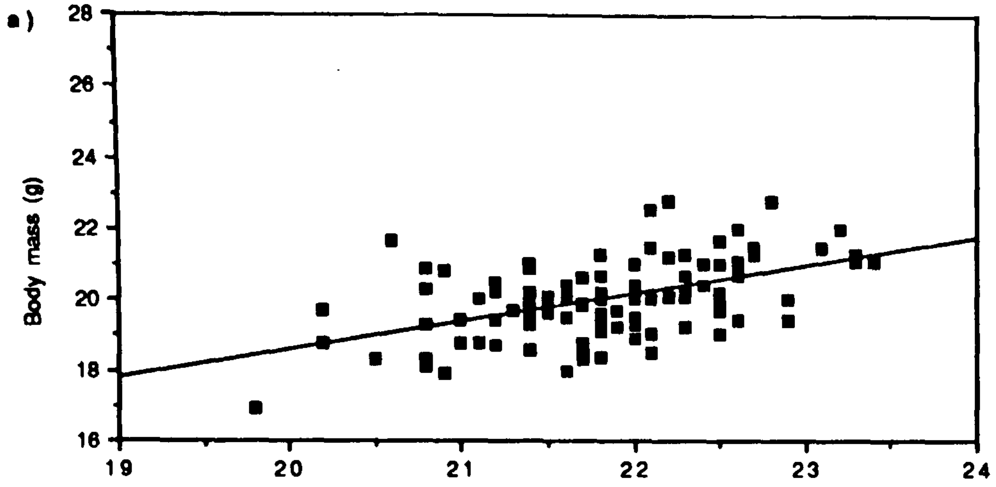
a - independent variables included in analyses were: wing, outer tail, inner tail, head-to-bill and keel-length (1987 to 1989). Trends were similar in each year so only pooled data are presented. For each bird a mean value per year was calculated. Inclusion of onlya mean value per individual measured in successive seasons, did not alter results.

Eqn. 1: $\text{All}_{male}\,Y_{mass} = (.368^{*}K) + (.334^{*}HB) + (.067^{*}W) - (.013^{*}OT) - 5.6324$

Eqn. 2: $\text{All}_{fem}\,Y_{mass} = (.685^{*}K) + (.088^{*}W) - 5.135$

Eqn. 3: $\text{Inc}_{male}\,Y_{mass} = (.794^{*}K) + 2.699$

Eqn. 4 $\text{Inc}_{fem}\,Y_{mass} = (.947^{*}K) + 0.364^{*}HB) - 0.9386$



y = 2.6985 + 0.79427x r^2 = 0.260, r = 0.51; n=99, p<0.000

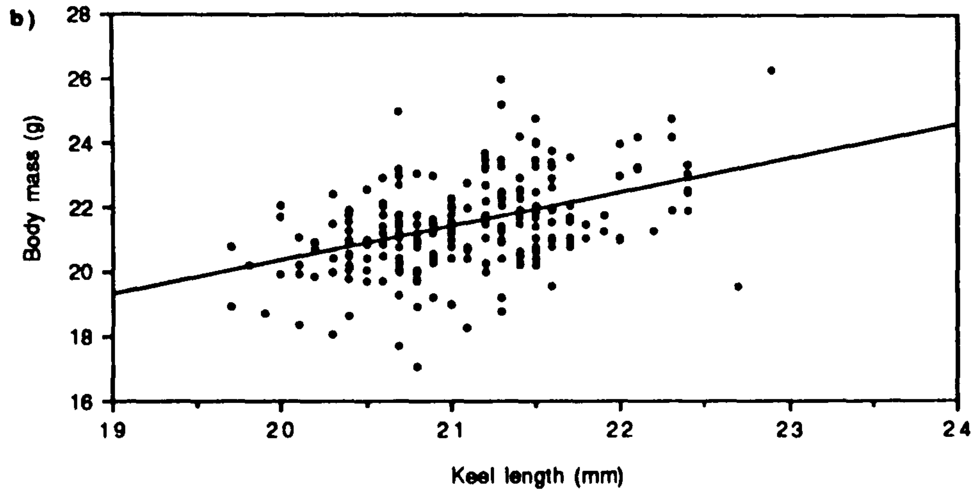


Fig 7.10 Relationship of keel length and average body mass during the incubation period: a) Males and b) Females

note: data are for 1987, 1988 and 1989 and, first and second broods combined. For individuals which were captured more than once a mean value was computed

y = - 0.92985 + 1.0623x r^2 = 0.192, r=0.44; n=215, p<0.000

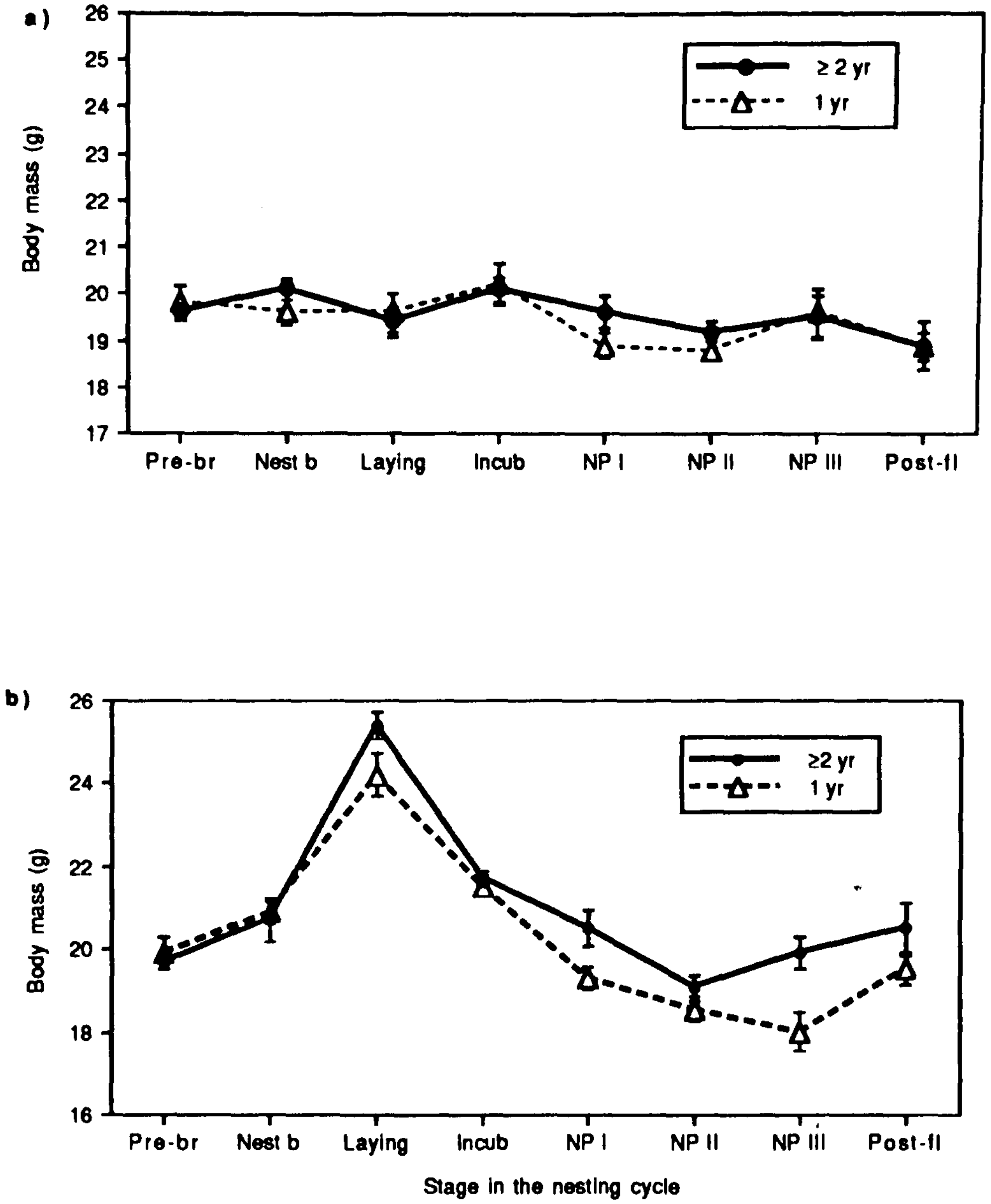


Fig 7.11 Variation in adult body mass at different stages in the nesting cycle (1st brood), by age class: a) Males and b) Females

Mean and se values are plotted; sample sizes are as given in Appendices 7.5a and 7.5b for males and females respectively

To standardise mass in relation to body size, therefore, residual mass was calculated as: $\text{Mass}_{\text{Obs}} - \text{Mass}_{\text{Exp}}$ (see Table 7a).

7.3.5.3 Age-related variation in mass and change in mass

There appeared to be no consistent differences in male body mass with age during the nesting cycle (Table 7.10a, Fig 7.11a). Yearling males were heavier during Pre-breeding, "Laying", Incubation and NP III, but lighter during Nest building, NP I and NP II stages of first broods (all differences were non-significant, Table 7.10a). Yearlings males were lighter in residual mass at all stages (except Incubation), significantly so for Nest building, NP I and NP II ($p<0.05$, Table 7.10a). Yearling females were lighter than older females at all first brood stages, except Pre-breeding and Nest building (both ns), laying (25.4 v 24.2, $p<0.05$) and nestling rearing (NP I, II, III, $p=0.01$; Table 7.10a, Fig 7.11b).

In general both actual and percentage mass loss were greater in yearlings than in older birds, significantly so for change in mass of males between Incubation and Nestling feeding during first (-1.4 vs -2.5, $p=0.048$) and second (-1.4 vs -2.5, $p=0.037$) broods. Mass changes were similar for females (-1.1 vs -0.6, ns). Older females tended to lose more mass (Table 7.10b) between first- and second-brood incubation, and first- and second-brood nestling rearing.

7.3.6 RELATIONSHIP OF BODY MASS , FAT SCORES AND ULTRA-SOUND READINGS

The ultra-sound device was used to measure fifty-six males and eighty-one females comprising a total of 207 readings (MUS) (all were measured during second broods). Body mass and fat scores (MFS) were also taken for this sample of birds. Mass, MFS and MUS were positively inter-correlated in both sexes: Mass vs MFS: $r=0.49$, $r=0.69$ (Fig 7.12a, Fig 7.13a); Mass vs MUS: $r=0.38$, $r=0.69$ (Fig 7.12b, 7.13b); MFS vs MUS: $r= 0.20$, $r=0.45$ (Fig 7.12c, 7.13c), for males and females respectively (all $p<0.000$, except male MUS vs MFS where $p=0.056$).

The relationship of mass and MFS was confirmed for a sample of about 800 birds which were fat-scored and weighed throughout 1988 ($r=0.42_{n=348}$, $r=0.62_{n=439}$, both $p<0.000$ for males and females respectively). As observed for the smaller sample the relationship was stronger for females indicating that they were scored more accurately than males. Visible fat may be more easily scored for females because they have a full brood patch (*cf.* males).

7.3.6.1 Change (Δ) in mass and MFS

Mass and mean fat scores generally changed in the same direction; correlation coefficients (r) varied from 0.67 to 0.75 (males, Fig 7.14a) and 0.52 to 0.61 (females, Fig 7.14b), depending on the delta value (Table 7.11).

Table 7.10a Comparison of body mass (Mass) and size-adjusted[a] body mass (Residual) between one year (1) and older (≥2) Swallows at each stage of the first brood nesting cycle, split by sex, 1988 and 1989 combined. Using the Students t-test

	Males				Females			
Stages in the nesting cycle	Mass		Residual		Mass		Residual	
	t^b	sig	t	sig	t	sig	t	sig
Pre-breeding	0.49	ns	-0.52	ns	0.36	ns	0.38	ns
Nest building	-1.39	ns	-2.18	*	0.37	ns	-0.08	ns
Laying	0.38	ns	-0.41	ns	-2.40	*	-2.25	*
Incubation	1.78	0.084	0.97	ns	-0.85	ns	-0.73	ns
NP I	-1.65	ns	-2.44	*	-2.44	*	-2.42	*
NP II	-1.37	ns	-2.52	*	-1.94	*	-1.76	0.084
NP III	0.15	ns	-0.59	ns	-2.49	*	-1.70	ns
Nestling (All)	-1.50	ns	-1.65	ns	-2.36	* *	-2.21	*
Post fledging	0.00	ns	-0.42	ns	-1.51	ns	-1.23	ns

a - size adjusted masses were calculated using equations 1 (males) and 2 (females) above

Table 7.10b Comparison of changes[a] in body mass (actual) between different stages in the nesting cycle of one year (1) and older (≥2) Swallows, split by sex, 1988 and 1989 combined. Using the Students t-test

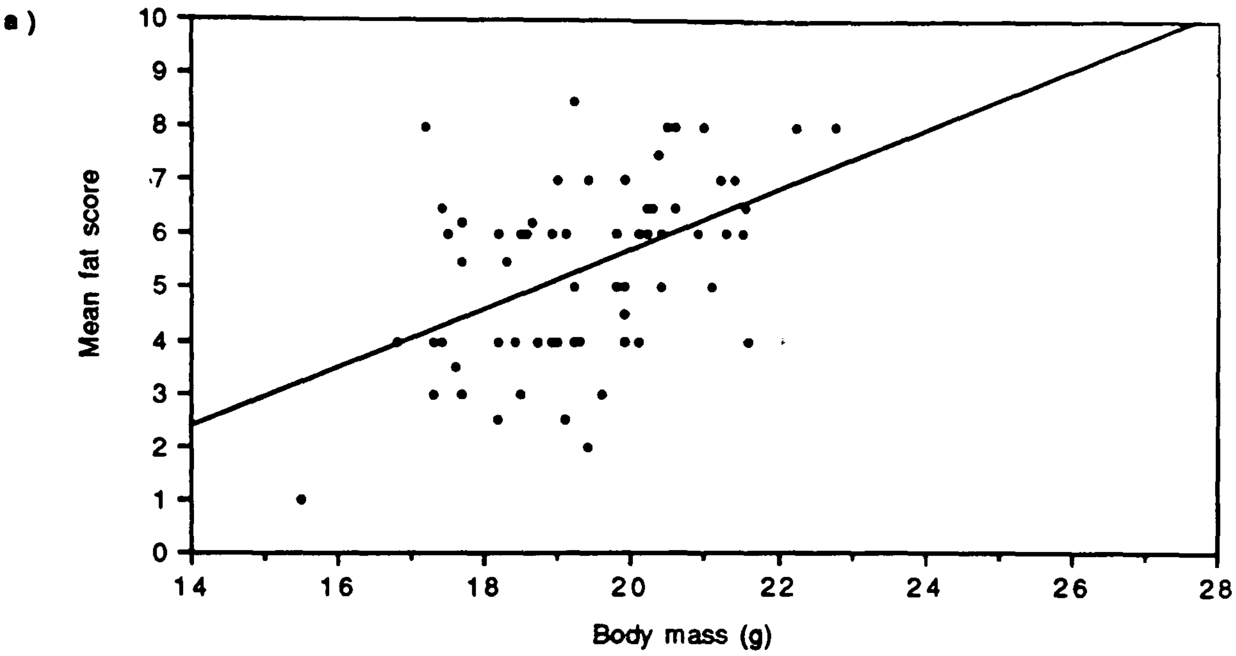
Stages in the nesting cycle	Sex	Age class 1	>2	n	t-test t	df	p
Pre-br(1st)->Incub(1st)	M	-0.2 (.3)	-0.5 (.3)	11,14	0.75	23	0.460
Incub(1st) ->Nestl(1st)	M	-1.1 (.3)	-0.6 (.3)	12,17	-1.26	27	0.223
	F	-3.2 (.2)	-2.5 (.3)	27,24	-2.03	49	0.048
Incub(2nd) ->Nestl(2nd)	F	-2.5 (.3)	-1.4 (.4)	10,11	-2.24	19	0.037
Incub(1st) ->Incub(2nd)	F	-0.77 (.5)	-1.13 (.2)	11,12	0.64	13.8	0.534
Nestl(1st) ->Nestl(2nd)	F	-0.28 (.3)	-0.72 (.3)	12,9	1.13	19	0.271

a - change in mass between two stages in nesting cycle was calculated as follows:
eg. $\Delta\text{Mass}_{\text{Incub(1st)} \rightarrow \text{Nestl(1st)}} = \text{Nestling rearing}_{\text{mass}} - \text{Incubation}_{\text{mass}}$

Table 7.11 Correlation of change in individual mean ultrasound measures (ΔMUS) with changes in mean fat scores (ΔMFS) and body mass (Δmass) in live adult Swallows[a], split by sex (r and significance)

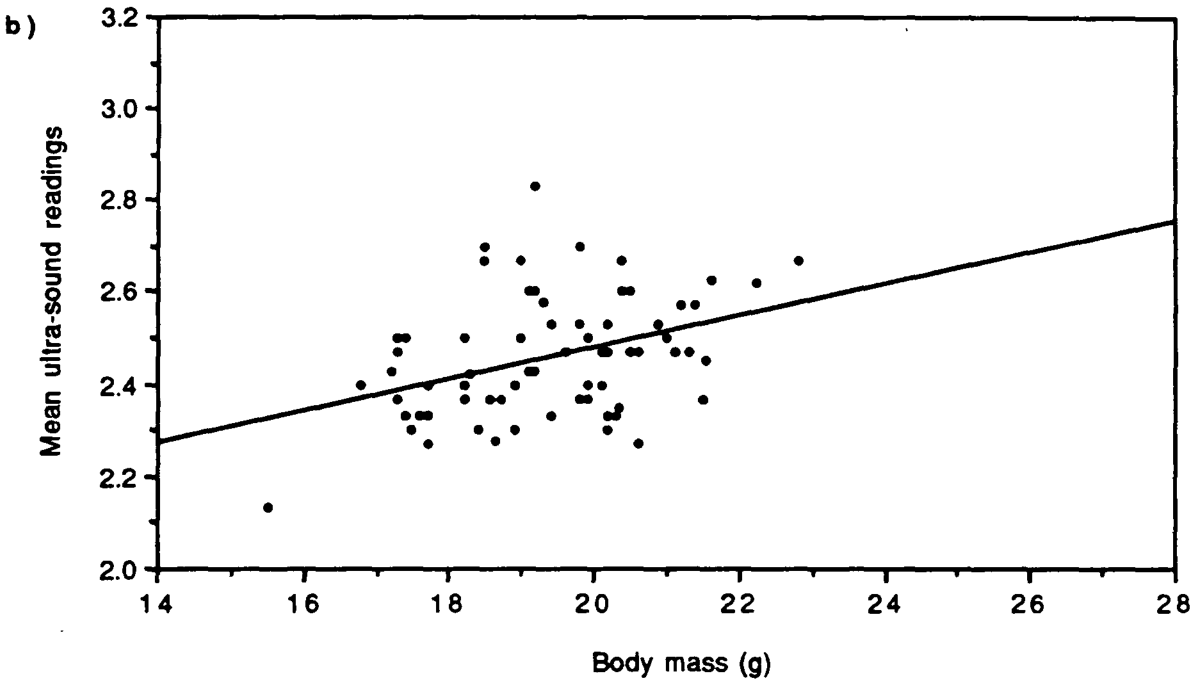
	All			Pairs			Mean	
	ΔMFS	ΔMUS	‖	ΔMFS	ΔMUS	‖	ΔMFS	ΔMUS
Males								
ΔMass	0.67 ***	0.62 ***	‖	0.68 ***	0.61 **	‖	0.75 **	0.61 *
ΔMFS	-	0.72 ***	‖	-	0.72 ***	‖	-	0.71 **
Females								
ΔMass	0.61 ***	0.64 ***	‖	0.52 **	0.66 ***	‖	0.52 **	0.67 ***
ΔMFS	-	0.30 *	‖	-	0.24 ns	‖	-	0.25 ns

a - sample sizes for males = 29, 23,15; Females = 40,33,26 for Mass, MFS and MUS



note: includes only subset of data where ultra-sound readings were also taken

y = - 5.5202 +0.56087x r^2 = 0.237; n=69, p<0.000



y = 1.7928 + 3.4295e-2x r^2 = 0.144; n=69, p<0.001

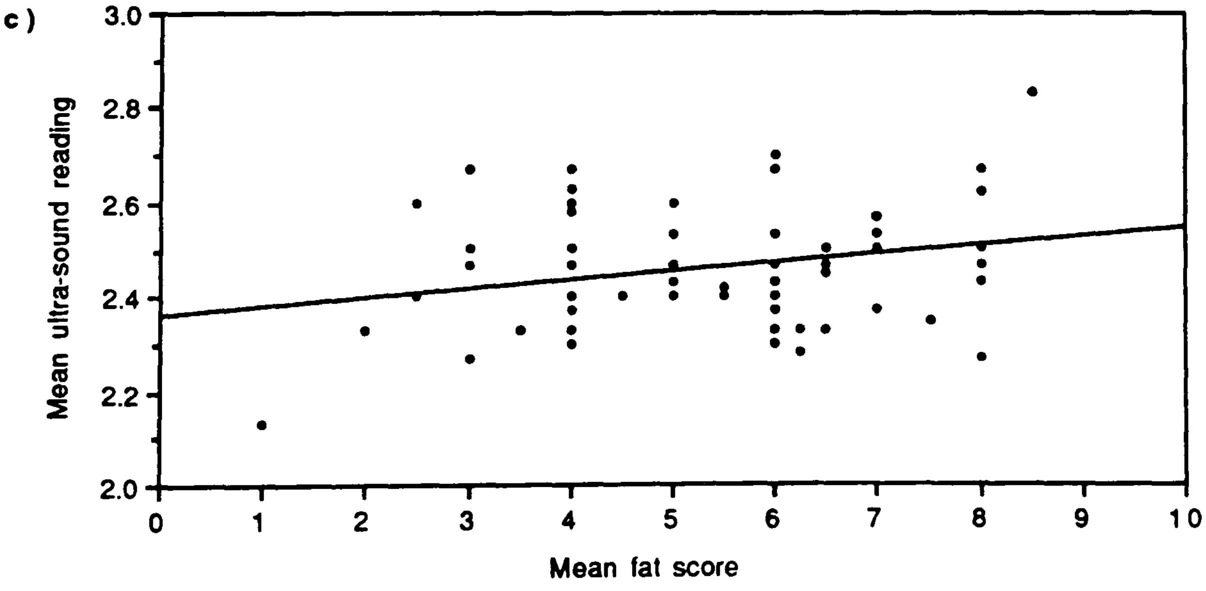
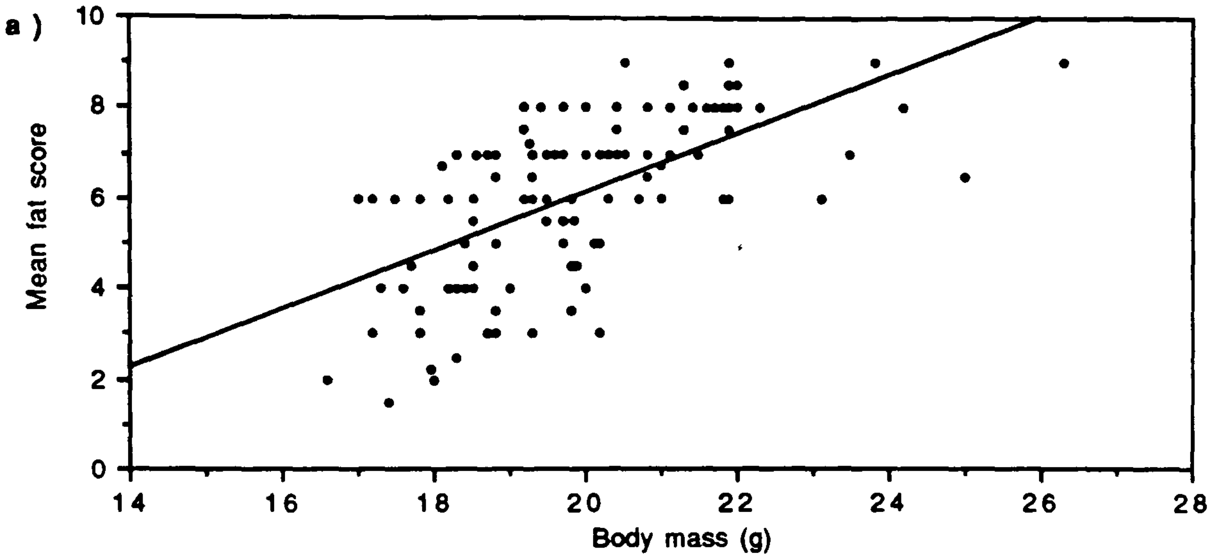


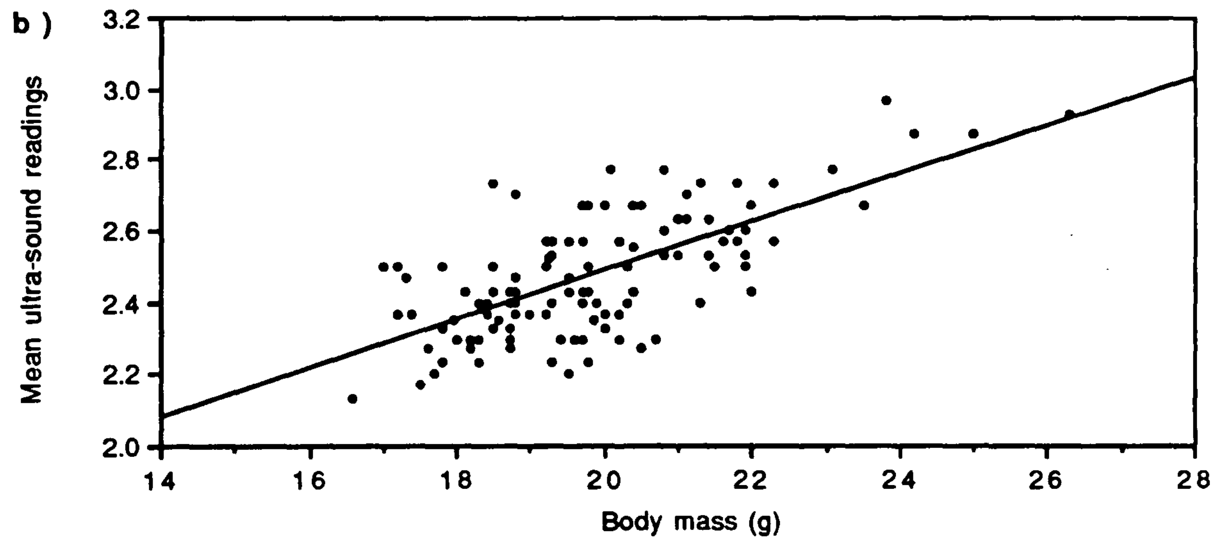
Fig 7.12 Relationship of: a) Body mass and Mean fat score (MFS); b) Body mass and Mean ultra-sound reading (MUS) and c) MFS and MUS in live male Swallows

y = 2.3612 + 1.7933e-2x r^2 = 0.053, n=67, p=0.056



note: includes only subset of data where ultra-sound readings were also taken

y = - 6.7980 +0.64649x r^2 = 0.394; n=112, p<0.000



y = 1.1335 +6.7610e-2x r^2 = 0.473; n=112, p<0.000

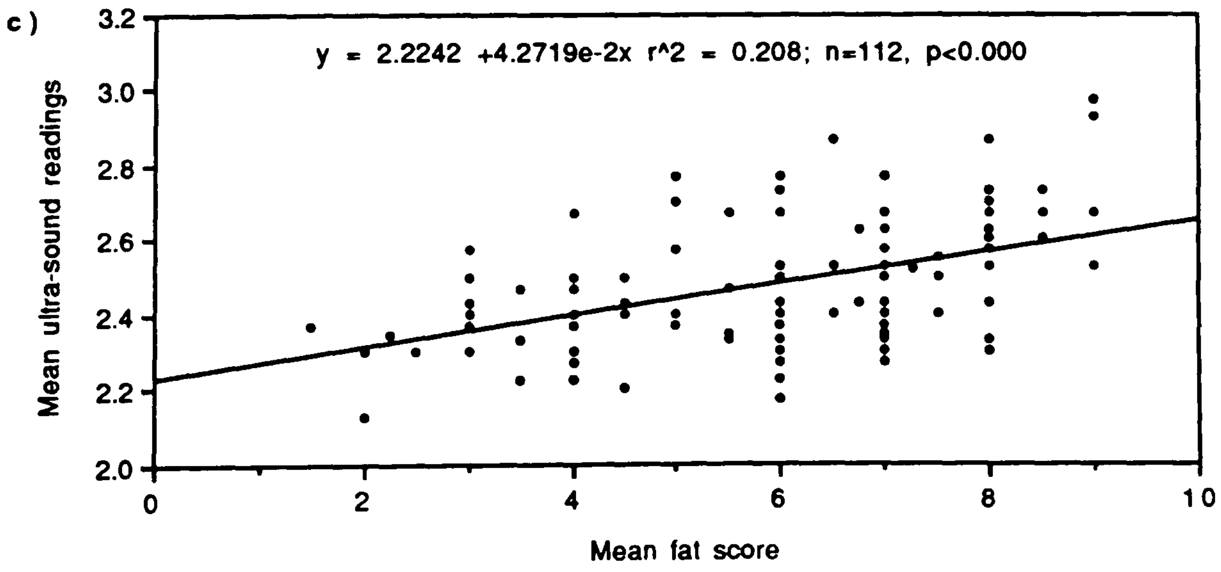
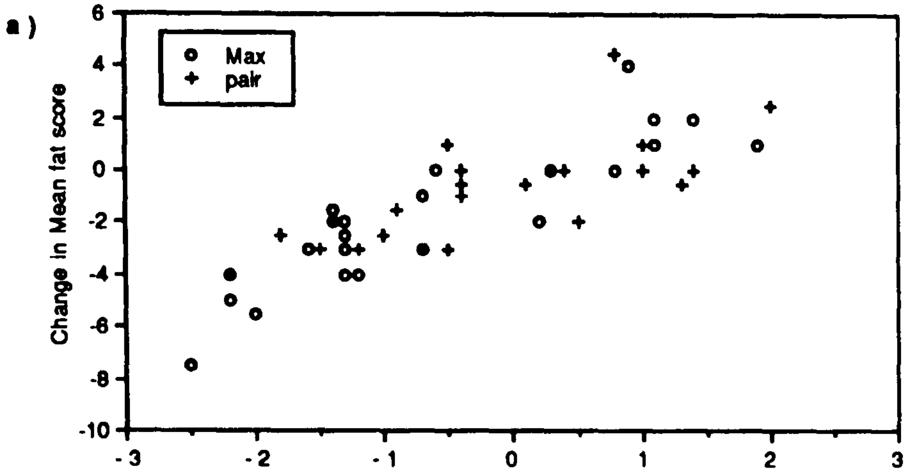


Fig 7.13 **Relationship of: a) Body mass and Mean fat score (MFS); b) Body mass and Mean ultra-sound readings (MUS) and c) MFS and MUS in live female Swallows**



Max: $y = -0.65356 + 1.8581x$ $r^2 = 0.770$; n=24
Pairs: $y = -0.65814 + 1.3594x$ $r^2 = 0.564$; n=24
All : $y = -0.68488 + 1.6563x$ $r^2 = 0.690$; n=48

Max refers to Δmass calculated between max and min values recorded for any individual; pairs to birds which were only measured twice; All is based on all delta values calculated (see text)

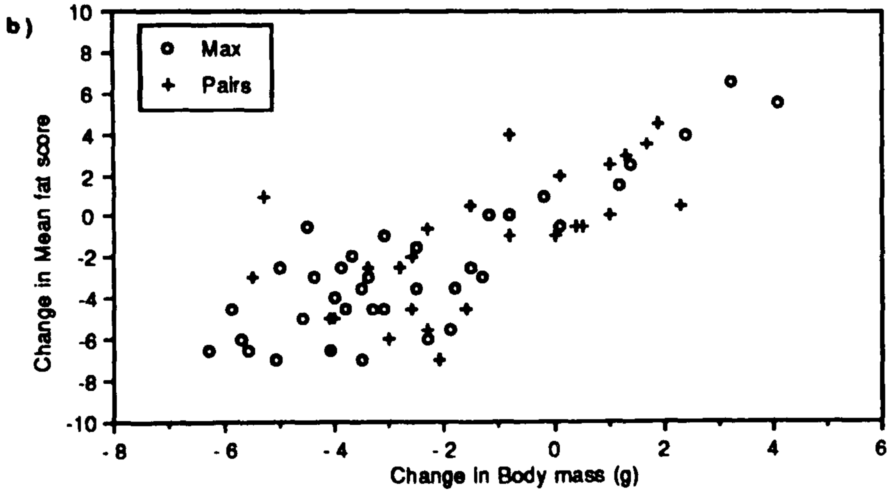
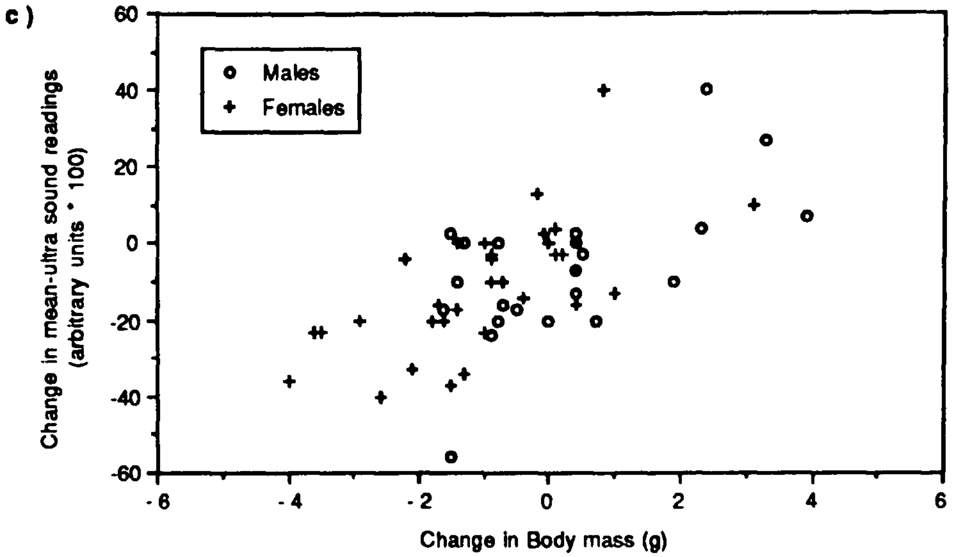


Fig 7.14b Relationship of change in body mass and the associated change in Mean fat score in adult Swallows : a) Males and b) Females

Pairs: $y = 9.3071e{-2} + 1.0003x$ $r^2 = 0.443$; n=27
Max: $y = 0.35197 + 1.1340x$ $r^2 = 0.725$; n=37
All : $y = 0.22312 + 1.0851x$ $r^2 = 0.630$; n=64



male: $y = -8.2017 + 7.0567x$ $r^2 = 0.373$, p<0.001, n=23
female: $y = -3.8834 + 7.3990x$ $r^2 = 0.435$, P<0.000, n=33

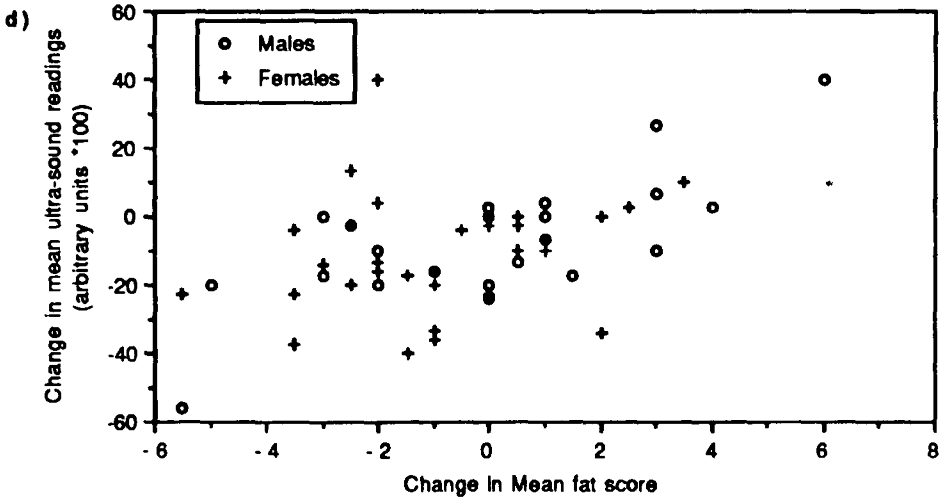


Fig 7.14 Relationship of change in mean ultra-sound readings and associated change in: c) Body mass and d) Mean fat score in adult Swallows, by sex

male: $y = -6.5011 + 4.7373x$ $r^2 = 0.523$, p<0.000, n=23
female: $y = -9.2748 + 1.9248x$ $r^2 = 0.055$, p<0.0.94, n=33

7.3.6.2 Change in mass and MUS

In 36 of 56 cases (64%), body mass and MUS changed in the same direction (Fig 7.14c). The maximum increase and decrease in change of mass over this period was: (Males: Δ+ 3.9, Δ- 1.5g and Females: Δ+3.1, Δ-4.0g). These changes were accompanied by associated changes in MUS of: Δ+7, Δ-3, Δ+10 and Δ -36, for males and females respectively. On only four occasions was a decrease in mass associated with an increase in MUS and on only 10 occasions was an increase in mass associated with a decrease in MUS. Mass changes (Δ mass) explained 37% to 38% and 41% to 45% of MUS for males and females respectively (Table 7.11). This indicated that although body mass and MUS changes were generally positively correlated, changes in body mass might also be associated with changes in other body components (eg. lipid).

7.3.6.3 Change in MFS and MUS readings

Changes in male MFS and MUS were significantly correlated (~ $r=0.70$, all $p<0.001$, Table 7.11). The positive correlation, however, was much weaker for females and was only significant for ΔAll: ($r=0.30$; $p<0.05$, Table 7.11). MUS and MFS changed in the same direction in just over 50% of cases (*cf.* 61% for males, Fig 7.14d). Females were fat scored more accurately than males, so the weaker female correlations for change in fat score were unexpected. Closer inspection revealed that the male correlation was exaggerated by two outliers. Excluding them, however, still yielded a higher r^2 than for females ($r^2=0.26$). Only females showed a lower MFS with higher MUS. Indeed, excluding these two points plus a third outlier (where a small change in fat was associated with a large change in MUS), gave an r^2 of 0.29. There was no obvious reason to account for their departure from the general trend, however.

7.3.7 VARIATION IN ADULT BODY MASS WITH DAY IN THE NESTING CYCLE

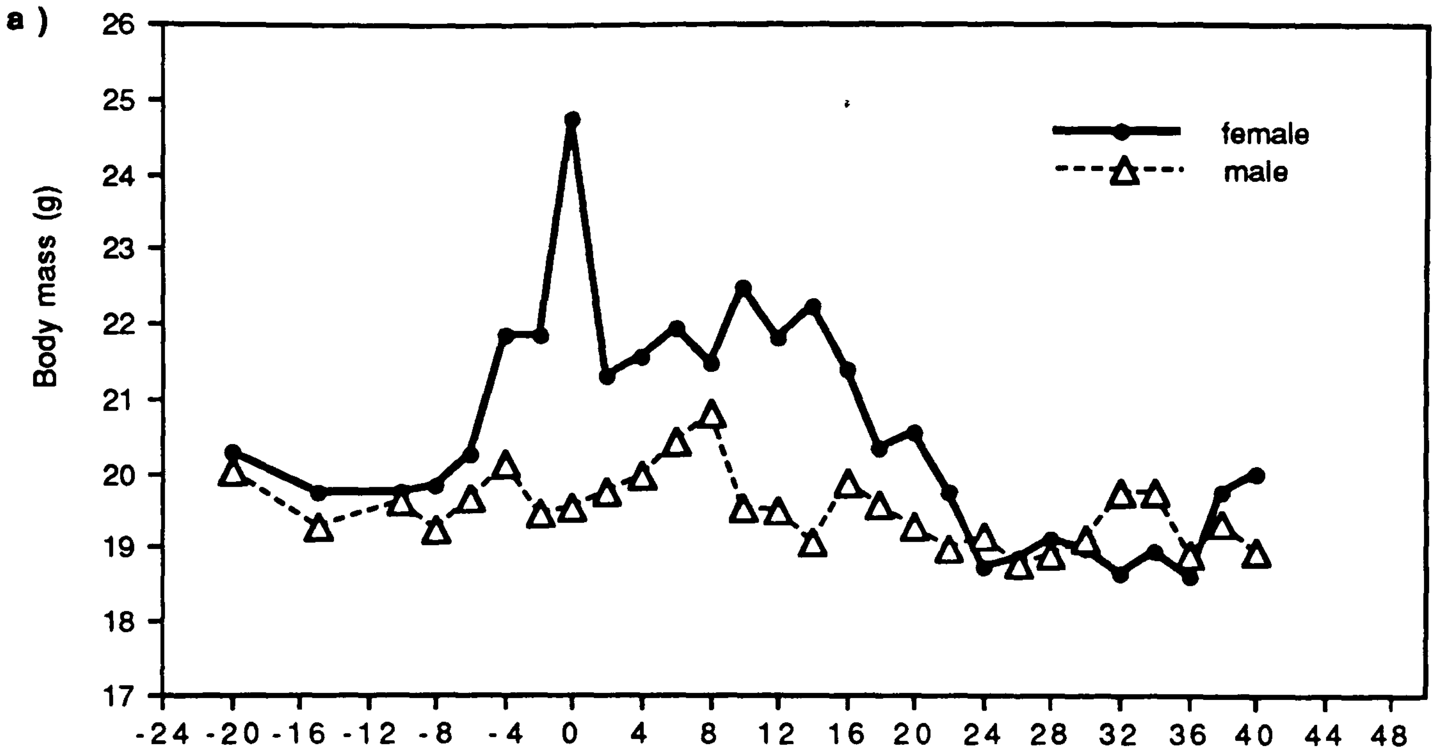
Variation in male and female body mass by day in the nesting cycle (Pre-breeding to Post-fledging) for first and second broods are plotted in Fig 7.15a and 7.15b for first and second broods respectively.

7.3.7.1 Males

There were no significant regressions of mass on day in the nesting cycle at each of the following stages: Pre-laying period 1st, Fig 7.16); Incubation period: (1st, 2nd & both), but overall mass declined through the Nestling Period (1st & 2nd, Fig 7.17a,17b); almost significantly for second broods ($r=0.26$, $p=0.07$). Closer inspection showed that the relationship was not linear but concave. Although males were lighter than females when nestling feeding started from Day 13, they were consistently heavier only showing a lower mass at Day 21, when most nestlings fledged.

7.3.7.2 Females

During the Pre-laying period of first broods, female mass increased significantly with



Female : y = 21.45423 - 0.05821x r^2 = 0.156, p<0.000, n=473

Male : y = 19.58685 - 0.01306x r^2 = 0.004, p<0.000, n=336

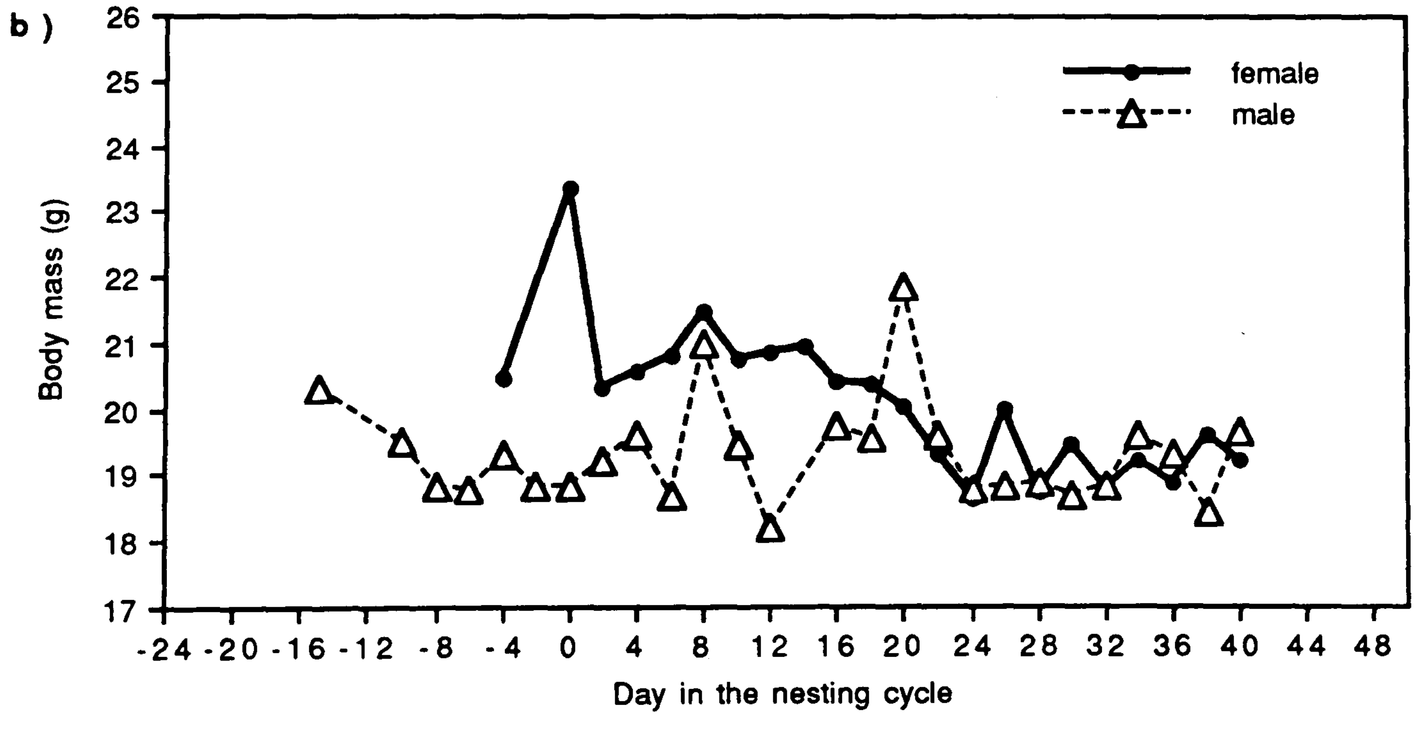


Fig 7.15 Variation in adult body mass of male and female Swallows by day in the nesting cycle: a) First and b) Second broods

Female : y = 21.57752 - 0.07522x r^2 = 0.279, p<0.000, n=193

Male : y = 19.22936 - 0.00417x r^2 = 0.002, p<0.615, n=113

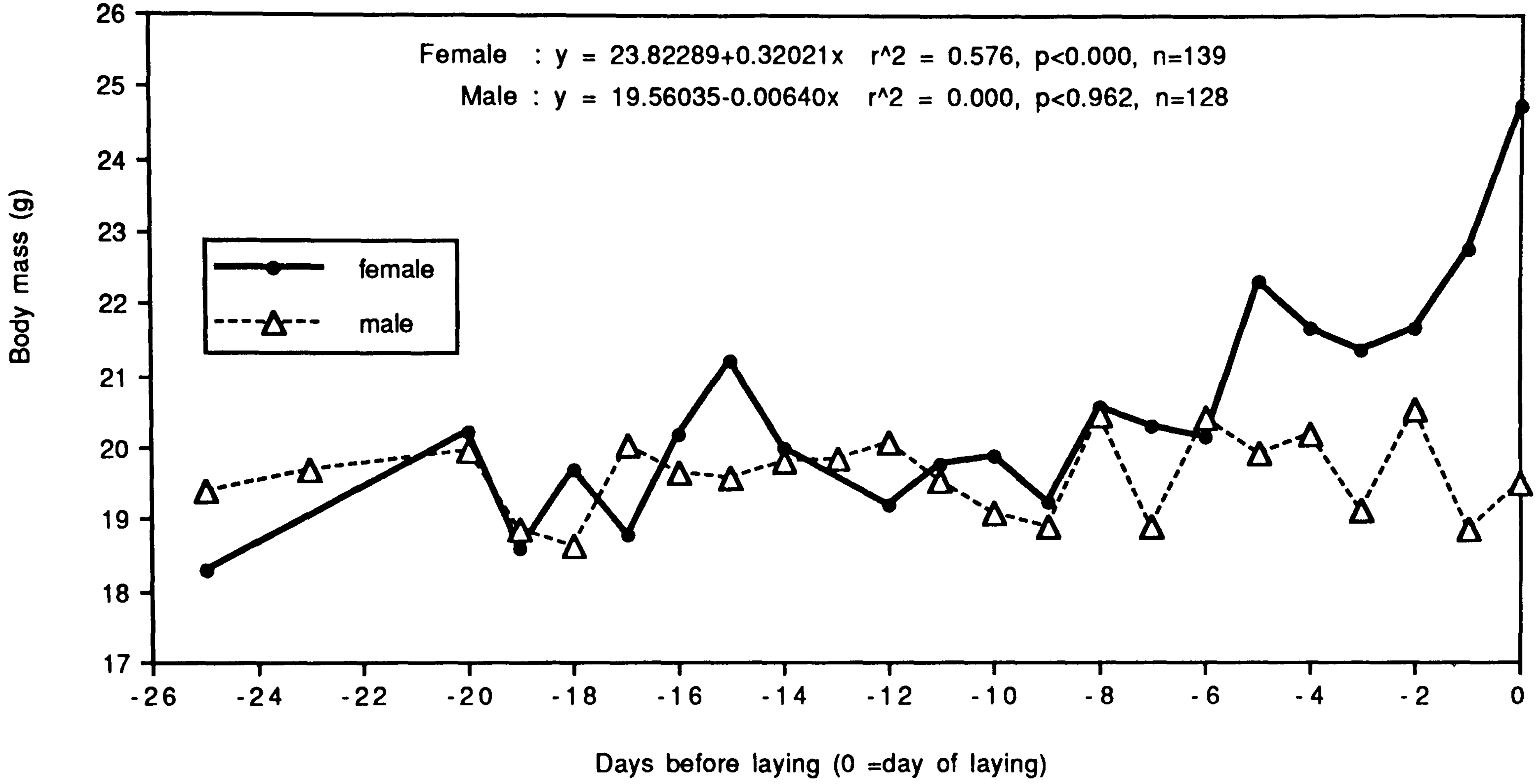


Fig 7.16 Variation in adult body mass of male and female Swallows during the pre-laying period (first brood)

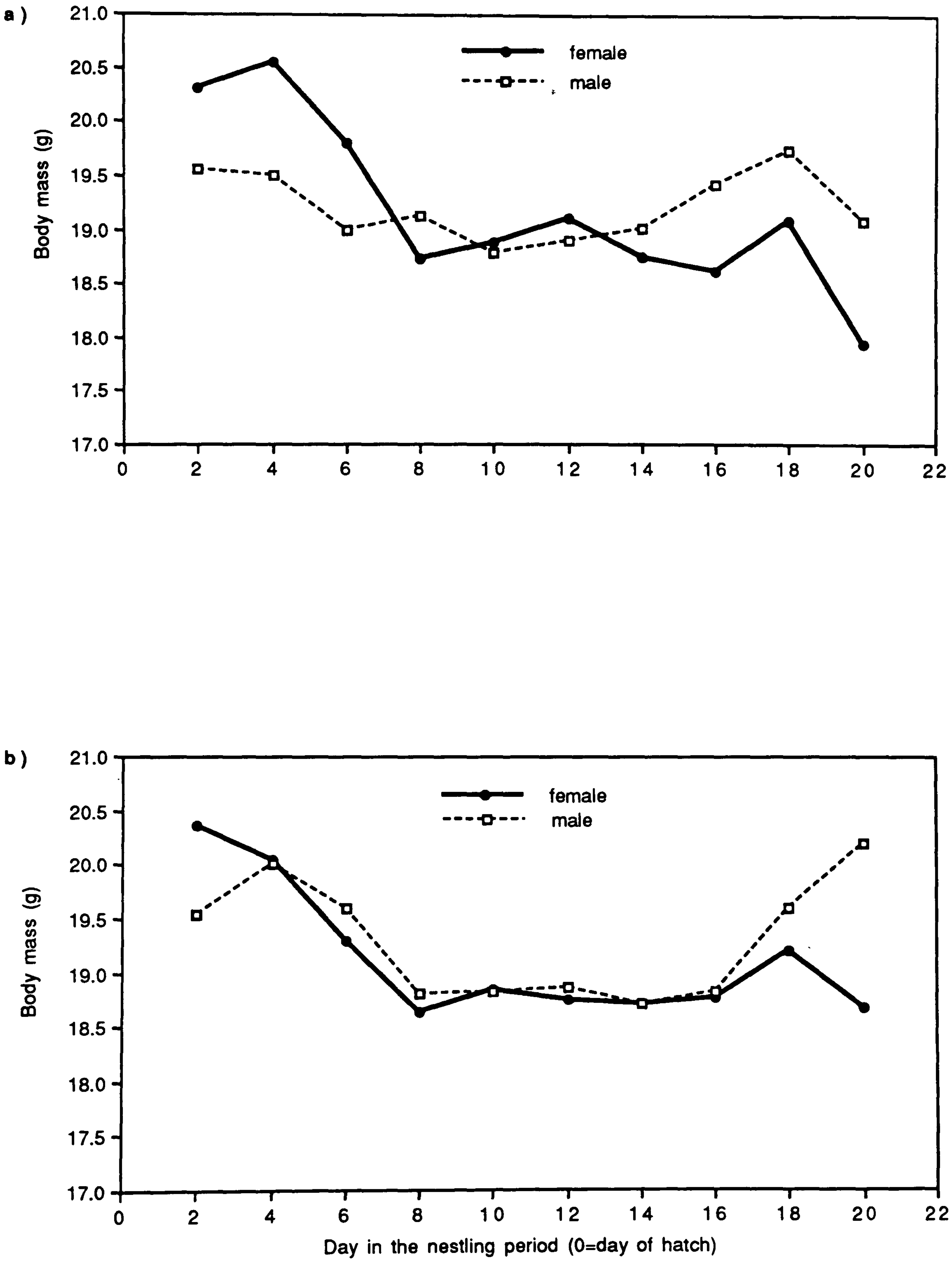


Fig 7.17 Variation in adult body mass during the nestling period, by sex: a) First and b) Second broods

days before laying (r=0.58, p<0.000; Fig 7.16). Mass increased slightly during Incubation but the trend was not significant for first- or second-broods. Greater variation occurred during Nestling rearing; mass declined significantly as nestlings aged (first brood r=-0.41, Fig 7.17a; second brood r=-0.37, Fig 7.17b, both p<0.000). Trends were similar so data were pooled. Mass peaked during the first few days following the hatch and steadily declined through the brooding phase (NP I ≤ 8 days). It was more stable in the middle (NP II) before decreasing to a minimum at fledging, after which it increased.

7.3.8 VARIATION IN ADULT BODY AND MUSCLE THICKNESS DURING THE NESTING CYCLE

7.3.8.1 Males

During first broods, body mass was remarkably constant with never more than a 3% change between successive stages (Fig 7.18): Pre-breeding to Nest building (Δ +0.2g) ; "Laying" period to Incubation period (Δ+0.5g); Incubation period to NP I (Δ-0.6g); and NP III to post-fledging (Δ-0.1g). Maximum (incubation) and minimum (NP II) masses differed by only 1g, representing a mean overall change of only 5% (*cf.* females). Ranking stages, starting from the heaviest, gave:

Incubation> Nest b >Pre-br>Laying>NP I>NP III>Post-fl >NP II

A similar pattern was present in second broods but greater variation existed between successive stages (~Δ -1.6 to +4.5%). The maximum difference occurred between the laying period (18.7g) and post fledging period (20.1g) [Δ 1.4g, 7%]. Males were heaviest after breeding had finished and lightest during the IBI (Fig 7.18):

Post breeding > NP I > Incubation > NP III > NP II > Laying > Inter-brood

Muscle thickness during second broods was highest during "Pre-laying" and Incubation and lowest during the latter stages of Nestling period (NP II and III) (Fig 7.19c)

7.3.8.2 Females

Females increased significantly in mass from arrival on the breeding grounds (Pre-breeding) to Nest building (+6%) and increased further by 15% before peaking during Laying. During Incubation females decreased by 14% followed by further decreases of 9% and 11% from Incubation to NP I and then to NP II (Fig 7.18). There was little difference between NP II and NP III (-2%). After fledging, mass increased by around 10% (Fig 7.18). The greatest difference between any two stages in the nesting cycle was between Laying and NP II (6.2g;~Δ 25%). Excluding laying birds, the maximum difference was between Incubation (21.7g) and NP II (18.5g; Δ=3.2g; 15%), still much greater than the maximum change for males (see above). The lowest change in mass was between NP II and III (0.3g, Δ1.6%) and was not significant. The pattern of mass change

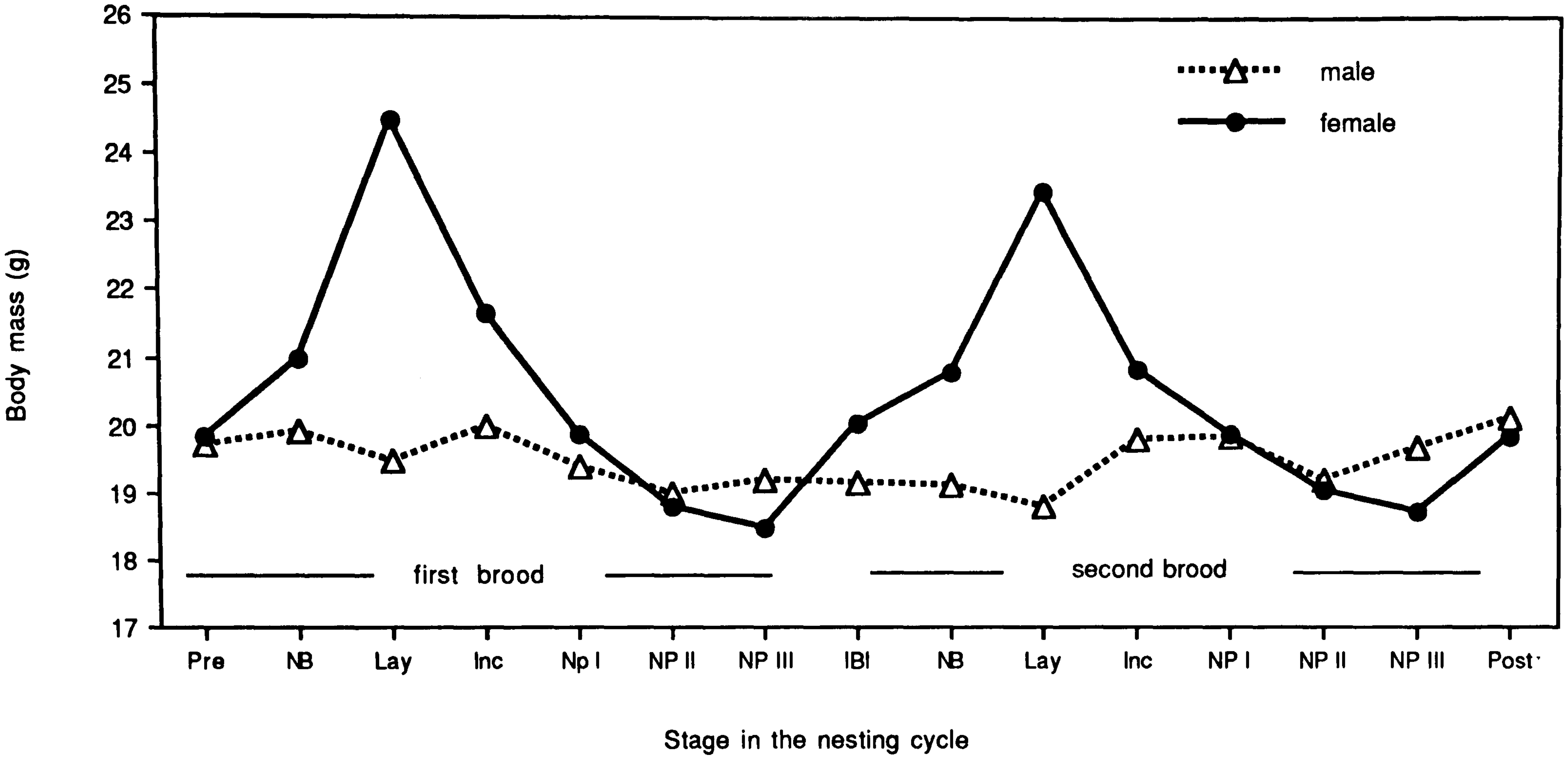


Fig 7.18 Variation in adult Swallow body mass during different stages in the nesting cycle (1st and 2nd broods), by sex

Mean values are plotted; sample sizes and se values are given in Appendices 7.3a and 7.3b for first and second broods respectively. Data are for all years combined.

was similar during second broods (Fig 7.18). Ranking the data in descending order, gave:
First - Laying > Incub > Nest building >Post fl > NP I > Pre-br > NP II > NP III
Second - Laying > IBI > Incubation > NP I > Post -br > NP II > NP III
Measurements of muscle thickness during second broods revealed that protein reserves in females were highest for "Pre-laying" and Incubating females reaching a minimum lowest during the latter stages of Nestling period (NP II and III), but increasing after the young had fledged (Fig 7.19c).

For the same subset of data Mass (Fig 7.19a) and MFS (Fig 7.19b) showed similar trend to MUS (Fig 7.17c) except that while data on body mass indicated a peak during Laying, results based on MFS and MUS showed that a peak occurred while females were Incubating. The increase in mass came, therefore not from an increase in condition but from the presence of an egg and other reproductive material, confirming earlier carcass analysis results.

7.3.9 COMPARISON OF BODY CONDITION BETWEEN SEXES AND BROODS DURING DIFFERENT STAGES OF THE NESTING CYCLE

Males were larger so size-adjusted masses (residual) were also analysed. Data for muscle thickness refer only to second broods (Appendix 7.6).

7.3.9.1 Sex differences

Females were heavier than males (Fig. 7.20a,b) during Pre-breeding (ns, p<0.001), Nest building, Laying and Incubation (both p<0.000), NP I (p<0.05) [*two p values refer to first and second brood differences; a single p means that significance is the same for both*]. Only during NP II (ns) and NP III (p<0.05) were males heavier. Pooling all Nestling rearers (Nestling All) yielded no significant differences between sexes during first (19.2 v 19.2) or second (19.5 v 19.3) broods (Table 7.12a). During the Post-fledging period first brood females were significantly heavier (p<0.001), whereas second broods females were lighter (ns) than males.

Males had heavier residual mass at all first brood stages except Nest building (ns), Laying (p<0.000) and Incubation (p<0.000; Table 7.12a). Trends were more consistent during second broods but residual mass was heavier in males (t=2.04, p=0.045) during NP II whereas actual mass showed the opposite (t=-0.15, ns; Table 7.12a). Differences in muscle thickness between sexes were non-significant for all stages (Table 7.12b, Fig 7.19c).

7.3.9.2 First versus second broods

For both sexes, during Laying (p<0.05,p<0.001) and Incubation (ns, p<0.000), birds were heavier during first- than second-broods [*two p values refer to male and female differences; a single p means that the significance is the same for both sexes*] (Tables 7.13, Fig 7.21a & b for males and females). Males were heavier during the Pre-laying

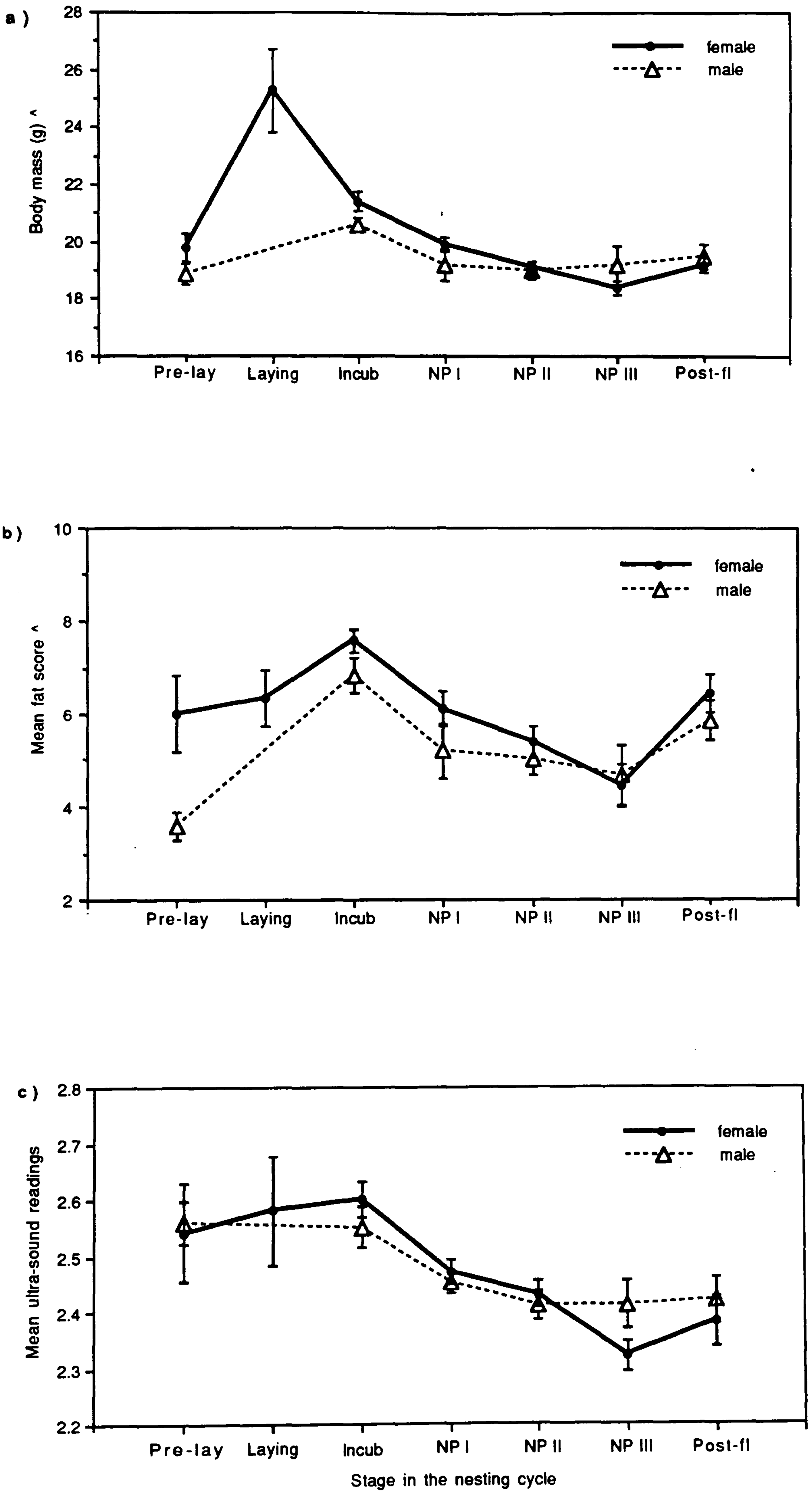


Fig 7.19 **Variation in: a) Body mass; b) Mean fat score and c) Mean ultra-sound of Swallows at different stages of the nesting cycle (2nd br), by sex**

^ includes only subset of data where ultra-sound readings are also taken

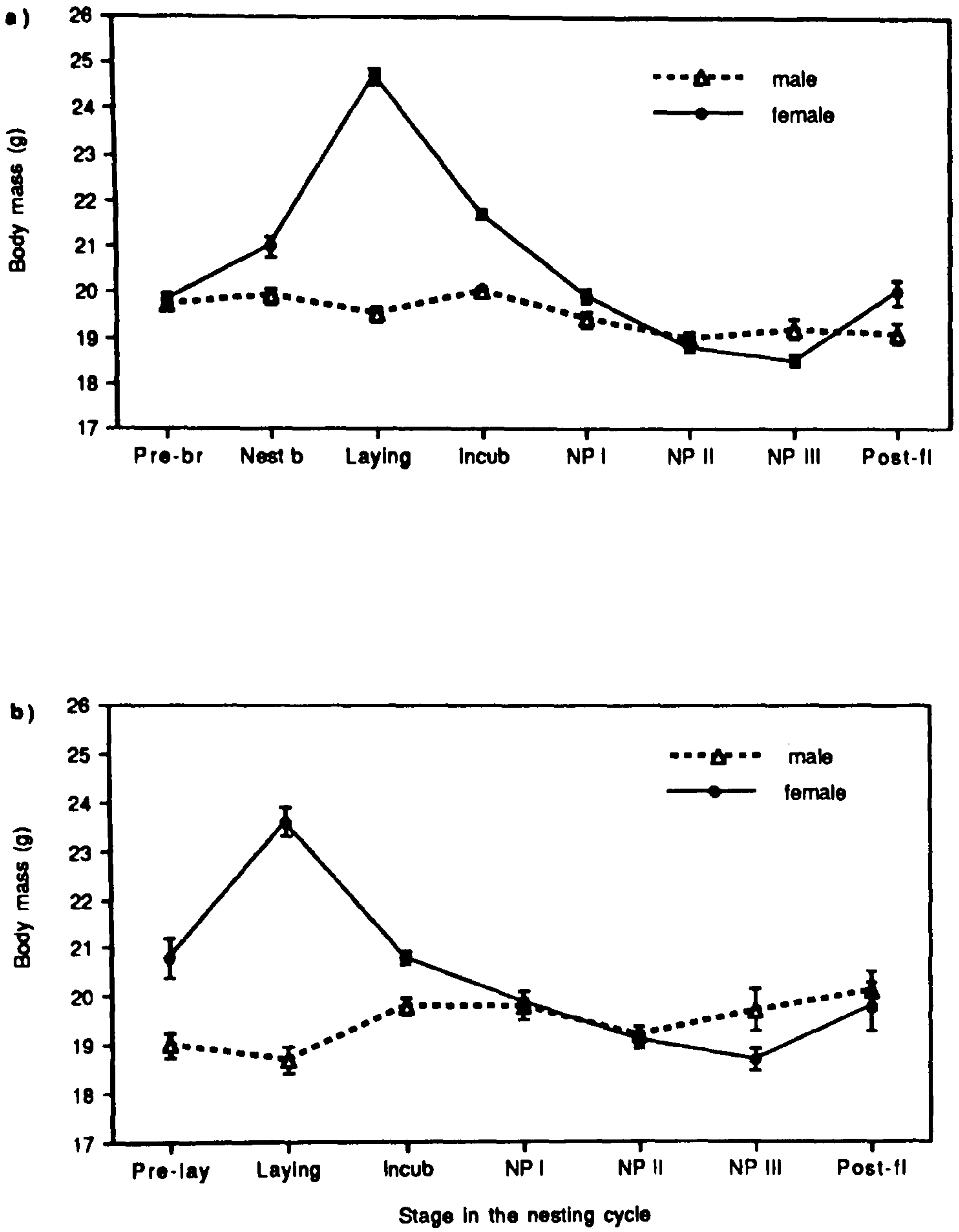


Fig 7.20 Variation in adult body mass at different stages of the nesting cycle, by sex: a) First and b) Second broods

Data are for all years combined. Mean and se values are plotted; sample sizes are as given in Appendices 7.3a and 7.3b for first and second broods respectively

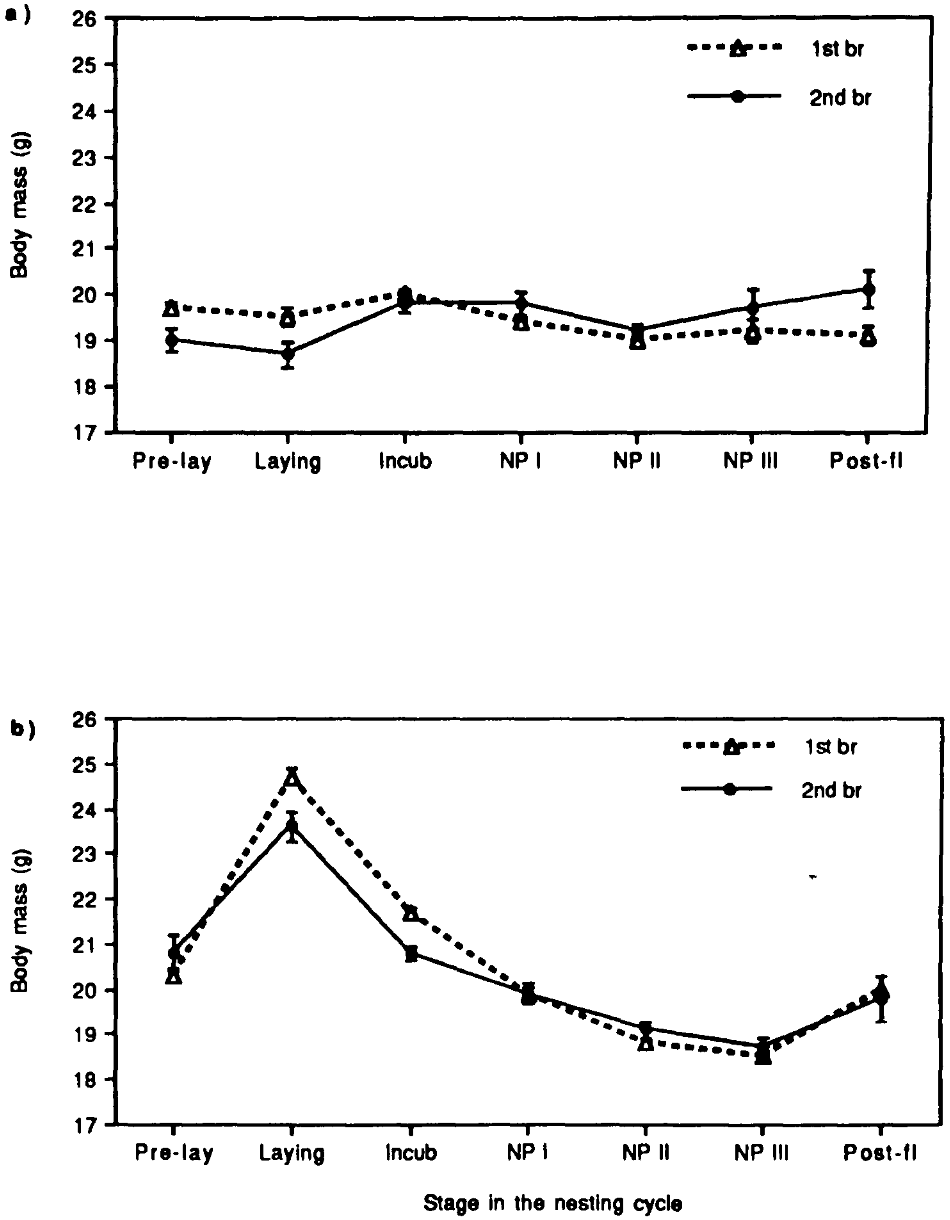


Fig 7.21 Variation in adult body mass at different stages of the nesting cycle, by brood number: a) Males and b) Females

Data are for all years combined. Mean and se values are plotted and along with sample sizes are given in Appendices 7.3a and 7.3b, for first and second broods respectively

Table 7.12a Comparison of body mass (Mass) and size-adjusted[a] body mass (Residual) between sexes at each stage of the nesting cycle, by brood number, using the Students t-test

	First brood				Second brood			
	Mass		Residual		Mass		Residual	
Nesting stage	t[c]	sig	t	sig	t	sig	t	sig
Pre- breeding	-0.78	ns	3.30	* *	-3.82[b]	* *	-2.14[b]	*
Nest building	-4.11	* * *	-0.86	ns	-	-	-	-
Laying^	-18.1	* * *	-17.1	* * *	-10.42	* * *	-11.71	* * *
Incubation	-9.69	* * *	-5.61	* * *	-3.98	* * *	-0.77	ns
NP I	-2.16	*	1.37	ns	-0.15	ns	2.04	*
NP II	1.21	ns	6.43	* * *	0.62	ns	4.57	* * *
NP III	2.26	*	4.76	* * *	2.12	*	4.03	* * *
Nestling (All)[d]	-0.09	ns	6.34	* * *	0.79	ns	3.87	* * *
Post-fledging	-2.64	*	2.04	*	0.41	ns	1.60	ns

a - size adjusted masses were calculated using equations 1 and 2 above for males and females respectively

b - data for Pre-breeding (inter-brood) and Nest building were combined

c - negative values are where females are heavier than females (see also below)

d - data for NP I, NP II and NP III combined.

Table 7.12b Comparison[a] of ultra-sound readings, fat scores and body mass at different stages in the nesting cyclebetween sexes, using Students t-test

Stage in the nesting cycle	Body mass t	Body mass sig	MUS t	MUS sig	MFS t	MFS sig
Pre-laying	-1.59	ns	0.15	ns	-2.93	*
Incubation	-1.90	0.066	-0.92	ns	-1.71	ns
Nestling period I	-1.21	ns	-0.35	ns	-1.35	ns
Nestling period II	-0.33	ns	-0.44	ns	-0.73	ns
Nestling period III	1.37	ns	1.60	ns	0.27	ns
Post-fledging	0.44	ns	0.56	ns	-0.97	ns

a - comparisons are based on mean and se values given in Appendix 7.6.

Table 7.13 Comparison of body mass (Mass) and size-adjusted[a] body mass (Residual) between first and second broods at each stage of the nesting cycle, split by sex, using the Students t-test

	Males				Females			
Stages in the	Mass		Residual		Mass		Residual	
nesting cycle	t[b]	sig	t	p	t	p	t	p
Pre-laying	-2.71	* *	3.44	* *	-0.70	ns	-0.46	ns
Laying	2.20	*	2.58	*	3.37	* *	3.34	* *
Incubation	0.82	ns	1.18	ns	4.35	* * *	5.30	* * *
NP I	1.46	ns	-1.13	ns	-0.02	ns	0.13	ns
NP II	-0.94	ns	-0.34	ns	-1.34	ns	-1.05	ns
NP III	-1.03	ns	-0.75	ns	-0.87	ns	-1.02	ns
Nestling (All)	-1.81	ns	-1.29	ns	-1.02	ns	-1.26	ns
Post fledging	-2.12	*	-2.51	*	0.35	ns	0.57	ns

a - size-adjusted masses were calculated using equations 1 and 2 above for males and females respectively

b - negative t vales are where mass is higher for second relative to first broods.

period (19.7 v 19.0, $p<0.05$), and the Post-fledging period ($p<0.05$; Table 7.13) of first broods. Both sexes tended to be heavier while feeding nestlings during second broods, though differences were small (≤ 0.5g). Overall, males (ns, Fig 7.21a) and females (20.3 v 20.8, ns, Table 7.13, Fig 7.21b) were generally heavier during second broods.

PART III PARENTAL BODY CONDITION, FECUNDITY AND SURVIVAL

7.3.10 PARENTAL BODY MASS AND BROOD SIZE AFTER MANIPULATION

7.3.10.1 Comparison of first brood manipulation treatments

Male or female mass during the nestling period (NP I, II and III) in general did not differ between first brood manipulation categories (Reduced, Control or Enlarged), but females which reared additional nestlings were on average 1.5g lighter during the inter-brood interval than females which reared Control or Reduced broods (both $p<0.05$, Table 7.14a). Neither body-size effects nor initial mass prior to manipulation led to a general absence of significance during first broods (data not presented). Change in mass during nestling rearing (ΔMass= NP II - Incubation) also did not differ significantly between treatments although in general parents which reared Control broods lost about 0.5g more than experimental birds (Enlarged and Reduced) (Table 7.14a).

7.3.10.2 Comparison of second brood manipulation treatments

Parents of Enlarged or Reduced second broods did not differ significantly in mass but small sample sizes reduced statistical power. Overall, parents which reared Control broods were heavier than those which reared Enlarged [significantly so for females during NP I and NP II (both $p=0.025$) and for males during NP II ($p=0.050$)] or Reduced([all ns) broods (Table 7.14b). Sample size was too small to make comparisons during the Post-fledging period.

7.3.10.3 Effect of brood size and change in brood size after manipulation (1st)

Male or female body mass at different stages in the nesting cycle (first broods) before [(Pre-breeding, Laying, Incubation (Fig 7.22a, Fig 7.23a] or after manipulation [NP I, II (Fig 7.22b, Fig 7.23b)] was not significantly related to the number of young reared to independence nor was it significantly related to the number of young on day 13 (B13) or to a change in brood size at Day <u>13</u> (BAM_{13} - $BRS_{\underline{0}}$) (Table 7.15a and b, for males and females respectively). The general lack of a significant negative correlation of mass (male and female) during the nestling period and brood size (B13, D13 or NYF) was not due to any differences in initial mass since a change in mass over the period between Incubation and NP II was also non-significant. For males but not females mass loss was negatively correlated with the size of brood reared to independence (NYF) such that males which fledged the most young tended to lose more mass ($r=-0.29$, Table 7.15a) (*cf.* females $r=0.02$, Table 715b).

Table 7.14 Comparison of adult body mass(g) (Mean (se)) at different stages in the nesting cycle before and after manipulation of brood size, all years combined, using one-way ANOVA

a) First brood size

Adult body mass at different stages in nesting cycle	Sex	Reduced	Control	Enlarged	‖	Summary of results One-way ANOVA R v C	C v E	R v E
NP I	M	19.4 (.3) (9)	19.4 (.2) (33)	19.3 (.5) (11)	‖	ns	ns	ns
	F	19.9 (.4) (12)	20.1 (.2) (41)	20.6 (.3) (13)	‖	ns	ns	ns
NP II	M	19.2 (.3) (15)	19.1 (.2) (39)	18.9 (.3) (18)	‖	ns	ns	ns
	F	19.1 (.3) (17)	19.0 (.2) (46)	18.9 (.3) (22)	‖	ns	ns	ns
NP III	M	19.5 (.7) (8)	18.9 (.4) (15)	18.9 (.5) (8)	‖	ns	ns	ns
	F	18.1 (.9) (4)	18.4 (.2) (12)	18.2 (.3) (6)	‖	ns	ns	ns
Inter-brood	M	19.0 (.4) (6)	19.1 (.3) (22)	19.2 (.3) (14)	‖	ns	ns	ns
	F	20.9 (.2) (6)	20.8 (.3) (17)	19.3 (.3) (11)	‖	ns	*	*
ΔMass[a]	F	2.8 (.3) (12)	3.2 (.3) (24)	2.7 (.3) (16)	‖	ns	ns	ns

a - ΔMass = Mass$_{\text{NP II}}$ - Mass$_{\text{Incubation}}$

Table 7.14b **Second brood size[a]**

Adult body mass at different stages of nestling period	Sex	Reduced	Control	Enlarged	‖	Summary of results One-way ANOVA R v C	C v E	R v E
NP I	M	18.2 (.4) (4)	19.7 (.4) (19)	19.2 (.2) (5)	‖	ns	ns	ns
	F	18.9 (.6) (7)	20.1 (.3) (26)	18.7 (.6) (7)	‖	0.036	0.025	ns
NP II	M	19.4 (.3) (11)	19.6 (.3) (23)	19.2 (.5) (10)	‖	ns	ns	ns
	F	19.0 (.5) (6)	19.6 (.3) (30)	18.4 (.3) (12	‖	ns	0.025	ns
NP III	M	18.5 (.7) (4)	19.9 (.5) (10)	18.0 (1.0) (5)	‖	ns	0.050	ns
	F	18.8 (1.2) (4)	18.8 (.3) (12)	18.6 (.8) (5)	‖	ns	ns	ns

Table 7.15 Pearson correlation coefficients[a] of brood size at Day 13 (B13), and Day 18 (NYF) and change in brood size at Day 13 (D13) after manipulation with parental body mass of Swallows at different stages of the nesting cycle before and after manipulation (first brood). Data are for all years and age classes combined:

a) Males

Brood size/				Stages in the nesting cycle (first brood)						Second br
age	stats	Pre-br	Laying	Incubation	NP I	NP II	NP III	IBI	Δmass[b]	Incubation
B13	r	0.09	-	0.00	-0.10	-0.08	-0.25	-0.15	0.26	-0.13
	n	(95)		(69)	(49)	(71)	(28)	(39)	(23)	(25)
	p	ns		ns	ns	ns	ns	ns	ns	ns
D13	r	0.05	-	-0.06	-0.20	-0.14	-0.30	-0.07	0.22	-0.10
	p	ns		ns	ns	ns	ns	ns	ns	ns
NYF	r	0.10	-	0.04	0.07	0.12	-0.23	-0.17	-0.29	-0.13
	n	(94)		(69)	(48)	(70)	(28)	(38)	(23)	(25)
	p	ns		ns	ns	ns	ns	ns	ns	ns

---

a - only nests where at least one young was known to fledge are included in the above analyses; significance levels did not alter when all birds which raised at least one or more nestlings at least until day 12

b - $\text{Mass}_{(\text{NP II})} - \text{Mass}_{(\text{Incubation})}$

Table 7.15 Contd. b) Females

Brood size/				Stages in the nesting cycle (first brood)						Second br
age	stats	Pre-br	Laying	Incubation	NP I	NP II	NP III	IBI	ΔMass	Incubation
B13	r	0.08	-0.12	-0.03	0.14	0.01	-0.11	-0.51	-0.03	0.19
	n	(74)	(44)	(154)	(63)	(83)	(18)	(27)	(51)	(55)
	p	ns	ns	ns	ns	ns	ns	0.006	ns	ns
D13	r	0.14	-0.06	-0.03	0.10	0.03	0.19	-0.34	0.00	0.20
	p	ns	ns	ns	ns	ns	ns	ns	ns	ns
NYF	r	0.10	-0.10	0.05	0.21	0.14	0.12	-0.27	-0.02	0.20
	n	(740	(43)	(154)	(61)	(82)	(18)	(27)	(51)	(55)
	p	ns	ns	ns	ns	ns	ns	ns	ns	ns

a - only nests where at least one young was known to fledge are included in the above analyses; significance levels did not alter when all birds which raised at least one or more nestlings at least until day 12

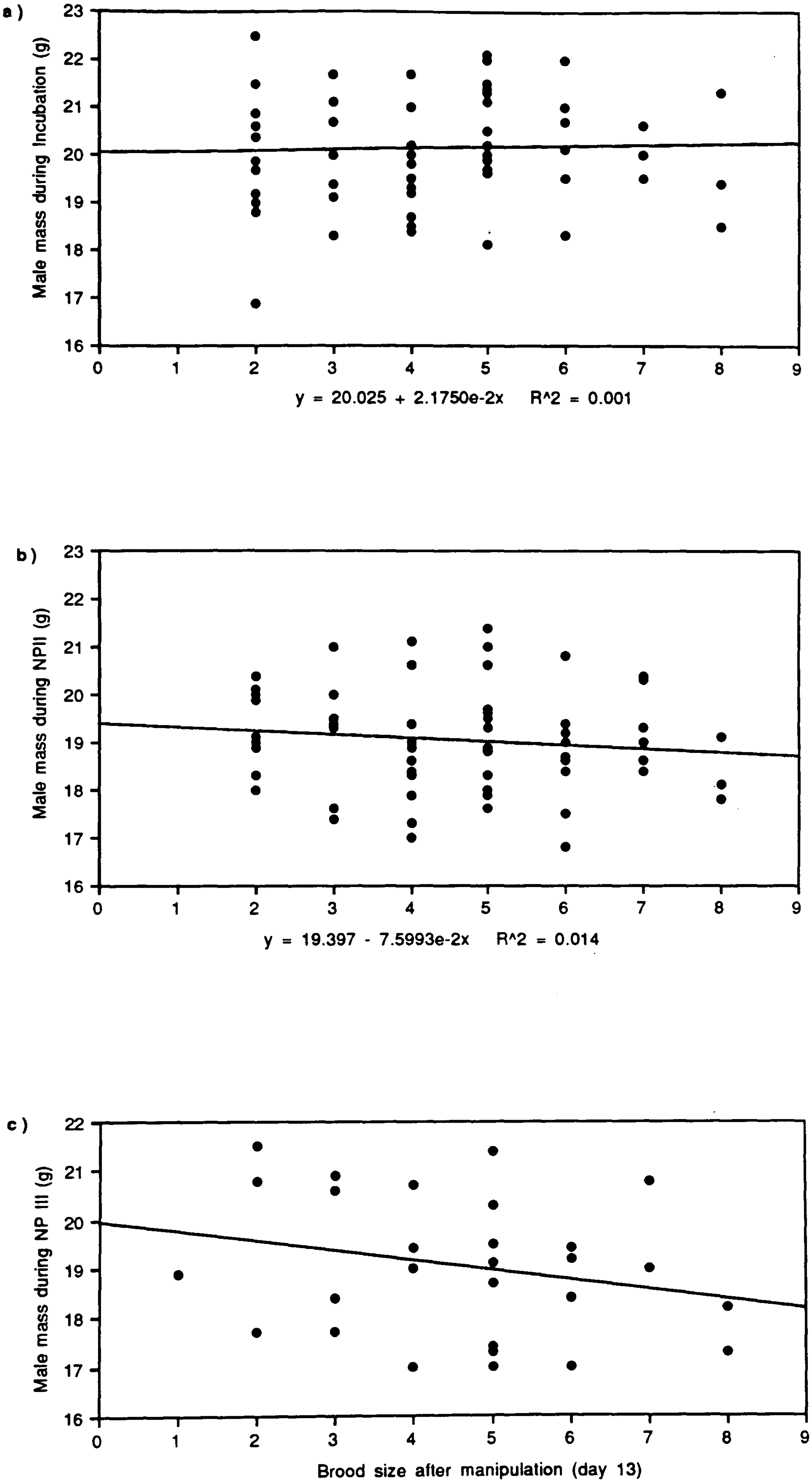
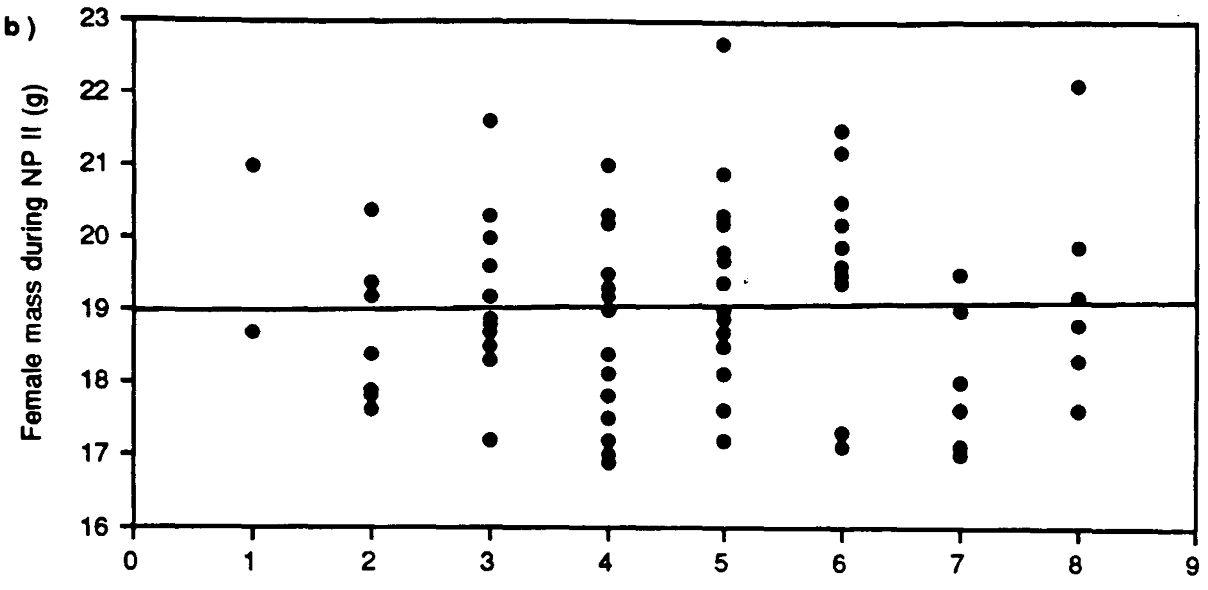
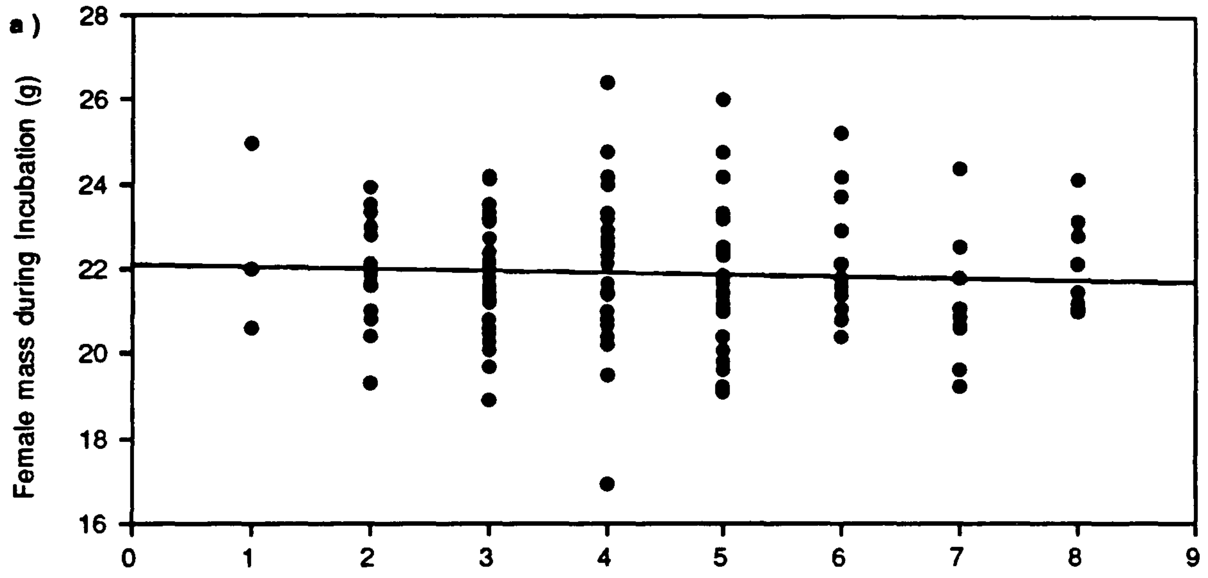


Fig 7.22 Relationship of brood size (1st) after manipulation (Day 13) with male mass during: a) Incubation, b) Nestling period II (NP II) and c) Nestling period III (NP III)

y = 19.934 - 0.19807x   R^2 = 0.063



y = 18.950 + 1.8728e-2x R^2 = 0.001



y = 22.037 - 3.8424e-2x R^2 = 0.002

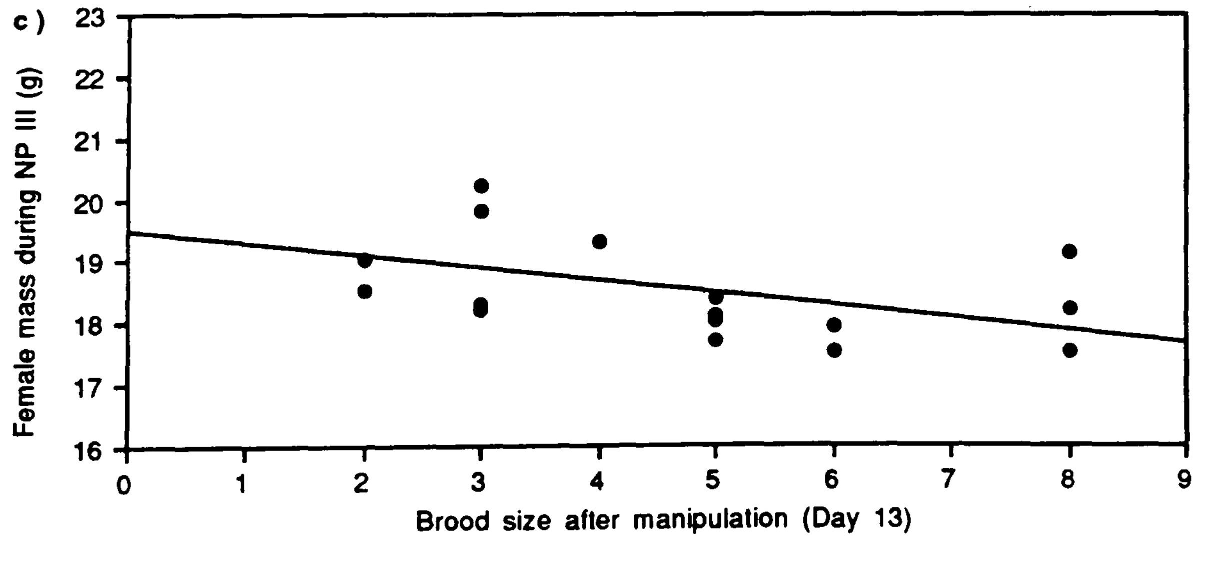


Fig 7.23 Relationship of brood size (1st) after manipulation at Day 13 with female mass during: a) Incubation, b) Nestling period II (NP II) and c) Nestling period III (NP III)

y = 19.493 - 0.20107x R^2 = 0.240; p<0.05

Females which had reared most young at least until day 13 were observed to be lighter at or after fledging (NP III, Fig 7.23c). The pattern was the same for males but the trend was not significant (Fig 7.22c).

7.3.11 PARENTAL BODY MASS AND THE INTER-BROOD INTERVAL (IBI)

Combining the data for both experimental and control broods there was no significant relationship of parental body mass (actual and residual) at different stages in the nesting cycle [Pre-breeding, Incubation, NP I, NP II , NP III and Post-fledging] to the length of the inter-brood interval, except that the interval increased as female mass increased during the laying period ($r=0.45$ and $r=0.58$, both $p<0.001$ actual and adjusted body mass respectively, Table 7.16). Partialling out date of hatch (correlated with IBI, see Chapter 6) did not alter any of the results. There was also a non-significant tendency to re-nest sooner for females which were heavier during the final stages of nestling rearing and after fledging. Moreover, parental body mass (individually or in combination) was not included as a significant variable in a multiple regression analyses to explain variation in the duration of the length of the IBI (data not presented).

Trends were similar when only Control broods were analysed; parental body mass (male or female) was not significantly correlated with IBI at any stage (data not presented).

7.3.12 PARENTAL BODY MASS AND OCCURRENCE OF SECOND BROODS

Males and females which attempted a second brood tended to be heavier during their first brood than single- brooded birds (Table 7.17). These differences were more marked for females and were significant during the laying period (23.8g vs 24.8g) and post-fledging period (19.3g vs 20.4g, both $p<0.05$). Double-brooded females were also heavier during NP II and NP III and lost less mass between incubation and nestling rearing. None of these differences were significant, however ($p>0.05$; Table 7.17).

7.3.13 PARENTAL BODY CONDITION AND SURVIVAL

7.3.13.1 Males

Males which survived tended to be heavier during first broods than those which died. This was particularly marked during nestling rearing (Nestling All: 18.7 vs 19.4 , $p<0.001$, Table 7.18a). Examination by nestling age during this period revealed that the critical phases were during NP II and NP III when surviving males were about 1g heavier than those which died (NP II 18.3 vs 19.3, $p<0.002$; NP III: 18.6 vs 19.7, $p>0.05$) and these difference persisted for size-corrected mass.

Table 7.16 Pearson correlation coefficients of inter-brood interval (IBI) with parental body mass (actual) and size-adjusted body mass (Residual) of Swallows during the nesting cycle (first brood). Data are for all years, age classes, Control and experimental broods combined

			Stages in the nesting cycle (first brood)						
Parameter	Sex	stats	Pre-br	Laying	Incubation	NP I	NP II	NP III	IBI
Actual	Male	r	0.11	a	0.12	-0.23	0.06	0.05	0.08
		n	(60)		(44)	(28)	(44)	(17)	(27)
		p	ns		ns	ns	ns	ns	ns
Residual[b]		r	0.16	a	0.19	-0.16	0.01	0.25	0.24
		p	ns		ns	ns	ns	ns	ns
Actual	Female	r	0.01	0.45	-0.11	0.09	0.13	-0.14	0.21
		n	(48)	(31)	(100)	(39)	(53)	(14)	(18)
		p	ns	*	ns	ns	ns	ns	ns
Residual[b]		r	0.10	0.58	-0.09	0.14	0.07	-0.29	-0.07
		p	ns	**	ns	ns	ns	ns	ns

a - sample size too small

b - sample size as given for comparisons based on actual mass

Table 7.17 Comparison of measures of body mass (g)(Mean (se)) at each stage of the nesting cycle between single- and double-brooded adult Swallows, years combined analysed, using the Students t-test

Stage in the nesting cycle	Sex	Number of broods Single	 Double	n	||	t	df	sig
Pre-br	Male	19.5 (.2)	19.7 (.1)	24,71	||	-0.94	93	ns
	Female	19.9 (.3)	20.2 (.2)	16,57	||	-0.85	71	ns
Laying	Female	23.8 (.4)	24.8 (.2)	10,36	||	-2.03	44	0.049
Incubation	Male	20.0 (.2)	20.1 (.2)	17,49	||	-0.44	64	ns
	Female	22.0 (.2)	21.8 (.1)	35,115	||	0.54	148	ns
NP I	Male	19.5 (.2)	19.4 (.3)	18,32	||	0.50	47.8	n
	Female	20.3 (.3)	20.2 (.2)	12,49	||	0.16	59	ns
NP II	Male	19.1 (.2)	19.0 (.2)	18,49	||	0.40	57.3	ns
	Female	18.7 (.2)	19.1 (.2)	19,61	||	-1.49	56.1	ns
NP III	Male	18.8 (.4)	19.0 (.4)	8,18	||	-0.26	24	ns
	Female	17.8 (.4)	18.5 (.2)	6,14	||	-1.56	18	ns
IBI	Male	19.3 (.3)	18.9 (.2)	5,32	||	0.56	35	ns
	Female	19.3 (.4)	20.4 (.3)	6,21	||	25	-2.44	0.05
ΔMass	Male	0.1 (.6)	1.1 (.3)	6,15	||	-1.43	19	ns
	Female	3.5 (.4)	2.8 (.2)	10,38	||	46	1.47	ns

Table 7.18 Comparison of body mass (Mass) and size- adjusted[a] body mass (Residual) at each stage of the nesting cycle of non-surviving (Died) and surviving (Survived) adult male Swallows, years combined, using One-way ANOVA, (Mean (se,n)):

a) First brood nesting cycle

Stage in the nesting cycle	Measure of mass	Died	Survived	one-way ANOVA		
				df	F	p
Pre-breeding	Mass	19.7 (.2) (33)	19.7 (.2) (31)	1,62	0.06	0.816
	Residual	0.10 (.19)	0.22 (.21)	1,62	0.17	0.678
"Laying"	Mass	19.4 (.5) (8)	19.5 (.7) (4)	1,10	0.02	0.902
	Residual	0.15 (.28)	-0.13 (.81)	1,10	0.17	0.691
Incubation	Mass	20.1 (.3) (21)	19.9 (.3) (20)	1,39	0.56	0.449
	Residual	0.13 (.25)	0.57 (.20)	1,50	1.92	0.165
NP I	Mass	19.3 (.3) (11)	19.5 (.3) (16)	1,25	0.17	0.686
	Residual	0.06 (.23)	-0.09 (.18)	1,25	0.24	0.626
NP II	Mass	18.3 (.2) (15)	19.3 (.2) (19)	1,32	10.98	0.002
	Residual	-1.02 (.22)	-0.14 (.19)	1,32	10.04	0.003
NP III	Mass	18.6 (.4) (6)	19.7 (.3) (9)	1,13	2.40	0.146
	Residual	-1.22 (.47)	0.15 (.23)	1,9	8.29	0.013
Nestling (All)	Mass	18.7 (.2) (32)	19.4 (.1) (46)	1,76	9.47	0.003
	Residual	-0.65 (.18)	-0.05 (.11)	1,76	8.92	0.004
Post fledging	Mass	19.2 (.4) (15)	19.3 (.4) (13)	1,26	0.01	0.915
	Residual	-0.28 (.33)	-0.49 (.36)	1,26	0.182	0.674

b) Second brood nesting cycle

Stage in the nesting cycle	Measure of mass	Died	Survived	one-way ANOVA		
				df	F	p
Inter-brood	Mass	19.4 (.4) (5)	18.6 (.5) (8)	1,11	1.32	0.277
	Residual	-0.31 (.16)	0.95 (.48)	1,11	1.20	0.299
Incubation	Mass	20.1 (.4) (12)	20.0 (.2) (13)	1,23	0.17	0.684
	Residual	0.71 (.33)	0.38 (.18)	1,23	0.83	0.371
NP I	Mass	19.4 (.4) (14)	20.1 (.5) (11)	1,23	1.08	0.310
	Residual	-0.11 (.42)	0.49 (.41)	1,23	1.01	0.325
NP II	Mass	18.8 (.3) (16)	19.6 (.3) (19)	1,33	3.30	0.078
	Residual	-0.58 (.22)	-0.23 (.27)	1,33	1.00	0.325
NP III	Mass	19.4 (1.0) (5)	19.9 (.4) (6)	1,9	0.23	0.642
	Residual	-0.41 (.81)	0.11 (.34)	1,9	0.40	0.545
Nestling (All)	Mass	19.1 (.3) (35)	19.8 (.2) (36)	1,69	3.71	0.050
	Residual	-0.37 (.22)	0.05 (.20)	1,69	1.96	0.166
Post fledging	Mass	19.9 (.7) (8)	19.6 (.9) (5)	1,11	0.07	0.793
	Residual	0.52 (.57)	0.10 (.83)	1,11	0.19	0.672

Surviving males were heavier while feeding nestlings during second broods, significantly so for combined data (NP I, II, III) data (19.1 vs 19.8, p=0.05; -0.4 vs 0.1, p<0.05, actual and residual respectively, Table 7.18b). The critical period again appeared to be during NP II (18.8 vs 19.6, p=0.078). Males which died were generally heavier during the IBI and after second broods had fledged. The sample size and non significant difference limit interpretation of these findings, however. More data need to be collected during these potentially critical periods.

Males which survived had thicker muscles (i.e greater protein reserves by implication) during the nestling and post-fledging period than those which did not return in 1989, significantly so for nestling rearers (2.5 vs 2.2, p<0.003, Table 7.20).

7.3.13.2 Females

Female body mass was not significantly related to overwinter survival. Comparisons of residual mass and inclusion of date as a covariate (data not presented) also failed to reveal any significant differences. Results differed slightly between first- and second broods (Table 7.19a & b respectively). Incubating and nestling-rearing females which survived tended to be slightly heavier and lighter respectively, than females which died whereas during second broods the opposite trend was observed. Females which survived during NP II (2nd broods) were 0.7g lighter than those which died (19.5 vs 18.8, p=0.096) whereas during NP I survivors were 0.4g heavier (19.7 vs 20.1, p>0.05, Table 7.19b). Females which survived or died also did not differ in muscle thickness at any stage (all p> 0.5, Table 7.20).

Table 7.19 Comparison of body mass (Mean) and size-adjusted[a] body mass (Residual) at each stage of the nesting cycle of non-surviving (Died) and surviving (Survived) adult female Swallows, years combined, using One-way ANOVA, (Mean (se,n)):
a) First-brood nesting cycle

Stage in the nesting cycle	Measure of mass	Died	Survived	one-way ANOVA df	F	p
Pre-breeding	Mass	20.5 (.3) (29)	20.5 (.3) (22)	1,49	0.04	0.843
	Residual	-0.01 (.27)	0.09 (.26)	1,49	0.08	0.783
Laying	Mass	25.0 (.6) (8)	24.8 (.3) (14)	1,20	0.06	0.814
	Residual	4.52 (.40)	4.27 (.28)	1,20	0.27	0.607
Incubation	Mass	21.7 (.2) (52)	22.0 (.4)	1,88	1.03	0.312
	Residual	1.24 (.19)	1.74 (.20)	1,88	2.54	0.115
NP I	Mass	20.4 (.3) (18)	20.0 (.3) (16)	1,32	0.93	0.341
	Residual	0.24 (.27)	-0.49 (.29)	1,32	3.06	0.090
NP II	Mass	18.9 (.2) (32)	18.8 (.4) (16)	1,46	0.13	0.717
	Residual	-1.42 (.19)	-1.50 (.33)	1,46	0.04	0.838
NP III	Mass	18.5 (.3) (8)	18.5 (.4) (9)	1,15	0.01	0.915
	Residual	-1.91 (.36)	-1.89 (.39)	1,15	0.00	0.969
Nestling (All)	Mass	19.3 (.2) (58)	19.2 (.2) (42)	1,98	0.16	0.685
	Residual	-0.97 (.18)	-1.19 (.21)	1,98	0.60	0.442
Post fledging	Mass	20.23 (.4) (20)	20.0 (.5) (14)	1,32	0.11	0.741
	Residual	-0.24 (.34)	-0.47 (.53)	1,32	0.07	0.787

b) Second brood nesting cycle

Stage in the nesting cycle	Measure of mass	Died	Survived	one-way ANOVA df	F	p
Inter-brood	Mass	20.6 (.9) (5)	20.6 (.6) (7)	1,10	0.00	0.983
	Residual	.24 (.79)	.12 (.57)		0.02	0.897
Laying	Mass	21.4 (.9) 10	23.1 (.7) 10	1,18	2.33	0.144
	Residual	1.16 (.84)	2.59 (.63)		1.75	0.202
Incubation	Mass	20.9 (.3) 36	20.8 (.3) 25	1,59	0.20	0.653
	Residual	.08 (.21)	.43 (.27)		0.21	0.649
NP I	Mass	19.7 (.3) 21	20.1 (.3) 27	1,46	0.83	0.365
	Residual	-.48 (.32)	-.18 (.3)		0.47	0.494
NP II	Mass	19.5 (.30 24	18.8 (.3) 24	1,48	2.89	0.096
	Residual	-1.02 (.24)	-1.50 (.18)		2.44	0.125
NP III	Mass	18.7 (.3) 9	18.9 (.3) 9	1,16	0.10	0.762
	Residual	-1.66 (.28)	-1.40 (.28)		0.38	0.547
Post fledgling	Mass	19.7 (.7) 7	19.5 (.6) 5	1,10	0.03	0.857
	Residual	.47 (.71)	.80 (.56)		0.11	0.743
Nestling (All)	Mass	19.5 (.2) 56	19.4 (.2) 60	1,114	0.00	0.971
	Residual	-.92 (.18)	-.88 (.18)		0.02	0.880

Table 7.20 Comparison of muscle thickness [ultra-sound readings (MUS)] before (Pre), during (Nestling) and after (Post) nestling rearing between non-surviving (Died) and surviving (Survived) adult Swallows, for a sample of birds measured during second broods in 1988 including both experimental and control birds, split by sex

Stage in the nesting cycle	Sex	Died	Survived	one-way ANOVA df	F	p
PRE-nestling	Male	2.57 (.05) (5)	2.57 (.06) (7)	1,10	0.00	0.995
	Female[a]	2.61 (.04) (18)	2.57 (.07) (7)	1,23	0.31	0.586
NESTLING	Male	2.39 (.02) (13)	2.48 (.02) (10)	1,21	11.14	0.003
	Female	2.43 (.03 (29)	2.45 (.02 (17)	1,44	0.28	0.603
POST-nestling	Male	2.34 (.02) (5)	2.42 (.06) (8)	1,11	1.20	0.296
	Female	2.34 (.04) (13)	2.35 (.03) (8)	1,19	0.01	0.929
All	Male	2.42 (.02) (19)	2.49 (.03) (21)	1,38	4.14	0.049
	Female	2.47 (.02) (40)	2.47 (.03) (22)	1,60	0.00	0.955

a - laying birds have been excluded

7.4 DISCUSSION

"Condition" has been applied in a wide range of studies and is often assumed to be a function of total body lipids relative to body mass. Birds can metabolise both fat and lean (mainly protein) components which may vary independently (but see Evans & Smith 1975; Marcström & Mascher 1979) and so any reliable index of body condition should attempt to reflect the status of both lipid and protein reserves. "Good" condition implies a state where an individual has sufficient reserves for current activities, or short term periods of adversity while "poor" condition indicates a state of declining or depleted reserves (Bryant 1988a). Indices of condition would, therefore, be expected to carry fitness implications. Having manipulated reproductive effort and demonstrated the presence of both intra- and inter-seasonal costs in Swallows (Chapter 6), in this final section a number of predictions linking reproductive costs and parental body condition (Results Part III) were tested. Central to making such predictions, however, is an ability to obtain an accurate measurement of body "condition" and to demonstrate how it changes throughout the nesting cycle (Results Part I & II).

7.4.1 MEASURING BODY CONDITION IN DEAD INDIVIDUALS

Analyses of a small sample of carcasses enabled the body condition of breeding adult Swallows to be determined precisely here (Results Part I) and also in a later study by Ward (1992). Lipid reserves were measured directly through lipid extraction and the lean dry mass of pectoralis muscles (major and minor) of Swallows was assumed to be a reliable measure of protein reserve since it explained 77% of the variation in total lean dry material (see Introduction for rationale). This agreed closely with a figure obtained for Dippers (74%, Newton, S.F 1989) and was higher than that observed for Sand Martins (52% Jones 1987d). Differences occurring between sexes in total body or component dry masses but not lean dry masses, should indicate variation in lipid reserves and *vice versa*. Where DMs and LDMs vary in the same manner then this suggests that breeding Swallows utilise their lipid and protein reserves in parallel (Newton, I 1968, 1972). Sample sizes were too small to make any meaningful comparisons across stages in the nesting cycle.

Female Swallows had a higher overall total lipid content and tended to have higher component lipid indices than males but in general differences were not significant. Major lipid 'stores' in 'healthy' Swallows were the body shell, skin and body feathers and wings. Since most of this is subcutaneous it is, therefore, readily mobilisable representing potential energy reserves of an individual. By comparison components with very low lipid indices mainly contain structural lipid (i.e not normally mobilisable as an energy source). The lipid content of two starved males was almost one third lower than measured for 'healthy' males (5.2 *cf.* 14.8) and lipid content of all main stores was lower than that measured for healthy birds. It was concluded that: a) there was very little difference in either mobilisable or structural lipids between sexes; b) major stores of mobilisable lipid were the skin and contour feathers and body shell and, c) components which were mainly comprised of structural lipid were in general characterised by having the lowest lipid indices, an exception being the gut. Females not only tended to have higher lipid but also showed greater protein reserves than males as indicated by a significantly higher total lean dry mass. Healthy birds had proportionately the highest amount of lean material in the pectoralis muscles and the percentage LDM of pectoralis muscles was highest for females and lowest for starved birds.

The high degree of inter-correlation between lipid content and: (i) total lean dry mass and, (ii) pectoralis lean dry mass (Table 7.5), implies that lipid and protein reserves changed in parallel. Apparent structural lipid and protein reserves from deep tissues (i.e not main stores) was the last to be mobilised but during times of extreme food shortage, both lipid and protein reserves were utilised. These were drawn fairly evenly from stores all around the body eventually resulting in starvation. This latter point is of relevance if the lipid or protein content of particular components or selected stores reliably reflect an individual's lipid or protein status.

7.4.2 MEASURING BODY CONDITION IN LIVE INDIVIDUALS

Body condition needs to be assessed in relation to the demands at a particular point in time (Evans and Smith 1975). Since there are marked variations in body mass and condition during different stages in the nesting cycle comparisons of individuals should be made between birds at a similar stage in the nesting cycle. Technique (s) which accurately distinguish between lipid and lean components in live birds enable variations in condition over time to be monitored, and also allow measurements from a larger, and more representative sample of the population to be taken. In the present study adult Swallows were fat-scored and their muscle thickness measured in an attempt to estimate an individual's lipid and protein reserves respectively.

The method of fat scoring applied here explained just under two thirds (62%) of the variation associated with the total body lipid content in adult Swallows. This was less accurate than the results presented for Sand Martins (Jones 1985, 1987d) and House Martins (Bryant and Westerterp 1983), where fat scores accounted for over three quarters of the total variation in lipid. Jones (1985) reported that fat scores tended to be more accurate for extreme levels of fat (high or low). The reduced accuracy of fat scores in predicting lipid content in this study may be related to the fact that over two thirds of the birds scored were between three to seven (overall range = 0-10). House Martins carry more fat than Swallows (Bryant *et al.* 1984) which is further consistent with this explanation. A weaker correlation for males was attributed to their lack of a brood patch resulting in fat being not so easily viewed and thus scored. Jones (1985) concluded similarly for Sand Martins.

The thickness of the flight muscles was measured in live adult Swallows in the field with the use of a portable ultrasonic flaw detector (ultra-sound). This has been previously been tested in Mute Swans (Sears, 1988) and Dippers (Newton, S.F 1989, 1993) and in both of these studies ultrasonic readings explained over ninety percent of the total variation associated with muscle thickness (as measured using hypodermic needle). The relationship was stronger for Mute Swans than Dippers (99% vs 91% respectively). More recently, similar correlations have been reported for Japanese Quail (Ward 1992) and for Robins (I G Johnston *pers comm*). Muscle thickness as measured by the ultra-sound was not compared with needle thickness estimates in the present study, but given the above findings, together with the result that MUS was significantly correlated with Swallow carcass analysis measurements (LDM & PLDM), it was assumed that thickness of flight muscles as measured by the ultra-sound device could be taken as a reliable indicator of protein reserves in adult Swallows (also see Introduction).

7.4.3 CAN BODY MASS BE TAKEN AS A RELIABLE INDICATOR OF BODY CONDITION IN BREEDING ADULT SWALLOWS

The interpretation of parental mass loss while breeding has generated considerable debate in the literature. Although body mass is often taken as an indicator of condition it has been argued that since mass may vary independently of body reserves, the validity of such an assumption is questionable (see Introduction and also below). For instance water loss, defecation or time since last feed could all cause an individual to have a low or lowered mass, but which would be unlikely to carry any fitness implications (for discussion see Jones 1985). Furthermore consumption of different prey items could result in differential gains in mass which need not necessarily be proportional to their energetic or calorific content. Again this could lead to changes in mass but not condition. If body mass and condition are found to be covariates, such that a change in mass also implies a change in both lipid and protein reserves, then this would allow mass to be used in the present study to examine the relationship of parental body condition and reproduction costs (Results, Part III).

The reliability of body mass as an indicator of body condition in breeding Swallows was confirmed in the present study. In a sample of carcasses live body mass (mass) was found to be significantly and positively correlated with both total lipid and protein (lean dry mass and pectoralis lean dry mass). Mass was a better predictor of total body lipid than fat scores but explained less variation in protein reserves (PLDM) than MUS or MUS volume (58% vs 66% vs 67% respectively). Notably using size adjusted measures of mass (Residual) only marginally improved the level of prediction of lipid and protein reserves. Since male and female mass was found to show a good correlation with field measures of body reserves which were taken from a large sample of live birds across all stages, this provides firm evidence to support mass as a reliable index of body condition in Swallows. Moreover, the high degree of inter-correlation of all three measures is further consistent with earlier findings from carcass analysis that lipid and protein reserves were deposited or utilised in parallel.

In order to make valid comparisons between sexes, years or broods where appropriate, it is necessary to be able to adjust body mass for seasonal- or body size-related differences. A failure to do so would limit the interpretation of the results. Although it has been demonstrated that body mass of birds sometimes varies from year to year depending on factors such as climate, food availability or territory quality (eg. Cooch *et al.* 1960; Redfield 1973; Korpimaki 1990a) such trends have generally only been reported for bigger species (> 25g). Body mass of Swallows during the breeding cycle did not differ significantly between years (except during pre-laying period), and so the analyses were performed only for the pooled data set. By comparison, across all stages fat scores were lower in 1989. Given that there were no differences in mass for the same sample of birds, these differences were not related to variation in lipid reserves between years, but rather that birds were unintentionally scored lower in the second year. An obvious explanation for this result is that the accuracy of fat-scoring increased with the benefit of a years experience. Body mass was more strongly correlated with total body lipid anyway and as mass did not differ significantly between years, fat scores were not analysed further in the present study.

Significant correlations of body size with mass were evident for both male and female Swallows. Based on a simple linear regression model keel-length proved to be the single best predictor of body mass here. Similar trends have been reported for other studies on hirundines (Bryant 1979, 1989; Jones 1987d; Ward 1992). The relationship was strengthened through using a model which incorporated wing and head-to-bill along with keel-length. Including only incubating birds (or the partners of incubating females) explained the greatest amount of variation (26% and 19% for males and females respectively). Principal Component Analyses failed to explain greater amounts of the variation in body mass when compared to multiple regression models or even for keel length alone. Weaker relationships for females suggested that a greater proportion of variation in their mass was related to changes in body reserves (*cf.* skeletal size). Since: a) mass varies significantly with body size, b) males are larger than females and, c) double- tended to be bigger than single-brooded birds (Chapter 4), size-adjusted masses (Residual mass) should be used to make comparisons between sexes and broods.

7.4.4 VARIATION IN BODY CONDITION DURING THE NESTING CYCLE

Patterns of mass change have been studied in considerable detail in association with annual and breeding cycles including (Bryant 1975a; Lessells *et al.* 1979; Pinowska 1979; Dowsett-LeMaire & Collette 1980; Freed 1981; Norberg 1981; Silverin 1981; Westerterp *et al.* 1982; Village 1983; Newton *et al.* 1983; Ricklefs & Hussell 1984; Jones 1985, 1987d; Crick & Fry 1986; Gaston & Jones 1989; Dijkstra *et al.* 1990; Korpimaki 1990a, reviewed by Moreno 1989a). Males and females may differ in their body mass throughout the breeding cycle (Moreno 1989a) it is necessary to ensure that birds of a similar stage in the nesting cycle are being compared and the division of duties understood (Chapter 3).

Mass of male Swallows varied very little during the breeding season, never changing by more than about three percent between successive stages and reaching a maximum while their partner was laying and a minimum during nestling rearing, specifically from day nine onward (NP II & NP III). Similar trends have been reported in other studies (Moreno 1989a; Korpimaki 1990a and references therein). In some species males may lose mass due to territoriality and courtship activities but for reasons already mentioned these were not considered to be important for male Swallows. Energetic costs and possible implications associated with mate -guarding or EPCs have yet to be investigated. Females by comparison, exhibited marked changes in mass during the nesting cycle; increasing steadily from arrival on the breeding grounds (which was sometimes three to four weeks before laying started) when they weighed about 19g, through nest building (21g) and rising to a peak of around 25g during laying. While the marked increase in mass associated with laying is largely due to the presence of reproductive material (enlarging gonads as well as the actual egg and other egg follicles (Ward 1992), it may also be associated with changes in lipid, protein or water content (Jones and Ward 1976; Hirons *et al.* 1984; Ward 1992).

Based on a very small sample of carcasses analysed here lipid content increased from pre-breeding to laying and peaked during incubation whereas lean dry mass and water content were at a minimum and maximum during the pre-breeding and laying periods respectively. In other studies it has been suggested that a decrease in mass from laying to incubation is caused by a decline in size of the ovary and oviducts (see Ricklefs 1974) but also through utilisation of lipid and protein stores necessary for egg formation (*cf.* Jones and Ward 1976). Data from carcass analysis, fat scores and muscle thickness indicated that while protein reserves and water content may have decreased slightly between laying and incubation, lipid reserves appear to have increased as implied by a peak during incubation. Changes in lipid and reproductive material which were studied by Ward (1992) showed that the increase in mass during laying was almost entirely explained by the additional mass of egg plus reproductive material (oviducts). Ward (1992) pointed out that analyses based solely on mass changes would have led to the erroneous conclusion that the non-reproductive portion of the female remained at the incubation level throughout laying when in fact there was a build up of lipid during the final four day period of rapid follicular growth, balanced by a decrease in water content which resulted in the non-reproductive mass being constant.

Female mass at incubation was usually about 22g which was significantly heavier than males (also see Ward 1992). Female Swallows (*cf.* Barn Swallows, Ball 1983a) took sole responsibility for incubation and males were never observed to feed their partner during this time (Chapter 3) nevertheless females usually managed to maintain their mass during the incubation period (also see Jones 1987e). Such incubatory mass constancy (IMC) is more often observed in species where both sexes take an equal role in incubation (Moreno 1989a). Since females have reduced foraging potential while incubating, increased reserves may be necessary to overcome adverse weather when food availability is lowered. This may also explain why mass was higher during the early part of the season when aerial food supply tended to be more unpredictable (Chapter 5). Only during the pre-laying and laying periods was female mass significantly heavier during first- compared to second-broods. This further suggested that additional reserves (as indicated by higher body mass) during the early stages of incubation served as a buffer against unpredictable food resources. Jones (1987e) demonstrated that female Swallows were heaviest during warm condition when they spent less time incubating both because: a) the eggs did not cool so quickly and, b) food was more abundant enabling birds to forage at a higher rate.

Maintaining condition during incubation might be important for a number of other reasons including : a) an ability to re-lay promptly following disturbance, or b) the capacity to care for the young during the first week when they also require to be brooded. It has been shown in an earlier study of Swallows (Jones 1987e) and also in the Sparrowhawk (Newton 1986) that females may desert their clutch if circumstances are such that their mass drops to a critically low level (equivalent to that known to be attained while successfully feeding nestlings). Desertion by females incubating un-manipulated clutch sizes were very few in this study and in those cases where desertion followed clutch reduction, body mass was at normal incubatory mass. The incubation pattern of female Pied Flycatchers which incubated experimentally enlarged clutch sizes changed from a constant to a declining mass (Lifjeld & Slagsvold 1986) and clutch enlargements in the Dotterel also lead to greater mass losses than normal (Kallas & Lofaldi 1987).

Incubation behaviour in relation to energetic costs (Mertens 1977a, 1980; Walsberg & King 1978a,b; Gessaman & Findell 1979; Biebach 1981, 1984; Vleck 1981; Yom-Tov & Hilborn 1981; Jones 1985, 1987e, 1989; Ward 1992), clutch size (Biebach 1981, 1984; Lifjeld and Slagsvold 1986; Kallas & Lofaldi 1987; Tarburton 1987; Baltz & Thompson 1988) or body condition (Aldrich & Raveling 1983; Lifjeld & Slagsvold 1986; Kallas & Lofaldi 1987; Jones 1985, 1987e, 1989; Ward 1992) have been studied in both the field and laboratory species but was outside the scope of the present analyses.

A decrease in mass (relative to incubation) was observed for both male and female Swallows during first broods. But, whereas males showed a minimum mass during NP II (19g, *cf.* females =18.8), females reached a minimum when nestlings were slightly older at NP III (18.5 *cf.* males=19.2). Only during NP II (ns) and NP III ($p<0.05$) were males heavier than females. Trends were the same during second-broods except that after offspring from the first brood had fledged females were significantly heavier than males (the opposite was true during the post-fledging period of second broods, ns).

Measurements of muscle thickness revealed that protein reserves were also lowest for both sexes during the latter stages of the nestling period. A decrease in mass while feeding nestlings (*cf.* incubation) has been described in many species (Nice 1937; Kluyver 1952; von Haartman 1954; Newton 1972; Bryant 1975a; Dowsette-LeMaire & Collette 1980; Freed 1981; Westerterp *et al.* 1982; Nur 1984 a, Jones 1985, 1987; De Laet and Dhondt 1989; Johnson *et al.* 1990, but see Reid 1987) and has been variously interpreted (Freed 1981; Norberg 1981; Murphy and Haukioja 1986; Jones 1987; Gaston and Jones 1988) summarised in three hypotheses: (i) the "stress" hypothesis, (ii) the "adaptive " hypothesis and, (iii) the "threshold" hypothesis.

The principal tenet of the "stress" hypothesis is that mass loss while rearing nestlings (see above) was symptomatic of a fitness cost. Intuitively this seemed an attractive idea since there was evidence to show a negative correlation between fecundity (Nur 1984a and references therein), survival (Coulson et al. 1983; Reid 1987) and weight loss in a number of species. This idea was challenged by Freed (1981), however, who proposed that being lighter during this period was in fact adaptive, thus termed the "adaptive" hypothesis. Freed (1981) argued that since a decrease in mass could reduce flight costs (Pennycuick 1975; Norberg 1981 and also see Lima 1986) and thus energy requirements, it may have neutral or indeed beneficial effects. In this hypothesis a loss in mass is not associated with a parallel loss in "condition" and since mass loss itself has no survival implications (see above) it can not, therefore, be seen as being costly. Three findings documented in the literature added support to Freed's proposition. Firstly, mass loss was often achieved prior to the period of maximum food demand (Dowsette-LeMaire and Colette 1980; Freed 1981; Ricklefs and Hussell 1972; Jones 1987). Secondly, it was independent of natural (Freed 1981) and experimental (De Steven 1981; Ricklefs and Hussell 1984) brood size. Thirdly, in some species it was found to occur in females but not males even when males fed at an equal rate.

Although these two hypotheses are alternative, they are not necessarily mutually exclusive explanations for interpreting patterns of mass loss. Rather, the significance of the mass change might depend upon both the amount and the timing concerned. Implicit within this third idea is that a critical threshold of body mass for maximising success exits (Jones 1987; Gaston and Jones 1988, but also see Nur 1984a). If mass falls below a certain point or threshold, then an individual is likely to suffer deleterious consequences, whereas if it stays above the threshold it could be highly adaptive. These hypotheses were examined in relation to data collected fro male and female Swallows in relation to both natural and manipulated brood sizes.

7.4.5 PARENTAL BODY CONDITION AND REPRODUCTIVE COSTS

Results presented earlier showed that although most pairs of Swallows could rear additional young to independence when these were added to their broods shortly after hatch, parents incurred a cost (Chapter 6). It has commonly been assumed that such trends are manifest because an enlargement in brood size (increase in parental reproductive effort assumed), caused a deterioration in parental body condition (Drent & Daan 1980; for review see Dijkstra *et al.* 1990) which meant they were less likely to attempt a second brood or have a lowered probability of survival. Firm evidence to support this assumption, however, is generally lacking (Bryant 1988a), and in a number of studies no link between condition and intra-seasonal reproductive costs has been demonstrated (Finke *et al.* 1987; Hegner & Wingfield 1987; Smith *et al.* 1987; Tinbergen 1987; Lindén 1988). Condition, therefore, might not be the mechanism through which reproductive costs are expressed. Other factors such as an increased risk of predation (eg. ecological costs) perhaps associated with increased parental care or time spent around the nest could put an upper limit on the number of young which can be fed. Alternatively, clutch size might be limited by some other stage in the breeding cycle (Chapter 8).

Equally a link between the two could be masked if condition was not properly measured or if parents failed or decided not to respond to manipulation (i.e by not increasing effort). The latter could result in the parents paying no direct cost (effort related to fitness, by implication) with instead an effect on nestling quality being observed. Further, a failure to identify critical periods in the nesting cycle could also cause costs to be underestimated or not demonstrated. If parents responded to experimental enlargement of brood size by prolonging the period of parental care (rather than increasing effort), then recruitment of offspring might not be reduced but an effect on parental condition might become apparent after the young have fledged. Few studies have collected data over this period, however. Moreover, in double-brooded species there may be differing consequences of manipulation of first- and second-broods and, depending on division of duties between sexes, for males and females. For example a prolonged period of parental care during first broods might result in lowered probability of second broods whereas during second broods an effect on parental or offspring survival might be more likely.

Analyses of body mass during the nesting cycle indicated that for both sexes, first- and second-broods, condition was poorest during nestling rearing, specifically (NP II and NP III). A number of predictions (see Introduction) following from the assumption that parental condition was related to current and: a) future fecundity and, b) survival are discussed.

7.4.5.1 Is parental condition negatively related to the size of brood reared ?

Neither male nor female mass was significantly correlated with brood size (natural or experimental) and the lack of a significant relationship was not attributed to effects of body size or initial mass (i.e at Pre-breeding, Laying; Incubation). Comparisons between treatment categories (Control, Enlarged and Reduced) in general yielded non significant differences (except at or after fledging, see later) confirming these results. Differential mortality of Enlarged broods did not explain the lack of a significant negative result, as expected from Prediction 1. Moreover, body mass was not significantly related to either clutch or brood size (data not presented). Based on these results, therefore, it was concluded that rearing additional nestlings does not result in a trade-off against the body condition. Based on this finding mass loss during the post-hatching period was not interpreted as being symptomatic of a fitness cost. Similar results have been described in House Sparrows (Hegner & Wingfield), House Wrens (Finke *et al.* 1987) and Great Tits (Tinbergen 1987; Smith *et al.* 1987, 1989; Orell & Koivula 1987; Lindén 1988).

In a number of other studies, however, parental mass was significantly reduced following brood enlargement (Hussell 1972; Nur 1984a, 1988; Askenmo 1977, 1979; Reid 1987; Dijkstra *et al.* 1990). Female Tree Swallows, showed a tendency to lose more mass but the difference was not significant though a small sample reduced statistical power (DeSteven 1980). Where sexes differed in their response, males usually showed reduced mass loss relative to females (Hussell 1972; Nur 1984b, 1988; Dijkstra *et al.* 1990). A possible explanation to account for differences between species might relate to whether they are single- or double brooded (also see below).

7.4.5.2 Does parental condition during first brood influence the time taken to start, or the occurrence of second broods ?

The size of the first brood has an effect on the timing and probability of an individual attempting a second brood (Chapter 6 and references therein) and it was predicted that the underlying mechanism to account for such a trend was parental body condition. This seemed a reasonable prediction given the following: a) body mass and condition has been linked to food availability (Jones 1987e) and, b) food resources (natural and experimental) have been directly (or indirectly) and significantly related to: (i) length of the IBI (Kluyver *et al.* 1977); Eden *et al.* 1989), (ii) nestling growth (Bryant 1978a; Blancher and Robertson 1987; Johnston 1990; Wiggins 1990b) and, (iii) the percentage of pairs which attempted two or more broods in a season (for review see Martin 1987; Arcese & Smith 1988; Tinbergen & van Balen 1988; Riley 1992).

From the data collected here, however, it was concluded that there was no evidence to suggest that parental body mass while rearing first brood nestlings influenced either the duration of the IBI or the probability of attempting a second brood. This applied to parents rearing both natural and experimental broods. The lack of significance was not attributed to differences in initial body mass, since changes in mass (NP II $_{mass}$ - Incubation $_{mass}$) and (NP II $_{mass}$ - Pre-breeding $_{mass}$) were also non significant. Similar conclusions were made for studies on Great Tits (Tinbergen 1987; Smith *et al.* 1989). For both sexes there was a general tendency for Swallows which were heaviest during first broods to be heavier. These differences were more marked for females and were significant during the Laying and the Post-fledging period. Female mass was also only significantly related to the IBI during the Laying period. No comparable data has been presented for these stages in other studies. Given that female mass was not related to clutch or brood size it is difficult to see how mass at laying could be causally related to the duration of the IBI or number of broods attempted. One possibility is that it is an artefact of seasonal variation; earlier birds were heavier and started their first broods significantly earlier. This needs further investigation.

The lowered mass of single-brooded birds during the post-fledging period, on the other hand could indicate that the condition parents are in after the young fledge, is of greater importance (*cf.* during nestling rearing as predicted). Although this idea is consistent with the finding that nestlings from Enlarged broods were of poor quality and parents were significantly less likely to attempt a second brood the lack of a temporal difference in timing of second broods (Control v Enlarged) argues against this point. Lindén (1988) suggested that comparisons between single- and double-brooded females were not valid during the post-fledging period, since the mass of females which invested in a second clutch would be influenced by Gonadal growth. The implication of this suggestion would be that the heavier mass of double-brooded birds, as observed here, is neither a function of their condition nor the effort they expended while feeding nestlings. This was not considered to be a valid criticism, however, because only Swallows which were caught at least six days before the onset of laying were included in the analyses. Differences in mass (as a result reproductive material) only become evident from about four days before laying (Ward 1992). In order to give a clearer interpretation of these findings more data relating to the condition of parents and their offspring during the post-fledging period, together with feeding rates and the role of both sexes need to be collected. It remains to be determined whether lowered mass during this period was costly or adaptive. A significantly relationship of lowered mass with overwinter mortality would support the former while no difference would favour the latter.

7.4.5.3 Is parental survival related to body condition

Manipulation of brood size affected parental survival in Swallows; males or females which reared a Reduced first or second brood survived better than those which reared Control or Enlarged broods. Moreover, females responded differently to second brood manipulation, most notably those rearing Enlarged second broods showed much higher survival compared to those which reared Enlarged first broods (Chapter 6). Other workers have also reported that parents which reared reduced broods tended to survive better, and those with additional young fared worse (*cf.* Control broods) (for reviews see Partridge 1989; Dijkstra *et al.* 1990; Lessells 1991). Decreased survival of birds raising larger broods could be a consequence of increased exposure to predation or risk of injury. Reid (1987) suggested that the timing of adult mortality in the Glaucous-winged Gull, indicated that ecological costs were unlikely to account for increased mortality of parents rearing enlarged broods. Similarly, predation was also thought to be unimportant for adult Swallows during the breeding season (Chapter 3) but more data are needed to demonstrate this conclusively.

Indirect evidence, supports the idea that poor body condition of adult birds could carry a mortality risk, for example: (a) heavier individuals survive periods of short term fasting longer than lighter birds (Ketterson and King 1977; Steube and Ketterson 1982) and, (b) a positive correlation between natural food abundance in winter and survivorship (Perrins 1966; van Balen 1980; Kallander 1981; Enoksson and Nilsson 1983; Nilsson 1985, 1987). A positive relationship of male or female body condition and overwinter survival has been previously demonstrated (Fretwell 1968; Coulson *et al.* 1983; Haramis et al. 1986; Reid 1987; Conroy et al. 1988; Newton 1981; Evans 1969; Marcstom and Kenward 1981; but see Lehikoinen 1986; Krementz et al. 1989 and Dufour and Ankney 1990) although for only a few passerines (Patterson *et al.* 1988; Newton, S.F 1993). Both male and female Swallows were expected to be most at risk during nestling rearing as indicated by minimum mass and muscles thickness during these stages.

The data were only partly in agreement with this prediction. Males but not females showed a significant association of measures of body condition to survival. Specifically that surviving males were significantly heavier during nestling rearing (1st & 2nd broods) and the critical period was during NP II as predicted. Males which survived also had significantly thicker muscles (as measured by an ultra-sound device) while rearing nestlings (data for second broods only). Newton (1993) was the first to demonstrate that indices derived from an ultra-sound device had implications for overwinter survival; adult male but not female Dippers which survived had significantly thicker muscles. In both Dippers and Swallows, significant differences were maintained whether or not body size corrections were used. Notably, while the relative condition of the pectoralis muscles varied independently of body mass in Dippers, this was not the case for Swallows. This explains why analyses of either body mass or muscle thickness in Swallows lead to similar conclusions, whereas in Dippers there was no relationship between overwinter survival and body mass. Significant differences based on ultra-sound condition indices in male Dippers were all independent of mass (Newton 1993). Good agreement of mass and ultra-sound with respect to predicting probability of survival gives further confirmation that in Swallows mass provides a good indicator of body condition and that lipid and protein reserves are utilised simultaneously.

The question remains as to why body condition was only important in shaping overwinter survival in male, but not female Swallows (also in Dippers, Newton, S.F 1993). The precise reasons for this are not clear, but given that females had poorer condition during NP II & NP III the finding was unexpected. Possibly the two sexes have different critical threshold, below which survival is threatened. Males may work harder (or maximally rather than optimally) than females. The discovery of a male which had almost certainly starved to death while feeding an enlarged brood of eight, while his partner went on to successfully rear a second brood with a new partner, lends some support to this idea. On Day 14 of the nestling period this male weighed 17.9g whereas at the same stage his partner was almost 1g lighter 17.0g. Thus whereas as the female probably abandoned the brood in order to allocate resources to self-maintenance, the male appears to have continued feeding the brood. Males might be expected to show higher effort than females if their overwinter mortality was higher and their residual reproductive success thus potentially lower. This too did not appear to be the case, however, since males in generally survived slightly better than females (see Table 3.9a,b).

In order to account for such differences direct measurements of daily energy expenditure are necessary for males and females of pair while at the same stage in the nesting cycle. Such data has been recently been collected for Swallows by Bryant *et al.* and these results are awaited with interest. A drawback of the present analyses was that the it comprised a pseudo-random sample of males and females which reared both natural and experimental (reduced and enlarged) broods. Future analyses will attempt to look in more detail at the inter-relationship of treatment, condition and survival (eg. Dijkstra *et al.* 1990).

7.4.6 STRATEGIES OF SINGLE AND DOUBLE BROODED BIRDS

A notable distinction between studies which did or did not show a decline in mass with increasing brood size was whether they were single- or multi-brooded. Parental condition of Swallows (this study), House Sparrows (Finke et al. 1987), House Wrens (Hegner & Wingfield) and Great Tits (Tinbergen 1987; Smith et al. 1987, 1989; Orell & Koivula 1987; Lindén 1988) which are all predominantly multi-brooded was unrelated to brood size, whereas in single-brooded female Snow Buntings, Blue Tits, Pied Flycatchers, Tree Swallows, Glaucous-winged Gulls and Kestrels mass was significantly reduced when experimentally enlarged broods were reared (Hussell 1972; Nur 1984a, 1988; Askenmo 1977, 1979; DeSteven 1980, Reid 1987; Dijkstra et al. 1990 respectively). These difference could indicate different strategies for allocation of resources by single or multi-brooded species (see also discussion by De Laet & Dhondt 1989). For instance single-brooded species might do better by investing more heavily in its present reproductive attempt as their chance to breed again are likely to be reduced relative to that of an individual attempting the first of two or more broods in a season. Following on from this idea manipulation of first- or second-broods might be expected to carry differing consequences for multi-brooded species. There was some evidence to support this for Swallows. Males and females feeding experimentally Enlarged second broods had a significantly lower mass during NP II and NP III respectively compared to those rearing Control broods. Other published studies on multi-brooded species, however, appear not to have manipulated the size of second broods and so these results need to be confirmed. A further idea for future analyses would be to examine the relationship brood size and parental mass of single- or double-brooded individuals of the same species. This could provide further insight into distinguishing whether variation in the number of broods attempted in aseason is related to an alternative strategy or variation in individual quality. A negative relationship for single-brooded Swallows would lend some support the former whereas as no increase in effort would support the latter.

Chapter eight

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General Discussion

8 GENERAL DISCUSSION

8.1 PROBLEMS ASSOCIATED WITH MEASURING REPRODUCTIVE "SUCCESS" AND MANIPULATING REPRODUCTIVE "EFFORT"

8.1.1 MEASURING REPRODUCTIVE SUCCESS

An ability to contribute offspring to succeeding generations is the most crucial aspect of any animals' life. Natural selection favours those phenotypes which are the most "successful"; that is, produce the the largest number of offspring which subsequently recruit to the breeding population. This precise measure is difficult to determine, however, and so alternative ways of assessing "success" have been sought. Typically the number of young reared to independence during a season or across a lifetime has been collected (Clutton-Brock 1988, Newton, I 1989). Since other measures such as timing of breeding and clutch size are also closely related to the number of young fledged these too are often taken as indices of reproductive success. While such data have the advantage of being collected more easily they remain incomplete measures of fitness (Newton, I 1989). The validity of using the number of fledglings reared as an estimate of the number which were subsequently recruited into the breeding population has been confirmed in only a few studies (Newton, I 1989; Hötker 1988) and found to be unreliable in others (Gauthier 1989).

8.1.1.1 Assessing parentage

A further assumption necessary when trying to quantify reproductive success is that the adults which are observed to attend a brood are the true genetic parents. While this can often be justifiably assumed for monogamous species, in some including the Swallow (Møller 1987a,b) this might not be valid. Females can increase their fitness by intra-specific nest parasitism (INP) (Anderson 1984; Brown 1984; Møller 1987a,b). There was no evidence that INP occurred for the population of Swallows studied here (Chapter 3; Ward 1992) and it was therefore, concluded that measures of seasonal reproductive success used in the present study should be accurate for females. Males, by comparison have the opportunity to increase their fitness by engaging in extra pair copulations (EPC) and equally are at risk from cuckoldry. In order to ensure the certainty of paternity for all eggs in a given males nest the frequency of EPCs and how often they result in successful fertilisations (EPFs) needs to be determined. Since the advent of DNA or genetic fingerprinting parentage this can now be achieved with a high degree of certainty (Wetton *et al.* 1989; Burke *et al.* 1989). Although the frequency of EPFs was not quantified during the present study there was evidence to suggest that they occurred; males were observed to closely guard their partners and chase intruders. Whether this occurred because of the risk of EPFs obviously needs to be confirmed. In any case EPFs are not expected to be as high as the figure reported by Møller who showed that EPC (and associated activities) were more frequent at larger colonies (Møller 1985, 1987a) most colonies observed here had five or fewer pairs (Chapter 3). Attempted EPCs have also been shown to be more frequent from older, earlier breeders while younger, later breeders are more likely to be "victims" (Møller 1985, 1987a). If EPFs were proven to occur in the population of Swallows studied here, since it would probably have the effect of increasing some age-related differences in success it should not substantially affect interpretation of the majority of the relevant results described in Chapter 5.

In the present study the number of young fledged across a season is assumed to be a reliable measure of reproductive success. This is supported to some extent through the finding that the number of offspring which were recruited into the breeding population increased with brood size. No INP or EPFs are assumed but any conclusions will necessarily bear these three potential sources of error in mind.

8.1.2 MANIPULATING REPRODUCTIVE EFFORT

Manipulation of brood size has proved to be a key tool in studies of avian reproductive ecology. This approach assumes that parents accept additional nestlings as their own but a difficulty associated with this is whether individuals respond in an appropriate way to the treatment imposed. The lack of an effect could be due an absence of costs, or alternatively through a failure to induce or detect a response. Costs were detected in the present study and these were assumed to be a direct consequence of the experiment.

A second potential problem concerns the way in which brood size has been altered. The degree of manipulation has varied from one or two nestlings being added or removed to more extreme situations where brood size differed greatly from that of the original size (Røskaft 1985; Reid 1987; Nur 1984a,b, 1988; Tinbergen 1987; Smith *et al.* 1988). In the present study up to three nestlings were added or removed but all manipulated broods fell within the range of one to eight, which was just one outside the natural range (2-7). The validity of creating brood sizes far outside the range normally encountered has been debated (Lindén & Møller 1988). Preliminary analyses here identified that a pair of Swallows could rear a maximum of eight young. Nest size proved to be too small to accommodate brood sizes of nine or more (see Discussion Chapter 6). Thus for experiments carried out on natural populations extending the brood sizes much above the natural limit may not be feasible for practical reasons alone. In nest-box populations, where this is clearly not a problem, more experiments are needed to determine both the validity and usefulness of such an approach. Extreme manipulations are likely to exaggerate costs and in so doing make their detection easier. This could provide a clearer insight into the mechanism underlying reproductive costs. Whether any meaningful extrapolations can be made, however, is both crucial and uncertain. Ultimately the design of the experiment should depend upon the specific questions being addressed.

Thirdly, should hatch failures be compensated for ? Since hatching success was very high for Swallows this was not considered to be of relevance here. More generally, unless it can be shown that reduced hatching success is related to some other factor such as egg quality, egg size or incubation behaviour then in order to increase reproductive effort during nestling rearing eggs which fail to hatch should be replaced with a chick at hatch.

Fourthly, if parents which rear manipulated broods (or the offspring of these broods) were more likely to disperse than those of Control broods then conclusions relating brood size to survival or future fecundity are likely to be invalid. This was also not deemed to be a problem in the present study (see discussion Chapter 6).

Finally, experimentally altering brood size serves to manipulate only one phase of the breeding cycle. As discussed earlier other stages such as egg laying, incubation or the cumulative effects across all stages might prove to be more limiting.

8.2 THE ROLE OF FOOD AVAILABILITY AND TIMING OF BREEDING IN SHAPING REPRODUCTIVE SUCCESS

8.2.1 FOOD AVAILABILITY

The role of food abundance in shaping reproductive success and other life history parameters has been comprehensively reviewed (Martin 1987). For a wide range of species, natural food abundance was found to be positively correlated with several measures of seasonal breeding performance such as egg size and egg quality, laying intervals, clutch size, nestling growth and quality and the number of broods attempted in a season (Martin 1987). Since Swallows feed solely on aerial insects, factors which cause insect abundance to vary are expected to play an important role in shaping their reproductive success (Chapters 4 and 5). This was not intended as the main focus of the present study, however. The association of reproductive performance and environmental conditions are therefore largely speculative. To properly have linked the two would have required more precise data which focussed on the short-term consequences of variability in food supplies. Such data were collected for the population of Swallows studied here during a concurrent study of laying and incubation (Ward 1992) and in an earlier study on incubation (Jones 1985).

8.2.1.1 Laying anomalies

Laying anomalies occurred in about ten percent of all Swallow nests observed (Chapter 3, also see Ward 1992). If these were imposed by a shortage of food as has been suggested (Lack 1954; Bryant 1975a; O'Connor 1979), then it could be predicted that an irregular laying pattern would be most prevalent during the early part of the season or during periods of inclement weather (both of which were associated with a reduction in aerial insect abundance). This expectation proved to be only partly founded; laying anomalies have been detected during both first and second broods but in only two cases were they definitely linked to periods of low food abundance (Ward 1992). Moreover, the mass of females (at the start of incubation) which did not lay daily did not differ significantly from all other females (Ward 1992). This contrasted with House Martins where it was noted that females which suffered laying anomalies were significantly lighter than those which laid daily (Bryant 1979).

It is suggested that in both species laying anomalies are likely to be adaptive because an interruption in laying would allow for a large clutch size to be laid at the cost of only one or two days delay. Terminating laying on the other hand would result in a minimum delay of about twelve days (depending on clutch size, re-lay interval etc.). This longer delay could reduce not just the reproductive value of each egg (*sensu* Verhulst & Tinbergen 1991) but also the probability of a second clutch being attempted. There was no evidence to suggest that other strategies such as reducing egg size or egg quality would be likely to be more beneficial (Ward 1992).

8.2.1.2 Egg size and quality

An increase in egg size and quality with food abundance is consistent with the idea that food limits egg production (Bryant 1975b; Högstedt 1981; Murphy 1986). The size and composition of Swallow eggs was related to environmental conditions during, but not before, the periods of albumen formation; eggs were heavier and larger if they were formed during favourable conditions (i.e higher temperature, food abundance and lower rainfall) (Ward 1992). Notably, Swallows egg size was not correlated with laying order, clutch size, female body size or female age. Ward (1992) concluded that eggs were formed principally from food intake (i.e based on daily resources) and that egg synthesis was largely under energetic constraint.

Egg size may have fitness implications. Within species it has been demonstrated that smaller eggs have reduced hatching success and nestlings from them have lower growth rates and survival than from bigger eggs (Schifferli 1973; Davis 1975; Bryant 1978b; De Steven 1978; Lundberg and Vaisanen 1979; Moss et al. 1981; Ward 1992). Similarly, small Swallow eggs hatched smaller, lighter nestlings. Survival implications were not considered, however (Ward 1992). Notably egg size was unrelated to hatching success (Ward 1992). In Tree Swallows and Great Tits, although egg size was significantly correlated with nestling mass it was unrelated to survival (De Steven 1978 and Schifferli 1973 respectively).

8.2.1.3 Clutch size

Published data are equivocal in their support for an effect of food supply on clutch size. In experimental studies involving supplementary food a positive relationship has been detected in the Sparrowhawk (Newton & Marquiss 1981), Magpie (Högstedt 1981), Kestrel (Dijkstra *et al.* 1982), Song Sparrow (Arcese & Smith 1988) and Tengmalms Owl

(Hörnfeldt and Eklund 1990), yet in other studies no effect was demonstrated (Clamens and Isenmann 1989, for review see Martin 1987, Table 1 p461). Among other things differences in methodology regarding the period over which supplementary food was provided or a failure to control for effects of natural food abundance or timing of breeding during the experiments, could account for some differences between species (Martin 1987).

8.2.1.4 Nestling growth and quality

Environmental conditions, food availability and food quality have also been shown to have an effect on nestling growth. Results from studies carried out on laboratory populations demonstrated that both food 'quality' and food availability influenced nestling growth rates and that effects sometimes persisted to adult size (Boag 1987a, Johnston 1990). Variation in nestling diet quality can exist in the wild and this too can have an effect on nestling growth (Morse & Vohra 1971; Johnston 1990). A positive relationship between natural food availability and nestling growth has been demonstrated in the House Martin (Bryant 1978a; Johnston 1990) and Tree Swallow (Blancher and Robertson 1987; Wiggins 1990b). Variation in wing length attained by yearling House Martins in different years was explained by insect abundance in the year of hatch (Bryant 1989a).

Data were inconclusive as to whether similar trends occurred here for Swallows. Although yearlings (females) which hatched in 1987 had significantly longer wing lengths in the following year (*cf.* 1988), this was not linked to differences in food abundance during the nestling period. Moreover, peak nestling mass was not correlated with any measure of food abundance. A lack of significant trends might be explained if the suction trap method proved to be an inappropriate measure of the Swallow diet or if the analyses were not extensive enough to detect any differences. Earlier studies, however, have shown a close relationship between hand net sampling at specific study sites and suction trap catches as well as between growth, reproductive success of Swallows and suction trap catches (Turner 1980; Jones 1985). Future analyses should attempt to look in more detail at the inter-relationship of post-fledging development, parental care and food availability. Where possible the relative importance of both genotypic and phenotypic factors should also be evaluated (Alatalo *et al.* 1990).

8.2.1.5 Number of broods

In species which are known to be multi-brooded the percentage of pairs which attempted two or more broods in a season has been linked to variation in natural food abundance (Perrins 1965; Newton 1972; Bryant 1975, 1988; Blancher & Robertson 1982; Hussell 1983; Gavin 1984; Rodenhouse *et al.* 1986, in Martin 1987; Arcese & Smith 1988; Tinbergen & van Balen 1988; Riley 1992). More notable was that Willow Tits which were provided with supplementary food increased the probability of an individual attempting a second brood but did not increase their clutch size (Jansson & Bromssen 1980). The percentage of Swallows pairs which were double brooded decreased in each year of the study but this did not appear to be related to annual differences in food abundance (Chapter 5).

8.2.2 ROLE OF DATE OF ARRIVAL AND TIMING OF BREEDING IN SHAPING REPRODUCTIVE SUCCESS

8.2.2.1 Differential date of arrival

Swallows arrived on their breeding grounds from early April but continued to appear through May and into June. Possible benefits associated with early arrival include access to the best resources such as food, nest sites or mates (Coulson 1977; Newton *et al.* 1985; Stutchbury & Robertson 1987b). Specifically, Stutchbury&Robertson (1987) suggested that arrival patterns in Tree Swallows were a consequence of intense competition for nest sites. Nest sites did not appear to be limited for the population of Swallows studied here (also see Møller 1987b) and since, Swallows do not have feeding territories it remains to be shown that early arrival is advantageous (see below). Furthermore, what enables some birds to arrive at the breeding grounds earlier than others also needs to be considered. The finding that some birds arrived at their breeding site consistently earlier than others (*pers obs;* also Medvin et al. 1987) is consistent with the view that it could ultimately be under genetic control (Berthold 1990). It has also been reported, however, that older or more experienced birds arrived earlier than yearlings (Coulson & Horobin 1976; Crawford 1977; Nolan 1978; Stutchbury & Robertson 1987b, but see Afton 1984) and that this sometimes but not always (Stutchbury & Robertson 1987), resulted in earlier laying. Experiments which have demonstrated that females can advance their laying date and increase clutch size following the provision of supplementary food (Martin 1987) further suggest that at least in some species energy might be limiting early in the season (this was not tested in the present analyses, but see below). There was some evidence from this and other studies on hirundines to suggest that physiological differences between individuals are of importance.

Adult mortality has been shown to occur during the breeding season in the Swallow (this study), House Martin (Rheinwald 1971; Bryant 1979) and Tree Swallow (Lombardo 1986a and references therein) and that this was most prevalent early in the season before any breeding activity had started (this study; Lombardo 1986a). Specifically Lombardo (1986) reported that Tree Swallows which died early in the season: "were physiologically less able to withstand the metabolic stress of cold weather than those that survived". This conclusion was based on three measurements (dry weight; % dry weight; and nonfat dry weight) made on these carcasses. Moreover, three quarters of all known casualties were yearlings. Perhaps a greater susceptibility to unseasonable weather either on migration or in the breeding area, may partially explain why yearling hirundines often return and commence breeding later than older birds.

The underlying pattern regulating arrival dates to the breeding grounds could, therefore, be related to variation in physiological tolerances such that each individual will arrive and remain at a site when it is physiologically able to do so. If individuals which arrived first had a lower daily energy expenditure or metabolic rate combined with an ability to forage more efficiently then this would enable them to tolerate poor or unpredictable environmental conditions during the early part of the season. It might be informative to examine body condition during the pre-breeding period, in particular how body condition relates to arrival date, onset of laying and subsequent breeding success. There are , however, likely to be considerable problems in studying this, not least because of the difficulties associated with catching an adequate sample of birds during this period. Moreover, if selection operates prior to arrival at the breeding grounds then any underlying trends may be obscured.

8.2.2.2 Timing of breeding

Earlier breeding should favour a prolonged breeding season which among other things will allow for a longer period to attain optimal breeding condition or to attempt subsequent broods or replacement clutches. This would assume that earlier breeding is favourable and that limits of time are an important determinant of multiple breeding attempts. Swallows and House Martins which arrived earliest were older and were also the earliest proven layers (*pers obs*; Bryant 1979). Arrival date and laying date was not linked in Tree Swallows, reflecting that for this species early arrival was more important to secure a nest site (Stutchbury & Robertson 1987b). Data supporting the advantages of early breeding are unequivocal for many species of birds (Perrins 1965; Møller 1988a; Kirkpatrick *et al.* 1990; Oring *et al.* 1992) and particularly in a variable seasonal environment it is likely to be an important component influencing fitness (for review see Stearns 1976).

The time at which breeding starts appeared to be a major factor shaping annual reproductive success in Swallows; clutch size decreased and the reproductive value of each egg declined with season. Moreover, pairs which were double -brooded, itself a major determinant or reproductive success, started their first broods significantly earlier than single-brooded pairs. It was also noted that there was a negative trend in clutch size for both first and second broods, single- and double-brooded pairs, and so the observed decline could not be wholly attributed to reduced breeding success associated with second broods. In other species clutch size has commonly been been observed to be larger and more successful earlier in the season compared to later (Klomp 1970; Perrins 1970; Daan & Dijkstra 1988) and possible reasons to explain such trends have been discussed (Lack 1954, 1966; Askenmo 1982; Murphy 1986; Verhulst & Tinbergen 1991 and Daan *et al.* 1991).

Lack (1954, 1956) suggested that seasonal trends could be attributed to a decline in food abundance during the season. This idea was supported by the finding that: a) in good food years or in association with an increase in natural food abundance females were observed to lay earlier and, b) where part of the population was provided with additional food (prior to egg laying) females laid significantly earlier than unfed birds (for review see Martin 1987; p124, Table 1). Although the relationship between laying dates and food abundance was not directly examined here for Swallows indirect evidence suggested that clutch size could not be wholly explained by energetic constraints upon egg production (also see Ward 1992). Firstly, clutch size decreased whereas food availability generally increased with season so that a decline in food abundance was observed only after most pairs had finished laying (Chapter 5). Secondly, when eggs were removed during first or second broods a similar sized clutch was usually laid within seven days. Results from experimental studies which failed to show an increase in clutch size in association with the provision of additional food also argue against Lack's theory (Martin 1987; Daan *et al* 1991). A decline in breeding performance with season was, therefore, largely independent of food abundance for Swallows studied here.

A second possibility is that females which laid later in the season were of lower "quality" (Askenmo 1982; Murphy 1986; Verhulst & Tinbergen 1991). A number of results from this study were consistent with this view: single-brooded birds tended to be yearlings which laid later in the season, were less successful and had a lowered probability of survival (*cf.* double-brooded) (Chapter 5; also Ward 1992). One way to experimentally test whether these differences were related to: a) their initial laying date and food availability or, b) individual differences, would be to manipulate the laying date of pairs. This could be achieved through clutch removal. Removal of clutches in females is known to induce females to lay a replacement clutch and so delay their start date by about twelve days (for a clutch size of five). This protocol should have the effect of altering laying date while "controlling" for quality. Where a delay did not reduce reproductive success or alter the probability of a second brood (relative to the control) this would indicate that individual quality was of greater importance than the initial start date. Laying itself might be costly, however. While the available data suggested that this did not appear to be the cases for Swallows (Ward 1992) this cannot be assumed across all species. If laying was found to incur a cost then interpretation of the results would not be so straightforward. Any experiment of the type proposed above should, therefore, attempt to estimate how costly the production of extra eggs is. If laying could be delayed by some other method such as interfering with nest building then such a group could act as a second control. To fully estimate the fitness consequences associated with variation in laying dates juvenile survival also needs to be considered. Moreover, since a relationship between laying date and fecundity, or survival in the following year, might be related to timing of breeding, these factors also need to be considered (For discussion see Verhulst & Tinbergen 1991).

8.3

THE ROLE OF INDIVIDUAL ATTRIBUTES AND OTHER FACTORS SHAPING REPRODUCTIVE SUCCESS OF INDIVIDUALS

Seasonal or lifetime reproductive success may directly or indirectly be affected by characteristics of individuals or by chance factors (reviewed in Clutton-Brock 1988, also see Chapter 5 and references therein).

8.3.1 BODY SIZE

Through its effect on a wide range of characteristics including individual recognition, mate choice, dominance, territoriality, foraging ecology, flight dynamics and energetics , body size has been shown to influence the behaviour and ecology of birds (see Introduction, Chapter 4 and references therein). Specifically, adult body size has been related to an individual's reproductive success (Downhower 1976; Perrins 1979, 1980; Banbura 1986; Murphy 1986; Møller 1988a, 1990a; Bryant 1988b, 1989a; Langston *et al.* 1990) as well as its probability of survival (Fleischer & Johnston 1982, 1984; Lehikoinen 1986a; Monaghan & Metcalfe 1986, but see Jones 1987c; Langston *et al.* 1990). Interrelationships such as these, are undoubtedly complex and may be complicated further if selection pressures differentially affect males and females (Johnston & Fleischer 1981; Clutton-Brock *et al.* 1982) or vary between years (Fleischer & Johnston 1984; Lehikoinen 1986b). Moreover, since large and small size can be advantageous at different points in the annual cycle a compromise in response to prevailing behavioural, physiological or ecological "pressures" can be anticipated.

Phenotypic characteristics of Swallows varied between individuals, sexes and years (this study; Banbura 1986) as well as populations (Smith & Montgomerie 1991). Sexual size dimorphism has previously been reported as being slight in the Swallow except for outer tail length or tail streamers (sensu Møller 1988a) and wing length (Turner & Rose 1989). Differences in adult body size were also most extreme for outer tail streamers in the present study, but significant differences were noted for all other measurements except tarsus length (Chapter 4). Only in the case of the inner tail were females bigger than males. Three hypotheses have been outlined to explain the evolution of sexual size dimorphism in morphological characters: (i) "female reproduction" hypothesis, (ii) feeding niche hypothesis and, (iii) inter- sexual selection; the second and the third are reviewed here specifically in relation to outer tail length.

8.3.1.1 Female reproduction hypothesis

The female-reproduction hypothesis asserts that since smaller females can replenish reserves faster or require less energy for self-maintenance they should be able to channel their resources into reproduction earlier than larger females (Downhower 1976; Searcy 1979; Price 1984a; also see Langston *et al.* 1990). As a consequence they would be expected to have a higher reproductive success when compared to bigger birds. This hypothesis makes three assumptions: (i) timing of breeding is variable and in some way constrained by resources; (ii) early breeding is advantageous; (iii) eggs are produced from food eaten on the breeding grounds and not from reserves accumulated elsewhere and, (iv) small birds gained food as fast as big birds. As evidenced by the results from this study, Swallows do not appear to fit predictions of the female-reproduction hypothesis: breeding performance was inconsistently correlated with any measure of female body size taken (Banbura 1986; Møller 1990a; Ward 1992). In general all correlations were weak and non significant and if anything there was a tendency for bigger birds to be slightly more successful. A failure of the data to support the hypothesis was not attributed to any violation of the assumptions since all three outlined above were fulfilled: (i) there was marked variation associated with time of arrival and the onset of laying; (ii) birds which laid earlier had larger clutch sizes, fledged more young and were more likely to be double brooded and, (iii) resources necessary for egg formation were primarily based on food collected during laying (Ward 1992). Evidence in support of the female reproduction hypothesis has also been found to be equivocal for other species; smaller females bred earlier or produced more young than bigger conspecifics in Great Tits (Dunn 1976; Perrins 1979, 1980), Darwin's Finches (Downhower 1976; Price 1984a), Dippers (Schmidt & Sphznagel 1985) and Eastern Kingbirds (Murphy 1986) whereas larger female Pied Flycatchers laid earlier then smaller birds (Järvinen & Vaisanen 1984).

8.3.1.2 Feeding niche hypothesis

In the feeding niche hypothesis sexual dimorphism is linked with a reduction in inter-sexual competition for resources and differentiation in foraging strategies and diet selection (Selander 1966; Ligon 1968; Price 1984a). This was not examined during the present study but data collected from other studies suggest that since Swallows feed communally and there appears to be no differentiation in prey selection (Vietinghoff-Riesch 1955; Turner 1980; Jones 1985, 1987c; Møller 1990a), so sexual dimorphism in the outer tail length is not attributed to the feeding niche hypothesis. It has been noted, however, that while the size of prey taken did not normally differ between males and females (of a pair) male Swallows carrying experimentally elongated tails captured smaller insects relative to their partner (Møller 1989a).

8.3.1.3 Inter-sexual selection

Females will be selected to respond to a trait only if it varies markedly among potential mates (Searcy 1982; Cherry 1990). Tail length of Swallows studied here varied more than all other morphological traits and was significantly correlated between mates (Chapter 4). Controlling for the effects of age revealed that tail length was only significantly correlated between mates which were two years or older (see Banbura 1986). It is difficult to give a conclusive interpretation, however, because the trend was apparent only within one age group. Since pairing may be closely related to arrival date and age, and tail length was significantly correlated with both of these parameters the exact role that tail length plays in shaping mate choice can only be determined through manipulation experiments.

Results from experimental studies demonstrated that males which carried elongated tails attempted EPCs more frequently (Møller 1988a), acquired mates more easily and as a result had a shorter pre-laying period (Møller 1988a, 1989a, 1990a; Smith & Montgomerie 1990, also see Anderson 1982 and Barnard 1990). Results from both natural and manipulative studies are at least in part consistent with the idea that female Swallows use tail length as a cue to mate choice. As a consequence of this, females which mate with long tailed males would therefore be expected to be more successful. There was evidence to support this conclusion from this study (Chapter 5) as well as others (Banbura 1986; Møller 1988a; Smith& Montgomerie 1991).

Partners of males with longer outer tails (natural) started laying significantly earlier (this study; also Banbura 1986, Table III; p 133), fledged more young during the first brood and were more likely to be double brooded than those which had shorter tails (Chapter 5). Similarly, for partners of males with experimentally elongated tails, their partners commenced laying earlier (Møller 1988a; Smith& Montgomerie 1991) and fledged more young during a season (Møller 1988a, but see below) than those which were paired to males with shortened tails. Although Møller (1988a) noted that males with experimentally enlarged tails were significantly more likely to attempt a second brood compared to those with reduced tails (Fig 2, p 641) the opposite was found by Smith & Montgomerie (14% Vs. 38% enlarged and reduced respectively, n=15; Table 3, p199), who suggested that their finding could be linked to a low percentage (20%) of the population which was double brooded (*cf.* Denmark ~ 50%, Møller 1988a) (Smith & Montgomerie 1991). These conflicting results could reflect differences in experimental procedures or genuine differences between the populations (eg. %double brooded; seasonal trends; only male Barn Swallows incubate). Equally, it might reflect error related to the small sample sizes involved in both experimental studies.

8.3.2 PARENTAL AGE AND INDIVIDUAL DIFFERENCES

Adult Swallows could not be reliably aged using any morphological character and, therefore, had to be aged via their ringing history. As the return rate of juveniles to their natal area was low relatively few yearlings were identified. In other studies of hirundines it has been suggested that if a population has been completely marked in one season, and all of the individuals re-caught in the following season, then an unringed bird which appears is likely to be a new recruit (Bryant 1979; Crooks & Shields 1987). The validity of this approach is dependent on proving that: (i) adults are site faithful and, (ii) the majority of birds were captured in the first year.

Less than five percent of all adult Swallows were identified as moving between sites (Section 3.5) and so dispersal is expected to have a minor influence on the ability to correctly identify yearlings. The second assumption, however, was more difficult to confirm. Although an attempt was made to catch all birds in the study area, inevitably some evaded capture. This created a need to distinguish between unringed birds which were new recruits and those which had evaded capture in the previous season (s). Based on the level of observation as well as the percentage of birds which were estimated to be captured at that site in the previous season each unringed bird was assigned a code (Section 2.4). Two categories were established: (i) assumed to be new recruits and, (ii) at least one year old (probably a mixed age group). Comparisons of body size (Chapter

4) and breeding performance (Chapter 5) between "known" and "assumed" one year old birds, which in this (based on known-aged birds Chapter 5) and other studies of Swallows have been shown to be age-related (Banbura 1986; Møller 1988a, 1990b), yielded encouraging results. Measures of body size, plumage scores and breeding performance of assumed one year old males and females did not differ significantly from known one year old birds, but did differ for all measures from birds which were "at least two years old" (≥ 2). It, therefore, seemed valid to pool the data for "known" and "assumed one year old" birds.This enabled age related trends to be examined.

8.3.2.1 Distinguishing between age and breeding experience

The effects of age and breeding experience are often difficult to distinguish in short-lived passerines (Harvey *et al.* 1984, 1988; Sæther 1990). They may differ, however, if individuals do not all start to breed at the same age. Where this is apparent, and the the two groups (experienced vs inexperienced) are compared at the same age, birds which entered the breeding population at an older age should do poorly relative to those which entered at a younger age. This idea was not readily testable for Swallows, however, since most birds attempted to breed in their first year and those which were identified as non breeding either died or failed to return to the breeding area in the following season (Chapter 5). Nol & Smith (1987) further suggested that for multi-brooded species the performance of individuals with different levels of breeding experience could be compared within the same season. They predicted that if experience was an important factor then performance would increase with each breeding attempt (second > first). For this prediction to hold true and be valid, however, requires that conditions are stable across the period being monitored. Conditions were were not stable across the season in the House Martins (Bryant & Westerterp 1983) and were unlikely to be stable in the Swallows observed here, and so the comparison is not valid. Following on from Nol & Smith (1987), a third possible way in which age and breeding experience could be distinguished would be to compare the breeding performance in the second of two successive years of breeding between individuals of the same age which had been single- or double-brooded in the previous season. This also proved not to be testable here, however, because on average only one fifth of the population was single- brooded and since a majority of these did not return the following year, there was an insufficient sample size to make such a comparison. In any case this analyses would be flawed if it were also demonstrated that selective mortality operated on the population or that the strategies were derived from genotypic or phenotypic differences (see below).

8.3.2.2 Age-related trends in breeding performance

Breeding performance of Swallows improved with age as evidenced by the results of this study (Chapter 5). Specifically, it was noted that yearling females laid later, had a smaller clutch size and raised fewer young to independence during first broods compared to older birds (also see Ward 1992). Age-related patterns associated with arrival to the breeding grounds were discussed above. Yearlings also reared fewer young across the season. In a study of Blackbirds, Desrochers (1992) suggested that young birds fledged fewer offspring per year than older birds because they started breeding on average about two weeks later. This resulted in a smaller number of broods being attempted each season. While this was found to be partly true for Swallows it did not entirely explain reduced fledging success because comparisons made only on double-brooded birds, yearlings and adults yielded a similar result (Chapter 5, also see Desrochers 1992). Moreover, when the number of young fledged was expressed as a proportion of the initial clutch size, at any given attempt older birds still reared more young to independence. Since fledging success was also lower for yearlings this may indicate they were less successful at feeding their brood (below). Age-related trends were similar, though slightly weaker for comparisons between male age classes. Since yearling males were slightly more likely to fail to breed (also see Hemery *et al.* 1979 in Turner & Rose 1989; Crook & Shields 1987; Møller 1988b) and as it has been suggested that EPCs are more frequent from older males (Møller 1985, 1987a) results reported here are likely to underestimate age-related differences in success for males.

Although differences in breeding performance were most pronounced between one and two year old birds, females which were at least three years old started laying earlier and had a larger clutch size compared to birds which were categorised as being at least two years old. The latter, however, actually raised more young to independence during their first brood. There were insufficient data to compare differences across the season but it was suspected that the result was an artefact of a small sample. Further data are necessary, however, to discount an effect of ageing. Published results of senescence have so far only been convincingly demonstrated for two short-lived species: the Great Tit (Perrins & Moss 1974; Weber 1975; Dhondt 1987, 1989) and the Blue Tit (Dhondt 1987, 1989). Effects of ageing have included later laying dates (Perrins & Moss 1974; Dhondt 1987), smaller clutch sizes, lower hatching success and reduced numbers of young fledged (Dhondt 1987). There were slight differences between species, sexes and studies (Dhondt 1989). Since a difference between two and three year old Swallows was only detected for the number of young fledged it is suggested that this was not due to an effect of ageing and so the main difference remains that between yearlings and older birds.

Similar age-related trends in reproductive performance between yearlings and adults have been described for a wide range of other passerines species (for recent review see Sæther 1990). Differences were also most pronounced between one and two year old birds, and for almost all species studied, older birds started breeding earlier, had a larger clutch size and fledged more young (summarised in Appendix 8.1). Similar trends have also been observed for non-passerines (Sæther 1990). There appeared to be only a few exceptions to this trend but notably all were multi-brooded species. For instance there was no significant difference in laying dates with female age in the Savannah Sparrow and the Wrentit (BéDard & LaPointe 1985 and Geupel & DeSante 1989 respectively) and older female Savannah Sparrows (BéDard & LaPointe 1985) and Song Sparrows (Nol & Smith 1987; Geupel & DeSante 1989) did not have a larger clutch size or fledge more young. Notably for Song Sparrows in two earlier studies, older birds did advance their laying date relative to yearlings (Smith & Roff 1980; Smith 1981) and so for this species at least detection, and the exact extent, of age-related differences may be related to variation in environmental conditions (i.e food availability) (also see discussion below).

Other studies have also examined age-related differences in egg size and quality which could influence reproductive success. Although yearlings often laid smaller eggs than adults (DeSteven 1978; Nice 1937; Crawford 1977; Nolan 1978 reviewed in Sæther 1990) differences in hatching success were less inconsistent. Depending on the species, yearlings showed both a higher (Bryant 1979; Reese & Kadlec 1985) and lower (De Steven 1978; Nol & Smith 1987 and Perrins and Moss 1974 , references in Sæther 1990) hatching success. Notably hatching success was generally high for all age classes of Swallows observed here (Chapter 5, also Ward 1992). This suggested that egg quality or the ability to incubate clutches was not age-related. Ward (1992) reported that egg size in Swallows was not related to age but that it was highly repeatable for individual females.

Not only the number of offspring, but also their quality, has been observed to vary with parental age in Red-winged and Yellow-headed Blackbirds (Crawford 1977), Ipswich Sparrow (Ross 1980b) and the Swallow (Languy & Vansteenwegen 1989 respectively) and also in non-passerines (Myberget 1986; Hannon and Smith 1984). If older parents reared more young earlier and which are of better quality then one would predict that they also ought recruit more into the breeding population. Comparatively few studies on passerines have examined this (but see Rheinwald 1975; Ross 1980b; Perrins & McCleery 1985; Dhondt 1987; Geupel & DeSante 1989; Lessells & Krebs 1989, Appendix 8.1) and in general the data yielded inconsistent findings. Only Bee-Eaters (Lessells & Krebs 1989) and House Martins (Rheinwald 1976) recruited more offspring as adults. No difference was observed in other studies even though older parents had reared more young to independence (Geupel & DeSante 1989; Perrins & McCleery 1985; Dhondt 1987; Ross 1980). Older Swallows in this study actually produced fewer recruits than yearlings, though the difference was not significant. Lessells & Krebs (1989) suggested that variation in parental foraging ability could account for differential post-fledging survival of offspring reared by yearlings and adults.

In multi-brooded species the number of broods attempted in a season has also been shown to be age-related. All studies listed in Appendix 8.1 showed that older birds attempted more broods in a season that yearlings (Middleton 1979; Ross 1980; (Boer-Hazewinkel 1987; Geupel & DeSante 1990; Crawford 1977; Reese & Kadlec 1985; Nol & Smith 1987; Ross 1980b;Pinowski 1977; Geupel & DeSante 1989; DeSteven 1980; Bryant 1979; Desrochers 1992). Similarly older female Swallows attempted two broods significantly more often than yearlings and while a similar pattern was evident for males the difference was not significant.

Given that breeding success, the number of broods attempted and the probability of being recruited decreased as the season advanced then an individual could increase its fitness by producing as many young as early in the season as possible. This could at least in part be achieved through reducing the length of the breeding cycle (Tinbergen & van Balen 1988; also see below). A reduction in the time taken between finishing one brood and starting the next, termed here as the inter-brood interval (IBI), for instance might increase the probability of a second brood being attempted as well as the reproductive value of each second brood egg . A reasonable prediction might therefore be that older birds would reduce the duration of their inter-brood interval relative to yearlings (possible ways this could be achieved are considered below). Burley (1980) reported that experienced birds re-nested sooner than inexperienced ones and, older Savannah and Ipswich Sparrows took less time between broods than younger birds (Bédard & LaPointe 1985 and Ross 1980 respectively). The data collected here for Swallows, however, did not appear to support this idea. IBI of parents rearing control broods did not differ between male or female age classes (Table 6.17) and trends were conflicting when the relationship was re-examined for manipulated broods. Both older male and females Swallows which reared Enlarged first broods had a slightly (ns) longer IBI than yearlings. Only older birds which reared reduced broods conformed to the predicted pattern. The lack of a consistent trend was not attributed to older birds having an earlier date of hatch or larger brood size (both of which were negatively related to IBI, Chapter 6). The finding that females reduced their IBI by about three days in their second of two successive years of breeding is, however, consistent with the above suggestion. Ross (1980b) also reported that there was no significant differences in parental age to re-nest or re-lay after a clutch or brood was removed (i.e predated or abandoned). This suggests that differences were related to parental abilities in rearing broods rather than to the time needed to accumulate reserves for egg formation. Similarly in the present analyses the re-lay interval was consistent between age classes.

In almost all of the studies mentioned in Appendix 8.1, breeding performance also declined seasonally. The smaller clutch size and reduced number of young reared by younger birds may, therefore, simply reflect their later laying date. After controlling for laying date in Swallows (this study), Tree Swallows (De Steven 1978), Blackbirds (Desrochers 1992) but not Bee-Eaters (Lessells & Krebs 1989), differences in clutch size were still apparent. For all other parameters compared in this study including the number of broods attempted (also see Desrochers 1992) while part of the reduced breeding success of yearlings was explained by their later laying date, differences were still significant after variation in timing had been allowed for, and so some other factor must account for this pattern.

8.3.3 OTHER FACTORS

8.3.3.1 Mate-fidelity

In monogamous birds the quality of an individual's mate will be an important component shaping reproductive success. Breeding experience (Coulson 1966; Brooke 1978), age (Coulson and Horobin 1976; Mills 1973; Bryant 1987) or phenotypic characters (Chapter 4 and references therein), have been shown to influence mate choice. There was evidence to suggest that Swallows mated assortatively within two age classes (Chapter 5). The role of morphological attributes was less clear. Although outer tail and head-to- bill length were significantly correlated between pairs both these parameters also increased with age (Chapter 4). If, pairing takes place soon after arrival and arrival is age-related (as demonstrated for Swallows, this study), this could provide one obvious and simple route as to why individuals of a similar age often paired.

Although maintaining a pair bond has been shown to be advantageous in many species separation has also been shown to be widespread particularly following 'poor' breeding success (for review see Rowley 1983; but see Perrins and McLeery 1985). Maintenance of the pair bond both within as well as between seasons was not related to breeding success in Swallows. This provided a marked contrast to House Martins where: (i) intra-seasonal separation occurred more frequently following an unsuccessful first brood, (ii) individuals performed better following re-mating and, (iii) of 17% of pairs in which both partners survived from one season to the next none was detected as re-pairing (Bryant 1979). Why House Martins should shows such a high degree of infidelity , yet Swallows remain together regardless of performance is intriguing ? Poor breeding performance could occur as a result of chance factors such as inclement weather, disturbance or predation, rather than reflecting the quality of an individual. Where the likelihood of finding a new mate or a mate of better quality cannot be guaranteed separation may be more risky than fidelity. A second possibility is that infidelity is a mechanism to minimise in-breeding. Why such factors should differ for the Swallow and the House Martin, however, is not clear. Age composition and the sex ratio are also likely to be important in determining how costly or beneficial separation is likely to be. A shortage of alternative partners was not thought to be a factor explaining the observed trend for Swallows.

8.3.3.2 Nest re-use

The reasons and possible importance surrounding nest choice have been addressed by Barclay (1988) and reviewed in Shields *et al.* (1988). The consensus explanation for nest re-use is that it requires less time and, therefore, energy (Shields *et al.* 1988). During this study pairs which built a new nest started laying about four days later than those which re-used an old nest. This was attributed to the extra time taken to build a new nest (Chapter 3). Shields *et al.* (1988) also reported that the only pairs which successfully raised two broods were those which used old nests for both attempts. Since earlier arriving and double-brooded birds were older, improved performance with nest re-use may just be age-related. This was not investigated in the present analyses, however. Future analyses could attempt to examine more precisely the exact relationship between arrival date, nest choice and male and female age. Moreover since Swallows which attempted two broods in a season were the most successful, the decision to build a new or occupy an old nest might be related to whether an individual attempted a second brood. Indirect evidence supports this idea. Three quarters of all double-brooded pairs re-used an old nest during their first brood and just over two thirds of these attempted their second brood in an old nest. By comparison a majority of single-brooded pairs occupied new nests (Table 3.1c). Those which re-used an old nest would be be able to re-nest quicker and so would have more time in which to attempt a second brood. Double-brooded pairs which occupied an old nest might, therefore, be expected to have a shorter inter-brood interval. This remains to be examined but research on House Sparrows which has demonstrated that pairs which occupied nest boxes had a shorter interval between clutches opposed to those which occupied natural sites supports this proposition (McGillvray 1983). It was suggested that this could be due their being reduced thermoregulatory or nest maintenance costs associated with occupying a nest box (McGillvray 1983).

Given the potential time savings, which could be particularly critical for a double-brooded species, why then do all pairs not choose to utilise an old nest. For instance it was noted here that a failure to occupy an old nest was rarely due to an old nest not being available. Furthermore only 16% of double brooded pairs re-used their first brood nests. Nest re-use may be associated with a number of potential costs. A number of hypotheses have been proposed.

First, as nests age they will have a higher probability of falling down and (Shields and Crook 1987). Shields and Crooks (1987) found that nest falls were a significant source of nestling mortality in their study but the results from the present study did not support this idea; nest falls occurred rarely and also included new nests. This first hypothesis also makes the assumption that the birds are able to assess nest age. There is no evidence from the literature to indicate that this is a valid assumption.

Second, old nests have been shown to provide an ideal climate for ectoparasites (reviewed in Brown 1984; Shields and Crook 1987; Barclay 1988). Ectoparasites have been demonstrated as causing both lethal (Møller 1987a; Shields and Crook 1987) and sublethal effects in nestling Swallows (Møller 1987a, 1988b). If continuous use of old nests facilitated the growth of ectoparasite populations then this might explain why intermittent use of old nests appears to be favoured. This view is supported by the finding that double brooded pairs observed here built new second brood nests even after the first brood had been successful (Chapter 3). Møller's (1988b) made a similar observation but also noted that new nests were built more frequently following a high parasite load which led him to conclude that nest rotation was a possible means of parasite avoidance. No estimation of parasitic load was made in this study or in previous studies carried out on the same study area and so Møller's conclusion cannot be confirmed. Shields's (1984b) observation that pairs were more likely to change their nest following an unsuccessful breeding attempt is not consistent with this, however. Nest re-use was recorded following both successful and unsuccessful breeding attempts here. If ectoparasites did play role in shaping nest choice for it to function it would have to rely on birds being able to assess whether a nest was infested with parasites. This seems a likely possibility, however, since du Feu (1992) noted that fewer visits were made to infested nest-boxes when the number of fleas around the entrance had been experimentally manipulated.

8.3.3.3 Colony size

Swallow sociality varies not only among genera and species, but also among populations. While in some studies they have been reported as breeding in large groups, others have found them to be more or less solitary. The population of Swallows observed here ranged between one and fourteen pairs per colony. The advantages and disadvantages of coloniality have been extensively studied in the swallow family (for review see Shields *et al.* 1988 and references therein). Demonstrable costs associated with group living have included increased: (i) intra-specific nest parasitism (Møller 1987b); (ii) ectoparasitic loads (Møller 1987a; Shields and Crook 1987); (iii) levels of mate guarding (Møller 1985, 1987c,d); (iv) attempted EPCs (Møller 1985); (v) levels of sexually selected infanticide (Møller 1988b, but see Crook & Shields 1985) and finally, (vi) competition for mates, nest sites or other limiting resources. Observations made at colonies of varying sizes might explain some marked differences in the occurrence of certain activities documented between studies.

In Denmark, about 16% of all eggs laid were thought to be parasitic (Møller 1987b), whereas in the present study there was no evidence of any egg-dumping (Chapter 3). The difference between studies was not attributed to a failure to detect parasitic eggs here, but was related to the smaller colony sizes observed in central Scotland (also see Ward 1992). That the probability of victimisation increased with colony size in Denmark (Møller 1987f) is further consistent with this view. Similarly, infanticide has been observed in some studies of Swallows (Møller 1987a, 1988b; Crooks and Shield 1985, 1987) yet in this study and others (Myers and Waller 1977; Medvin *et al.* 1987) it was concluded that it was absent or exceptionally rare. Møller (1987a) found that the incidence of infanticide occurred more frequently on a per-nest basis in larger colonies and was more likely to be practiced by un-mated males (Møller 1988b). Six factors were proposed as being important in favouring the evolution of sexually selected infanticide: colonial and asynchronous breeding, a prolonged breeding season, skewed sex ratio, low relatedness between colony members and a high annual adult mortality rates (Møller 1988). While five of these points held true for the population of Swallows observed here a notable difference again concerned colony size; even the largest colony (~ 14 pairs) was over three times smaller than colonies where infanticide has been observed (Møller 1987a, 1988b; Shields and Crook 1987). Moreover, the number of males which failed to breed was thought to be considerably smaller than the estimated one in eight observed in large colonies in Denmark (Møller 1988a). Thus it was concluded that the most likely reason to explain the absence of intra-specific nest parasitism and infanticide during the present study in comparisons to studies made by others was related to differences in colony size.

Since there appear to be a number of demonstrable costs associated with group living, why should Swallows choose to live in groups at all. Of ultimate importance is whether colony size has any fitness consequences. Studies which have compared the reproductive success between solitary pairs with those in larger groups yielded inconsistent findings (for review see Shields *et al.* 1988). Snapp (1976) concluded that there was no demonstrable effect of colony size on reproductive success. Similarly Shields & Crook (1987) also reported no significant differences between solitary pairs with those living in smaller groups though they did detect a significant reduction in clutch size, hatching success and nestling survivorship of pairs in the larger group which they primarily attributed to parasitism. Improved anti- predator mechanisms and foraging efficiency have been suggested as potential benefits associated with group living (for review see Shields *et al.* 1988). This seems unlikely to be the ultimate factor favouring coloniality in this or other populations of Swallows, however, since : (i) levels of nest and adult predation have generally been reported as being low (this study, but see Shields 1984a; Møller 1984) and, (ii) there appears to be no clear benefit from foraging in groups (for discussion see Snapp 1976; Møller 1987a; Shields and Crook 1987). Alternatively the number of pairs in a colony may primarily be related to the availability of nest sites (Shields 1984a; Shields and Crook 1987 in Shields et al. 1988). Møller (1987a), however, ruled out nest-site limitation as a factor in his population because the number of breeding pairs could double between seasons and late-arriving birds were more likely to settle nearer to other breeding pairs than away from them (see also Shields 1984b). These points were supported by the results from the present study and so it was also concluded here that limitation of nest sites could not wholly explain colony size and thus some unknown factors(s) appear to encourage a moderate tendency to nest in groups.

8.4 FACTORS AFFECTING THE NUMBER OF BROODS ATTEMPTED BY INDIVIDUALS EACH SEASON

An important component of variation in the reproductive performance of Swallows was that some individuals successfully reared two broods in a season whilst others made only a single attempt. Tinbergen and van Balen (1988) proposed that an individuals decision to produce a second clutch was based on limitations of time. If there was a particular date after which a second clutch was not initiated (cut-off date) then other things being equal, timing of breeding (date of first egg) and the length of the breeding cycle (that is the time taken to complete a previous attempt before another brood can be attempted) would together determine whether an individual "decided" to produce a second clutch. An individual would be more likely to attempt a second brood if it started breeding earlier or reduced the length of the breeding cycle.

The length of the breeding cycle of Swallows could be influenced by a variety of factors including time taken to mate or build a nest, laying interval, clutch size, incubation period, number and quality of young reared to independence, nestling period and period of post-fledging care. While some of these probably play only a minor role (most eggs were laid daily, incubation period was consistent at around fifteen to sixteen days and 85% of all first clutches laid were four or five eggs) other stages such as nest building and post-fledging care have the potential to be more variable. For example nest re-use by Swallows could potentially reduce the nesting cycle by on average eight days (also see Section 8.4.3.2 above). As the number of young reared to independence increased, nestling quality decreased but the duration of the inter-brood interval increased. It was concluded that parents compensated for the poorer quality of nestlings by extending the period of parental care thereby causing a delay, or in some cases a failure to attempt a second brood (Chapter 6 and below). The presence of an end of season cut-off date together with the result that double-brooded birds started their first brood significantly earlier than single-brooded birds are both consistent with the view that time was a limiting factor shaping the number of broods attempted during a season by Swallows (also see Bryant 1979; Riley 1992). It was also noted, however, that some pairs attempted third broods (and second brood relay attempts) beyond the postulated end of season cut-off date. This implied that a shortage of time could not always explain why some pairs failed to attempt a second brood (Chapter 5, also see Middleton 1979). Other factors must play some role and the possibility that it was related to differences in individual quality which could have both a genetic and phenotypic component was explored. There was evidence to support this idea from the present study.

Some Swallows arrived consistently earlier than others and the onset of regrowth of the brood patch was found to be variable between individuals. More notably, breeding was never attempted after the brood patch had regrown. Gonadal regression has also been found to start earlier in some individuals than others (see Middleton 1977a; 1978; Bryant *pers comm*). Moreover, nearly all female Swallows attempted the same number of broods in successive years regardless of their partner. Males, by comparison were less consistent between seasons. When and how do individuals decide whether or not to attempt a second brood? It is suggested that it would 'pay' an individual to make an early decision not to attempt a second brood only if laying were costly. It was suspected that this was not the case for Swallows since replacement clutches were usually laid within in six or seven days. This was confirmed in a later study by Ward (1992) who measured the energetic costs of egg laying. The question remains as to how such a 'decision' might be made ? Theoretically individuals could gauge their future prospects based on their current situation using cues such as their own body condition or environmental conditions during varying stages of the first brood. For instance in a study of House Martins there was evidence to suggest that levels of food abundance could influence the decision of later layers to attempt a second brood (Bryant 1975b; Riley 1992). The prediction tested here that lowered mass or an increase in mass loss (also taken to indicate condition) while rearing a first brood would result in a reduced probability of a second brood being attempted (Section 7.1.5) is discussed below (see 8.6).

8.5 HYPOTHESES TO EXPLAIN AGE-RELATED PHENOMENA

Several non- exclusive hypotheses have been outlined to explain why older birds consistently show higher reproductive success than yearlings: (i) "Constraint" hypothesis, (ii) "Restraint" hypothesis and, (iii) "Selective mortality" hypothesis (for reviews see Curio 1983; Nol & Smith 1987; Pugesek & Diem 1990; Sæther 1990).

8.5.1 CONSTRAINT HYPOTHESIS

The constraint hypothesis first proposed by Curio (1983) states that breeding performance of yearlings is constrained by some necessary resources or skills. Effects of such a mechanism may manifest itself in a number of ways; performance may increase as a result of cumulative breeding experience or because as individuals age they improve essential skills such as their mating, foraging, fighting or predator-avoidance skills. A lack of these skills may result in an inability to find a mate, a nest-site, an ability to forage efficiently or provide or care for young. Published data generally support such a view; older birds (usually the males) occupy larger or optimal territories (Crawford 1977; Newton *et al.* 1981; Loman 1984; Reese & Kadlec 1985; Reid 1988). Furthermore since older birds are often bigger (Chapter 4) and dominant over juveniles (Smith *et al.* 1980) this can result in them having a superior competitive ability and thus prior access to resources. Swallows are not territorial and nor are they agonistic, however, and so the above factors can be discounted as playing a role in shaping reproductive success for this species.

This leaves the idea that older Swallows are more efficient foragers or that breeding improves through experience. Although it has commonly been assumed that foraging abilities improve with age (Perrins & Moss 1974; Bryant 1975b; DeSteven 1980) this has has generally only been demonstrated for non-passerines (Orians 1969; Pugesek 1981; Reid 1988; Burger 1988, but see Desrochers 1992). These differences have included older birds spending an increased time foraging (Pugesek 1981; Reid 1988) though not necessarily with improved efficiency. It is not known whether foraging techniques, (efficiency or time) varies with male or female age in Swallows, nor indeed for other hirundines. It has been noted, however, that although the size of prey taken did not differ between males and females (of a pair), male Swallows carrying experimentally elongated tails captured smaller insects relative to their partner (Møller 1989a). Since tail length was age-related (Chapter 4), foraging efficiency could be age-related. Circumstantial evidence however, does not lead to the prediction that younger Swallows would be disadvantaged. For instance Pennycuick (1969) demonstrated that smaller birds have reduced flight costs and Anderson and Norberg (1981) found that in five out of six aspects of flight, individuals with shorter wings were faster and more efficient foragers than larger ones. Moreover , in a comparative study of flight costs between British hirundines it was concluded that each species was morphologically adapted to its own feeding niche (Waugh 1978). Specifically, an individuals wing length, bill length and bill shape influenced maneuverability, mode of flight and an ability to handle different prey items.

Theoretically, if age-related differences in breeding performance were solely related to foraging success then yearlings which were provided with supplementary food should breed as well as older birds. This been experimentally tested in Great Tits (Kallander 1974); Dunnocks (Davies & Lundberg 1985) and more recently in Blackbirds (Desrochers 1992). Where laying dates are advanced in both age classes then the onset of laying would appear to be limited by food restraints. If yearlings advance their laying dates significantly more than do adults then this would suggest age-related differences in acquisition or an ability to accumulate reserves. Supplemental food advanced the laying dates of yearling, but not for older Great Tits and Blackbirds, strongly suggesting that yearlings were constrained from breeding as early as older birds because they were either on poorer territories or were less successful at foraging. A failure by adult birds to advance laying dates implied that the onset of breeding must be limited by some other constraints. Davies & Lundberg (1985), however, reported that supplemental feeding of Dunnocks affected both age classes. Differences between species could be related to variation in natural food availability at the time of the experiment: if food was scarce birds from all age-classes would benefit from provision of additional food. Alternatively Desrochers (1992) suggested that foraging success would only be expected to vary with age where foraging methods improved with learning experience. The implication being that Dunnocks use a simple feeding method whereas Blackbirds and Great Tits 'use a "difficult" foraging method (i.e require a long learning period to perfect)' (Desrochers 1992, p1130).

A further important point to note from Desrochers' experiment was that although yearling Blackbirds (which were provided with supplemental food) started laying at the same time as older birds they remained less successful than older birds. Timing of breeding was therefore insufficient to account for all of the age-related differences. Similarly, in the present analyses differences in clutch size and number of young fledged were still apparent when initial differences in laying dates were controlled for (Chapter 5). This suggests that acquisition of reserves was not just a problem associated with reduced food availability early in the season but also persisted throughout the season. Since the available data suggested that hatching success was inconsistently related to age and appeared not to be important in egg size and quality, this further suggests that yearlings were less successful at providing or caring for young. Studies which have demonstrated a significant association between nestling quality and parental age lend support to this idea. Few studies, however, have examined the relationship between male and female age, feeding visits and nestling growth. Languy & Vansteenwegen (1989) noted that nestlings born from older Swallows were heavier at asymptote . Pugesek (1983) suggested that such age-related differences were related to a larger investment in offspring being made by older parents (see below) but other explanations cannot be discounted (see Languy & Vansteenwegen 1989). In order to disentangle the possible interactions of foraging ability, age and subsequent breeding success, experiments are necessary. Although the Swallow offers a number of advantages for such studies (Chapter 1), an inability to manipulate food availability of adults, together with potential difficulties in measuring foraging efficiency, may cause problems for collection of sound data.

8.5.2 RESTRAINT HYPOTHESIS

If there is a trade-off between current and future fecundity then natural selection may favour a reduction in reproductive effort of younger birds since this may increase their chances of surviving to breed again and in doing so increase their lifetime productivity (Williams 1966; Charnov & Krebs 1974; Pianka and Parker 1975). This has been termed the "restraint hypothesis" (Bryant 1979; Curio 1983; Reid 1988; Pugesek and Diem 1990). Reproductive effort would be expected to increase with age if the probability of survival decreases with age (Pugesek 1981, 1983; Curio 1983; Reid 1988, but see Nur 1984d). As yet, however, no conclusive evidence exists for this idea (Hails & Bryant 1979; Reid 1988). If older birds have a greater cost of reproduction as a consequence of an increase in the allocation of resources to current reproduction (Clutton-Brock 1984; Reid 1987) it would support the idea that reproductive effort increases with age. Although the finding that more yearlings survived to the following season than older birds (significantly so for males (Section 5.3.20) is consistent with the restraint hypothesis, definitive demonstration would require showing that cost of reproduction increase with age. Insufficient data were analysed here to examine this possibility.

8.5.3 SELECTIVE MORTALITY OR INDIVIDUAL DIFFERENCES

A third hypotheses to explain age-related trends in breeding performance proposes that if successful individuals are selected against then poor individuals will die earlier than those of superior quality, resulting in higher reproductive performance among older birds (Curio 1983; Nur 1984d; Nol & Smith 1987; Reid 1988). Data collected for Swallows strongly suggested that double-brooded birds were more successful than single-brooded birds both in terms of the number of young and recruits produced across a season. Double-brooded House Martins were also more successful than single-brooded birds (Bryant 1979). It, therefore, seems reasonable to use the number of broods attempted in a season as a unit of success. If double-brooded Swallows or House Martins were both more likely to survive compared to single-brooded birds then this would lend support to the selective mortality hypothesis. If on the other hand they showed a higher probability of mortality and given that the number of broods was age-related in both species this would imply that a trade-off existed between the probability of a second brood being attempted and adult survival, so favouring the restraint hypothesis (also see below).

Double-brooded House Martins were less likely to survive than single-brooded birds suggesting a trade-off between effort and survival (Bryant 1979). Double-brooded female Swallows, however, were more than twice as likely to survive until the following breeding season than single-brooded birds (also see den Boer-Hazewinkel 1987; Geupel & DeSante 1990). Male survival in Swallows was not significantly related to the number of broods attempted but the trend was in the same direction as for females. So there appeared to be no cost of being double-brooded for Swallows. Further, surviving males reared one more young to independence in a season compared to those which died and this difference was significant.

Selective mortality and individual differences could not entirely explain age related differences, however. Results from an analyses which attempted to control for selective mortality, revealed that females which were at least two years old still laid earlier and had a bigger clutch size (*cf.* yearlings) (also see Perrins & McLeery, 1989) indicating that age-related differences in clutch size are not just an artefact of the positive correlation between individual quality and survival. There was no difference, however, in the breeding performance of females in successive seasons, apart from an earlier laying date. Controlling for initial age (yr (n)) yielded similar non-significant results. The latter two results are further consistent with the idea that variation in reproductive performance is largely explained by differences in individual quality. Females almost always attempting the same number of broods in consecutive seasons further supports this suggestion. Higher quality individuals would also be expected to be more successful during their first brood than single-brooded birds. This was confirmed for Swallows. Double-brooded female Swallows bred earlier and fledged more young during their first brood than single-brooded birds.

In conclusion reproductive performance of Swallows appeared to be shaped by both seasonal and true age effects, together with individual differences and selective mortality as evidenced by the results of the present study. Differences in foraging skills or parental care were not determined. The exact interpretation of age-related trends, however, seemed to depend upon the specific measure under consideration. Significant differences in laying date for known individuals in successive seasons firmly supports the idea that a genuine age effect was apparent for this parameter. Other measures such as clutch size, which only showed a slight tendency to improve with age, might be largely under genetic constraints.

8.6 REPRODUCTION COSTS ON PARENTS AND THEIR OFFSPRING: THE EVOLUTION OF CLUTCH SIZE IN SWALLOWS

Life-history theory provides an elaborate answer to the rather simple question of what limits clutch size in birds in a stable population. Individuals must reproduce at a rate which enables them, at the very least to replace themselves. A failure to achieve this will result in their genotype being selected against and so liable to extinction. A challenge for avian ecologists, therefore, has been to explain the great diversity in life-history tactics which exist to achieve this end amongst species, populations and individuals. For instance, in the population of Swallows observed here some pairs reared as many as eleven young in a season while others were partly or wholly unsuccessful. An important component of this variation was that some birds reared two broods in a season whilst others made only a single attempt. In other species, similar variation in reproductive success has been related, at least in part, to differences in territory quality (Clutton-Brock 1988). Since Swallows use communal feeding grounds, occupy nest sites which are usually close together (Bryant 1988a; Møller 1989b) and nest sites were not thought to be limiting , the role of territory in regulating fitness was assumed to be unimportant for this species (Chapter 1). Moreover, variation in reproductive success of Swallows did not appear to be constrained by food availability to laying females. Explanations for variation in annual reproductive success in this species must, therefore, be sought elsewhere.

Previous studies on the Swallow (Turner 1983a; Jones 1985), as well as the present study, have demonstrated that Swallows can successfully raise additional young when these are added to broods. This is now established as a widespread phenomenon: almost all birds given additional young at hatch are able to rear more young than their original clutch size (Introduction Chapter 6, for review see Dijkstra *et al.* 1990). Specifically, it was noted Swallows which reared experimentally Enlarged broods fledged more young than pairs whose original brood size was either unaltered (Control) or Reduced. This sometimes resulted in a maximum of eight nestlings being reared to independence during any single breeding attempt or up to sixteen across a season. Given that clutch size did not appear to be limited by the ability of parents to feed their offspring, and the important fitness contribution of rearing two or more broods in a season; what prevented parents from normally rearing additional nestlings ? One possibility, which relates to the idea that reproduction is costly , was investigated here.

It has been argued that individuals are faced with a number of trade -offs which are unavoidable given an inability to simultaneously invest maximally in reproduction and self-maintenance. This forces a compromise in allocation of resources between for instance: a) offspring number and offspring quality as well as, b) current or future fecundity. Through manipulation of brood size, these possible trade-offs were examined (Chapter 6) along with the idea that reproductive costs were linked to parental condition (Chapter 7).

8.6.1 OFFSPRING NUMBER VERSUS OFFSPRING QUALITY

In order to demonstrate that Enlarged broods are more productive, it is necessary to show that these fledglings are equally likely to be recruited. For many species determining post-fledging or overwinter survival has proved to be very difficult (Newton, I 1989 and references therein) and so a measure of nestling quality is more usually taken as a predictor of an individual's survival prospects (see below).

Peak nestling mass declined significantly with increasing brood size but despite nestlings from Enlarged broods being significantly lighter (*cf.* Control), no direct link between nestling quality and brood size was observed. Comparisons of mass of recruits versus non recruits also failed to demonstrate any significant differences in Swallows. Reducing parental effort (via removal of nestlings) improved nestling quality but lowered the probability of being recruited compared to Controls. In studies of Great Tits and Collared Flycatchers the number of recruits was maximised when pairs reared their own clutch size (Pettifor *et al.* 1988; Gustafsson & Sutherland 1988). These results favour the hypothesis that each individual lays a clutch size which is adapted to its own ability (eg. individual optimisation hypothesis, see General Introduction). That the probability of being recruited increases with natural brood size (this study, Perrins 1965; DeSteven 1980; Ross & McLaren 1981; Nur 1984b) is further consistent with this view. More data need to be gathered for Swallows to confirm this hypothesis, however, since the above conclusions are based on only two years of data, where there was marked variation in juvenile survival and other life-history components (Chapters 5 and 6). Although a positive relationship between peak nestling mass and juvenile survival has been demonstrated in at least fourteen studies (for reviews see Martin 1987; Magrath 1991) the mechanism underlying the assumed correlation between weight and survival is unclear. Perrins (1965) suggested that heaviest nestlings or fledglings also have greater fat reserves and so might be less likely to starve during periods of food shortage shortly after fledging. But as Garnett (1981) has pointed out, the total fat content of even the heaviest fledglings is on average low and if relied upon for existence would be expended within one day. Further evidence against this idea is that in many species, including the Swallow, the heaviest nestlings lose more weight prior to fledging than do light ones (Zach and Mayoh 1982, see also Bédard and Lapointe 1985). Alternatively, increased mass of nestlings might support better overall growth, or reflect good feeding conditions which could increase both nestling growth and juvenile survival independently (Garnett 1981; Sullivan 1989 and also see above). Analyses based on the mass and size at fledging of Swallows might prove to be a better predictor of survival prospects (also see Smith *et al.* 1989). Moreover, because of intra-brood variation, analyses based only on means is probably inadequate to demonstrate any differences (also see Nur 1984b).

8.6.2 CURRENT VERSUS FUTURE FECUNDITY

Costs of reproduction imply an inverse relationship between current and future fecundity (Stearns 1992). Results from the present study supported this prediction since the number of young reared during the first brood was significantly related to the timing, occurrence, size and success of second broods as well as to parental survival, specifically:

(i) Brood size (natural and manipulated) was negatively and significantly correlated with the inter- brood interval such that Swallows which reared Reduced broods started their second brood significantly earlier than Control and Enlarged broods which themselves did not differ significantly

(ii) Parents rearing Reduced broods were only slightly more likely to be double-brooded, while parents rearing additional young were significantly less likely to produce a second clutch than those rearing Control broods.

(iii) Differences in the size and success of second broods were independent of any effect on the duration of the IBI.

(iv) Males or females which reared a Reduced first- or second -brood survived better than those which reared a Control or Enlarged brood

Attempting to determine the relationship between adult survival and manipulation of brood size in Swallows was complicated by four findings: (i) not all pairs were double brooded; (ii) single brooded females survived less well than double brooded females; (iii) pairs rearing experimentally Enlarged first broods were less likely to attempt a second brood or were less successful relative to Control broods and (iv) not all pairs were manipulated during their first and second brood (also see (i) above). Even those which were not necessarily manipulated to the same degree or even in the same direction. To overcome these potentially confounding factors a number of steps were taken: a) only double-brooded birds were included in the analyses, b) males and females were analysed separately and, c) first- and second -brood manipulations were distinguished. Only one other published study has examined the relationship of manipulation of brood size to parental survival in a predominantly multi-brooded species, the House Sparrow (Hegner & Wingfield 1987) (Dijkstra *et al.* (1990) also summarise unpublished data of Tinbergen (1987) for continental Great Tits which are facultatively double-brooded). Moreover, no published study has systematically altered both first- and second-broods to examine their differential effect on parental survival.

Results obtained here were compared with other studies and possible explanation for observed trends were discussed (Chapter 6). The idea that Enlarged broods required an extended period of parental care (and the above results were a temporal "knock-on" effect) could not be accepted since timing of second broods did not differ significantly for parents rearing Control or Enlarged broods. It was suggested that there was an upper limit to the inter-brood interval and as rearing an Enlarged first brood was also associated with a reduced probability of attempting a second, then differences in the IBI would be not be expected (also see Lindén 1988).

There was no evidence to support the prediction that parental body mass while rearing first brood nestlings influenced either: a) the duration of the IBI or, b) the probability of attempting a second brood (Chapter 7). This applied to parents rearing both natural and experimental broods. The significantly higher mass of females during the IBI of double-brooded birds, however, indicated that perhaps the condition of parents after the young had fledged, was of greater importance. More data are needed during this period, in particular the relative roles of males and females in any post-fledging care, in order to provide an accurate interpretation of such a result. While differences in mass between surviving and non-surviving individuals would be consistent with the idea that mass loss was costly (Chapter 7) it could, instead be related to a reduction in flight costs while feeding nestlings outside of the nest (see below). Although brood size effects on survival were marked for female Swallows, no relationship between female body condition at any stage in the nesting cycle or on overwinter survival was detected. By comparison during both first- and second-broods, male mass during NP II was significantly higher for survivors.

Similar results between current and future fecundity have also been demonstrated in continental populations of Great Tits (Tinbergen and Albers 1984, Smith *et al.* 1987, 1989; Tinbergen 1987; Lindén 1988; De Laet & Dhondt 1989) though the results differed slightly between studies and years. For instance while Tinbergen (1987) and Lindén (1988) observed that parents of enlarged broods were double -brooded less often than parents of control broods Smith *et al.* (1987) reported an increase in the probability of having a second brood if the first brood had been Reduced. Two other species: the House Wren, typically double-brooded and the House Sparrow which is multi-brooded (Finke *et al.* 1987 and Hegner and Wingfield 1987 respectively) failed to show significant effects.

Tinbergen (1987) proposed a model to explain how Great Tits should allocate resources between first- and second-broods. There were three principal assumptions associated with the model. Firstly, that time is the main liming factor in determining whether one or two broods was attempted. Secondly, that the probability of recruitment is dependent on the condition of the nestling at dependency (not necessarily at fledging). Finally, that the probability of recruitment declines seasonally. In order for parents to optimise seasonal productivity, Tinbergen (1987) suggested that Great Tits should aim to start a second clutch when the expected combined pay-off from first and the second broods is maximised. Thus a trade-off exists between investment in the first- or second - brood (ie whether to tend the first brood or start the second).

Experimentally enlarging brood size has the effect of lowering nestling quality (see above). Then following Tinbergen's proposal parents are faced with a dilemma as to whether to continue tending the first brood until they are fully developed and increasing the chances of each offspring being recruited (balanced against the likelihood that this will reduce the time available to start and successfully complete a second clutch), or to abandon these fledglings in favour of starting a second clutch. Tinbergen suggested that under most circumstances parents would do best by providing additional care to the first brood since as the season progresses successive fledglings will be of lowered fitness. The reduced occurrence of second broods in Great Tits was therefore not thought to be constrained by an inability of the female to produce a second clutch. If the results from the present study complied with this model, this could provide a plausible explanation as to why female condition was not related to the inter-brood interval, number of broods attempted or with overwinter survival. This implies, however, that females are able to continually regulate their effort to maximise fitness, whereas males in contrast could be viewed as victims of variability in female strategies. They need not necessarily suffer deleterious consequences, however, if they pair with a good quality female. These ideas are supported by two findings from the present study: a) Swallows mated assortatively with respect to age and as indicated above older birds were more successful and, b) females which survived from one season to the next almost always attempted the same number of broods in a season (usually they were double-brooded, Chapter 5). Males by comparison more frequently changed from one season to the next, in accordance with their partner.

Given that the probability of recruitment is higher for earlier rather than later fledglings one final theoretical point concerns why double-brooded species do not just rear a single large first brood. Two obvious possibilities are that females might be constrained by the number of eggs which can be successfully laid or incubated. Laying did not appear to be costly in Swallows as evidenced by direct measurements of energy expenditure (Ward 1992). Although short term enlargements of up to eight eggs were successfully incubated (also see Jones 1985) it remains to be seen whether this could be maintained until hatch. Ward (1992), has suggested that an inability of females to cover Enlarged clutch sizes might put an upper limit on the number of eggs laid. Clearly, this needs to be tested. Ideally the potential costs of laying additional eggs, as well as incubating these also needs to be evaluated (also see Verhulst & Tinbergen 1991; Ward 1992 and Section 8.2.2.2).

Continued efforts should be made to investigate all possible costs at all stages of the reproductive cycle. Moreover, the costs of pairing in monogamous species and of post-fledging care is virtually unexplored. If, in addition, long-term manipulation of clutch sizes could be combined with monitoring effects on hatching and fledging success, along with offspring and parental survival (shown here across two broods) then cumulative effects from incubation and nestling rearing could be more accurately determined. Incomplete measures may cause studies to under- or overestimate fitness costs (Nur 1988b). Moreover it often remains unclear if costs are apparent whether they actually outweigh the immediate benefits and so reduce inclusive fitness. For instance, although Swallows which reared Reduced broods, fledged and recruited fewer young, they also had a higher survival and so the net benefit may still be positive. It is clear that research on life-history tactics of birds along with other animals requires still closer interrogation of observational, manipulative, and physiological approaches than has been achieved to date if the exact role of reproductive costs in shaping breeding parameters is to be fully evaluated.

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Appendices

Appendix 1 List of common and Latin bird names given in the text

American Goldfinch	*Carduelis tristis*
Bank Swallow	*Riparia riparia*
Barn Swallow	*Hirundo rustica*
Bee-Eater	*Merops apiaster*
Black-billed Magpie	*Pica pica*
Blackbird	*Turdus merula*
Blue Tit	*Parus caeruleus*
Bullfinch	*Pyrrhola pyrrhola*
Bobolink	*Dolichonyx oryzivorus*
Canary	*Serinus canaria*
Cliff Swallow	*Hirundo pyrrhonota*
Collared Flycatcher	*Ficedula albicollis*
Dipper	*Cinclus cinclus*
Dipper	*Cinclus cinclus aquaticus*
Dunnock	*Prunella modularis*
Eastern Kingbirds	*Tyrannus tyrannus*
Glaucous-winged Gull	*Larus glaucescens*
Great Tit	*Parus major*
Hooded Crow	*Corvus corvus cornix*
House Martin	*Delichon urbica*
House Sparrow	*Passer domesticus*
House Wren	*Troglodytes aedon*
Ipswich Sparrow	*Passerculus sandwhichensis princeps*
Japanese Quail	*Coturnix coturnix japonica*
Kestrel	*Falco tinnunculus*
Magpie	*Pica pica*
Mute Swan	*Cygnus olor*
Pied Flycatcher	*Ficedula hypoleuca*
Red-winged Blackbird	*Agelaius phoeniceus* T
Robin	*Erithacus rubecula*
Rock Pipit	*Anthus spinoletta*
Rook	*Corvus frugilegus*

Sand Martin	*Riparia riparia*
Savannah Sparrow	*Passer sandwhichensis* T
Snow Bunting	*Plectrophenax nivalis*
Song Sparrow	*Melospiza melodia*
Sparrowhawk	*Accipiter nisus*
Starling	*Surnus vulgaris*
Swallow	*Hirundo rustica*
Tawny Owl	*Strix aluco*
Tengmalms Owl	*Aegolius funereus*
Tree Sparrow	*Spizella arborea arborea*
Tree Swallow	*Tachycineta bicolor*
Willow Tit	*Parus montanus*
Wrentit	*Chamaea fasciata*

Appendix 3.1 Names and locations of Swallow sites and the number of breeding pairs, by year and brood number (see Fig 2.1).

Site	Grid Ref	1987 1st	1987 2nd	1988 1st	1988 2nd	1989 1st	1989 2nd
Baad	NS 764946	a	a	1	0	0	0
Bankend	NS 765934	6	5	10	4	4	1
'Bothy'	NS 758955	1	1	0	0	0	0
Blair Mains	NS 828965	2	2	4	2	3	3
Brierlands	NS 743984	a	a	7	6	b	b
Broom	NS 817964	2	2	2	1	1	2
Broom Cottage	NS 814948	2	2	a	a	0	0
Cambusdrenny E	NS 749943	1	1	3	0	1	1
Cambusdrenny W	NS 753944	5	4	6	5	5	6
Carrat	NS 748971	b	a	b	a	b	a
Chalmerston	NS 732952	3	a	3	a	a	a
Cowden	NS 767948	3	1	6	3	4	2
Craigarnhall	NS 753986	4	4	5	4	4	3
Craigniven	NS 750936	1	1	1	0	1	1
Craigton	NS 813959	2	2	5	4	4	2
Dasherhead	NS 009950	a	a	9	6	5	3
Drip end	NS 753962	b	a	b	a	a	a
Drumbrae	NS 862977	2	2	1	0	a	a
Easter Gogar	NS 835964	2	a	a	a	a	a
Easter Row	NS 752993	1	1	2	0	1	0
Glenhead	NN 754000	5[c]	3	10	9	8	5
Grangehall	NS 817952	1	1	2	1	a	a
Greystone	NS 743998	3	2	4	3	4	3
Heathershot	NS 764973	0	0	1	0	0	0
Hill of Drip	NS 766950	6	5[d]	9	7	11	6
Kier	NS 773995	5[c]	5[c]	6[c]	6[c]	b	b
Kier Cottage	NS 773992	1	1	1	1	0	0
Inverardoch	NN 739007	4	3	5	5	7	3
"Kennels"	NS 776984	1	1	2	1	1	1

a - site not checked
b - breeding pairs present but accurate census not made
c - minimum estimate
d - three broods attempted

Appendix 3.1 Contd.

		1987		1988		1989	
Site	Grid Ref	1st	2nd	1st	2nd	1st	2nd
Kersebonny S	NS 774773	3	4[d]	4	2	1	0
Kersebonny N	NS 774940	b	b	a	a	a	a
Knockhill	NS 782972	3	2	3	1	1	1
Logie Villa	NS 824966	a	a	2	2	3	2
Mains	NS 722945	a	a	4	2	3	3
Manor	NS 829954	2	1	3	2	2	a
Manor Powis	NS 825949	0	0	1	0	1	1
Manor Steps	NS 833950	2	2	3	3	4	3
Midlecropt	NS 777978	8	6	10	7	7	4
Netherton	NS 784965	1	1	a	a	a	a
Nyadd	NS 742975	5	b	a	a	a	a
Old Kier	NS 764978	3	2	3	3	5	4
Old Kier cottage	NS 765975	0	0	0	0	0	0
Offers	NS 716954	2	1	1	1	1	1
Park of Kier	NS 784992	10[c]	10[cd]	14[c]	14[c]	10[c]	10[c]
Pendreich	NS 803991	7	5	9	7	4	4
Powis	NS 818959	1	1	2	1	2	2
Powis Cottage	NS 818962	0	0	1	1	1	1
Redhall	NS 727943	2	2	4	1	3	3
Shaw	NS 746945	3	3	5	5	7	5
Steeds	NS 765975	2	2[d]	2	1	2	1
Touch	NS 754930	4	2	5	4	4	3
West Carse	NS 733944	1	1	2	2	2	2
West Drip	NS 755956	10	7	11	9	7	6
West Rossburn	NS 725969	1	1	2	2	2	0
West Rossburn Cott	NS 726968	1	0	0	0	0	0
Wester Row	NS 735945	5	4	7	4	3	a
Westwood	NS 735945	1	1	1	0	1	0
Westwood Lane	NS 744954	0	0	2	2	1	1
Whitehouse	NS 769934	3	1	2	0	1	1

a - site not checked
b - breeding pairs present but accurate census not made
c - minimum estimate
d - three broods attempted

Appendix 3.2a Intra-seasonal dispersal of adult Swallows in seasons 1987, 1988 and 1989, by sex

Ringing Information				‖ Recapture Information			
Date Ringed	Ring No	Sex	Date Capt[a]	Site	Date	Site	Notes
21/6/87	E080199	M	21/7	Knockhill	15/8	Midlecropt	1
25/5/87	C702151	M	25/5	Pendreich	07/7	Park of Kier	2
28/5/87	C702154	M	28/5	Bankend	17/8	Whitehouse	3
16/5/88	E936038	M	16/5	Kennels	21/6	Midlecropt	
11/6/88	E936162	M	11/6	Knockhill	03/7	Park of Kier	4
19/7/88	F073550	F	19/7	Whitehouse	21/8	Bankend	5
04/5/88	E649989	F	04/5	Midlecropt	03/8	W Wood Lane	
11/5/89	F145633	F	11/5	Manor	03/6	Manor Steps	6
22/6/89	F145784	F	28/6	Inverardoch	15/7	Greystone	
24/5/89	F145661	F	27/5	Knockhill	29/5	Midlecropt	

a - date of last capture at site of ringing

1 - recaptured back at Knockhill on 1/9/87 and 11/9/87, recaptured at Knockhill on 25/4/88

2 - recaptured at Park of Kier on 12/5/88

3 - recaptured at Whitehouse on 11/5/88

4 - recaptured at Park of Kier on 22/6/89

5 - recaptured at Bankend on 28/8/88

6 - found dead at Manor steps on 11/5/89.

Appendix 3.2b Intra-seasonal dispersal of juvenile Swallows in 1987, 1988 and 1989, analysed by sex

Ringing Information			‖ Recapture Information			
Date Ringed	Ring No	Date Capt	Site	Date	Site	Notes
21/6/87	E080121	28/6	Midlecropt	01/9	Knockhill	1
09/6/87	E080186	17/6	Shaw	18/7	Touch	
15/7/87	C702335	15/7	Park of Kier	11/9	Knockhill	
12/7/88	F073530	25/7	Midlecropt	05/8	Craigarnhall	
21/6/88	E936380	21/6	Craigton	02/9	University	

1 - recaptured at Knockhill on 26/5/88

Appendix 3.3 Inter- seasonal dispersal of adult Swallows, analysed by sex

Ringing Information				Recapture information	
Date	Ring No	Sex	Site	Date	Site
17/6/87	E080196	M	Craigton	05/5/88	Manor Steps[a]
28/6/87	E080214	M	W Drip	28/5/88	Hill of Drip
23/6/87	E080259	M	W Row	26/6/88	Greystone[a]
21/8/87	E649803	M	Inverardoch	25/8/88	Wester row
13/7/87	C702323	M	Old Kier	05/5/88	Midlecropt
25/7/87	C702379	M	Greystone	13/5/88	Easter Row
13/8/87	C702438	M	Hill of drip	17/5/88	E Camb
09/7/88	F073514	M	Baad	28/6/89	Cowden
17/6/88	E936275	M	W Wood	21/5/89	Westwood Lane
22/6/89	F145784	M	Greystone	27/7/90	Inverardoch[b]
16/7/86	C702434	F	Sunnylaw	07/6/87	Park of Kier
26/6/87	E080235	F	Offers	04/5/88	Dasherhead[a]
07/5/87	C114455	F	Craigton	10/6/88	Grangehall[c]
27/8/87	E649866	F	Knockhill	13/6/88	Midlecropt[c]
23/8/87	E649818	F	Grangehall	19/6/89	Powis
10/6/88	C114455^	F	Grangehall	23/5/89	Broom
30/6/88	E649538	F	Midlecropt	16/5/89	Knockhill
13/6/88	E649866	F	Midlecropt	15/5/89	Kennels
12/8/88	F073799	F	Whitehouse	05/6/89	W Camb
02/6/88	E936089	F	Manor Steps	24/5/89	Logie Villa
07/6/88	E936113	F	Powis	08/5/89	Broom

a - recaught at the same site in the following year

b - first caught in 1989 at Inverardoch then moved to Greystone and returned to Inverardoch in 1990

c - dispersed in successive years.

Appendix 3.4a **Inter-seasonal dispersal of juvenile Swallows ringed in or before 1987, by sex.**

Ringing Information			Recapture Information		
Date	Ring No	Site	Date	Site	Sex
15/7/86	C702417	Pendreich	19/8/87	Pendreich	M
15/7/86	C702418	Pendreich	06/7/87	Park of Kier	M
16/7/86	C702438	Midlecropt	13/8/87	Hill of Drip	M[a]
19/6/87	E080102	Whitehouse	15/5/88	Bankend	M
20/6/87	E080104	W Drip	12/8/88	W Camb	M
21/6/87	E080121	Midlecropt	24/5/88	Knockhill	M
16/6/87	E080192	Bankend	30/8/88	W Carse	M
01/7/87	E080249	Bankend	23/7/88	Touch	M
01/7/87	E649503	Pendreich	29/5/88	Midlecropt	M
04/7/87	E649519	Hill of Drip	19/8/88	Craigarnhall	M
07/7/87	E649574	W Drip	01/6/88	Craigniven	M
09/8/87	E649583	S Kerse	03/6/88	Bankend	M
27/8/87	E649880	Grangehall	21/6/88	Blair Mains	M
01/6/87	C702175	Steeds	17/5/88	Hill of Drip	M
23/6/87	E080144	S Kerse	04/5/88	Bankend	F
01/7/87	E080247	Whitehouse	03/6/88	Bankend	F
26/6/87	E080285	Craigarnhall	14/6/88	Midlecropt	F
04/7/87	E495022	Shaw	24/5/88	Cowden	F
05/7/87	E649538	Craigniven	30/6/88	Midlecropt	F
21/8/87	E649813	W Camb	09/8/88	Craigton	F
22/8/87	E649816	Park of Kier	15/5/88	Park of Kier	F
06/6/87	C702190	Knockhill	27/5/88	Manor	F
13/7/87	C702319	Old Kier Cott	10/7/88	Craigton	F
20/6/84	C114395	Old Kier	11/5/87	Wester Row	M
20/6/85	C114270	Midlecropt	02/7/88	Park of Kier	M
09/8/87	E649586	S Kerse	21/5/89	W Camb	M
10/8/87	E649607	Bankend	08/5/89	Whitehouse	M
21/8/87	E649809	W Camb	29/5/89	Steeds	M
14/7/87	C702326	Touch	14/5/89	Shaw	M
15/7/86	C702423	Pendreich	14/7/88	Park of Kier	F
05/7/87	E495041	Hill of Drip	23/7/89	Pendreich	F
26/8/87	E649859	Shaw	17/5/88	E Camb	?
28/6/87	E080207	Bothy	11/9/88	Sussex[b]	?[b]
29/8/87	E649893	Craigarnhall	30/9/89	Essex[b]	?[b]

? - sex not determined

b - information based on BTO ringing returns

a - dispersed in successive years.

Appendix 3.4b **Inter-seasonal dispersal of juvenile Swallows ringed in 1988, by sex.**

Ringing Information			Recapture Information		
Date	Ring	Site	Date	Site	Sex
13/7/88	F073542	Pendreich	18/5/89	Park of Kier	M
12/8/88	F073789	W Cambusdrenny	19/6/89	Craigarnhall	M
20/8/88	F145524	Brierlands	28/5/89	Old Kier	M
20/8/88	F145581	Shaw	20/7/89	Hill of Drip	M
14/6/88	E936211	Pendreich	25/5/89	Pendreich	M
20/6/88	E936360	W Drip	21/7/89	W Camb	M
21/6/88	E936371	Manor	30/5/89	Manor Steps	M
24/6/88	E936449	Midlecropt	22/5/89	Midlecropt	M
25/6/88	E936934	Greystone	08/6/89	Greystone	M
27/6/88	E936967	Hill of Drip	06/6/89	Shaw	M
05/8/88	F073672	S Kerse	22/5/89	Midlecropt	F
16/6/88	E936240	Shaw	12/6/89	Cowden	F
16/6/88	E936251	W Rossburn	25/5/89	Offers	F
19/6/88	E936329	Bankend	30/5/89	Manor Powis	F
22/6/88	E936425	Dasherhead	26/6/89	Shaw	F
03/7/88	E936824	W Drip	13/5/89	Manor	F
11/7/88	F073547	Craigarnhall	16/5/89	Old Kier	?
23/6/89	F574511	Craigton	31/5/90	Manor steps	M[a]
27/6/89	F574632	Greystone	13/6/90	Glenhead	M[a]
23/7/89	F574772	W Carse	28/5/90	W Camb	F[a]
29/7/89	F574836 sw	Mains	24/5/91	Mains	M[a]
12/6/90	F781524 sw	Broom	31/5/91	Manor Steps	F[a]

? - sex not determined

a - data collected by Sally Ward

Appendix 3.5 Frequency distribution of clutch sizes laid by Swallows, by brood number.

				% clutch sizes encountered					
Author	Location	Brood	Mean	2	3	4	5	6	7
This study	Central Scotland	1st	4.9	ne	3.1	18.2	64.3	13.6	0.7
		2nd	4.5	0.6	9.6	40.1	44.3	5.4	ne
		Both		0.2	5.6	26.4	57.3	10.0	0.4
Turner 1980	Central Scotland	All	4.7[a]	ne	4.0	26.0	66.0	4.0	ne
Adams 1957	U.K	All	?	2.0	9.0	41.0	43.0	5.0	<1
McGinn and Clark 1978	Southern Scotland	All	4.7	1.0	2.0	34.0	51.0	12.0	ne
McGinn 1979	N E Scotland	All	4.4	ne	9.0	47.0	38.0	6.0	ne
in Cramp 1988	W Germany	1st	4.9	ne	2.0	25.0	60.0	12.0	1.0
		2nd	4.3	ne	10	56	32	2	ne

ne - clutch size not encountered during study

a - calculated from data presented in Appendix 6 ' productivity of hirundines'

? - data not presented

Both - 1st and 2nd broods combined

All - brood number not specified

Appendix 6.1 Number of young[a] added (ADD) or removed (REM) from nests during manipulation of: (i) First and (ii) Second broods

Year	Manipulation categories	Sample	Mean (se) ADD/REM	No of nestlings Added or Removed 0	1	2	3	4
a)	**First broods**							
1987	Reduced	1	3.0 (.0)	-	-	-	1	-
	Control	82	0.0 (.0)	82	-	-	-	-
	Enlarged	3	3.3 (.0)	-	-	-	2	1
1988	Reduced	30	2.6 (.1)	-	2	12	13	3
	Control	58	0.0 (.0)	58	-	-	-	-
	Enlarged	26	2.7 (.2)	-	1	8	15	2
1989	Reduced	35	2.1 (.2)	-	6	14	13	1
	Control	58	0.0 (.0)	58	-	-	-	-
	Enlarged	24	2.4 (.1)	-	2	12	11	-
1988/89	Reduced	65	2.3 (.1)	-	8	26	26	4
	Control	116	0.0 (.0)	116	-	-	-	-
	Enlarged	60	2.5 (.1)	-	3	20	26	2
All years	Reduced	66	2.3 (.1)	-	8	26	27	5
	Control	217	0.0 (.0)	217	-	-	-	-
	Enlarged	54	2.5 (.1)	-	3	20	28	3
b)	**Second broods**							
1987	Reduced	8	2.6 (.3)	-	1	2	4	1
	Control	44	0.0 (.0)	44	-	-	-	-
	Enlarged	8	3.3 (.2)	-	-	-	5	3
1988	Reduced	19	2.4 (.2)	-	4	3	12	-
	Control	58	0.0 (.0)	58	-	-	-	-
	Enlarged	15	2.7 (.2)	-	1	4	9	1
1989	Reduced	6	1.5 (0)	-	4	1	1	-
	Control	73	0.0 (.0)	73	-	-	-	-
	Enlarged	2	1.5 (0)	-	1	1	-	-
1987/88	Reduced	37	2.4 (.2)	-	5	5	16	1
	Control	102	0.0 (.0)	102	-	-	-	-
	Enlarged	23	2.9 (.2)	-	1	4	14	4
All years	Reduced	33	2.3 (.2)	-	9	6	17	1
	Control	175	0.0 (.0)	-	-	-	-	-
	Enlarged	25	2.8 (.2)	-	2	5	14	4

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a - Pairs which failed during days 0-7 of the nestling period are not included

Appendix 7.1a **Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage total lipid of dissected body components of male Swallows (n=9). All dry and lean dry masses are measured in grammes[a].**

Male components	DM x	 se	LDM x	 se	LI[b] %	Total lipid %
Wing and tail feathers	0.6114	0.100	0.6114	0.010	-	-
Skin and body feathers	1.3549	0.046	1.1176	0.024	21.2	20.5
Legs	0.3410	0.018	0.2465	0.004	38.3	8.2
Wings	0.6822	0.037	0.5264	0.021	29.6	13.5
Pectoralis major	0.9109	0.066	0.7987	0.055	14.0	9.7
Pectoralis minor	0.0667	0.005	0.0604	0.005	10.4	0.5
Pectoralis [c]	0.9691	0.062	0.8578	0.051	13.0	9.6
Body shell	1.0688	0.063	0.8093	0.034	32.1	22.5
Head	0.5337	0.014	0.4406	0.009	21.1	8.1
Neck	0.1553	0.010	0.1313	0.009	18.3	2.1
Oesophagus	0.2259	0.012	0.2037	0.010	05.2	1.9
Lungs	0.1020	0.006	0.0935	0.005	09.1	0.1
Heart	0.0952	0.009	0.0851	0.008	11.9	0.9
Liver	0.2650	0.033	0.2098	0.020	26.3	4.8
Gut	0.1995	0.025	0.1417	0.017	40.8	5.0
Kidneys	0.0741	0.008	0.0623	0.007	18.9	1.0
Gonads	0.0220	0.004	0.0189	0.004	16.4	0.3
Total	6.7117		5.5559			100

a - same notation is used for Appendices 7.1b-g

b - Lipid index

c - Pectoralis = pectoralis major + pectoralis minor

Appendix 7.1b Means (x) and standard errors (se) for mean dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage total lipid of dissected body components of female Swallows (n=13)

Female	DM		LDM		LI	Total lipid
component	x	se	x	se	%	%
Wing and tail feathers	0.5669	0.020	0.5669	0.020	-	-
Skin and body feathers	1.6010	0.120	1.1223	0.032	42.7	27.5
Legs	0.3848	0.022	0.2611	0.006	47.4	7.1
Wings	0.7121	0.027	0.5589	0.018	27.4	8.8
Pectoralis major	1.0292	0.047	0.9123	0.037	12.8	6.7
Pectoralis minor	0.0752	0.005	0.0700	0.005	07.4	0.3
Pectoralis	1.1044	0.050	0.9823	0.040	12.4	7.0
Body shell	1.2597	0.098	0.8518	0.025	47.9	23.5
Head	0.5421	0.012	0.4345	0.009	24.8	6.2
Neck	0.1622	0.008	0.1292	0.005	25.5	1.9
Oesophagus	0.3363	0.042	0.2950	0.040	14.0	2.4
Lungs	0.0997	0.006	0.0893	0.005	11.6	0.6
Heart	0.1066	0.007	0.0924	0.006	15.4	0.8
Liver	0.4092	0.037	0.2977	0.017	37.5	6.4
Gut	0.3054	0.021	0.2225	0.014	37.3	4.8
Kidneys	0.1062	0.006	0.0870	0.005	22.1	1.1
Gonads	0.1225	0.142	0.0906	0.105	25.6	1.8
Total	7.8191		6.0815			100.6

Appendix 7.1c Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage total lipid of dissected body components of adult Swallows (n=22)

Adult	DM		LDM		LI	Total lipid
components	x	se	x	se	%	%
Wing and tail feathers	0.5851	0.013	0.5851	0.013	-	-
Skin and body feathers	1.5003	0.076	1.1204	0.021	33.9	25.4
Legs	0.3669	0.016	0.2551	0.004	43.8	7.5
Wings	0.6999	0.022	0.5456	0.014	28.3	10.3
Pectoralis major	0.9841	0.039	0.8690	0.033	13.2	7.7
Pectoralis minor	0.0720	0.004	0.0663	0.004	08.6	0.004
Pectoralis	1.0491	0.041	0.9314	0.033	12.6	7.9
Body shell	1.1816	0.066	0.8344	0.020	41.6	23.2
Head	0.5387	0.009	0.4370	0.006	23.3	6.8
Neck	0.1594	0.006	0.130	0.005	22.5	2.0
Oesophagus	0.2912	0.028	0.2577	0.025	13.0	2.2
Lungs	0.1007	0.004	0.0910	0.003	10.7	0.6
Heart	0.1020	0.005	0.0894	0.005	14.1	0.9
Liver	0.3502	0.030	0.2618	0.016	33.8	5.9
Gut	0.2621	0.019	0.1895	0.014	38.3	4.9
Kidneys	0.0931	0.006	0.0769	0.005	21.1	1.1
Gonads	0.0816	0.061	0.0613	0.045	33.1	1.4
Total	7.3619		5.8667			100.1

Appendix 7.1d **Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage of total lipid of dissected body components of fledgling Swallows (n=5)**

Fledgling	DM		LDM		LI	Total lipid
components	x	se	x	se	%	%
Wing and tail feathers	0.5095	0.008	0.5095	0.008	-	-
Skin and body feathers	1.4294	0.149	1.0131	0.023	41.1	29.2
Legs	0.3850	0.047	0.2556	0.01	50.6	9.1
Wings	0.6019	0.039	0.4600	0.013	30.8	9.9
Pectoralis major	0.7793	0.071	0.6943	0.057	12.2	6.0
Pectoralis minor	0.0530	0.009	0.0482	0.008	10.0	0.3
Pectoralis^	0.8323	0.074	0.7426	0.060	12.1	6.3
Body shell	1.1183	0.159	0.7695	0.047	45.3	24.4
Head	0.4788	0.023	0.3934	0.016	21.7	6.0
Neck	0.1546	0.015	0.1290	0.008	19.8	1.8
Oesophagus	0.2403	0.019	0.2004	0.011	19.9	2.8
Lungs	0.0870	0.007	0.0796	0.007	09.3	0.5
Heart	0.0826	0.009	0.0727	0.007	13.6	0.7
Liver	0.2451	0.027	0.2156	0.022	13.7	2.1
Gut	0.2531	0.044	0.1616	0.017	56.6	6.4
Kidneys	0.0758	0.009	0.0642	0.007	18.1	0.8
Gonads	-	-	-	-	-	-
Total	6.4937		5.0667			100

Appendix 7.1e Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and percentage total lipid of dissected body components of all Swallows: adults and fledglings combined (n=27)

All birds	DM		LDM		LI	Total lipid
components	x	se	x	se	%	%
Wing and tail feathers	0.5711	0.012	0.5711	0.012	-	-
Skin and body feathers	1.4872	0.067	1.1005	0.019	35.1	26.1
Legs	0.3702	0.015	0.2552	0.004	45.1	7.8
Wings	0.6817	0.020	0.5298	0.013	28.7	10.2
Pectoralis major	0.9447	0.038	0.8354	0.031	13.1	7.4
Pectoralis minor	0.0683	0.004	0.0629	0.004	08.6	0.004
Pectoralis	1.0089	0.039	0.8964	0.032	12.6	7.6
Body shell	1.1699	0.060	0.8224	0.0190	42.3	23.4
Head	0.5276	0.009	0.4289	0.007	23.0	6.6
Neck	0.1585	0.005	0.1299	0.004	22.0	1.9
Oesophagus	0.2817	0.023	0.2471	0.021	14.0	2.3
Lungs	0.0981	0.004	0.0889	0.003	10.3	0.6
Heart	0.0984	0.005	0.0863	0.004	14.0	0.8
Liver	0.3307	0.026	0.2532	0.014	30.6	5.2
Gut	0.2604	0.017	0.1843	0.012	41.3	5.1
Kidneys	0.0899	0.005	0.0745	0.004	20.7	1.0
Gonads	0.0665	0.061	0.0499	0.045	33.1	1.1
Total	7.2008		5.7184			99.7

Appendix 7.1f Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage total lipid of dissected body components for two males which were suspected of starving to death

Starved male components	DM		LDM		LI	Total lipid
	x	se	x	se	%	%
Wing and tail feathers	0.6466	0.029	0.6466	0.029	-	
Skin and body feathers	1.2031	0.007	1.1745	0.011	2.5	12.6
Legs	0.2596	0.019	0.2547	0.014	5.7	2.2
Wings	0.5401	0.020	0.5220	0.034	3.7	8.0
Pectoralis	0.7744	0.126	0.7351	0.112	5.2	17.3
Body shell	0.7993	0.126	0.7671	0.115	4.1	14.2
Head	0.4717	0.021	0.4313	0.0025	9.4	17.8
Neck	0.1355	0.021	0.1323	0.021	2.5	1.4
Oesophagus	0.1928	0.016	0.1883	0.013	2.3	2.0
Lungs	0.0819	0.001	0.0760	0.004	8.0	2.6
Heart	0.0637	0.013	0.0612	0.011	4.1	1.1
Liver	0.1524	0.007	0.1392	0.002	9.6	5.8
Gut	0.1330	0.052	0.1077	0.033	23.5	11.2
Kidneys	0.0444	0.006	0.0398	0.005	11.6	2.0
Gonads	0.0362	0.006	0.0316	0.006	14.9	2.0
Total	5.5343		5.2981			100.2

notes:

1 - one male was known to die while rearing an artificially enlarged first brood; the second male came from a carcass analysed by G Jones. This individual was found dead (very fresh) in the suction trap on 31/7/81. The stage in the nesting cycle was unknown.

2 - data for Pectoralis major and minor are not given separately as they were not distinguished between in one of the birds in G Jones sample

3 - Lipid indices have been calculated from raw data.

Appendix 7.1g Means (x) and standard errors (se) for dry masses (DM), lean dry masses (LDM), lipid indices (LI) and the percentage total lipid of dissected body components of male Swallows excluding two individuals which were suspected of having died through starvation (n=7)

Male components	DM x	DM se	LDM x	LDM se	LI %	Total lipid %
Wing and tail feathers	0.6013	0.029	0.6013	0.007	-	-
Skin and body feathers	1.3983	0.047	1.1014	0.029	27.0	21.1
Legs	0.3643	0.012	0.2468	0.005	47.7	8.4
Wings	0.7228	0.032	0.5277	0.026	37.0	13.9
Pectoralis major	0.9563	0.056	0.8316	0.051	15.0	-
Pectoralis minor	0.0684	0.006	0.0613	0.005	11.6	-
Pectoralis	1.0247	0.059	0.8929	0.054	14.8	9.4
Body shell	1.1458	0.040	0.8214	0.035	39.5	23.1
Head	0.5514	0.009	0.4433	0.010	24.4	7.7
Neck	0.1610	0.012	0.1310	0.011	22.9	2.1
Oesophagus	0.2353	0.013	0.2081	0.012	13.1	1.9
Lungs	0.1078	0.005	0.0985	0.004	9.4	0.7
Heart	0.1043	0.008	0.0919	0.008	13.5	0.9
Liver	0.2972	0.033	0.2300	0.019	29.2	4.9
Gut	0.2185	0.026	0.1515	0.019	44.2	4.9
Kidneys	0.0826	0.007	0.0687	0.007	20.2	1.0
Gonads	0.0185	0.006	0.0153	0.004	20.9	0.2
Total	7.0037		5.6297			100.2

Appendix 7.2 Adult Swallow body mass and fat scores for all birds captured by year and brood

		Body mass				Mean fat score[a]			
Year	Brood	Mean	se	range	n	Mean	se	range	n
Males									
1987	All	19.8	0.09	16.9-22.8	181	-	-	-	
	1st	19.7	0.13	16.9-22.8	81	-	-	-	
	2nd	19.9	0.19	16.9-22.5	48	-	-	-	
	?	19.7	0.16	18.0-22.8	52	-	-	-	
1988	All	19.4	0.07	16.2-24.0	366	5.43	0.09	1.5-9	348
	1st	19.4	0.09	16.2-23.5	200	5.30	0.12	1.5-9	189
	2nd	19.4	0.14	16.2-24.0	115	5.63	0.16	1.5-9	112
	?	19.6	0.15	17.1-22.4	51	5.51	0.25	2.0-8	47
1989	All	19.5	0.08	15.5-22.5	214	3.51	0.12	1.0-9	203
	1st	19.5	0.09	15.5-22.5	170	3.56	0.13	1.0-9	165
	2nd	19.0	0.19	17.5-20.6	24	3.39	0.47	1.0-9	18
	?	19.4	0.20	17.7-21.1	20	3.20	0.36	1.0-6	20
All	All	19.5	0.05	15.5-24.0	761	4.72	0.08	1.0-9	551
	1st	19.5	0.06	15.5-23.5	451	4.49	0.10	1.0-9	354
	2nd	19.5	0.10	16.2-24.0	187	5.31	0.16	1.0-9	130
	?	19.6	0.10	17.1-22.8	123	4.82	0.24	1.0-8	67
Females									
1987	All	20.8	0.14	16.8-26.1	207	-	-	-	
	1st	21.0	0.19	17.1-26.1	115	-	-	-	
	2nd	20.2	0.23	16.8-25.5	65	-	-	-	
	?	21.1	0.34	18.3-25.6	27	-	-	-	
1988	All	20.4	0.09	16.2-27.5	481	6.23	0.08	1.5-9	468
	1st	20.6	0.13	16.2-27.5	258	6.27	0.12	1.5-9	250
	2nd	20.1	0.13	17.0-27.2	187	6.15	0.14	1.5-9	183
	?	20.3	0.28	16.6-24.2	36	6.41	0.27	1.5-9	35
1989	All	20.8	0.13	15.6-27.9	291	5.67	0.13	1.0-9	275
	1st	20.9	0.15	15.6-27.9	244	5.70	0.14	1.0-9	235
	2nd	21.3	0.43	17.3-25.7	29	6.16	0.44	1.0-9	22
	?	19.4	0.38	17.0-21.7	18	4.75	0.47	2.0-8	18
All	All	20.6	0.07	15.6-27.9	979	6.03	0.07	1.0-9	743
	1st	20.8	0.09	15.6-27.9	617	5.99	0.09	1.0-9	485
	2nd	20.3	0.11	16.8-27.2	281	6.15	0.13	1.0-9	205
	?	20.4	0.20	16.6-25.6	81	5.85	0.26	1.0-9	53

a - no birds were fat scored in 1987

? - birds of unknown brood or non-breeding birds

Appendix 7.3 **Male and female body mass at different stages in the nesting cycle in 1987, 1988 and 1989 (mean (se)):**

(a) First broods

First brood		1987			1988			1989			All years		
Stage	Sex	mean	se	n	mean	se	n	mean	se	n	mean	se	n
Pre- breeding (Pre-br)	M	20.2	0.51	9	19.6	0.17	59	19.7	0.25	19	19.7	0.14	87
	F	20.4	0.53	7	19.8	0.16	49	19.6	0.46	12	19.8	0.15	68
Nest building (NB)	M	21.2	0.12	3	19.4	0.96	17	20.1	0.20	26	19.9	0.16	46
	F	22.4	0.83	4	21.0	0.40	13	20.8	0.28	30	21.0	0.22	47
Pre- Laying (Pre-lay)	M	20.5	0.40	12	19.5	0.14	76	19.9	0.16	45	19.7	0.10	133
	F	21.1	0.52	11	20.0	0.17	62	20.5	0.24	42	20.3	0.14	115
Laying	M	19.9	0.93	3	19.6	0.43	11	19.4	0.21	18	19.5	0.19	32
	F	24.3	0.54	9	24.9	0.38	18	24.6	0.24	29	24.7	0.18	55
Incubation (Incub)	M	20.1	0.29	21	19.8	0.21	31	20.1	0.23	24	20.0	0.14	76
	F	21.7	0.24	43	21.8	0.16	81	21.5	0.18	88	21.7	0.11	213
Nestling period I (NP I)	M	19.5	0.15	13	19.2	0.29	17	19.4	0.27	23	19.4	0.16	53
	F	20.0	0.24	17	20.2	0.25	26	19.5	0.27	32	19.9	0.15	75
Nestling period II (NP II)	M	19.2	0.16	9	18.8	0.18	32	19.1	0.20	42	19.0	0.13	83
	F	18.6	0.27	13	18.8	0.18	43	18.8	0.20	44	18.8	0.12	100
Nestling period III (NP III)	M	19.1	0.22	7	19.4	0.40	11	19.0	0.56	7	19.2	0.24	25
	F	18.6	0.22	5	18.4	0.33	13	18.1	0.20	2	18.5	0.11	20
Nestling (All)	M	19.3	0.16	29	19.1	0.15	60	19.2	0.16	72	19.2	0.09	161
	F	19.3	0.20	35	19.2	0.15	82	19.1	0.16	78	19.2	0.01	135
Post-fledging (Post-fl)	M	19.5	0.41	10	19.0	0.40	20	19.0	0.38	9	19.1	0.20	39
	F	20.8	0.44	10	19.5	0.32	15	20.0	0.40	6	20.0	0.27	31

Appendix 7.3 Contd. (b) Second broods

Second brood stage	Sex	1987 mean	1987 se	1987 n	1988 mean	1988 se	1988 n	1989 mean	1989 se	1989 n	All years mean	All years se	All years n
Pre- Laying	M	-[a]	-	-	19.0	0.33	14	19.1	0.06	6	19.0	0.25	20
	F	22.1	0.60	2	20.6	0.58	9	20.5	0.83	4	20.8	0.42	15
Laying	M	18.3	0.45	2	18.6	0.45	5	19.1	0.08	6	18.7	0.27	13
	F	24.3	0.40	2	23.3	0.57	11	23.8	0.37	11	23.6	0.31	24
Incubation	M	20.2	0.19	10	19.7	0.28	24	19.3	0.46	4	19.8	0.19	38
	F	20.8	0.37	15	20.9	0.18	65	20.5	0.21	7	20.8	0.15	87
Nestling period I	M	20.2	0.39	14	19.5	0.44	15	19.8	0.00	1	19.8	0.29	30
	F	20.0	0.36	17	19.8	0.25	35	-	-	-	19.9	0.21	52
Nestling period II	M	19.6	0.35	15	19.1	0.25	25	18.5	0.30	7	19.2	0.18	47
	F	19.1	0.34	21	19.1	0.19	37	18.8	0.45	7	19.1	0.16	65
Nestling period III	M	21.0	0.41	4	19.0	0.46	8	-	-	-	19.7	0.43	12
	F	19.6	0.95	2	18.6	0.23	16	-	-	-	18.7	0.23	18
Nestling (All)	M	20.0	0.24	33	19.2	0.20	48	18.7	0.32	8	19.5	0.15	89
	F	19.5	0.24	40	19.3	0.14	88	18.8	0.45	7	19.3	0.12	135
Post-fledging	M	19.5	0.93	3	20.2	0.45	20	-	-	-	20.1	0.41	23
	F	20.8	1.14	6	19.2	0.46	10	-	-	-	19.8	0.50	16

a - no data collected

Appendix 7.4 Male and female fat scores[a] at different stages in the nesting cycle in 1988 and 1989 (Mean (se)):

(a) First broods

First brood			1988			1989			Both years		
Stage	Code	Sex	mean	se	n	mean	se	n	mean	se	n
Pre- breeding	-2	M	5.65	0.20	55	4.32	0.43	19	5.30	0.20	74
		F	6.52	0.22	45	5.13	0.50	12	6.23	0.21	57
Nest building	-1	M	5.94	0.25	17	4.33	0.32	26	4.97	0.25	43
		F	6.46	0.24	13	5.82	0.27	30	6.01	0.20	43
Pre- Laying		M	5.72	0.16	72	4.32	0.26	45	5.18	0.22	117
		F	6.51	0.18	58	5.62	0.24	42	6.14	0.21	100
Laying	0	M	5.36	0.47	11	3.78	0.33	18	4.38	0.30	29
		F	7.30	0.33	18	6.85	0.33	27	7.03	0.24	45
Incubation	1	M	5.68	0.28	31	4.63	0.30	24	5.22	0.21	55
		F	7.45	0.14	80	6.93	0.15	88	7.18	0.11	168
Nestling period I	2	M	5.03	0.31	7	3.13	0.36	23	3.94	0.28	40
		F	6.08	0.30	25	5.25	0.38	30	5.63	0.25	55
Nestling period II	3	M	4.25	0.31	28	2.50	0.21	37	3.25	0.21	65
		F	4.52	0.20	42	2.90	0.20	39	3.74	0.17	81
Nestling period III	4	M	4.44	0.71	9	2.07	0.37	7	3.41	0.52	16
		F	4.15	0.60	13	3.00	1.90	2	4.00	0.57	18
Nestling (All)		M	4.53	0.22	54	2.67	0.50	67	3.50	0.32	121
		F	4.95	0.19	80	3.89	0.24	71	4.45	0.30	151
Post-fledging		M	5.16	0.45	19	3.22	0.31	9	4.54	0.36	28
		F	4.82	0.45	14	4.67	0.77	6	4.78	0.38	20

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a - birds were not fat scored in 1987

Appendix 7.4 Contd. (b) Second broods[a]

Second brood		1988			1989			Both years		
Stage	Sex	mean	se	n	mean	se	n	mean	se	n
Pre-laying	M	4.92	0.55	13	2.58	0.33	6	4.18	0.46	19
	F	5.39	0.32	9	5.38	1.33	4	5.38	0.43	13
Laying	M	4.20	0.58	5	4.25	1.18	6	4.23	0.67	11
	F	6.18	0.37	11	5.45	0.60	11	5.81	0.35	22
Incubation	M	6.67	0.23	24	4.38	0.24	4	6.34	0.25	28
	F	7.20	0.17	65	7.71	0.31	7	7.25	0.16	72
Nestling period I	M	5.57	0.43	15	1.50	0.00	1	5.31	0.47	16
	F	6.29	0.32	33	-	-	-	6.29	0.32	33
Nestling period II	M	4.92	0.27	24	1.00	0.00	1	4.76	0.30	25
	F	5.21	0.32	35	-	-	-	5.21	0.32	35
Nestling period III	M	5.06	0.66	8	-	-	-	5.06	0.66	8
	F	4.06	0.38	16	-	-	-	4.06	0.38	16
Nestling (All)	M	5.15	0.22	47	1.25	0.25	2	5.00		49
	F	5.42	0.21	84	-	-	-	5.42		84
Post-fledging	M	6.32	0.35	19	-	-	-	6.32	0.35	19
	F	6.40	0.49	10	-	-	-	6.40	0.49	10

a - birds were not fat scored in 1987

Appendix 7.5 Body mass of adult Swallows during first brood stages of the nesting cycle in 1988 and 1989, split by age class (1 v ≥2):

a) Males

First brood	1988		1989		Both years	
Stage	1	≥2	1	≥2	1	≥2
Pre-breeding	19.9 (.5) (15)	19.5 (.2) (32)	19.5 (.5) (5)	19.9 (.3) (13)	19.8 (.4) (20)	19.6 (.2) (45)
Nest building	19.2 (.3) (9)	20.1 (.2) (5)	20.2 (.4) (7)	20.0 (.3) (17)	19.6 (.3) (16)	20.1 (.2) (22)
Laying	20.3 (.6) (5)	18.9 (.7) (5)	18.9 (.6) (5)	19.7 (.3) (9)	19.6 (.4) (10)	19.4 (.3) (14)
Incubation	20.4 (.4) (13)	18.7 (.2) (9)	19.8 (.4) (9)	20.1 (.6) (10)	20.2 (.4) (22)	20.1 (.3) (19)
NP I	19.6 (.2) (7)	18.7 (.6) (7)	18.3 (.4) (9)	20.2 (.8) (10)	18.9 (.3) (16)	19.6 (.4) (17)
NP II	18.7 (.2) (9)	19.0 (.4) (15)	18.9 (.2) (15)	19.4 (.3) (22)	18.8 (.2) (24)	19.2 (.2) (37)
NP III	19.5 (.5) (4)	20.2 (.6) (4)	20. (1.6) (2)	18.9 (.6) (4)	19.6 (.5) (6)	19.5 (.5) (8)
Nestling (all)	19.2 (.2) (20)	19.1 (.3) (26)	18.8 (.2) (26)	19.5 (.2) (36)	18.9 (.1) (46)	19.4 (.2) (62)
Post-fledging	18.4 (.7) (5)	18.9 (.4) (10)	19.4 (.7) (4)	18.8 (.6) (4)	18.9 (.5) (9)	18.9 (.3) (14)

Appendix 7.5 Contd. (b) Females

First brood Stages	1988		1989		Both years	
	1	≥2	1	≥2	1	≥2
Pre- breeding	19.7 (.3) (11)	19.8 (.2) (26)	20.4 (1.3) (4)	19.3 (.3) (7)	19.9 (.4) (15)	19.7 (.2) (33)
Nest building	21.0 (.6) (8)	20.8 (.6) (3)	20.9 (.3) (19)	20.7 (.7) (8)	20.9 (.3) (27)	20.7 (.5) (11)
Laying	23.9 (.7) (6)	25.8 (.5) (7)	24.4 (.3) (14)	25.0 (.3) (11)	24.2 (.5) (20)	25.4 (.3) (19)
Incubation	21.8 (.3) (33)	21.9 (.3) (25)	21.3 (.2) (48)	21.6 (.3) (27)	21.5 (.2) (81)	21.7 (.2) (56)
NP I	19.9 (.5) (8)	20.0 (.55 (5)	19.1 (.31 (21)	21.0 (.6) (6)	19.3 (.3) (29)	20.5 (.4) (11)
NP II	18.5 (.4) (15)	19.1 (.4) (13)	18.4 (.3) (19)	19.1 (.3) (19)	18.5 (.2) (34)	19.1 (.2) (32)
NP III	17.9 (.6) (5)	19.9 (.4) (3)	18.5 (0) (1)	-	18.0 (.5) (6)	19.9 (.4) (3)
Nestling (All)	18.9 (.3) (33)	19.6 (.3) (26)	18.9 (.2) (47)	19.6 (.3) (26)	18.9 (.2) (79)	19.6 (.2) (52)
Post-fledging	19.3 (.4) (5)	20.5 (.8) (5)	19.8 (.6) (5)	20.8 (0) (1)	19.5 (.4) (10)	20.5 (.6) (6)

Appendix 7.6 Mean ultra-sound thickness (MUS) and corresponding measures of mean fat scores (MFS) and body mass at different stages in the nesting cycle[a] for live birds

Stages in the nesting cycle	Sex	Body mass Mean	Body mass se	MUS Mean	MUS se	MFS Mean	MFS se	n
Pre laying	M	18.9	0.37	2.56	0.038	3.58	0.30	6
	F	19.8	0.47	2.54	0.087	6.0	0.84	6
Laying	M	-		-		-		-
	F	25.3	1.44	2.58	0.097	6.33	0.601	3
Incubation	M	20.6	0.26	2.55	0.036	6.82	0.371	12
	F	21.4	0.33	2.60	0.031	7.57	0.245	24
Nestling period I	M	19.2	0.54	2.45	0.019	5.19	0.597	8
	F	19.9	0.25	2.47	0.023	6.13	0.376	21
Nestling period II	M	19.0	0.33	2.41	0.026	5.03	0.356	20
	F	19.1	0.21	2.43	0.024	5.39	0.327	32
Nestling period III	M	19.2	0.68	2.41	0.043	4.67	0.667	6
	F	18.4	0.24	2.32	0.027	4.46	0.437	12
Post-fledging	M	19.5	0.44	2.42	0.041	5.86	0.431	11
	F	19.2	0.26	2.38	0.045	6.45	0.425	10

a- data relates exclusively to a subset of data collected during second broods in 1988 during which period measures of ultra-sound thickness were taken on live birds. Results for fresh body mass and fat scores taken on the same individuals at corresponding captures are shown for comparative purposes. Where individuals were measured several times during the same stage in the nesting cycle a mean value was computed.

Appendix 8.1 Differences in measures of reproductive performance in relation to age of female

Passeriformes Species	Authors	Measures of reproductive performance: Date of first egg	Clutch size	No. fledged	No. Recruits	Breeding attempts
Bee-Eater	Lessells & Krebs 1989	+	+o	o	+	
Swallow	This study	+	+c	+c	o	+c
House Martin	Rheinwald *et al.* 1976			+	+	+
	Bryant 1979,1988	+		+		+
Tree Swallow	DeSteven 1978			+		
	DeSteven 1980	+	+	+		+
Wrentit	Geupel & DeSante 1989	+	o	o	o	+
Rock Pipit	Askenmo & Unger 1986	+	+			
Eastern Bluebird	Pinowski 1977	+		+		+
Pied Flycatcher	Harvey *et al.* 1979	+	+	+		+
	Harvey *et al.* 1985		+			+
Great Tit	Kluyver 1951	+s	+	+		
	Perrins 1965	+	+	+		
	Klomp 1970		+	+		
	van Balen 1973	+	+			
	Perrins & Moss 1974	+s	+c	+s		
	Perrins 1979		+s			
	Perrins & McCleery 1985	+	+	o	o	
	Dhondt 1987	+s	+s	+s	o	
Blue Tit	Dhondt 1987	+s	+s	+s	o	
Ipswich Sparrow	Ross 1980	+	+	+	o	+
Song Sparrow	Smith 1981		+			
	Smith & Roff 1980		+			
	Nol & Smith 1987	+	o	+		+
Savannah Sparrow	BéDard & LaPointe 1985	(o)	o	+		
Black-b Magpie	Reese & Kadlec 1985	+	+	+		+
Hooded Crow	Loman 1984		+			
American Goldfinch	Middleton 1979	+	+	+		
Blackbird	Desrochers 1992	+		+	+	
R-w Blackbird	Crawford 1977	+	+	+		+

notes:
+ adults breed earlier or have larger clutch size, fledge more young etc compared to yearlings
o - no difference in breeding performance
c - differences still apparent after controlling for age-related differences in laying date