

655

PARENT:OFFSPRING RESOURCE ALLOCATION STRATEGIES IN BIRDS;
STUDIES ON SWALLOWS (HIRUNDINIDAE)

Gareth Jones, B.Sc.

Thesis submitted for the degree of
Doctor of Philosophy

Department of Biological Sciences,
University of Stirling

February, 1985

8/85



He who know nothing, loves nothing. He who can do nothing understands nothing. He who understands nothing is worthless. But he who understands also loves, notices, sees ... The more knowledge is inherent in a thing, the greater the love ... Anyone who imagines that all fruits ripen at the same time as the strawberries knows nothing about grapes.

PARACELSUS

ABSTRACT

The use of precision automated electronic balances has allowed remote quantification of instantaneous and long term body mass changes in breeding swallows, Hirundo rustica. By means of observation, experiment and optimality modelling, the extent of mass changes during incubation and nestling rearing are described, and the fitness consequences of mass changes discussed.

An understanding of the causes and consequences of mass changes in swallows is developed from laboratory investigations of short term mass changes in canaries Serinus canarius, and from carcass analysis of breeding sand martins R. riparia, and swallows.

Parent:offspring resource allocation was investigated during incubation in swallows. A model is developed which assumes that fitness is maximised in individuals which spend most time on the nest as a result of maximising the difference between net gain while foraging and clutch reheating costs, measured in units of energy. The model is tested, and the most frequently observed inattentive period proves to be similar to that predicted to be the most energetically profitable.

The early decline in swallow body mass during nestling rearing is likely to represent a 'programmed' anorexia in females during the brooding phase, whereby mass loss is beneficial in reducing flight costs and releasing energy available for work. After termination of brooding, however, mass losses were associated with rapid feeding rates to the brood for both sexes, and were judged to be potentially costly in terms of adult survival.

By concurrent monitoring of resources for parents and offspring, investment in self-maintenance relative to investment in offspring is calculated, and the results interpreted in the wider context of life-history tactics and parental investment theories. Both sexes of swallow invested more in 'self' relative to 'offspring' when food was scarce or when feeding broods of small metabolic mass. Females appeared to risk their body mass falling to lower levels than that of their mates when feeding conditions were poor.

Overall, the study showed that the costs and benefits of mass changes in swallows differed according to the stage of the breeding cycle, and that detailed knowledge of the causes of mass changes allows insight into the evolution of reproductive strategies of birds of both sexes in relation to individual quality and resource availability.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr David Bryant, for his assistance throughout this study. The project grew out of his studies on house martins, and I am deeply grateful for Dr Bryant's constructive criticism, perception, and encouragement over the past three and a half years. Several colleagues discussed aspects of the work with me, and I especially thank Drs. Angela Turner, Paul Tatner, John Speakman and Nadav Nur for stimulating discourse. All participants in the Behavioural Ecology Discussion Group at Stirling also helped create and clarify ideas. Leslie Musk provided valuable information on Sahelian climate, and Stirling University Shared Technical Services assisted in devising and modifying equipment. Facilities were provided by courtesy of Professor W.R.A. Muntz in the Department of Biological Sciences.

This project would not have been possible without the co-operation of numerous landowners in the Stirling area, and I especially acknowledge Messrs. Fleming of Barbush quarry, Dunblane, and the McFarlands of Lecropt. Mrs. M. Abrahamson provided excellent typing services.

Angela Heaney, Iain MacGowan, June Randell, and Richard Teeuw were valuable friends during the study, and provided moral support and encouragement. Angie drew the frontispiece, and Iain's assistance in catching martins is much appreciated.

Financial support was provided by a NERC studentship.

CONTENTS

	Page
ABSTRACT	(i)
ACKNOWLEDGEMENTS	(iii)
1. INTRODUCTION	1
2. THE STUDY SPECIES AND STUDY SITES	
2.1 Introduction	8
2.2 Materials and Methods	
2.2.1 The distribution of sand martin colonies in the Stirling Region	9
2.2.2 Examination of individual birds and capturing techniques	10
2.2.3 Statistical procedures	12
2.3 Results	
2.3.1 The distribution of sand martins in Central Scotland and population changes 1982-1984	12
2.3.2 Colonisation patterns of sand martins at the main study site	15
2.3.3 Some aspects of the breeding biology of sand martins	18
2.3.4 Predators and parasites of sand martins	19
2.3.5 Morphometrics of sand martins at Barbush	20
2.3.6 Changes in morphometrics between years	26
2.3.7 Morphometrics and breeding biology measurements of swallows	30
2.4 Discussion	
2.4.1 The distribution, colonisation patterns, and population changes of the study population of sand martins	32
2.4.2 Factors responsible for sand martin population crashes	40
2.4.3 Natural selection and body size changes in bird populations	43

3.	RESOURCES AVAILABLE FOR BREEDING HIRUNDINES	
3.1	Introduction	49
3.2	Materials and Methods	50
3.3	Results	
3.3.1	Suction trap catches	53
3.3.2	Hand-net catches	55
3.3.3	Differences in insect abundance between years	67
3.3.4	A comparison of suction trap and hand-net catches	67
3.3.5	A summary of factors influencing resources available for breeding hirundines	70
3.4	Discussion	70
3.4.1	The implications of low levels of food abundance for hirundine feeding behaviour and body condition	71
3.4.2	The implications of short and long term fluctuations in food availability for hirundine breeding biology	73
4.	PHYSIOLOGICAL ASPECTS OF SHORT-TERM BODY MASS CHANGES IN BIRDS	
4.1	Introduction	75
4.2	Materials and Methods	76
4.3	Theory and Results	
4.3.1	A model of canary body mass changes: theory	80
4.3.2	Laboratory studies: short-term body mass changes in canaries and sand martins	83
4.3.3	A model of canary body mass changes: results	88
4.3.4	Short-term body mass changes in breeding swallows	90
4.4	Discussion	
4.4.1	The use of precision automated balances in studies of avian body mass changes	92
4.4.2	Short-term body mass changes in birds	94
4.4.3	Modelling avian body mass changes in the laboratory	100

5. THE BODY CONDITION OF BREEDING HIRUNDINES

5.1	Introduction	101
5.2	Materials and Methods	102
5.3	Results	
5.3.1	Lipid reserves of adult and fledgling sand martins	103
5.3.2	The role of protein reserves in body mass changes of breeding sand martins	117
5.3.3	The role of body water in body mass changes of breeding sand martins	119
5.3.4	The role of reproductive structures in body mass changes of breeding sand martins	122
5.3.5	Body condition of breeding sand martins - synthesis	123
5.3.6	The body condition of adult and fledgling swallows	126
5.3.7	Nestling body mass and body condition in sand martins	126
5.3.8	Body component development in nestling sand martins	129
5.3.9	The lipid content of body components in nestlings	132
5.3.10	Lipid index hierarchies within broods	134
5.3.11	Are the youngest or least nourished chicks in the brood age hierarchy relatively undernourished with respect to their age?	136
5.4	Discussion	
	The adaptive significance of body reserves in breeding sand martins and their broods: implications for parent:offspring resource allocation strategies	
5.4.1	Implications for the parents	138
5.4.2	Implications for the brood	145

6. MATE-GUARDING AND SEXUAL CHASES IN SAND MARTINS

6.1	Introduction	150
6.2	Materials and Methods	151
6.3	Results	
6.3.1	Diurnal and seasonal variation in mate-guarding behaviours	154
6.3.2	Which birds are chased by male sand martins?	156
6.3.3	Female body mass during breeding and sexual chasing	161
6.3.4	Female flight performance and reproductive condition	162
6.4	Discussion	
6.4.1	Mate-guarding behaviour and coloniality in birds	167
6.4.2	How body mass changes may affect flight performance in fertile female sand martins: cues for males to increase their fitness	170

CONTENTS (cont.)	Page
7. RESOURCE ALLOCATION DURING INCUBATION IN SWALLOWS	
7.1 Introduction	174
7.2 Materials and Methods	175
7.3 Theory and Results	
7.3.1 Body mass dynamics of incubating female swallows	176
7.3.2 The cost of incubation	182
7.3.3 Incubation strategies of swallows: a mode of optimal behaviour	187
7.3.4 The effects of changing costs and benefits on the optimality model - theory	188
7.3.5 Quantification of the parameters included in the model	189
7.3.6 Egg cooling rates	190
7.3.7 A test of the model of an optimal inattentive period	196
7.3.8 The effects of changing costs and benefits on the optimality model - results	200
7.3.9 Motivational factors influencing swallow incubation behaviour	204
7.4 Discussion	
Incubation from a parent:offspring resource allocation perspective	210
8. RESOURCE ALLOCATION BETWEEN PARENT SWALLOWS AND THEIR NESTLINGS	
8.1 Introduction	214
8.2 Materials and Methods	215
8.3 Results	
8.3.1 Adult body mass changes during nestling rearing	218
8.3.2 Adult masses during the brooding phase	220
8.3.3 Female brooding behaviour	225
8.3.4 Replacement experiments	225
8.3.5 Adult masses during the non-brooding phase	229
8.3.6 Brood size manipulation experiments	234
8.3.7 Parental foraging ecology and feeding behaviour during nestling rearing	237
8.3.8 Differences in parental investment by male and female swallows during nestling rearing	245
8.3.9 Factors influencing nestling growth	248
8.4 Discussion	
Optimal body mass of adult birds rearing nestlings	252

CONTENTS (cont.)	Page
9. GENERAL DISCUSSION: REPRODUCTIVE COSTS, REPRODUCTIVE EFFORT, AND PARENTAL INVESTMENT IN SWALLOWS	
9.1 Definitions	270
9.2 Body mass changes as an indicator of reproductive costs in birds	271
9.3 Life-history tactics and reproductive effort	272
9.4 Concurrent parent:offspring resource allocation in swallows	281
SUMMARY AND CONCLUSIONS	285
BIBLIOGRAPHY	
APPENDICES	

CHAPTER 1

1. INTRODUCTION

Resources gained during foraging by breeding animals may be allocated to either parents or their offspring. When breeding, the demands on a parent's time and energy are high (Drent and Daan 1980; Bryant and Westerterp, 1980), and those individuals which optimise the relative allocation of resources between self-maintenance and reproduction, with the goal of maximising lifetime reproductive success, are likely to be favoured by natural selection.

Most theories of life-history strategies assume that the reproductive effort expended by parents has evolved to reconcile the opposing effects on fitness of current and future levels of effort (Williams, 1966a, b; Charnov and Krebs, 1974; Pianka and Parker, 1975; Hirshfield and Tinkle, 1975; Stearns, 1976; Ricklefs, 1977; Calow, 1979). Reproductive activities are assumed to increase physiological stress or predation risks for parents, and therefore effort expended in reproduction may reduce the expectation of future life. Several studies of animals have revealed either an increase in mortality of breeders relative to non-breeders (Summers-Smith, 1956; Snow, 1958; Geist, 1971; Berger, 1972; Clutton-Brock, Guinness and Albon, 1983), or have shown an increased mortality rate related to increased fecundity (Lowe, 1969; Snell and King, 1977; Bell, 1981).

The level of reproductive effort expended by parents is difficult to quantify. Some studies on birds have reported no survival differences between adults rearing natural broods of different sizes (Lack, 1966, analysing data of B. Campbell; Bryant, 1979), while other work has observed a positive relationship between reproductive performance and adult survival (Högstedt, 1981; Smith, 1981).

The number of offspring reared by adults in natural situations however, may be a poor measure of reproductive effort, since higher quality individuals may rear more youngsters and incur less breeding stress than individuals of poorer quality rearing fewer offspring (Perrins and Moss, 1975). Studies relating reproductive effort to future survival or reproductive success must therefore overcome the effects of phenotypic variation in quality amongst individuals and are best approached through experimental manipulation of reproductive effort, altering the number of offspring reared by adults and detecting subsequent changes in parental survival or breeding productivity (Askenmo, 1979; De Steven, 1980; Nur, 1984a).

One problem in relating adult survival rates to reproductive effort is that the return rates of parents rearing different brood sizes may reflect differences in emigration rates, rather than changes in survival rates (Högstedt, 1981). Even studies of experimental modification of reproductive effort in birds are subject to criticism. If parents adjust their body condition during incubation in accordance with the number of young they are genetically or environmentally disposed to rear, then the body condition of adults when chicks hatch will reflect differences in cumulative investment involved in incubating clutches of different sizes. If laying or incubating a clutch is more costly to a bird than rearing a brood of nestlings (Yom-Tov and Hilborn, 1981), experimental manipulation of brood size alone may not impose reproductive costs at the critical time.

Evidence for the existence of reproductive costs in bird species is inconsistent. Double-brooded female house martins Delichon urbica show a higher annual mortality rate than single-brooded females (Bryant, 1979). Individual great tits Parus major rearing large brood sizes

within a season have a lower survival rate than those rearing fewer young (Kluyver, 1971). By experimental manipulation of brood size, Askenmo (1979) found a reduced return rate of male pied flycatchers, Ficedula hypoleuca rearing enlarged broods compared with males rearing natural brood sizes, but no such relationship was evident amongst females. The return rate of female tree swallows, Iridoprocne bicolor was found to be similar for birds rearing enlarged and normal brood sizes (De Steven 1980). In contrast, female blue tits, Parus caeruleus showed decreased survival rates when rearing enlarged broods compared with control and reduced brood sizes, though no effect of brood size on male survival rate was apparent (Nur, 1984a).

Parent birds obviously cannot be expected to predict changes in survival chances in order to evaluate options open to them at any time (Drent and Daan, 1980). Although the relationship between short term behaviour and lifetime reproductive success must be approached with caution (McNamara and Houston, 1982), it is feasible that breeding birds monitor their long term survival prospects in terms of short term changes in their energy balance (Drent and Daan, 1980). A short term deterioration in body condition may for example, be proximately detected by the parent through an increase in hunger motivation, mediated perhaps by sensory monitoring of lipid in blood plasma.

Adult passerine birds are normally lighter in mass when rearing young than during incubation (Nice, 1937; Newton, 1972; Bryant, 1975a, 1979; Dowsett-LeMaire and Collette, 1980; Freed, 1981; Westerterp, Gortmaker, and Wijngaarden, 1982; Nur, 1984a), and birds rearing experimentally enlarged brood sizes may (Hussell, 1972; Askenmo, 1977; Bryant, 1979; Nur, 1984a) or may not (De Steven, 1980), show increased rates of mass loss compared with birds rearing natural brood sizes.

The decreased body mass of adult birds feeding nestlings has sometimes been considered an indicator of physiological stress associated with rearing a brood (Nice, 1937; Ricklefs, 1974), and has been used as a predictor of subsequent adult survival prospects (Hussell, 1972; Askenmo, 1977). However, Freed (1981) and Norberg (1981) have suggested that mass loss by adult birds rearing young could be beneficial to the parents in reducing power requirements for flight and releasing energy available for work. Alternatively parental mass loss during rearing could be viewed as optimising the trade off between the costs and benefits of losing mass in terms of an individual's lifetime reproductive success (Norberg, 1981; Nur, 1984a).

One aim of this thesis is to evaluate adult body mass changes during breeding as an index of reproductive investment in swallows Hirundo rustica, through concurrent monitoring at the nest of resource balance for parents and young. Previous studies have generally considered parental allocation or offspring demands in isolation, although some recent work has analysed changes in adult body condition in direct relation to offspring demands (Fedak and Anderson, 1982; Ricklefs and Hussell, 1984).

Incubation is another phase of the nesting cycle where parental interests in self-maintenance may conflict with the offsprings' interests in being hatched successfully. Since offspring demands are more constant during incubation than when chicks are growing in the nest, behavioural decisions by parents may be less variable and hence easier to investigate. Another aim of this thesis, then, is to develop a model of optimal behaviour for incubating female swallows which assumes that fitness is maximised for individuals which spend as much time as possible on the nest by maximising their net energy gains

while foraging between incubation bouts. Previous studies of optimal feeding behaviour have concentrated on animals in non-reproductive situations (reviews in Krebs, 1978; Krebs, Stephens and Sutherland, 1983). Although central place foraging studies (Orians and Pearson, 1979) have considered adult birds feeding nestlings (Hegner, 1982; Bryant and Turner, 1982), the theory has only recently considered how resource allocation between parent and offspring may influence patch residence time (Kacelnik, 1984). The model of optimal incubation behaviour presented in Chapter 7 considers the constraints of egg cooling (investment in offspring), and adult feeding behaviour (investment in self) to predict an optimal time to leave eggs unattended.

The study species used in the investigation of parent:offspring resource allocation, the swallow and the sand martin R. riparia, are introduced in Chapter 2, and aspects of their population ecology and breeding biology are described. Resource allocation between parents and offspring is likely to depend on the quantity of resources available. For example, investment in brood growth during adverse conditions may occur at the expense of somatic maintenance by the parents. Food resources available to hirundines during the breeding season over the study period are described in Chapter 3.

It is necessary to understand the causes of short term body mass changes in birds so that, for example, instantaneous adult mass changes while foraging can be related to energy balance. Mass changes which occur as a result of food ingestion, water intake, metabolic water losses, and defaecations have to be measured and their dynamics understood if substantial conclusions about more significant mass changes are to be reached. In Chapter 4 a laboratory investigation of the causes of short term mass changes in canaries Serinus canarius (used

as a convenient laboratory model) is presented, and factors likely to be responsible for instantaneous mass changes in breeding swallows are described.

If parental body mass changes are to be related to changes in the body condition of breeding birds, a detailed knowledge of the bird's energy reserves while breeding is necessary. For example, loss of mass by females after laying may be associated with atrophy of ovaries and oviducts rather than decreases in energy reserves. Hence in Chapter 5 long term body mass changes of sand martins during breeding are related to changes in lipid and protein reserves by carcass analysis, and comparisons are made with a smaller sample of swallow carcasses. Changes in the energy reserves of adult sand martins and their broods are considered concurrently during the rearing period. The sand martin is included here because of a ready availability of individuals for carcass analysis, contrasting with swallows where removal of individuals would have interfered with the study population more severely.

In Chapter 6 the consequences for male reproductive success of female sand martins becoming heavy when they are fertile is described. If males are able to detect fertile females through female flight behaviour, itself associated with increased body mass, males may potentially increase their fitness by mating promiscuously with such females.

Knowledge of the causes of instantaneous and long term body mass changes in breeding hirundines developed in Chapters 4 and 5 is applied to studies of reproductive investment by swallows in incubation (Chapter 7) and during nestling rearing (Chapter 8). Through the use of precision automated nest balances, and by means of

observation, experiment, and optimality modelling, the significance of mass changes as a measure of reproductive investment and the fitness consequences of mass changes are described.

Over the study period a dramatic reduction of numbers occurred in local and national (U.K.) sand martin populations. At the same time a decrease in the average body size of individuals at the main study colony was observed. In Chapter 2, the adaptive significance of body size changes in bird populations is reviewed. The consequences of parental mass changes during breeding for theories of life-history tactics and parental investment are discussed in the final section, Chapter 9, and parent:offspring resource allocation in swallows is described by considering adult self-maintenance and investment in offspring simultaneously.

CHAPTER 2

2. THE STUDY SPECIES AND STUDY SITES

2.1 INTRODUCTION

The fieldwork for this study was performed on the swallow, Hirundo r. rustica, and the sand martin, R. riparia. In North America the sand martin is called the bank swallow, and a different subspecies of swallow, the barn swallow H. r. erythrogaster, is found. All species are summer migrants to their breeding grounds.

The breeding cycles of birds encompass a wide range of activities, each activity incorporating a variety of behaviours with different time commitments and energetic costs (Ricklefs, 1974; Bryant and Westerterp, 1980; Ettinger and King, 1980). In the sand martin, the breeding season incorporates prospecting for colonies, arrival at the colony, mate selection, mate guarding and sexual chases by males, egg formation, fertilization, and laying by females, incubation, and nestling rearing. Since the species is typically double brooded in Britain (Turner, 1980; Cowley, 1979, 1983), all of the activities following arrival may be duplicated within the breeding season. Accounts of the breeding biology of the sand martin are given by Asbirk (1976) and Turner (1980), and similar information exists for bank swallows in America (Stoner, 1936; Petersen, 1955).

Accounts of the breeding biology of the swallow are reviewed by Turner (1980). Only the female swallow incubates the eggs and broods young nestlings, whereas both sexes of sand martins (Turner, 1980) and barn swallows (Ball, 1983a, b) share these duties.

In this chapter, observations on the breeding biology of sand martins and swallows are presented, with emphasis placed on the arrival patterns and populations changes of sand martins over the study period.

The analysis of arrival patterns includes an investigation of which birds arrived at the colony earliest, and speculation on the costs and benefits of early arrival for sand martins. Settlement patterns were investigated within a major colony, and colony selection was studied on a wider geographical basis. The occurrence of a dramatic population crash over the course of the study allowed insight into quantitative changes in body size within a bird population after a period of high mortality, and speculation about the effects of such over-winter selection for optimal body size during the breeding season.

2.2 MATERIALS AND METHODS

2.2.1 The distribution of sand martin colonies in the Stirling Region

In order to assess the distribution and abundance of sand martins in the Stirling area and to select suitable study sites, surveys of local colonies were performed between 1982 and 1984. The area selected for the survey was the Stirling Region, arbitrarily defined for the British Association Conference at Stirling 1974 (Figure 2.2). The region includes part of the highland boundary fault, and is composed of a diverse range of habitats (Timms, 1974).

Sites were surveyed in late June and early July, corresponding to the period when most birds had constructed burrows for first broods at the main study colony at Dunblane (see results). Hence burrow counts are likely to estimate the maximum number of pairs attempting first broods at the sites surveyed. Colonies were located by following river courses and through contacts with local ornithologists, and it is likely that all of the major colonies (>50 pairs) in the Stirling Region were covered at some stage during the three summers of the study.

Sand martins often construct new burrows each year, and many birds dig new holes for second broods (Turner, 1980, pers. obs.). Burrows obviously not in use were not counted. Criteria for assessing occupancy were the presence of chicks, fledglings or adults at the burrow entrance, claw marks outside of the burrow, or lines of faeces below the burrow. Unused burrows often had vegetation growing out of them, or had cobwebs across the entrance (Harwood and Harrison, 1977). Such burrows were excluded from the counts.

Burrows which were not obviously out of use, but whose occupancy could not be confirmed were included in the counts. Hence considerable errors of over-estimation are possible, and the burrow counts are probably only of use in detecting large scale population changes.

The main study site

Most observations and studies were based at Barbush sand quarry, near Dunblane, Central Region (NN 787026), about 8 km north-west of Stirling University. The colony is the largest recorded in Scotland (Thom, in prep.), with about 920 pairs present in 1982, but numbers showed considerable fluctuations between years. Several subcolonies were present each year at Barbush, and one subcolony was studied intensively each year, supplemented with fewer observations made at other subcolonies. At Barbush subcolonies ranged in size from a single burrow to about 390 occupied burrows.

2.2.2 Examination of individual birds and capturing techniques

Adult birds and recently fledged young were captured using mist nets. Birds were netted during the evening (18.00h-22.00h), and other nets were left up overnight and emptied at dawn on the following day. Checking of nets before dawn showed that no birds remained in the nets overnight.

Wing-length (maximum chord, measured to the nearest 0.5 mm) and keel-length (measured to the nearest 0.1 mm) were recorded, and all birds captured were ringed. Individuals could be aged (recently fledged young or older) by plumage characteristics, and many adults were sexed by brood patch criteria (Svensson, 1975). Lipid reserves were scored in the tracheal pit and on the posterior edge of the keel, each on a 0-6 point scale. The two values were combined into an overall fat score. The percentage coverage of lipid on the abdomen was also estimated when possible (Figure 2.1).

A subsample of adults was colour marked, and the birds were traced back to their burrows. When parent birds were seen removing faecal sacs from the nests, the burrows were enlarged, and the nestlings were removed. Nestlings were processed and aged according to sand martin nestling growth curves (Turner and Bryant, 1979).

Having calculated nestling age, and assuming that brood size equalled clutch size, that incubation lasted 13 days, that one egg was laid each day, and that incubation began when the penultimate egg was laid (Turner, 1980), first egg dates could be calculated. Age determination for the brood also allowed adult body mass and fat score to be related to stage of the breeding cycle. Visits to the main study site were spread evenly over the breeding season.

Adult swallows were captured using mist nets, and were processed in the same way as described for sand martins.

Standard meteorological measurements were obtained from the weather station at Stirling University. Additional measurements of shade temperature, barn temperature, and estimates of windspeed using the Beaufort Scale were made in the field.

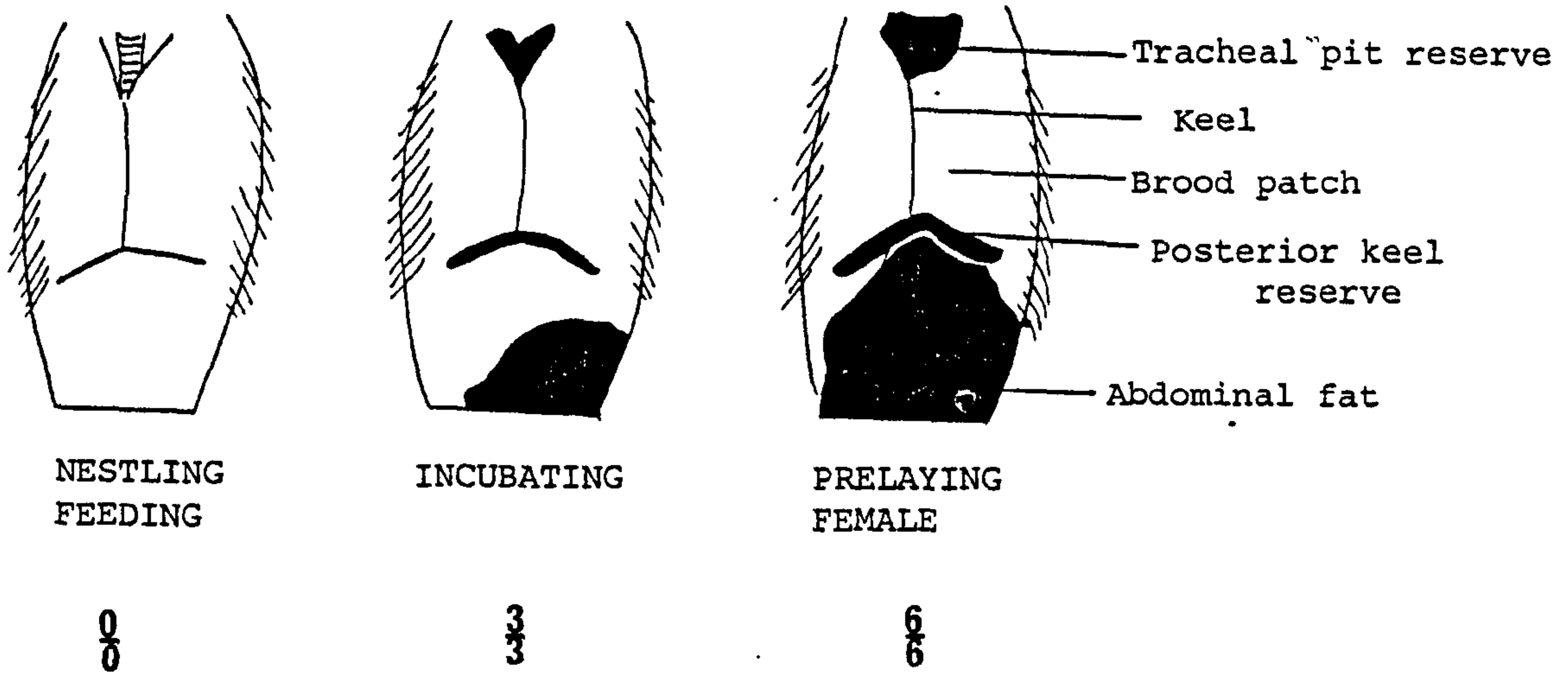


Figure 2.1

Fat-scoring system for hirundines. Lipid reserves were scored on a 0-6 point scale in the tracheal pit and at the posterior edge of the keel. Scores were added together for an overall fat score.

In some instances the percentage coverage of abdominal fat was also estimated.

Fat reserves are heavily shaded.

Numbers are fat scores, $\frac{(\text{tracheal})}{(\text{posterior keel})}$

2.2.3 Statistical procedures

Statistical procedures follow Zar (1974). Stepdown multiple regression analysis was used, and the presentation of information for this technique follows the reasoning of Kennedy and Southwood (1984).

For predictive purposes, stepdown regression should be halted when the next variable to be included has a non-significant t-value for entering the analysis. In the text, 'full analyses' included all variables used for the analysis, while in 'abbreviated analyses' computation was halted after the last significantly contributing variable had been entered.

When two variables, which taken separately might be almost equal predictors of variation in the dependent variable are intercorrelated, only one, the first one entered, may appear significantly in a stepwise regression (Kennedy and Southwood, 1984). Correlation matrices for variables used in multiple regression analyses are therefore also presented.

Statistics are given throughout as the mean \pm 1 s.d. unless otherwise stated.

2.3 RESULTS

2.3.1 The distribution of sand martins in Central Scotland and population changes 1982-1984

The burrow counts from the 1982-1984 Stirling Region colony censuses are presented in Appendix I. Counts were obtained from 27 colonies over 3 years, with 15 sites covered in all three years. In 1982 counts were spread over a longer period than in the two subsequent years. Early counts in 1982 were therefore likely to be under-estimates, since the Barbush study colony continued to increase after

counts were made at some sites. Hence the counts at such sites were increased by a factor which corresponded to the percentage change in burrow numbers at Barbush between the time when the counts were made and when peak numbers occurred at Barbush.

The largest colony recorded was at Barbush (site 5 in Appendix I), when an estimated 920 pairs attempted first broods in 1982. The smallest colony was of one burrow, at Northfield quarry, Denny (site 20) in 1983. Suitable sites for sand martin colonies can be short-lived, and the birds must be opportunistic in colony selection. For example, Roughmute sand quarry (site 18) held about 370 pairs in 1982, was largely reclaimed as grassland in 1982-3, and the colony has disappeared by 1984. Sand quarries are frequently disturbed, and river banks may collapse or be flooded, so sites may vary considerably in distribution and size from year to year. The distribution of the surveyed colonies in the Stirling region is presented in Figure 2.2. There were few colonies in the north-west of the Region, which is mainly high ground and includes few rivers with sandy banks. Most sites were concentrated in the south and east of the Region, especially along river courses where suitable banks exist for burrowing, or where glacial sand and gravel deposits have been quarried, leaving large cliffs for colonisation. Most river bank nests were found along the Allan Water, the River Devon, and the River Endrick. The Rivers Forth and Teith have few high sandy banks which are safe from flooding.

In Figure 2.3 a frequency distribution of colony sizes is plotted for each of the three years of the study. The splitting of the River Devon sites into three was arbitrary, since the nests were scattered along the river, and did not lie in discrete colonies. In each year, most colonies were in the 1-100 burrows class. The number

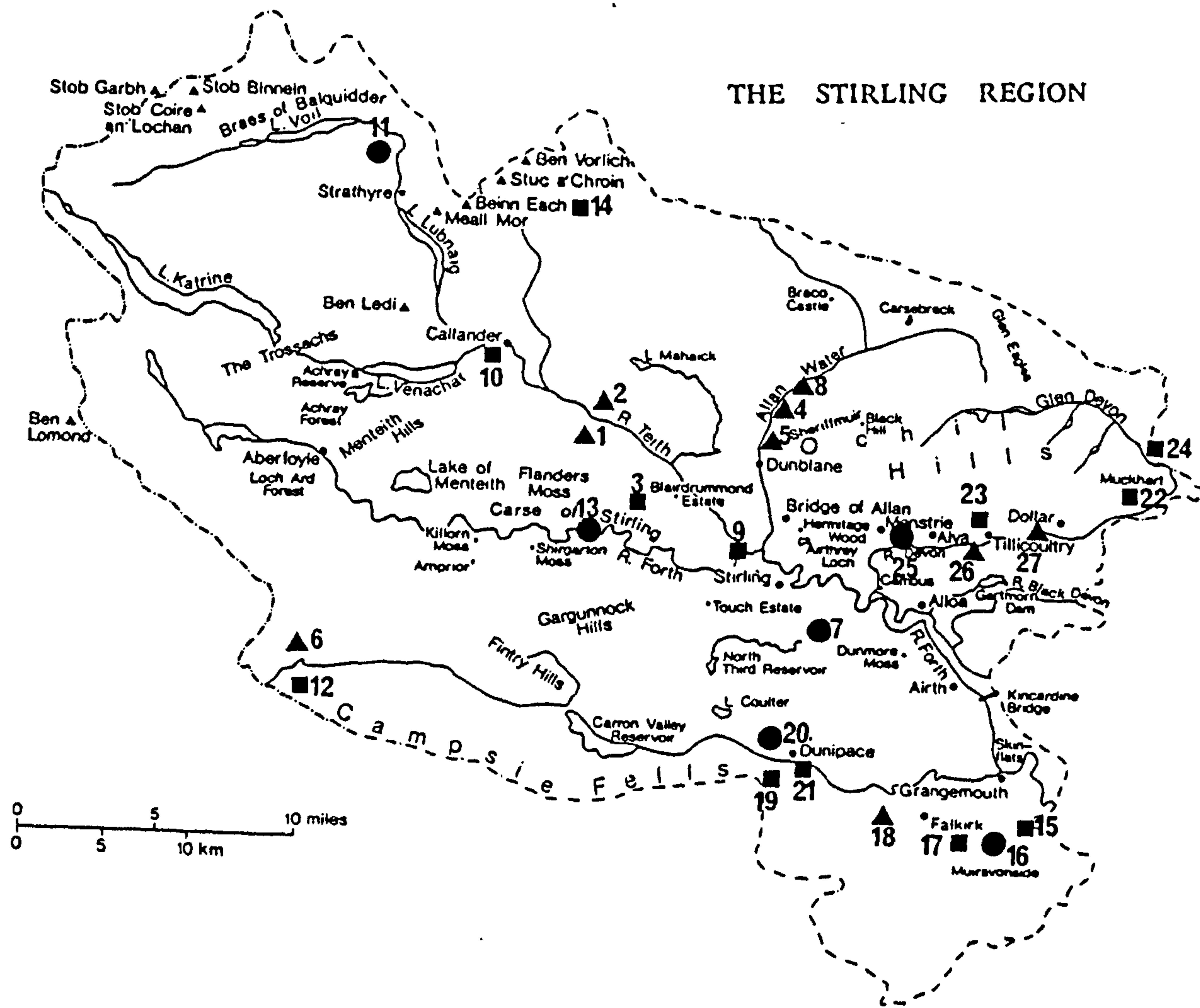
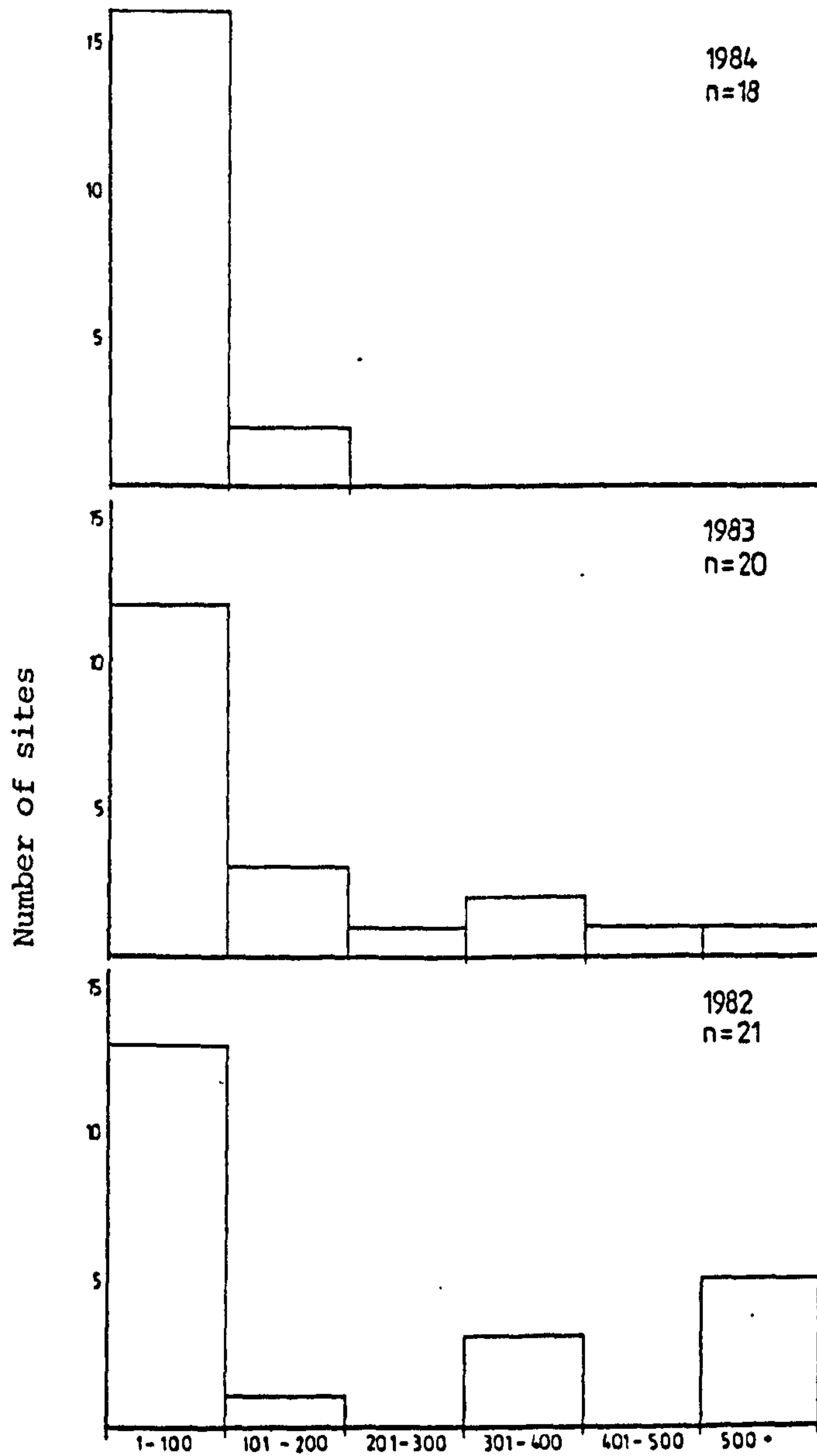


Figure 2.2

Sand martin colonies surveyed in the Stirling Region, 1982-1984.

Numbers refer to sites listed in Appendix I, and counts are the maximum recorded 1982-1984. The maximum number of pairs attempting first broods at each colony is estimated.

- Circles: 1-10 burrows
- Squares: 11-100 burrows
- Triangles: 101-1000 burrows



Colony size: estimated maximum number of pairs attempting first broods.

Figure 2.3

Frequency distributions of sand martin colony sizes in the Stirling Region, 1982-1984

of colonies containing more than 500 burrows declined from 5 in 1982 to 1 in 1983, whilst no colony exceeded 200 burrows in 1984.

(i) Colony site selection in the Stirling Region

The information on colony distribution is from the 1982 data, when sand martin numbers were the highest during the study period. Sites only covered in 1983 and 1984 had their numbers modified according to the average population changes for the Stirling Region over the years concerned, giving estimates of burrow numbers for 1982. Two small colonies initiated in 1983 were excluded from the analysis (Cowie quarry, site 7, and Dunipace cemetery, site 21).

It is estimated that in 1982 a maximum of about 4,074 pairs of sand martins attempted first broods in the Stirling Region. Of these, about 3,285 (81%) nested in sand or gravel quarries, about 723 (18%) nesting in river banks, 1% in a glacial esker. The calculated distribution of burrows in 1982 is illustrated as a pie-chart in Figure 2.4.

(ii) Population changes 1982-1984

As mentioned in Section 2.2.1, the census method was considered to be accurate enough only to detect large scale population fluctuations. Burrow counts for eight sites which were surveyed in all three years gives an indication of population trends over the study period. These sites were selected because of their lack of disturbance over the study period, and included 65% of all burrows counted during 1982. Data are presented for the five artificial and three natural sites in Figure 2.5. Information for a further two sites surveyed in 1983 and 1984 only (Drumbeg and Avon Glen) is also plotted.

Of the eight sites, five showed a decline in size between 1982

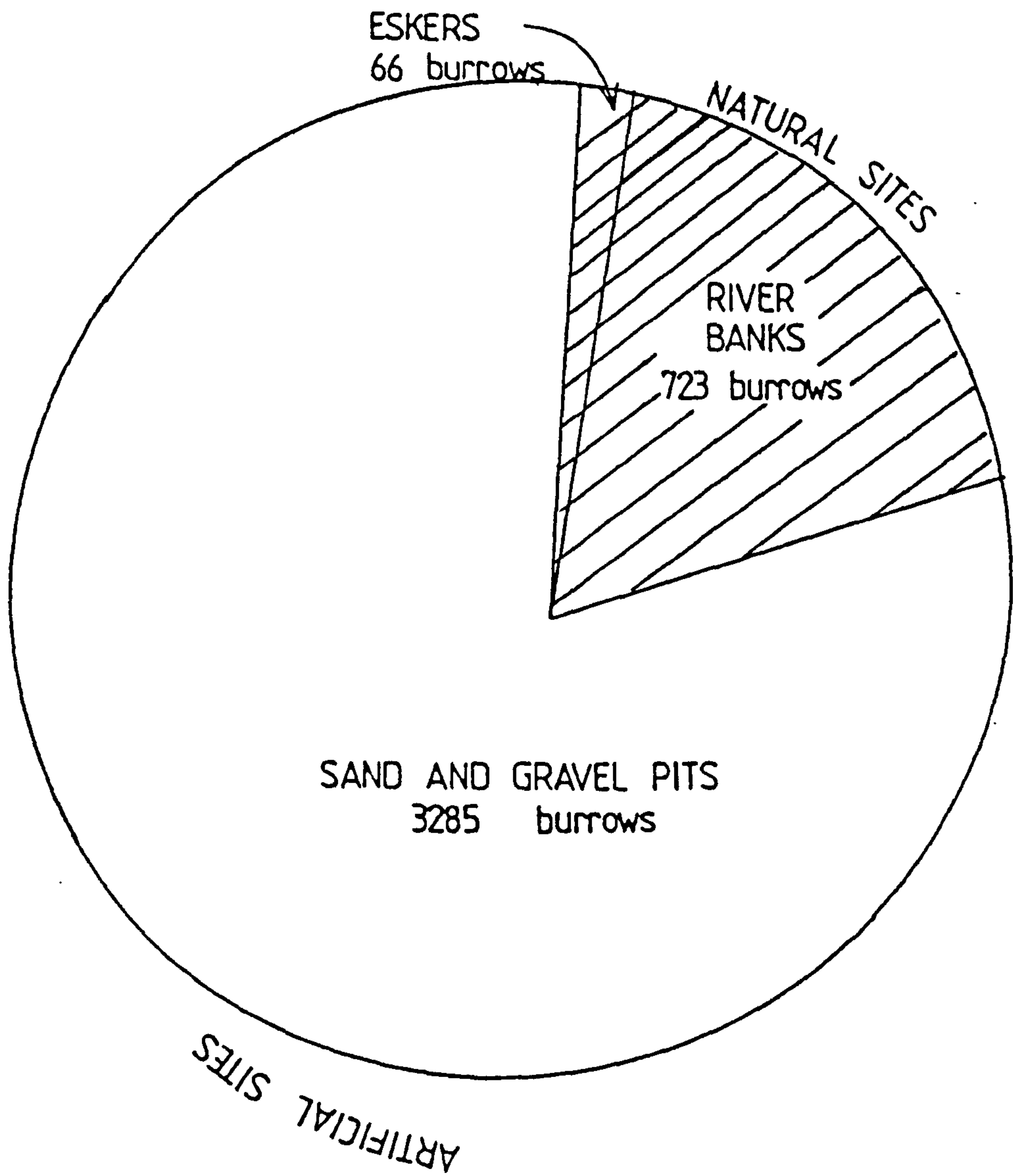


Figure 2.4

The distribution of sand martin burrows in different sites in the Stirling Region as calculated from the 1982 data. The proportion of burrows in natural sites is represented by cross-hatching.

Colony size: estimated maximum number of pairs attempting first broods

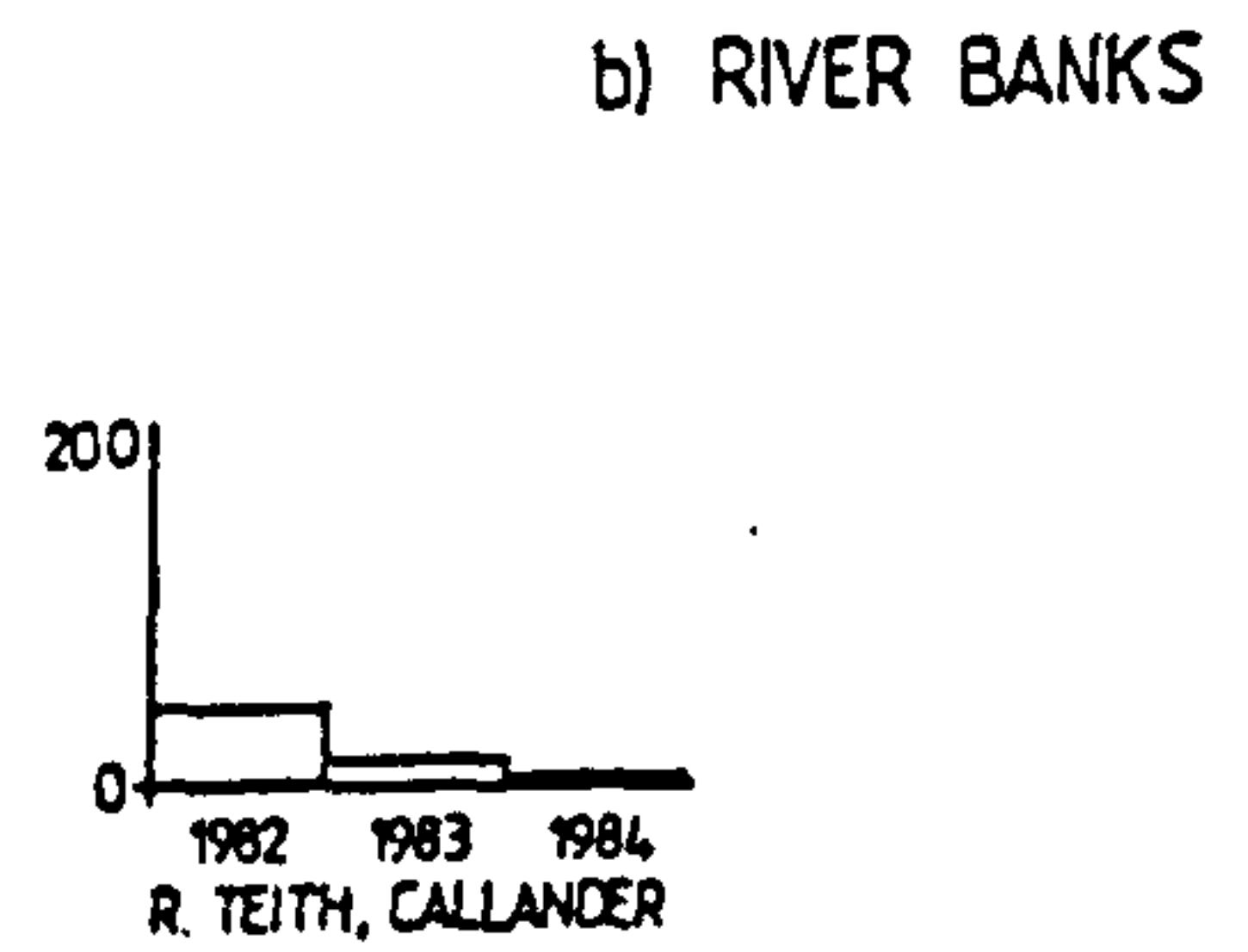
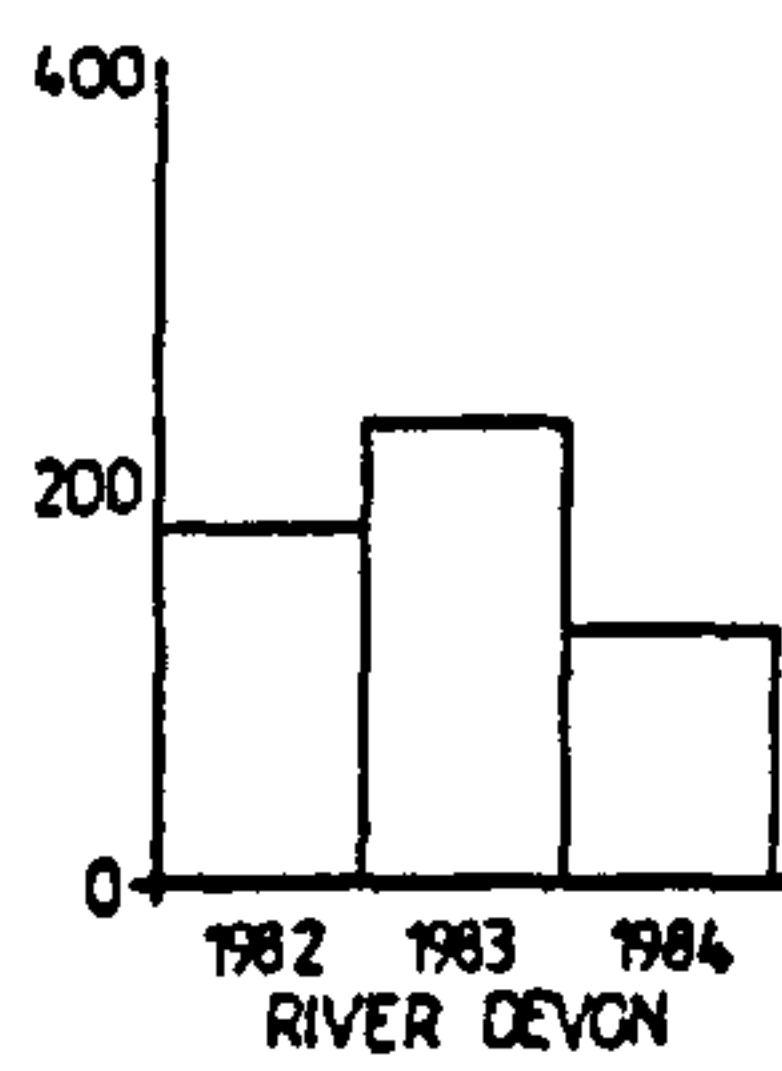
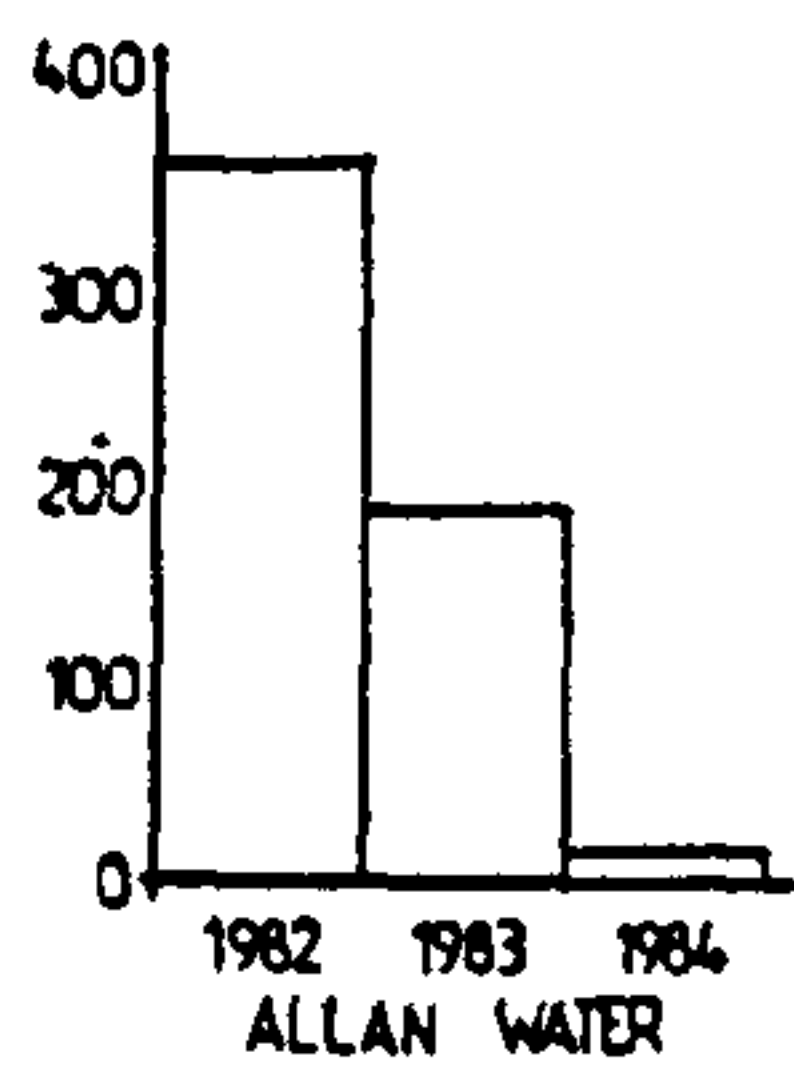
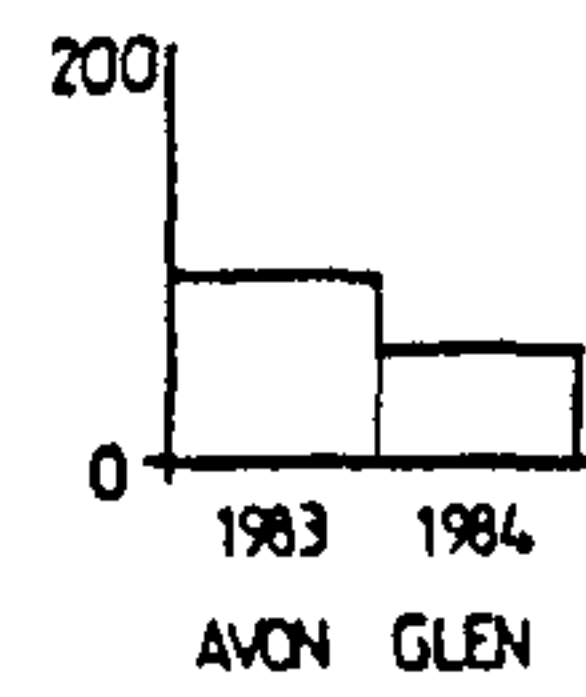
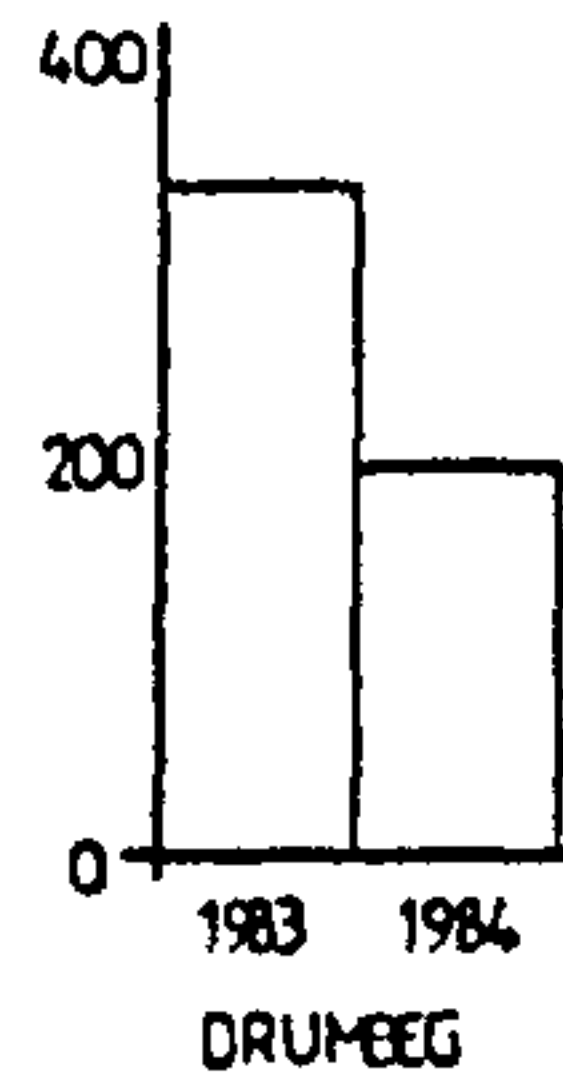
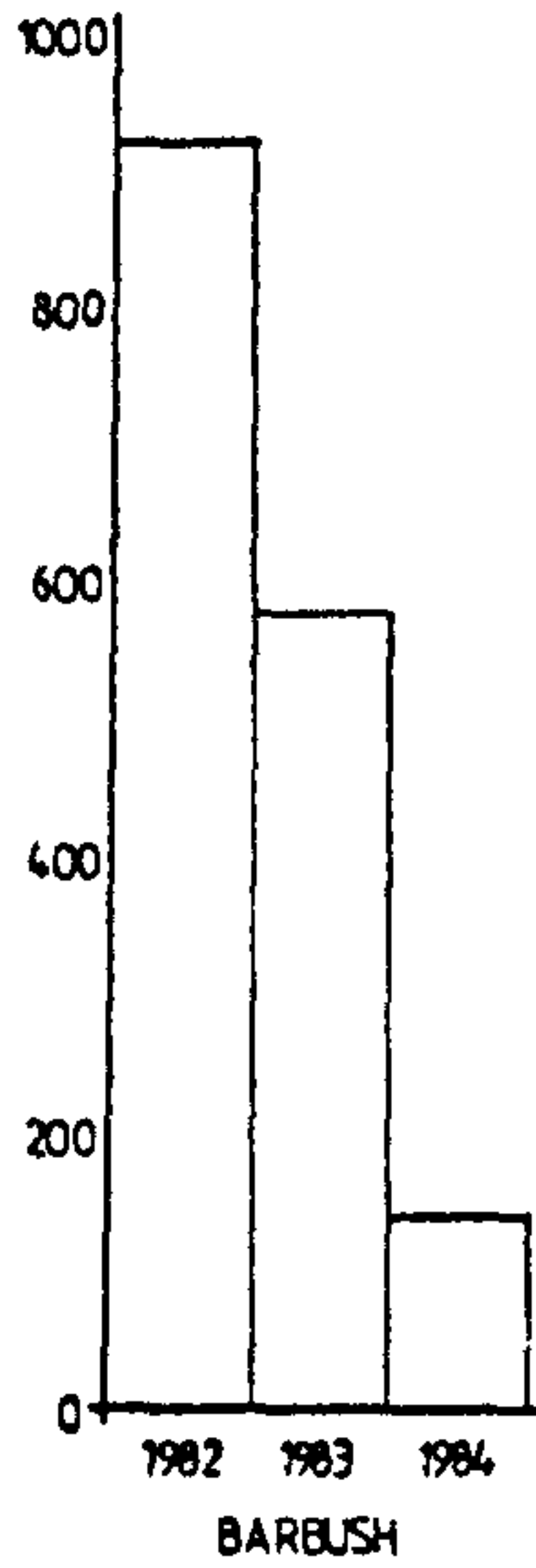
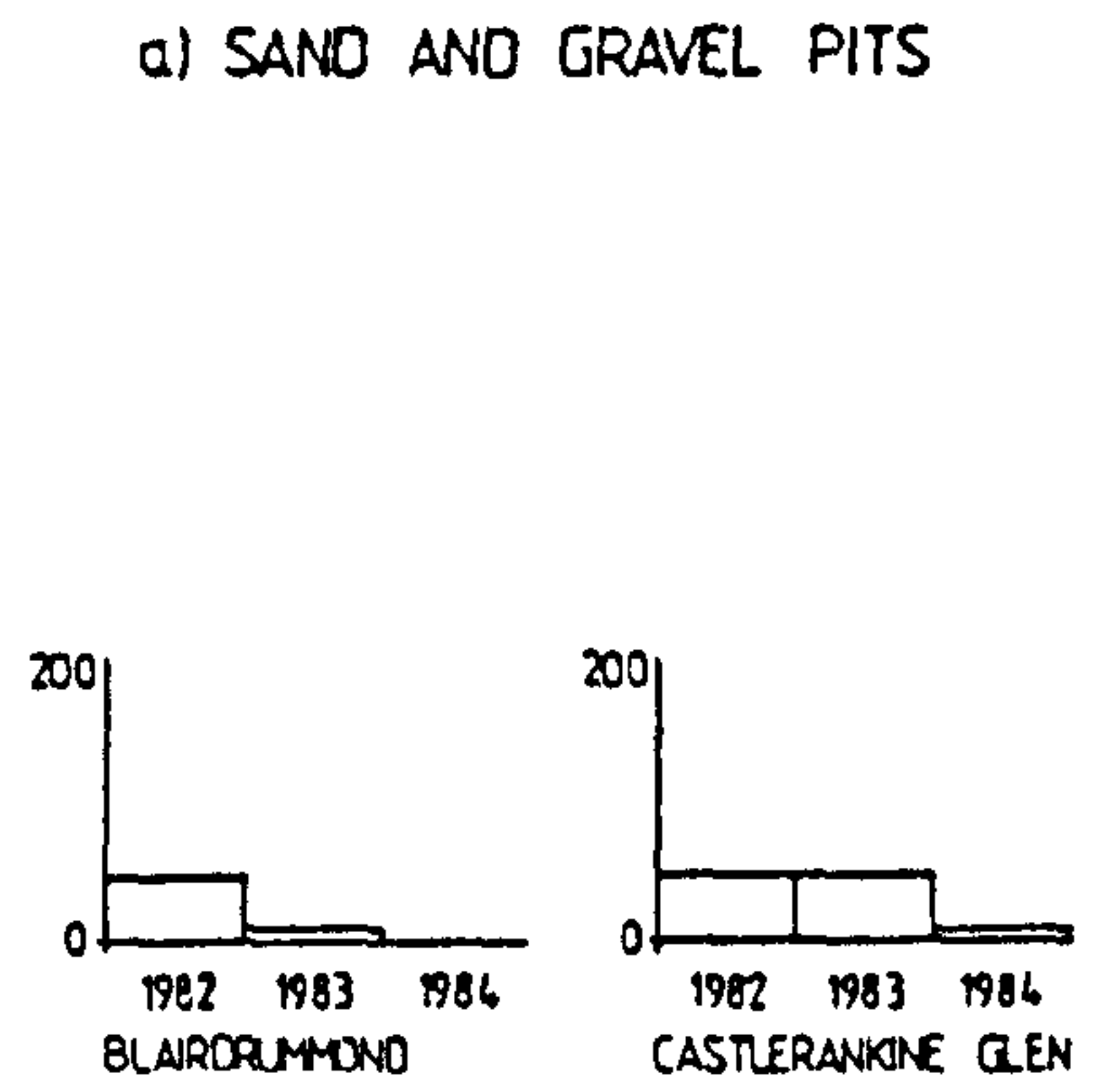
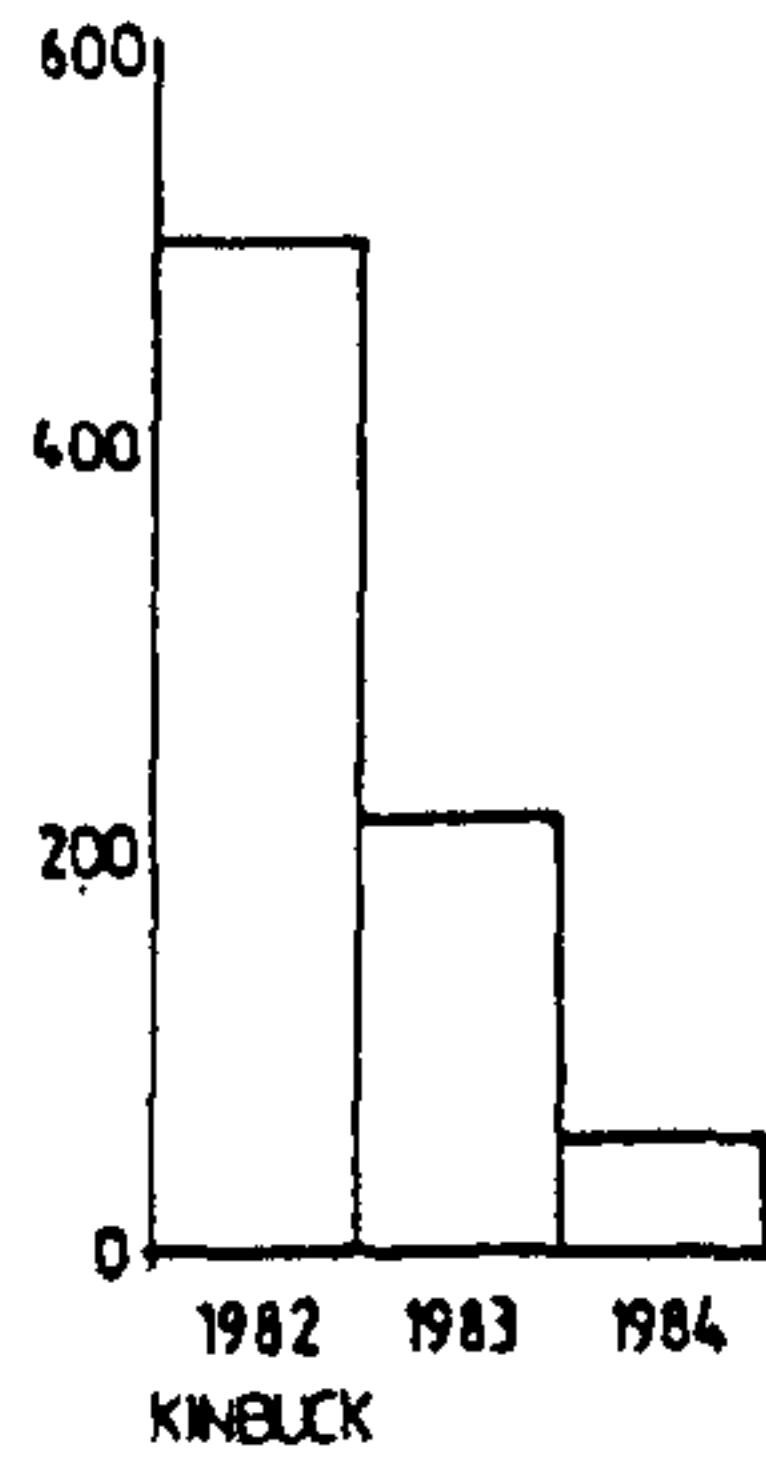
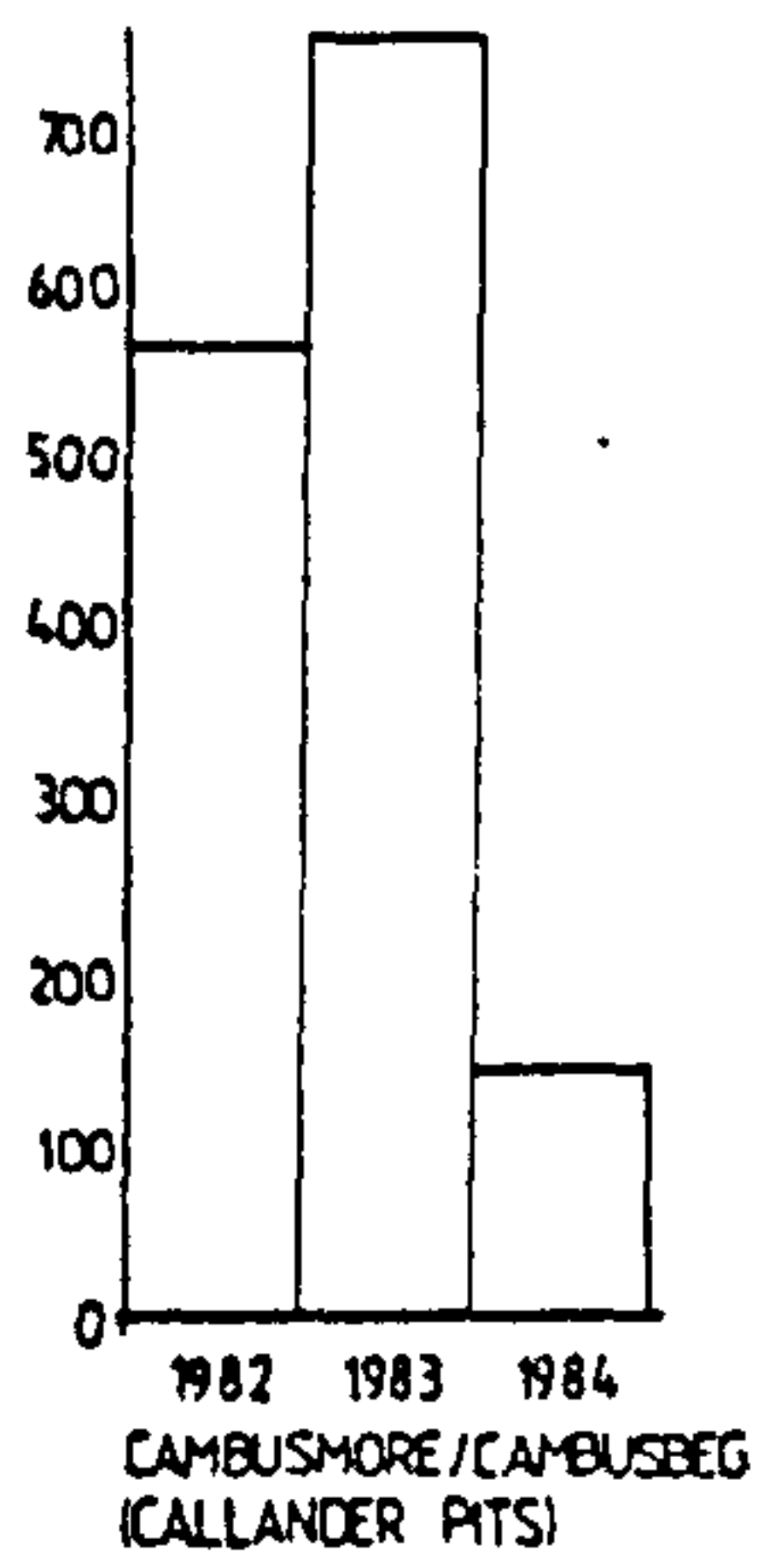


Figure 2.5

Sand martin burrow counts 1982-1984.

(a) Artificial sites

(b) Natural sites

and 1983, one remained the same size, and two increased in size. All eight sites were reduced in size between 1983 and 1984, as were the other two artificial sites included in Figure 2.5.

Combined data for the eight sites during each of the three years is plotted in Figure 2.6. Similar trends occur in natural and in artificial sites. In artificial sites, 1983 numbers were 76.5% of 1982 numbers, while 1984 numbers were 21.7% of 1983 numbers, 16.6% of 1982 numbers. For natural sites, 1983 numbers were 74.7% of 1982 numbers, the 1984 count was 36.7% of the 1983 total, 27.4% of the 1982 count. Hence, overall, for the eight natural and artificial sites combined, sand martin burrow numbers in 1983 were 76% of the 1982 total, while numbers in 1984 were 24.9% of 1983 numbers, and only 18.9% of the 1982 total.

Mean colony size at the eight sites showed a significant decline between 1982 and 1984, and 1983 and 1984, though not between 1982 and 1983 as determined by a paired sample t-test (t 1982, 1983 = 1.26 ns; t 1983, 1984 = 2.47, $P < 0.05$; t 1982, 1984 = 2.76, $P < 0.05$, $n = 16$ in all cases).

Besides large colonies declining in size over the study period, five small sites became extinct, resulting in the loss of 73 burrows (see Appendix I for details). Although two small sites were established in 1983, these only accounted for 22 burrows.

2.3.2 Colonisation patterns of sand martins at the main study site

In this sub-section the manner in which sand martins settled at Barbush quarry is described. Population changes over the three year study period are covered, and an analysis is performed in sub-section 2.3.6 to determine whether the birds surviving the population crash

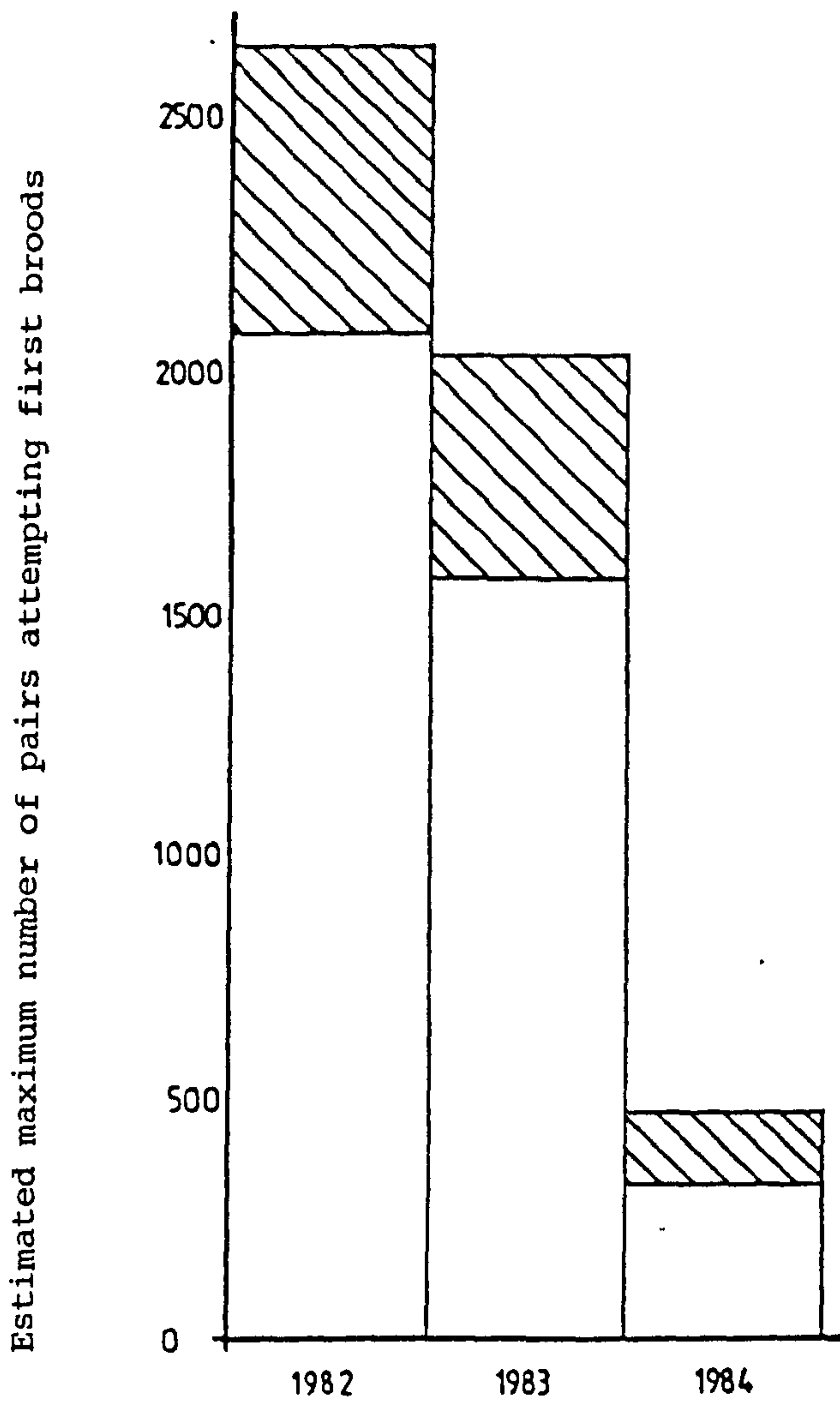


Figure 2.6

Sand martin burrow counts for eight sites combined, 1982-1984. Cross-hatched sections denote burrows in ^{natural} artificial sites.

of 1983-4 were morphologically different from the birds breeding at the colony in 1982 and 1983.

The estimated numbers of occupied burrows at Barbush over the seasons 1982-1984 inclusive are shown in Figure 2.7. About 55% of the 1982 number of pairs probably settled at Barbush in 1983, while 1984 numbers were 27% of the 1983 counts, 15% of the 1982 count. Hence the Barbush colony showed a decline in size over the three years of the study, especially between 1983 and 1984, as was shown by most other sites surveyed in the Stirling Region (section 2.3.1).

Figure 2.7 also shows that the settlement pattern of sand martins in each year is more or less linear between the date of first arrival until at least early June, and then reaches a plateau as most birds will have arrived by this time. The date on which the first birds arrived at the colony also varied by about 20 days over the study period, and was probably largely dependent on spring weather conditions over the migration route.

The Barbush colony was composed of several sub-colonies, which varied in distribution and number from year to year according to the distribution of sand extraction at the quarry. Nevertheless, one subcolony was present for all three years of the study, and was a relatively high, large and stable sand cliff no longer quarried and known as the 'main subcolony'. In each year the first birds to return to Barbush in Spring occupied the main subcolony, suggesting that it offered favoured breeding habitat, probably because of the cliff's stable composition, lack of disturbance and inaccessibility.

Colonisation patterns for the four largest subcolonies at Barbush in 1982 is shown in Figure 2.8. 1982 was particularly

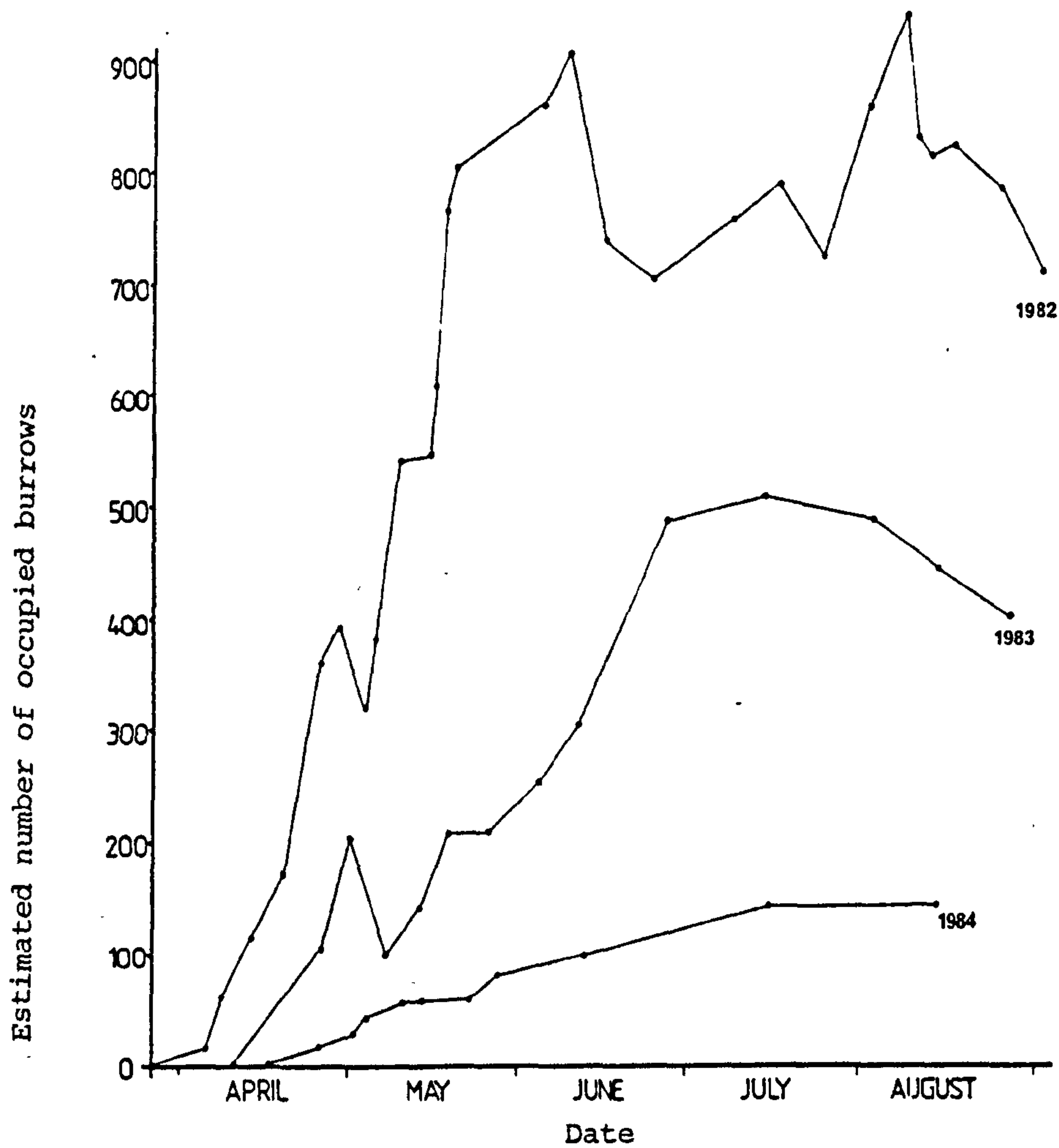


Figure 2.7

Seasonal changes in the estimated number of occupied sand martin burrows at Barbush, 1982-1984. Decreases often occurred as a consequence of sand cliff collapses.

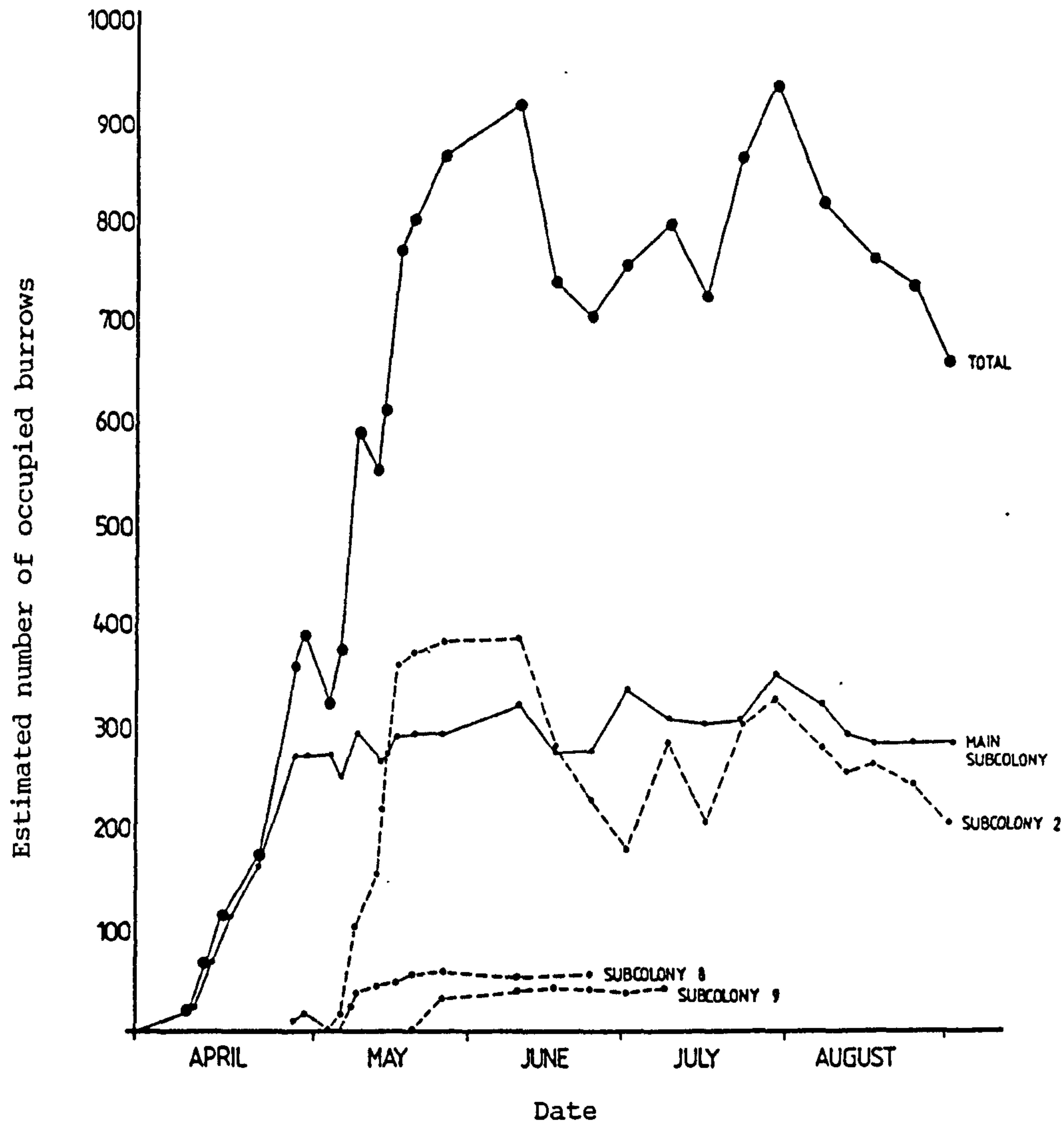


Figure 2.8

Colonisation patterns for the four largest sand martin subcolonies at Barbush in 1982.

favourable for an investigation of this type because all the previous year's burrows at the colony had been destroyed, so any burrows counted in 1982 were constructed during that year.

The 'main subcolony' was occupied by all birds arriving before the end of April. Subcolonies 2 and 8 were then utilized when the rate of colonisation in the main subcolony levelled off. When the settlement rate in subcolonies 2 and 8 reached a plateau, subcolony 9 was initiated. The first-settled sites are probably the most favoured subcolonies, so one of the benefits of early arrival may be access to the most favourable nesting sites.

To identify which birds occupied the 'main subcolony' an analysis of ringing retraps was performed.

In 1982, 251 adult sand martins, 58 fledglings, and 145 pulli were ringed at Barbush, and five birds were controlled, four of which were previously ringed at the colony. In 1983 25 birds were controlled, of which 22 were ringed at Barbush, and 19 were aged two years or older. One hundred and eighty four further adults, 74 fledged young, and 51 pulli were ringed. In 1984 22 birds of known age were controlled (including two first year birds), and a further 79 adults and 13 fledglings were ringed.

The cumulative patterns of ringing recoveries in 1983 and 1984 for birds of known age are shown in Figure 2.9. In both 1983 and 1984 second year or older birds were captured before first year birds. In 1983 the earliest first year bird was captured on 15th May, by which time seven second year or older birds had been controlled. An influx of first year birds probably occurred in the second half of May, with six controls in two weeks. In 1984 the earliest first year

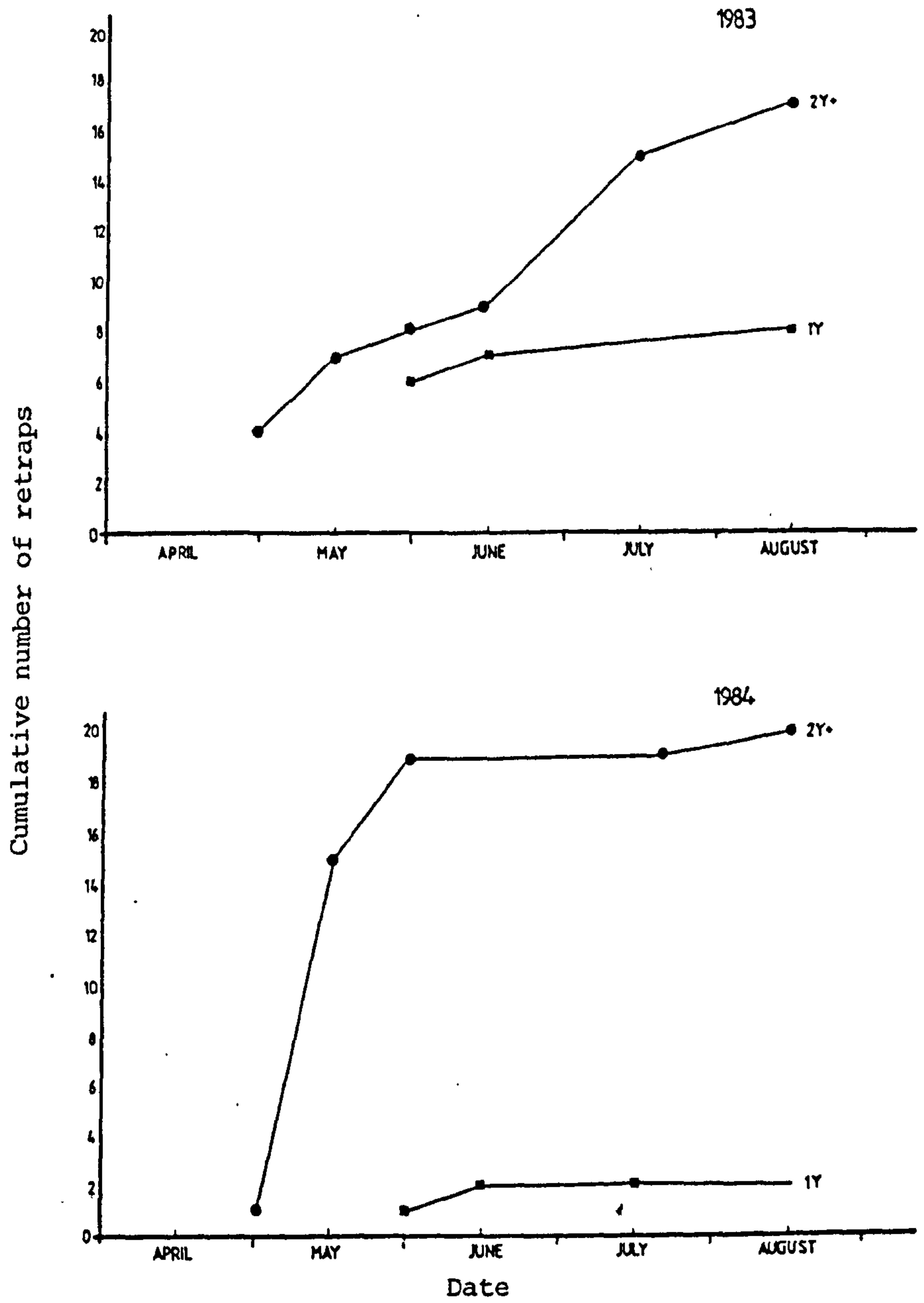


Figure 2.9

Recapture rates for sand martins of known age at Barbush in 1983 and 1984.

1Y : first year birds

2Y+ : second year or older birds

bird was controlled on 16th May, by which time 16 second year or older birds had been controlled. An influx of second year or older birds probably occurred in the first fortnight of May 1984, with 15 controls in two weeks. In 1984 the date of first arrival at the colony was later than in 1983 (Figure 2.7). Mead and Harrison's (1979a) large scale analysis of sand martin ringing recoveries showed that older birds normally arrived 2-3 weeks before first year individuals.

In 1984 all 20 second year or older birds controlled were captured at the main subcolony, even though this subcolony contributed only a half of all burrows present. In 1983 eight of 19 second year or older birds (42%) were controlled at the main subcolony, while all of six first year birds were controlled in subcolonies other than the main subcolony. Thus older birds, returning to the colony at a relatively early date, are likely to have the largest choice of subcolony.

2.3.3 Some aspects of the breeding biology of sand martins

In 1982 some measurements of the breeding biology of sand martins were made at Barbush. Mean clutch size was 4.38 ± 1.39 ($n = 13$). This is slightly lower than the mean for northern Britain given by Morgan (1979) because all data was collected from a subcolony which was colonised at a relatively late date, probably by late arriving, young birds. Clutch size decreases as the breeding season progresses and increases with adult age in house martins (Bryant, 1979).

In 1982 the mean brood size from nests examined over the entire colony was 3.65 ± 0.95 ($n = 49$), close to the mean value of 3.58 for northern Britain (Morgan, 1979).

The seasonal trend in brood size is plotted in Figure 2.10 for broods aged 7-17 days. Sand martins are often double brooded (Morgan, 1979; Cowley, 1983), and the data illustrated in Figure 2.10 is consistent with a seasonal decline in brood size within both first and second broods. Such a trend also occurs in swallows (McGinn and Clark, 1978).

The timing of laying for 58 nests at one subcolony in 1982 is shown in Figure 6.2 (subcolony 2 in Fig. 2.8). The first egg date distribution was bimodal, with peaks in early June and over most of July. Several of the late clutches laid in late July and early August were later deserted when chicks were in the nest. The bimodal distribution of first egg dates is consistent with Morgan's (1979) analysis of sand martin nest record cards, though the second first egg date peak at this subcolony contained a higher percentage of the total distribution and was more prolonged than in Morgan's analysis.

2.3.4 Predators and parasites of sand martins

Adult sand martins at Barbush were often pursued by sparrowhawks (Accipiter nisus), and on two occasions pursuit resulted in successful capture for the hawk. All other observed predation was directed at well developed youngsters at burrow entrances. Sparrowhawks, kestrels (Falco tinnunculus) and crows (Corvus corone) were seen to successfully predate such young. Black-headed gulls (Larus ridibundus) were the most persistent visitors to burrows, however, and were seen to capture young martins on at least five occasions, often attempting to pull chicks from burrow entrances. The nestlings were then carried away by the gulls, and one young martin retrieved from a flying gull was found to be dead. There appears to be no previous published record of black-headed gulls as active sand martin

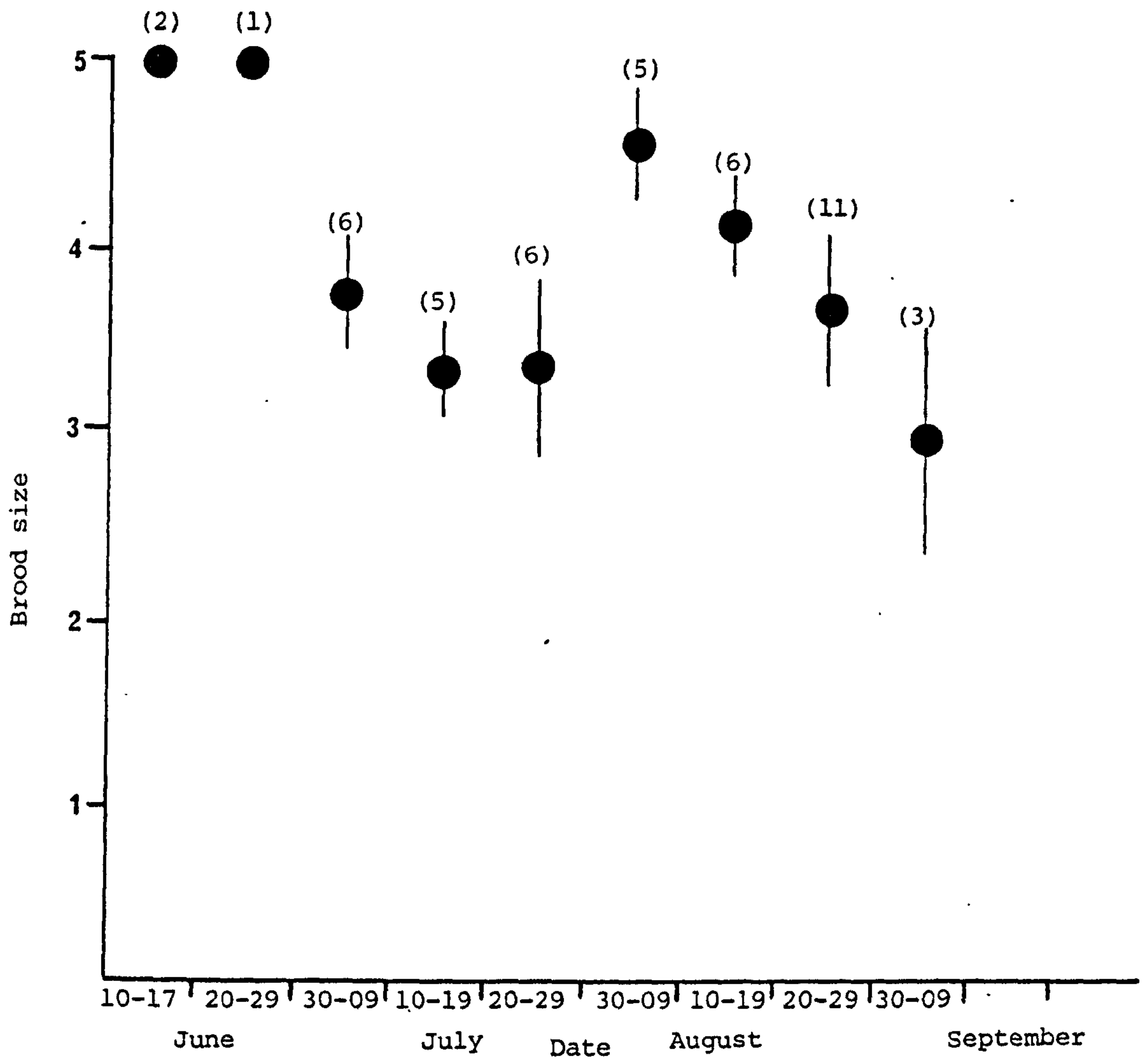


Figure 2.10

Seasonal trend in brood size for sand martins at Barbush, 1982. Broods aged 7-17 days are included (n = 49). Values plotted are means \pm sd, sample sizes in brackets.

predators (as opposed to scavengers) (Mead and Pepler, 1975), though at Barbush they appeared to be the most successful avian predator.

Mink (Mustela vison) tracks were often found on colony faces, and other potential mammalian predators observed at Barbush were weasels (M. nivalis) and stoats (M. erminea). With such a range of predators, there is likely to be intense selection for sand martins to choose subcolonies for nesting where predator accessibility is minimised.

A stuffed sparrow hawk and stoat presented to birds at the colony were persistently mobbed. All of the avian predators listed above were normally mobbed by the martins, as were weasels, stoats, and even occasionally rabbits (Oryctolagus cuniculus) which had burrows nearby.

Parasites present at the colony included hippoboscid flies (Sterepteryx hirundinis), sand martin ticks (Ixodes lividus), sand martin fleas (Ceratophyllus styx) and feather lice (Mallophaga). Up to 800 fleas were counted at a single burrow entrance.

2.3.5 Morphometrics of sand martins at Barbush

(a) Body mass

The body mass of sand martins varied according to the stage of the breeding cycle, the time of day, body size, sex, and food availability.

Variation attributable to the stage of the nesting cycle is described in Chapters 5 and 6. Histograms of evening body masses over the three years of the study for 172 females and 92 males of known wing-length and keel-length are presented in Figure 2.11. The heaviest male processed was 15.2g, birds heavier than this probably

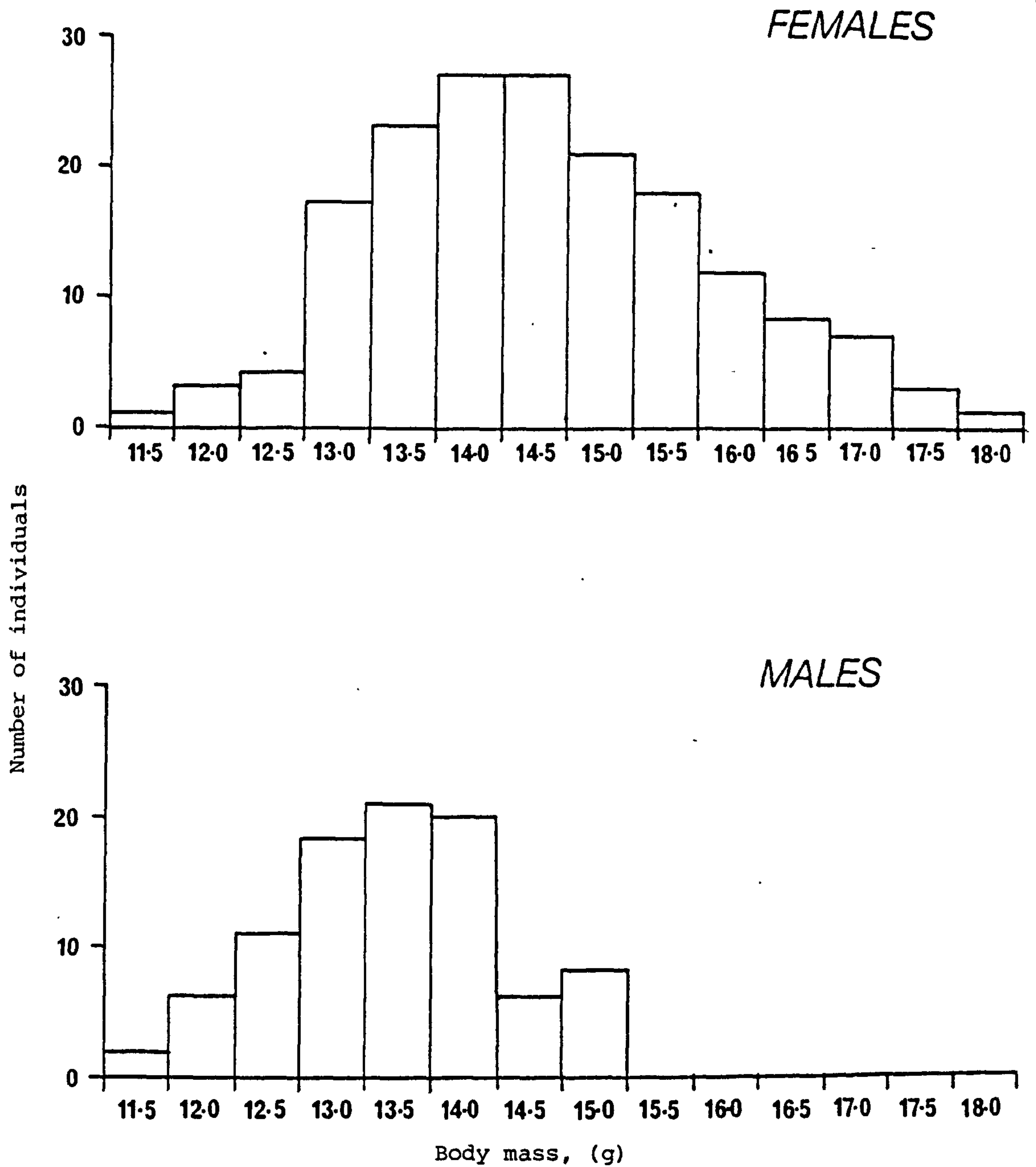


Figure 2.11

Frequency distributions of body mass for sand martins at Barbush, 1982-1984. Masses are only presented for birds of known wing-length and keel-length.

being laying or prelaying females. The heaviest female captured was 19.7g, but is not included on the histogram because no other morphological measurements were made on capture. Mean female evening body mass was 14.56 ± 1.28 g, mean male evening mass 13.43 ± 0.82 g, and the difference between means is statistically significant ($t = 7.68$, $P < 0.001$), probably because of the presence of heavy laying and prelaying birds in the female body mass distribution. The mass distributions were probably not representative of the colony as a whole because nestling-feeding adults which were light (Chapters 5 and 6) were under represented in the mist net catch. The mist nets tended to capture laying, incubating, or brooding birds which often remained in their burrows on approach.

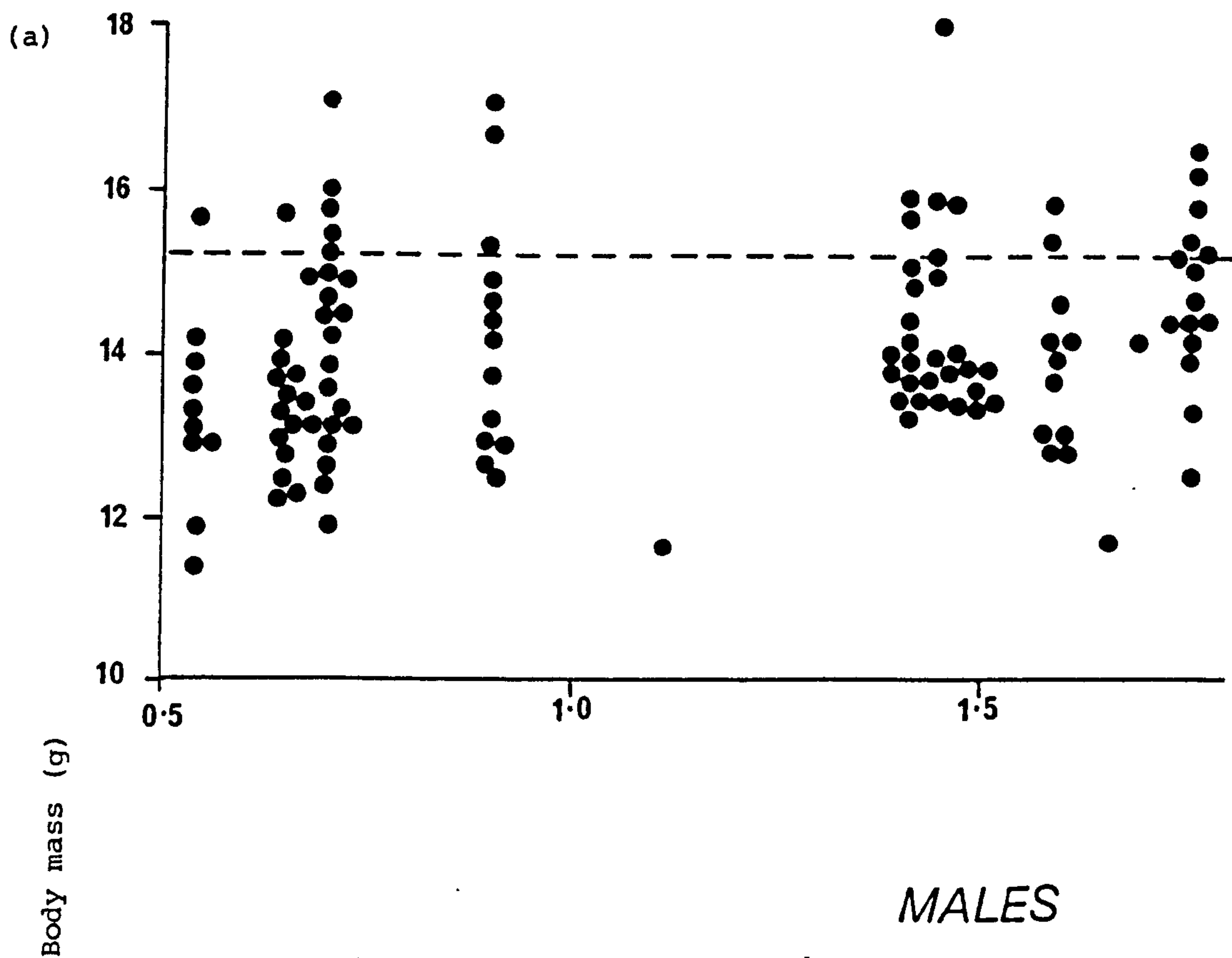
(i) Diurnal variation in body mass

The mean body mass of females captured at dawn was 13.77 ± 1.41 g ($n = 47$), compared with 14.56 ± 1.28 g for evening caught birds ($t = 3.83$, $P < 0.001$). The mean body mass of males handled at dawn was 12.82 ± 0.65 g ($n = 18$), compared with 13.43 ± 0.82 g for evening caught birds ($t = 2.97$, $P < 0.01$). Females caught at dawn are on average significantly heavier than males caught at dawn ($t = 2.74$, $P < 0.01$). Females tended to increase in average mass by 5.7% between dawn and evening, males by 4.8%.

(ii) Body mass and food availability

Evening body masses of 62 breeding male sand martins and 117 evening masses of breeding females during 1982 were related to food abundance as determined by the 12.2m suction trap (Chapter 3). The results are shown in Figure 2.12. Both sexes were heavier when food was more abundant. The correlation coefficient between male mass and food abundance was 0.33 ($P < 0.01$), and a similar significant positive correlation occurred with females ($r = 0.24$, $P < 0.01$).

FEMALES



MALES

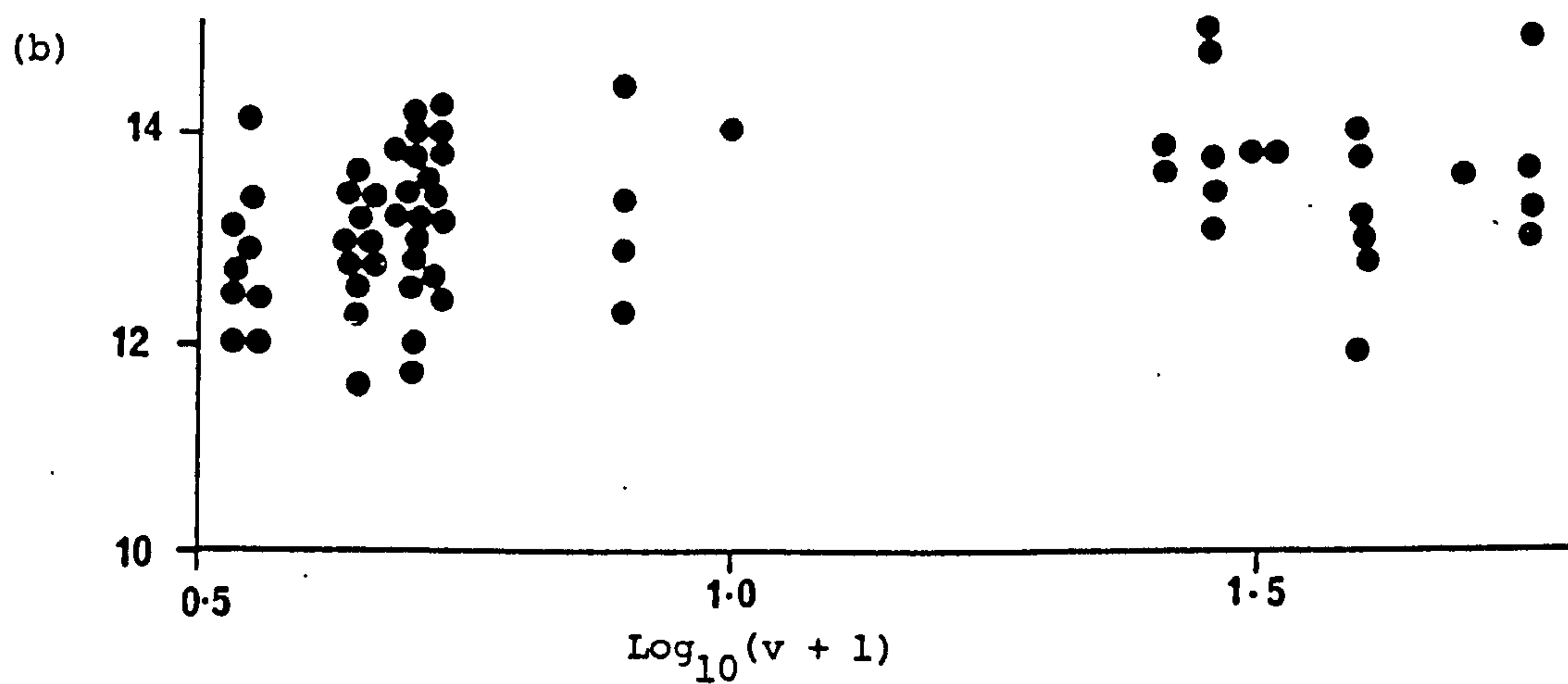


Figure 2.12

The relationship between body mass during the breeding season and food abundance as determined by the 12.2m suction trap.

(a) Females: $r = 0.24$, $P < 0.01$. The pecked line represents the mean mass of laying and pre-laying females.

(b) Males: $r = 0.33$, $P < 0.01$.

However, when birds arrived at the colony in Spring, they tended to be fat and heavy (Chapter 5) at a time when food was scarce (Chapter 3). Pre-breeding birds arriving at the colony during a period of low and unpredictable food availability are likely to carry substantial lipid reserves to buffer against food shortages. Moreover, birds are likely to fatten up in the autumn before migrating, as has been found in house martins (Bryant, 1975a).

(iii) Body mass and body size

Two potential measurements of body size were investigated in the study: wing-length (maximum chord, measured to the nearest 0.5 mm), and keel-length, measured to the nearest 0.1 mm. Correlation coefficients between body mass, wing-length, and keel-length for all birds, females only, and males only are presented in Table 2.1.

Body mass was significantly positively correlated with wing-length and keel-length for birds of both sexes combined and for females alone. Mass was significantly correlated with keel-length only in males. Wing-length was significantly positively correlated with keel-length when all birds were considered, but the correlation was lost when male or females are analysed in isolation.

Hence keel-length is probably a more reliable measurement of body size than wing-length since it correlates with body mass in both males and females, and correlation coefficients of mass/keel-length comparisons were greater or equal to those of mass/wing-length comparisons. Moreover, in a stepdown multiple regression analysis of body mass, taking keel-length and wing-length as independent variables, only keel-length entered as a significant variable (Table 2.2).

Table 2.1

Correlation matrices for body mass and morphometrics in sand martins

(a) males, females, and birds of undetermined sex, n = 423

	wing-length (mm)	keel-length (mm)
body mass (g)	0.11*	0.15**
wing-length (mm)		0.12*

(b) males only, n = 115

	wing-length (mm)	keel-length (mm)
body mass (g)	0.18 ns	0.21*
wing-length (mm)		0.09 ns

(c) females only, n = 220

	wing-length (mm)	keel-length (mm)
body mass (g)	0.14*	0.14*
wing-length (mm)		0.07 ns

Tabulated values are correlation coefficients, r.

ns : not significant

* : P < 0.05

** : P < 0.01

*** : P < 0.001

Table 2.2

Stepdown multiple regression analysis of morphometric determinants of body mass in sand martins

Analysis performed on 423 birds, males and females combined.

Independent Variable	r^2	Degrees of Freedom	Full Analysis			Abbreviated Analysis		
			Regression Equation	t	P	Regression Equation	t	P
keel-length, mm	2.3	1,421	$0.281x_1 +$	2.89	**	$0.303x_1 + 8.12$	3.13	**
wing-length, mm	3.1	2,420	$0.043x_2 + 4.01$	1.93	ns			
			F = 6.8			F = 9.8		
			P < 0.01 **			P < 0.01 **		

** : P < 0.01

Keel-length is also a better measurement of body size than wing-length in that it remains constant from year to year, and probably attains most of its maximum length at fledging or soon afterwards. (Chapter 5 shows no significant difference between the mean keel-length of samples of adults and fledglings.) Retrapped sand martins have been found to keep the same keel-length between years, whereas their wing-length increases with age (see below).

Histograms of keel-length and wing-length in male and female sand martins at Barbush between 1982 and 1984 are presented in Figure 2.13. There was no significant difference in mean keel-length between the sexes (male mean keel-length = 19.01 ± 0.63 mm (n = 125), females 18.95 ± 0.65 mm (n = 220), $t = 0.83$, ns), and mean wing-lengths were not significantly different between the sexes (male mean wing-length = 105.26 ± 2.73 mm, females 104.89 ± 2.68 mm, $t = 1.22$ ns).

The relationship of wing-length to age is shown in Figure 2.1~~3~~⁴, for average values of birds of known age, and for individuals measured in more than one year. Birds of known age and minimum known age are included in the same age class. The oldest bird controlled was four years or older.

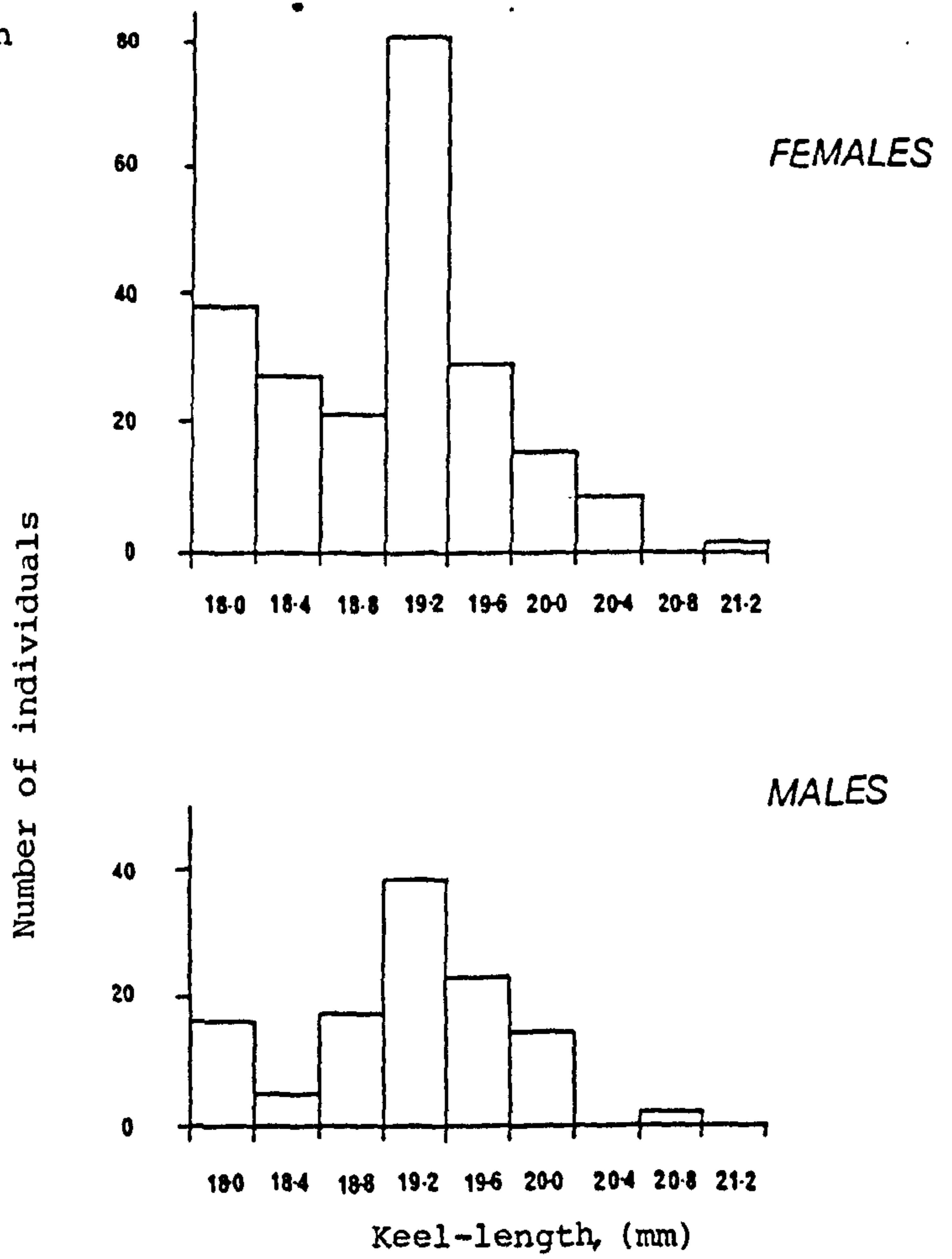
From both Figure 2.14a and b wing-length was shown to increase with age of the bird. The regression equation for wing-length as a function of age using the data in Figure 2.14a is wing-length (mm) = $104 + 1.28$ (age), $F = 6.3$, $P < 0.05$, $n = 46$, $r^2 = 12.4\%$.

In 20 out of 28 individuals controlled between years wing-length was found to increase with age, whilst in the remaining eight individuals, wing-length remained the same between years (Figure 2.14b).

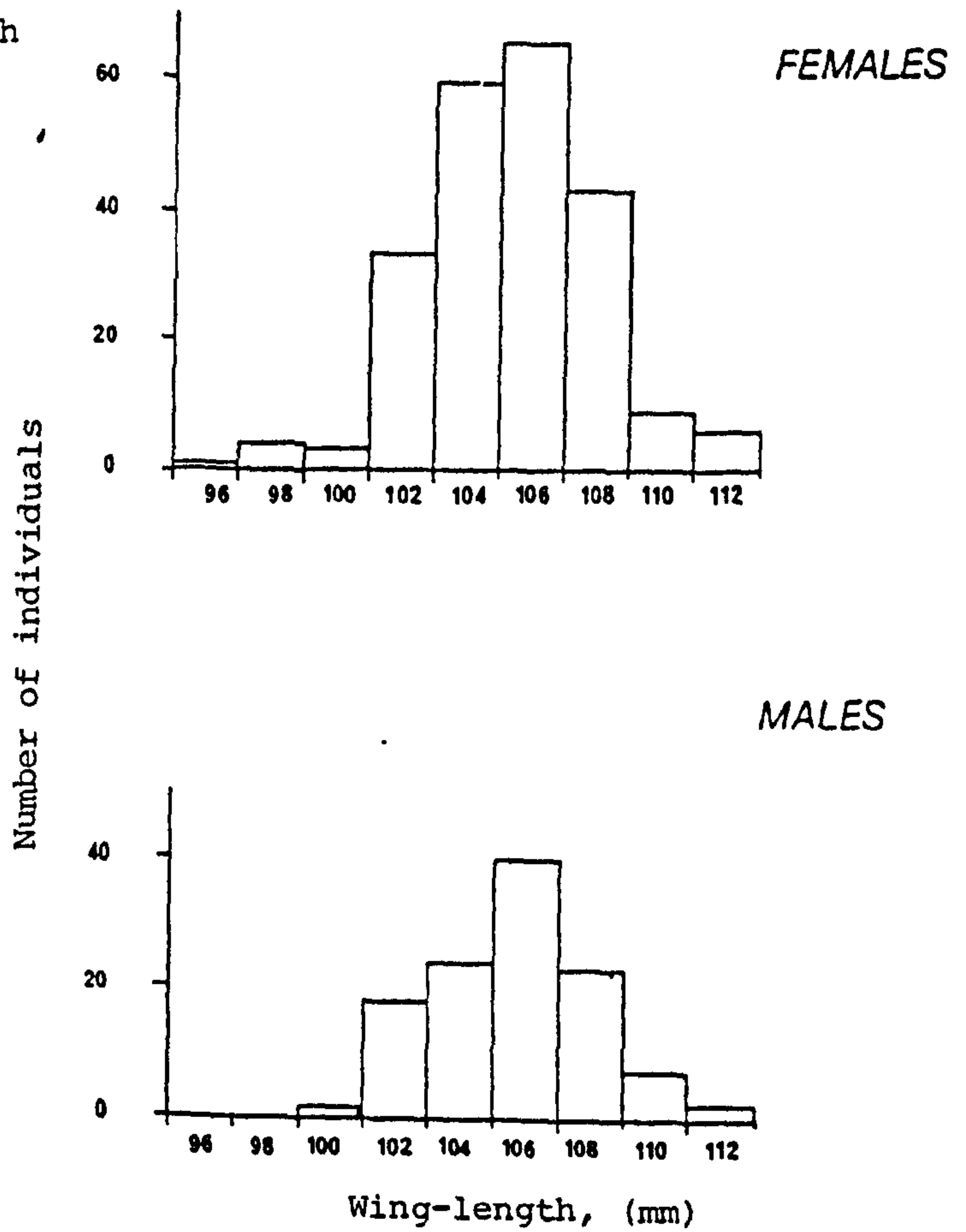
Figure 2.13

Frequency distributions of
(a) keel-lengths and
(b) wing-lengths
of male and female sand martins captured at
Barbush, 1982-1984.

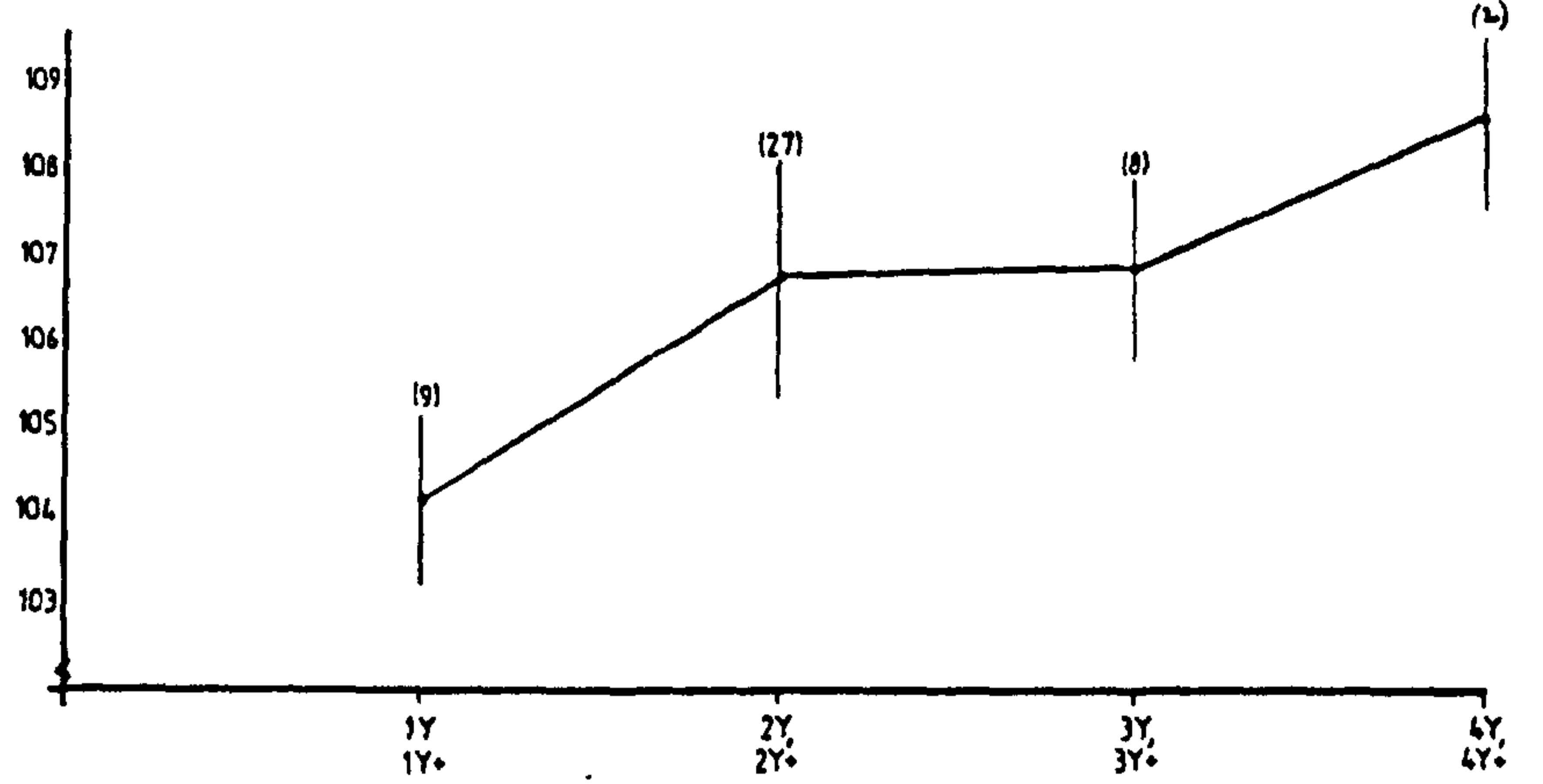
(a) Keel-length



(b) Wing-length



a)



b)

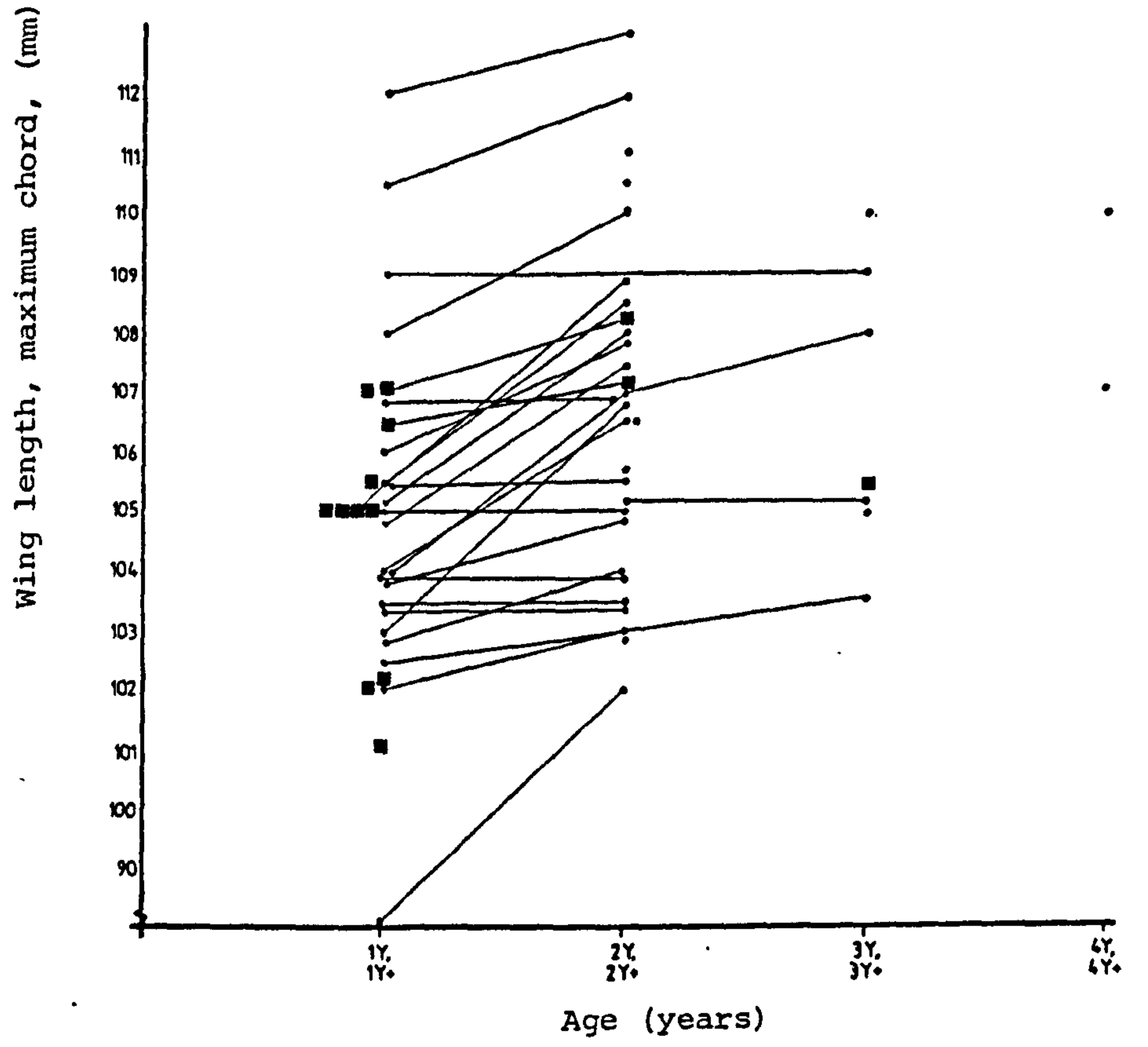


Figure 2.14

The relationship between wing-length and age in sand martins. Birds of minimum known age are included in the age classes.

- (a) Mean wing-length \pm sd for each age class.
- (b) Individuals trapped in two or more years.

Squares: birds of known age.

Circles: birds of minimum known age.

Hence wing-length is probably not a good indicator of body size in sand martins both because it is not consistently correlated with body mass, and wing-length varies according to the age of the bird.

2.3.6 Changes in sand martin morphometrics between years

Changes in sand martin mean wing-length and mean keel-length between years at Barbush were analysed in relation to changes in colony size. Separate analyses were performed on a sample of birds of both sexes combined and on males and females in isolation. Birds controlled in more than one year ($n = 47$) were included in the analysis for each year they were controlled.

(a) Wing-lengths

Differences in mean wing-lengths between years are presented in Table 2.3. Although mean wing-lengths of males were consistently longer than those of females, in no year was the difference large enough to be statistically significant. When data from birds of each sex were combined, mean wing-length was significantly shorter in 1982 than in both 1983 and 1984. There was no significant difference in mean wing-length between 1983 and 1984. The same significant trends seen in the combined sample of males and females occurred when females were considered in isolation. However, mean male wing-lengths were not significantly different between any of the years considered.

The mean increment in wing-length of 10 birds recaptured in 1983 and ringed in 1982 was 2.15 ± 1.40 mm. Of these, only one (10%) maintained an unchanged wing-length between years, all other birds returned with increased wing-length. The mean increment in wing-length for 17 birds controlled in both 1984 and 1983 was 1.09 ± 1.31 mm. Of these, 6 (35%) had not changed in wing-length, all other birds returning with increased wing-length. The difference in mean wing-

Table 2.3

Changes in mean wing-length of sand martins at Barbush 1982-1984

Analysis 1

There was no significant difference between the means of male and female wing-length (Fig. 2.14): $t = 1.22$, ns. Therefore combine data for males and females and birds of undetermined sex ($n = 423$).

<u>Year</u>	<u>Wing-length (max. chord) mm, $\bar{x} + sd$ (n)</u>
1982	104.43 + 2.58 (162)
1983	105.53 + 2.93 (165)
1984	105.58 + 2.48 (96)

t-tests:

	<u>1983</u>	<u>1984</u>
1982	3.61***	3.50***
1983		0.14 ns

Analysis 2

Using birds of known sex ($n = 335$, 220 females, 115 males).

	Wing-length		<u>t</u>	<u>P</u>
	<u>females $\bar{x} + sd$ (n)</u>	<u>males, mean + sd (n)</u>		
1982	104.29 + 2.56 (93)	104.77 + 2.67 (63)	1.13	ns
1983	105.19 + 3.04 (77)	105.88 + 2.74 (32)	1.11	ns
1984	105.57 + 2.02 (50)	105.80 + 2.71 (20)	0.39	ns

t-tests:

	Females		Males	
	<u>1983</u>	<u>1984</u>	<u>1983</u>	<u>1984</u>
1982	2.10*	3.06**	1982 1.90 ns	1.50 ns
1983		0.78 ns	1983	0.01 ns

ns : not significant; * : $P < 0.05$, ** : $P < 0.01$, *** : $P < 0.001$.

length increment over the two seasons was not statistically significant ($t = 1.98$).

Cowley (1979) attributed a decrease in the mean wing-length of sand martins after a population crash to decreased feather growth during moult in a Sahel drought. The present results suggest that differences in wing-length between years are more likely to reflect differences in the age structure of the colony between years, rather than differences in body size between years, since wing-length is not always a good predictor of body mass (Tables 2.1, 2.2), and wing-length increases with age (Figure 2.14). The significantly longer mean wing-length in 1983 and 1984 compared with 1982 may indicate increased levels of mortality in young birds during 1982-1983 and 1983-1984 compared with 1981-1982. Juvenile mortality has been shown to be very high during the population crash of 1968-1969 (Mead, 1979).

(b) Keel-lengths

Differences in mean keel-lengths between years are presented in Table 2.4. There was no significant difference in mean keel-length between 1982 and 1983 when data for both sexes were combined. However, there was a highly significant reduction in the mean keel-length of birds captured in 1984 compared with birds measured in both 1982 and 1983. Similar significant trends as those seen in the combined sample of males and females occurred when females were considered in isolation. No significant differences in male mean keel-length existed between years, although the trends were the same as in females. The sample sizes of males measured in 1983 and 1984 were small, however, totalling only 52 birds in two years. Frequency distributions of keel-lengths for each year are presented in Figure 2.15. For each graph, the most frequent keel-length class remained the same

Table 2.4

Changes in mean keel lengths of sand martins at Barbush 1982-1984

Analysis 1

There was no significant difference between the means of male and female keel-lengths (Fig. 2.14): $t = 0.83$ ns, $n = 220$ females, 115 males.

Therefore combine data for males, females, and birds of undetermined sex ($n = 423$).

<u>Year</u>	<u>Keel-length mm, mean \pm sd, (n)</u>	
1982	18.99 \pm 0.70	(162)
1983	19.06 \pm 0.58	(165)
1984	18.76 \pm 0.54	(96)
<u>t-tests</u>		
	<u>1983</u>	<u>1984</u>
1982	0.99 ns	2.77**
1983		4.13***

Analysis 2

Using birds of known sex ($n = 335$, 220 females, 115 males).

<u>Year</u>	<u>Females, $\bar{x} \pm$ sd, (n)</u>		<u>Males, mean \pm sd, (n)</u>		<u>t</u>	<u>P</u>
1982	18.99 \pm 0.73	(93)	18.99 \pm 0.67	(63)	0.00	ns
1983	19.04 \pm 0.57	(77)	19.14 \pm 0.61	(32)	0.82	ns
1984	18.74 \pm 0.55	(50)	18.87 \pm 0.50	(20)	0.92	ns
<u>t-tests</u>						
	<u>Females</u>		<u>Males</u>			
	<u>1983</u>	<u>1984</u>	<u>1983</u>	<u>1984</u>		
1982	0.19 ns	2.12*	1982	1.06 ns	0.74 ns	
1983		2.94**	1983		1.66 ns	

ns : not significant; * : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$

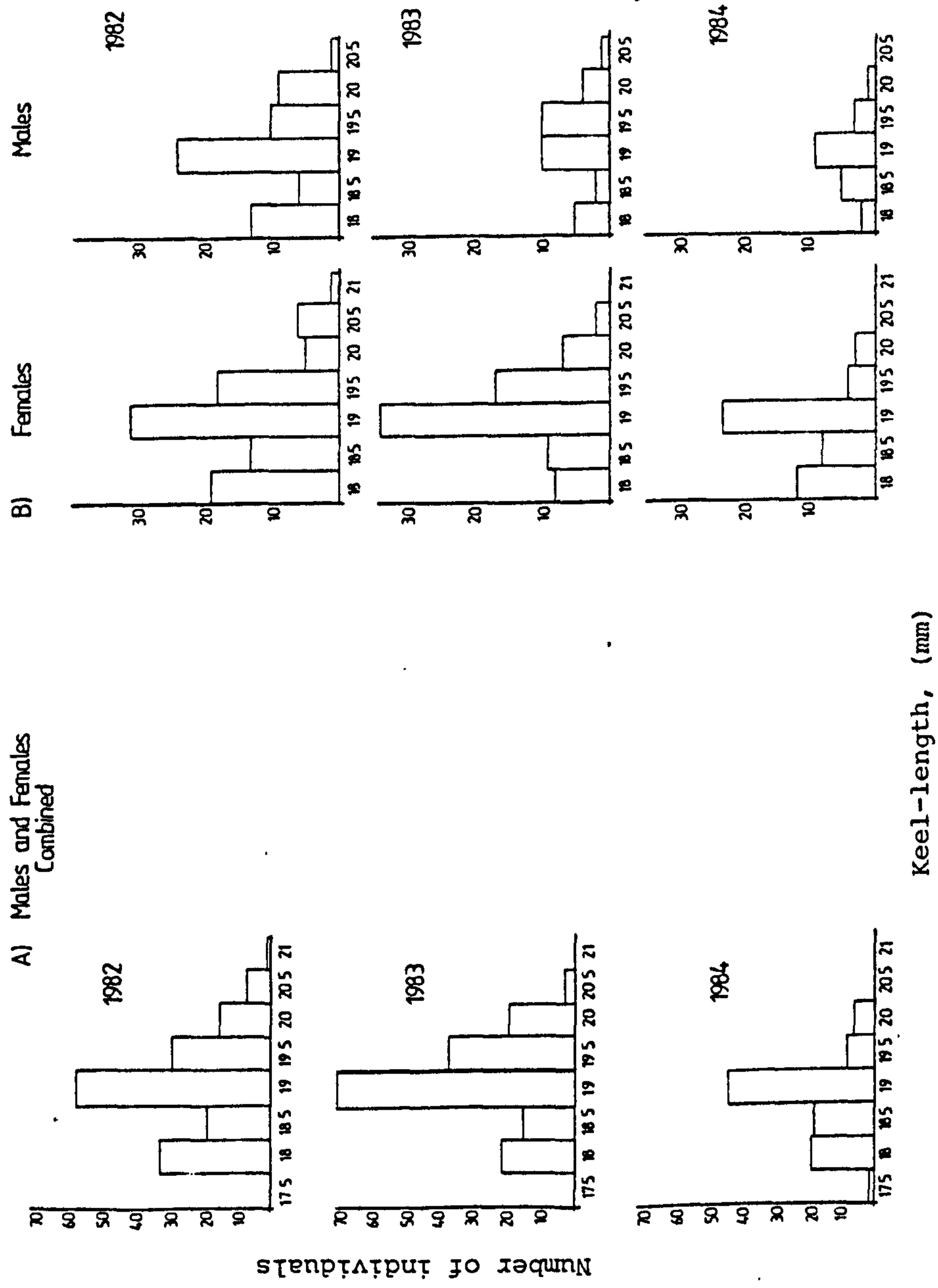


Figure 2.15

Frequency distributions of sand martin keel-lengths, 1982-1984.

(A) Males and females combined. (B) Male and female keel-lengths plotted separately.

(mid-interval 19 mm). Selection appeared to be acting against the biggest birds. In 1982 and 1983, ten of the 327 birds processed had keel-lengths greater or equal to 20.5 mm. By 1984 none of the 96 birds processed had keels this long. Moreover, in 1982, 32% of birds had keel-lengths longer than the modal class, compared with 35% in 1983, but only 15% in 1984.

2.3.7 Morphometrics and breeding biology measurements of swallows

Body size measurements of 54 swallows processed between 1978 and 1984 (including data of D.M. Bryant) is presented in Table 2.5. Although males captured were significantly lighter in body mass than females, males had significantly longer keel-lengths and wing-lengths.

Correlation matrices of body mass, keel-length, and wing-length for males, females, and both sexes combined (Table 2.6) show no significant correlations between variables for any groups considered. However, when body mass of incubating females measured by the precision electronic balance method at a standardised time of day was related to keel-length, a highly significant positive correlation existed (Chapter 7).

The mean clutch size of 58 swallow nests (including data of D.M. Bryant) was 4.66 ± 0.70 . The frequency distribution of swallow clutch sizes is shown in Figure 2.16. Modal clutch size was five, and clutches ranged in size from three to six eggs. The mean brood size from 40 nests was 4.28 ± 0.93 nestlings, and the mean number of fledglings raised from 19 nests was 4.11 ± 0.94 .

In 1982, 16 swallow nests were inspected at least once every other day. From 86 eggs, 81 chicks hatched, giving a hatching success of 94.2%. From 81 chicks hatched, 78 (96.3%) fledged successfully.

Table 2.5

Measurements of body size in swallows

	<u>Males</u> (n = 23)	<u>Females</u> (n = 31)	<u>t</u>	<u>P</u>	<u>Both sexes</u> (n = 54)
Body mass (g)	19.69 ± 1.50	21.66 ± 1.98	4.16	P < 0.001	20.82 ± 2.03
Keel-length (mm)	21.76 ± 0.89	20.95 ± 1.07	3.04	P < 0.01	21.30 ± 1.06
Wing-length (mm)	125.73 ± 3.00	124.00 ± 3.01	2.09	P < 0.05	124.74 ± 3.10

Table 2.6

Correlation matrices of swallow morphometrics

(a) Females: n = 31	body mass, g	keel-length, mm
	keel-length, mm	0.32 ns
	wing-length, mm	0.22 ns
		-0.24 ns
(b) Males: n = 23	body mass, g	keel-length, mm
	keel-length, mm	0.07 ns
	wing-length, mm	0.30 ns
		0.10 ns
(c) Both sexes: n = 54	body mass, g	keel-length, mm
	keel-length, mm	-0.02 ns
	wing-length, mm	0.02 ns
		-0.03 ns

Tabulated values are correlation coefficients, r.

ns : not significant.

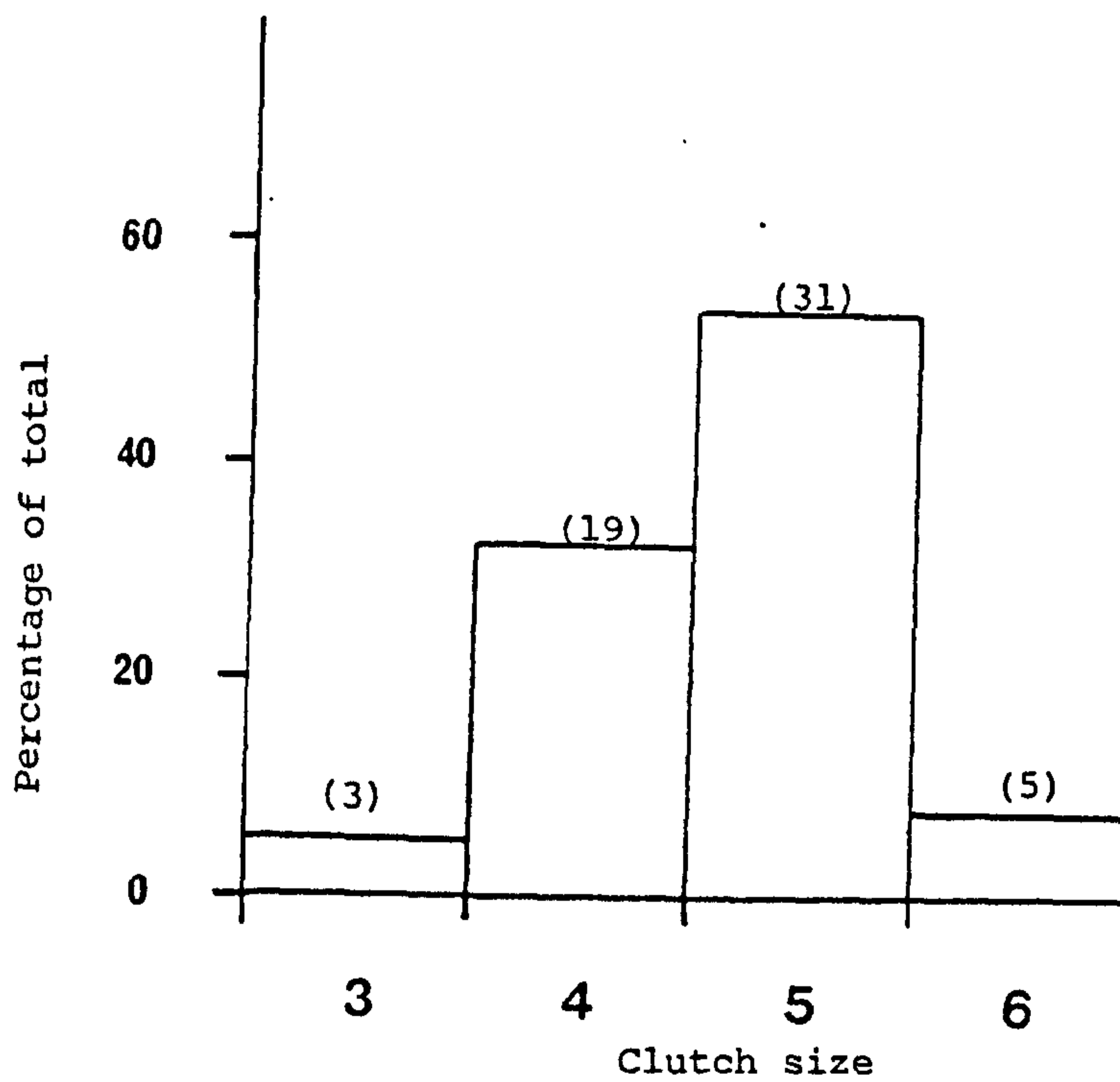


Figure 2.16

Frequency distribution of swallow clutch sizes over the study period.

Sample sizes in brackets.

Includes data of D.M. Bryant.

Of the three chick deaths recorded, only one was due to undernourishment, two others dying after falling from the nests. Hence hatching success and fledging success were very high in the swallows studied, and chick death from undernourishment was scarce. However, 1982 appeared to be a favourable year for swallow breeding, and breeding success may be lower in years of low food abundance.

Mean clutch size during the study was identical to that documented by McGinn and Clark (1978) for swallows nesting elsewhere in lowland Scotland.

2.4 DISCUSSION

2.4.1 The distribution, colonisation patterns, and population changes of the study population of sand martins

(a) Some costs and benefits of early arrival at sand martin colonies

Sand martins arriving early in the season at Barbush tended to be two years of age or older (Figure 2.9). The first arrivals at the colony will gain several benefits associated with the early season, but may also suffer some costs of early arrival. Some such costs and benefits will be described below.

Older birds returning to the colony early in the season will have a larger choice of nesting site than younger birds arriving later. Burrow numbers at Barbush subcolonies in 1982 tended to increase until a plateau was reached (Figure 2.8), the plateau probably corresponding to a burrow density above which interference between burrows or subcolony collapse may be precipitated.

Hence the best quality subcolonies will have limited burrowing sites, and early arriving birds will have first access to these sites. The 'main subcolony' at Barbush was the first subcolony to be occupied

during each of the three years of the study, and was probably favoured for three reasons:

- (a) The main subcolony sand cliff was high, steep, and hence relatively inaccessible to mammalian predators. Sieber (1980) found that sand martins nesting in the highest burrows in a colony suffered less predation by a beech marten (Martes foina).
- (b) The subcolony was no longer quarried and hence suffered little human disturbance during the breeding season.
- (c) The subcolony consisted of firm, compacted sand which was relatively stable and resistant to collapse.

Hence it seems likely that the older birds which returned early colonised the best quality subcolony until its density reached a level where it became more profitable for birds to settle elsewhere. Colonisation patterns probably follow a model similar to those developed for territoriality and breeding density by Brown (1969) and Fretwell (1972). Territoriality itself is unlikely to limit the number of sand martins settling in particular subcolonies, though there is likely to be a subcolony burrow density above which the probability of interference between burrows or subcolony collapse is high. A model of sand martin subcolony settlement patterns modified from Brown's (1969) theory of the effect of territoriality on breeding density is presented in Figure 2.17.

It is assumed that three subcolonies are available for settlement at a sand martin subcolony. Subcolony 1 is the highest quality subcolony, and could be likened to the 'main subcolony' at Barbush. Subcolony 1 is colonised until a critical burrow density ($*n_1$) is reached, whereupon birds would improve their reproductive success by

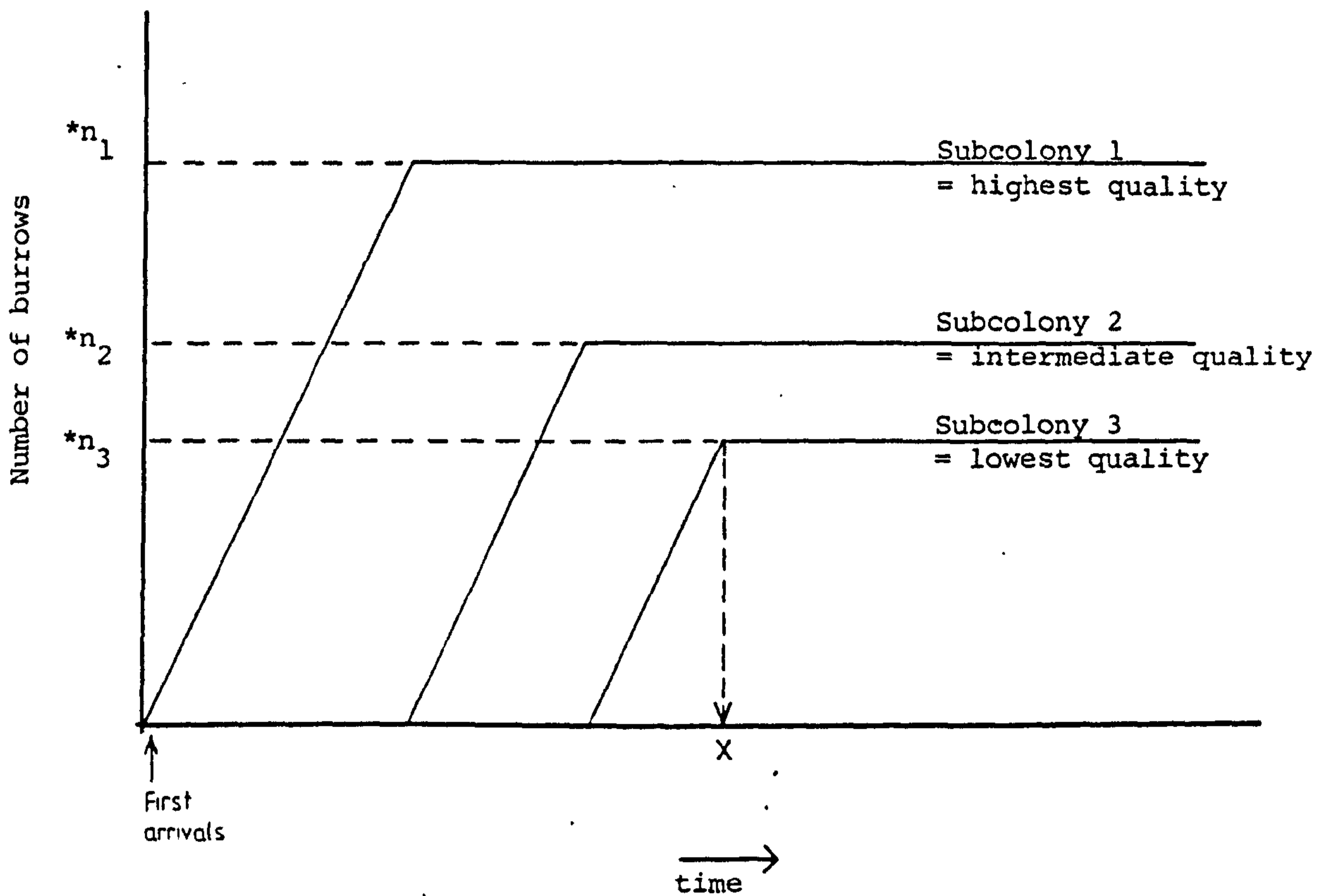


Figure 2.17

A model of sand martin colony settlement patterns.

See text for explanation.

n^* : critical burrow densities, above which birds improve their reproductive success by settling in another subcolony.

At X , birds which move to another colony have higher reproductive success than birds remaining to breed at the colony.

moving to subcolony 2. The critical density (n_c) is probably attained when the increased chances of burrow interference or subcolony collapse are likely to reduce the potential settler's likelihood of breeding successfully.

The second ranked subcolony, subcolony 2 is then settled to its critical density (n_{c2}). Although in Figure 2.17 $n_{c2} < n_{c1}$, n_{c2} could be greater or equal to n_{c1} , since inferior quality subcolonies may have a greater area available for burrowing than superior quality subcolonies. When the critical density of burrows in subcolony 2 is reached (n_{c2}), subcolony 3, the smallest and poorest quality site is colonised. When n_{c3} is attained, late arriving birds may increase their reproductive success by moving to another colony for nesting.

The model involves birds making similar decisions as to whether or not they join flocks of a given size (Sibly, 1983; Pulliam and Caraco, 1984), and can be tested through the prediction that nesting attempts in all subcolonies should be equally successful.

If all three subcolonies were of equal quality in terms of nesting habitat, the trend of sequential filling of subcolonies may still be observed. Critical burrow densities may then be determined by the number of pairs which optimises predator detection or maximises any benefits associated with social foraging for an individual.

In years of low population density most of a study population of Dutch titmice bred in mixed woodland, while in years of high population density some birds bred in pine woodland also (Kluijver and Tinbergen, 1953). Since titmouse reproductive success declines with density (Perrins, 1965), and in the Dutch study there was no

difference in reproductive success per pair in the two habitats, it is likely that individuals settled where they could expect the greatest reproductive success.

Glas (1960) showed that chaffinches Fringilla coelebs, settled in mixed woodland before pine woodland, and settled at a higher density in the former habitat. Sieber (1980) found that sand martin burrows excavated early in the season were higher up cliff faces than later ones, so martins may move to other subcolonies once a critical density of high altitude burrows is attained. Sieber's study also showed that birds settled in several subcolonies with increasing density, so that burrows were on average spaced 27-30 cm from each other.

Thus early arriving sand martins would be expected to settle in subcolonies which maximise their reproductive success, and the settlement patterns of early arriving, older birds will influence the manner in which later arriving, younger birds settle in subcolonies. Wheatear, O. oenanthe territories in which early breeding occurred were occupied in more breeding seasons than were territories where late breeding occurred and such territories were occupied by older males and were the first territories to be settled in at the start of the breeding season (Brooke, 1979).

Early arriving sand martins may also be able to renovate old burrows from the previous season, rather than spending time excavating new ones. However, the use of old burrows may carry a cost of a higher rate of ectoparasitism or chance of collapse. On May 9th, 1983, 34 burrows at the main subcolony, a site which contained a maximum of 350 burrows the previous year, had a mean number of 112 ± 155 sand martin fleas, Ceratophyllus styx, at their

entrance. Twenty-eight burrows at a newly established subcolony examined on the same date each had no fleas at their entrances.

Other parasites such as hippoboscids flies, Stenepteryx hirindinis, are also likely to be present in greater numbers in previously used burrows, and hippoboscids may utilise 2.7% of a house martin brood's assimilated energy (S. Guy, unpubl.). Sanguinivorous mites reduce maximum nestling mass in purple martins, Progne subis, (Wayne Moss and Camin, 1970), and Ixodes mites feeding off the blood of sand martin chicks may exert a similar effect. Hence any benefit arising from reuse of a limited supply of old burrows is likely to be counteracted by a significantly increased ectoparasite cost.

Early arriving sand martins may be able to select high quality mates if birds of the opposite sex also arriving early are of the best quality. Early nesting pairs may also rear larger broods: brood size appears to decrease over the season within first and second broods (Figure 2.10), though to what extent this is due to less experienced birds laying smaller clutches later is not known. Probably more importantly, early arrivals may be more likely to rear two broods in a season than later arriving birds. In 1983 subcolony 'NS' was not colonised until 19th May, and no second broods were raised here. Conversely, the 'main' subcolony was first colonised on 20th April, and most pairs there appeared to rear two broods.

Late breeding may also reduce the survival prospects of the fledglings. In great tits, young fledged late in the season have a lower chance of surviving until the subsequent breeding season than earlier hatched chicks (Perrins, 1965). Second brood house martin

fledglings show higher overwinter mortality rates than youngsters from first broods (Rheinwald, Gutscher, and Hormeyer, 1976).

Early arriving sand martins will be interacting with few conspecifics, and so will experience the costs and benefits associated with small group size. Large groups of sand martins may be able to better exploit unpredictably distributed food patches than smaller groups (Emlen and Demong, 1975), though the advantages of social foraging in bank swallows is disputed (Hoogland and Sherman, 1976). Early arrivals may benefit from reduced competition for nesting materials, though pay the costs associated with increased susceptibility to predators with small colony sizes (Hoogland and Sherman, 1976).

The most significant cost to early arrivals is likely to be an increased probability of encountering prolonged periods of food shortage. Suction trap catches are often low in volume for long periods early in the season (Chapter 3), and sand martin mortality in Britain appears to be highest at this time (Mead, 1979). Hence early arrivals often carry large lipid reserves (Chapter 5), presumably to buffer against such food shortages, though must pay the energetic costs of carrying this extra mass during flight (Chapter 8). One benefit of late arrival by sand martins would be the avoidance of any increased mortality risks associated with low levels of food abundance early in the season.

(b) The distribution of sand martins in the Stirling Region and implications for conservation

The British Trust for Ornithology (B.T.O.) breeding bird survey of the 1970's recorded sand martins in 75% of 10 km squares in Britain, with confirmed breeding in 84% of these (Sharrock, 1976). The species was absent from large areas of south and east England where calcareous rock formations in places restrict the availability of breeding sites.

In 1982, when sand martin numbers were high in the Stirling Region, 81% of burrows surveyed were found in sand or gravel quarries. From an examination of sand martin B.T.O. nest record cards, Morgan (1979) found that 44.2% of colonies in southern Britain were in sand and gravel quarries, compared with 32.8% in northern Britain, suggesting a greater dependence on natural sites in northern Britain. 42% of sand and gravel pits surveyed in the B.T.O. Register of Ornithological Sites contained breeding sand martins (Fuller, 1982).

In the Stirling Region 60% of sites surveyed were found in artificial situations. The Stirling Region probably has more artificial colonies than most areas in Britain because its rivers often have low banks which are susceptible to flooding, and the area is rich in glacial sands and gravels so there are many opportunities for quarrying.

Colonies in sand and gravel quarries can be considerably larger than natural colonies: in 1982 the four sites with over 500 nests were all in sand quarries. Hence sand pits in the Stirling Region are not only the most frequently used sites for breeding by sand martins, they also hold the largest colonies. The compactness of sand in quarries will also probably influence the density of sand martins settling there: Sieber (1980) found higher burrow densities in less compact sand cliffs.

It is probable that the sand martin's dependence on sand quarries over much of Britain for breeding has led to a change in the distribution or abundance of the species over the past century. In Figure 2.18 the production of sand and gravel in Britain between 1900 and 1970 is plotted (from Catchpole and Tydeman (1975), based on the data of Archer (1972)). Sand and gravel output has increased

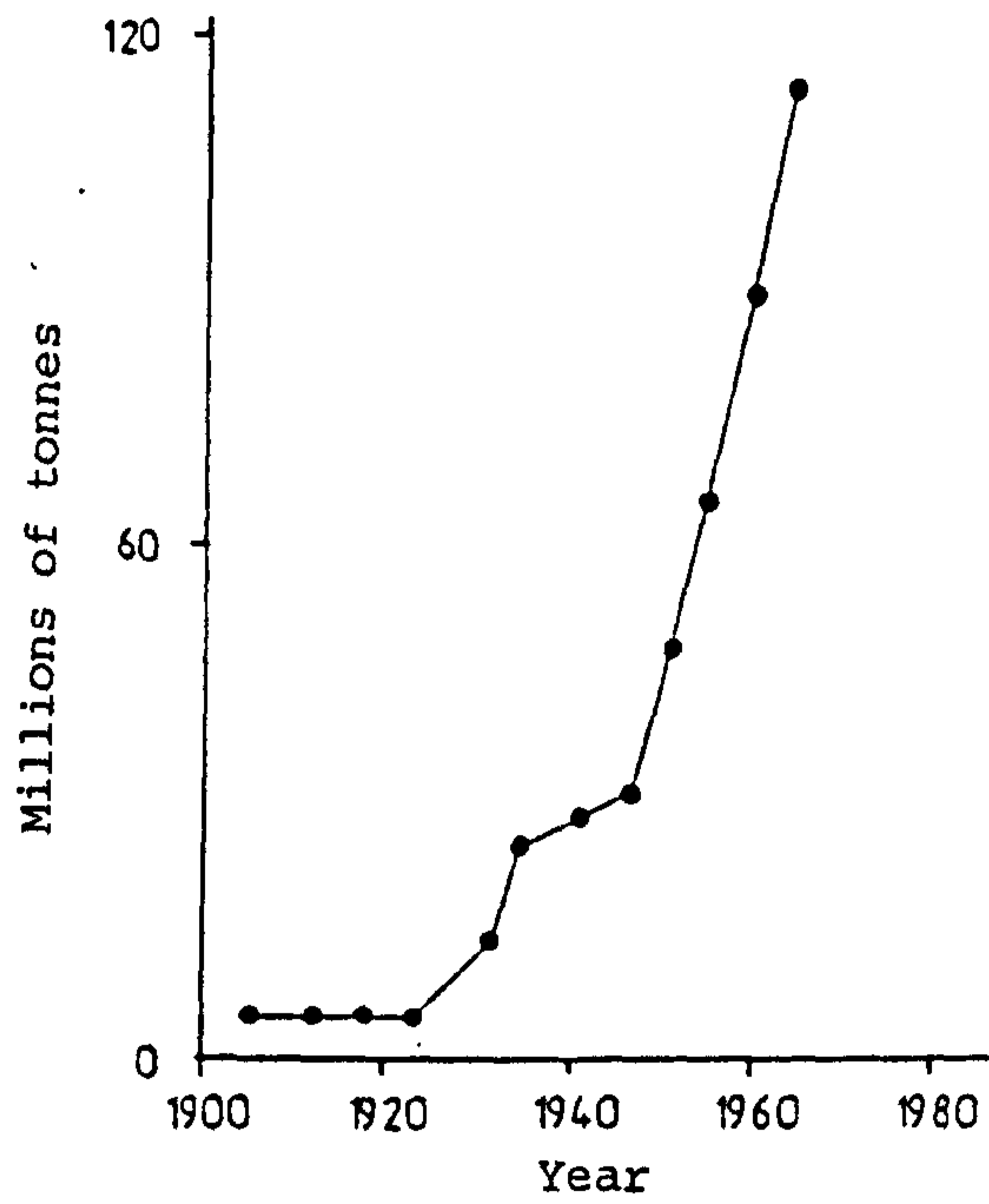


Figure 2.18

Sand and gravel production in Britain, 1900-1970.

From Catchpole and Tydeman (1975), based on the data of Archer (1972).

exponentially since the turn of the century, and projections up until 1980 predicted the trend to continue (Healing and Harrison, 1975).

Clearly the increased levels of quarrying of sand and gravel will have resulted in more artificial sites being available for sand martins, especially within the last 30 years. Parslow (1973) believes that the growth in the number of gravel pits in central and eastern England since 1950 has led to an increase in the sand martin population there.

However, some sand martin colonies in natural sites in Scotland decreased in size at least until the 1950's (Baxter and Rintoul, 1953). Hence the change in available sand martin nesting habitat over the past century may simply have resulted in a redistribution of nest sites rather than an increase in the population size of the species. Nevertheless, the largest colony recorded in the Forth area by Rintoul and Baxter (1935) was 300 burrows in a river bank on the River Almond. The Barbush colony in 1982 was probably the largest ever to exist in Scotland in recent years (up to 920 pairs in 1982), whilst Drumbeg sand pit has had up to 600 burrows documented, making it the second largest site recorded in Scotland (Thom, in prep.). Thus an increase in the sand martin population in Britain because of increased nesting habitat availability seems plausible.

The association of swallows and house martins nesting in human dwellings must be of ancient origin (Hosking and Newberry, 1946; Tate, 1981), but clearly sand martins are largely dependent on human activities for breeding at present. For a species which is probably highly susceptible to climatic changes in its wintering grounds (see below), the safeguarding of nests in sand and gravel quarries during

population crashes could be an integral part of sand martin conservation in Britain.

2.4.2 Factors responsible for sand martin population crashes

Sand martin populations declined in size severely in 1968-1969 and 1983-1984. Such dramatic reductions in numbers are not wholly explicable by events on the breeding grounds, so climatic conditions in the wintering area will be described.

British sand martins migrate through western France and Spain to spend winter in north-west Africa in the Sahel zone (12° - 18°N) south of the Sahara desert. The return migration is probably further to the east, with more ringing recoveries from the extreme north of Africa than in autumn (Mead and Harrison, 1979b).

The Sahel is normally a semi-arid zone, and has a single rainy season (July-September), with the abrupt alternation of dry and wet seasons resulting in a sharp seasonal increase in plants and invertebrates coinciding with the end of the northern summer period. Coupled with the absence of potential local competitive species, this usually makes the Sahel zone an ideal wintering ground for several bird species summering in Eurasia, including the sand martin, the redstart P. phoenicurus, the sedge warbler Acrocephalus schoenobaenus, the yellow wagtail Motacilla flava flavissima, and the whitethroat Sylvia communis (Morel, 1973).

During the 1950's rainfall in the Sahel was above that normally expected, but since 1968 it has been much below normal (Lamb 1982), probably partly because of a general weakening of the global atmospheric circulation (Winstanley, Spencer and Williamson, 1974). A severe drought occurred in the Sahel in 1968, and since then rainfall

has been below average (except in 1969), resulting in severe famine and desertification in north-west Africa (Derrick, 1984; Walsh, 1984).

Although the dry spell that started in 1967 may fall into a pattern of sparse, variable, and unevenly distributed rainfall that has prevailed in the region for the last 2,500 years, changes in land use and population growth has led to severe stresses being placed on fragile soils (Walsh, 1984). Moreover, the removal of vegetation, increased reflectivity, and reduced soil moisture induced by the drought have probably influenced the atmosphere in such a way as to strengthen the conditions that first produced the drought (Nicholson, 1982), so the drought is probably self-accelerating.

Precipitation during the Sahel wet season of 1968 was 25% below normal for the region as a whole, with rainfall the lowest since 1949 (Winstanley et al., 1974). The 1969 British breeding population of whitethroats fell to a level 77% below its 1968 value (Batten, 1971), and sand martin numbers in a Nottinghamshire study area were reduced by 45% over the same period (Cowley, 1979). For both the white-throat and the sand martin, the population crash in Britain was attributed to the sudden decrease in rainfall during the 1968 Sahelian wet season, reducing plants and insects available to birds in their wintering grounds.

During 1983 the river flood in the valley of the River Sénégal was the lowest recorded this century, largely as a result of poor rainfall in the mountains of northern Guinea (Dugan, 1984). However, it is unlikely that a severe Sahel drought was solely responsible for reducing 1984 sand martin numbers in the Stirling Region to about 25% of 1983 numbers: several other factors should be considered, including:

(i) Reduced fecundity in 1982 and 1983.

In 1982 a cold, wet spell in June reduced aerial insect abundance over about two weeks (Figure 3.1), and many sand martins at Barbush appeared to desert first broods. The 1983 Spring was prolonged, cold and wet, with aerial insect abundance low in the early season and also later in the season (compared with 1982), when weather conditions improved (Figure 3.2). Hence sand martins were late in arriving at the colony (Figure 2.7), and many pairs did not begin nesting until a relatively late date. Again, many first broods were deserted in the early season, and a large subcolony (c.200 pairs of an estimated c.500 at the colony) only reared one brood. Thus a reduced productivity during the 1982 and 1983 breeding seasons may have resulted in fewer birds than usual leaving Britain for the wintering grounds.

(ii) Conditions on spring and autumn migration

During the Spring of 1984 a persistent band of cold weather occurred in the Mediterranean at a time when hirundines would be migrating towards Britain (Mead, 1984). Hirundines can suffer high mortality rates when bad weather is encountered on migration (Alexander, 1933). Therefore many sand martins moving towards Britain in the Spring of 1984 may have perished in the area of the Mediterranean, or may perhaps have settled in Europe south of Britain. Conditions in the Mediterranean were probably responsible for the decline of the chiffchaff, Phylloscopus collybita, in Britain between 1983-1984, since this species winters in the Mediterranean and feeds on insects there (Mead, 1984).

Hence a series of catastrophic droughts in the Sahel zone of Africa, being especially marked in 1968, 1982, and 1983, have probably reduced British sand martin numbers to under 10% of their mid 1960's

numbers (Mead, 1984). After the severe drought of 1968 the reduction in sand martin numbers was largely attributable to a 3-6 fold increase in juvenile mortality, and a doubling of adult mortality (Mead, 1979; Cowley, 1979). Sand martins are relatively r-selected birds (Pianka, 1970) with potentially high fecundity rates, so population losses may be replaced within a relatively short time. The changes in physical attributes of the study population over the period of the 1983-1984 population crash will now be discussed from an evolutionary standpoint.

2.4.3 Natural selection and body size changes in bird populations

In this study keel-length was used as an index of body size because it positively correlated with body mass in males and females, attained a maximum length soon after fledging, and did not therefore vary with the age of the bird.

Body size is known to have a strong hereditary component in birds, whether measured through body mass or morphometrics (Boag and Grant, 1978; Smith and Zach, 1979; Van Noordwijk, Van Balen and Scharloo, 1980; Smith and Dhondt, 1980; Garnett, 1981; Boag, 1983). Garnett (1976) has shown that about three-quarters of the variation in tarsus length, an indicator of body size in great tits at Oxford, is caused by additive genetic variance. Thus it is likely that keel-length in sand martins also has a high heritable component and is thus likely to respond to selective pressures for changes in body size.

Climate is believed to influence the body size of organisms as reflected by the latitudinal trends in size between species (Mayr, 1956), and by geographical variation in skeletal characters within species (Niles, 1973). Extremes of weather may result in reduced fecundity rates (Schreiber and Schreiber, 1984), or heavy mortality rates of

birds (Boag and Grant, 1981; Johnston and Fleischer, 1981; Price et al., 1984). Severe weather outside of the breeding season can also produce significant changes in the distributions of size classes within bird populations through strong directional selection (Bumpus, 1899; Boag and Grant, 1981; Johnston and Fleischer, 1981; Price et al., 1984). Extreme climatic conditions can also select for a refinement of bodily proportions in house sparrows, Passer domesticus, (Fleischer and Johnston, 1982).

Most sand martin mortality occurs outside Britain (Mead, 1979). In 1984 the population of sand martins in the Stirling Region was 23% of its 1983 level, and the population crash was probably largely attributable to a severe drought in the winter quarters reducing food availability (section 2.4.2; Mead, 1984).

The severe Sahel climate and possibly poor conditions of spring migration, seemingly resulted in heavy mortality of sand martins and also directional selection for reduced body size (Table 2.4). Natural selection often affects the sexes in different ways (Johnston and Fleischer, 1981; Clutton-Brock, Guinness and Albon, 1982; Price, 1984a), and the same selective pressure may favour different morphological extremes in young and adults (Boag and Grant, 1981; Price and Grant, 1984). In this study the direction of overwinter selection acting on keel-length appears similar for both sexes, probably because of their similar morphology, though no statistically significant differences were obtained with males because of a small sample size.

Male and female Darwin's finches, Geospiza fortis, underwent directional selection towards large size over a drought in 1977 (Boag and Grant, 1981), and similar selection has occurred in subsequent dry spells (Price, et al., 1984). Large birds showed a higher

survival rate because they were able to crack the large and hard seeds that predominated in the drought with their large beaks (Grant, 1981). Additional directional selection for large size in males may occur through sexual selection (Price, 1984a). Directional selection for large size can be balanced by selection for small size in females (Price, 1984a) and in juveniles (Price and Grant, 1984).

Constraints on body size in one sex may affect selection on the size of the other sex. As yet, heritability estimates of body size in birds have been similar for males and females, at least in species with only slight sexual size dimorphism (Van Noordwijk et al, 1980; Price, 1984a). Females may mate selectively with large males, which may be high quality parents (Price, 1984b). However, smaller females may be at a metabolic advantage over larger females in having a reduced maintenance cost and being able to devote more resources to reproduction (Downhower, 1976), and small females may breed when younger (Price, 1984a). Hence a large male mating with a small female may pay the cost of fathering male offspring of reduced size and fitness than if size-assortative mating had occurred. The father would benefit however from rearing smaller females which may be at a selective advantage later in life over larger females resulting from size-assortative mating.

Extremely cold winters accentuate sexual size dimorphism in house sparrows, resulting in males becoming significantly larger after winter, females significantly smaller, this probably reducing intra-specific aggression over scarce food (Johnston and Fleischer, 1981). Great Tits in Ghent became smaller in wing-length between 1962 and 1975, probably because provision of nest boxes allowed the breeding of small birds which would be excluded from limited natural nest sites by larger individuals (Dhondt, Eyckerman and Huble, 1979).

It is easy to understand how large size could be selected for during food shortages if competition for food is intense and large birds are either more adept at foraging on scarce food (Grant, 1981), or if large birds are dominant to small birds and can exclude them from defendable food resources (Garnett, 1981). Why should small body size be selected for in sand martins during presumed food shortages however?

Outside of the breeding season, sand martins feed on aerial insects in Africa (Fry, Ash and Ferguson-Lees, 1970; Waugh, 1978). These are likely to be distributed in an unpredictable manner temporally and spatially, and will not be economically dependable, and hence there are likely to be few opportunities for large birds to exclude smaller individuals from food supplies. If martins with long keels also had long bills, they may be able to eat a greater variety of prey sizes than shorter billed individuals, as found in robins, Erithacus rubecula, (Herrera, 1978), so there may be some advantage of being large when food is scarce.

Selection for small body size is also likely to be influenced by the relationship of energy storage and expenditure to body size. Benefits of small body size may be associated with a reduced total energy expenditure (hence food requirements) compared with large birds (however, see Bryant and Westerterp, 1982, 1983b, for exception), and reduced flight costs through being light (Pennycuick, 1969, 1975). The benefits of being large are probably associated with an increased digestive capacity, lipid storage capacity (Schaffer and Elson, 1975), and a greater flight economy (Bryant and Westerterp, 1982).

The energetic costs of flight (Schmidt-Nielsen, 1972), and

existence energy (Kendeigh, 1970) bear an increasing allometric relationship with increasing body mass (related to size), while digestive capacity and lipid reserves (Schaffer and Elson, 1975) increase almost linearly on body mass increases. Hence the total costs of being large may increase more rapidly than the benefits when food is scarce, and when there are no behavioural advantages in being big. Small birds may thus be able to replenish reserves faster if food becomes available (Downhower, 1976). Small male red-winged blackbirds, Agelaius phoeniceus, for example have larger energy reserves in proportion to their size than do large males (Searcy, 1979). Horned larks, Eremophila alpestris, were smaller in areas of low productivity, though Niles (1973) interpreted this as an adaptation to the birds' heat budgets rather than using resource balance arguments.

If small body size is selected for in severe conditions outside the breeding season, what are the advantages of being large? Large males may be favoured by sexual selection (Searcy, 1979; Price, 1984a), and large male house martins have a higher lifetime reproductive success than smaller birds (Bryant, in prep.). Moreover, reproduction output per season is greater in large females than in smaller birds, probably because of improved flight efficiency in large individuals (Bryant and Westerterp, 1982), though a high reproductive output is counter selected to some extent by a greater reproductive cost of increased mortality rates in females rearing two broods per season (Bryant, 1979). Body size in hirundines may be subjected to normalising selection in both males and females, with different costs attributable to being large and small over different stages of the annual cycle. Hence there are probably advantages to being big during the breeding season, and although small females may pay smaller

mortality costs of reproduction overwinter than larger females, potential benefits may be with smaller birds of each sex in severe climatic conditions outside the breeding season.

Similar directions of change occurred in house martin morphology to those observed in sand martins over the same period in this study (D. M. Bryant, pers. comm.). Since body mass in hirundines is correlated with body size (section 2.3.5, Chapters 7, 8), masses inferred as being optimal (Chapters 7, 8) in a breeding population will be constrained by body size variation within the population, which in turn will be influenced by selective pressures outside the breeding season.

CHAPTER 3

3. RESOURCES AVAILABLE FOR BREEDING HIRUNDINES

3.1 INTRODUCTION

During the breeding season adult birds must decide about how much food and foraging time they allocate to themselves relative to allocation for reproductive activities. Parent:offspring resource allocation is likely to be affected by changes in environmental conditions or food availability. Environmental conditions have been shown to influence adult maintenance behaviours and brood provisioning rates in gray cat birds Dumetella carolinensis (Johnson and Best, 1982), and bobolinks Dolichonyx oryzivorus (Wittenberger, 1982).

If food becomes scarce during the breeding period, for example when invertebrate prey abundance is reduced by cold temperatures, parents may spend relatively more time self-feeding to maintain their body condition than in times of prey abundance. Parents are likely to rank their interests above those of their offspring since brood survival is ultimately dependent on parental care, and fitness is likely to be greater among individuals surviving for more than one breeding season.

British hirundines feed solely on insects (Bryant, 1975b; Waugh, 1978; Turner, 1980), whose abundance is greatly influenced by prevailing weather conditions (Williams, 1961; Johnson, 1969; Bryant, 1975b). Previous work on aerial insect abundance in the Stirling area has been reported by Waugh (1978), and Turner (1980).

Aerial insect abundance affects nestling growth in house martins (Bryant, 1975b), and breeding adults are heavier when insect numbers are high (Bryant, 1979). Previous studies have investigated the effects of food availability on brood growth or adult condition in

isolation however, and a detailed knowledge of resource availability would obviously be of importance in a study of concurrent parent: offspring resource allocation in aerial feeding birds, the specific objective of this project. In this chapter some factors influencing the abundance of aerial insects in the study area are described and some implications of variation in food supply for feeding ecology, body condition, and the breeding biology of hirundines are discussed.

3.2 MATERIALS AND METHODS

Resources available for breeding hirundines were sampled by two methods: a suction trap at Stirling University campus, and by hand-net sampling in areas where breeding swallows were feeding.

The suction trap

The suction trap sampled aerial insects at a height of 12.2m and was situated in the grounds of Stirling University, 3-8 km from the swallow nest sites studied, and 8 km from the sand martin study colony.

The trap samples air vertically downwards to avoid directional effects, and samples through 1 mm mesh gauze at a constant rate over the day. Samples are taken from a randomly dispersed aerial insect population, and the trap is non-selective with regard to insect size, and is neutral in attraction (Johnson, 1950; Taylor, 1962; Taylor and Palmer, 1972; Bryant, 1973). Massive insects not normally eaten by hirundines (for example bumble-bees Bombus spp.) were excluded from the suction trap catches.

Samples were removed from the suction trap at 10.00h daily, the contents stored in 10:1 methanol:glycerol solution, and the volume of the catch was estimated. For analysis volumes were transformed to \log_{10} , since house martin breeding biology is most closely related

to the logarithm of insect abundance as measured by a suction trap (Bryant, 1973). Hence suction trap catch data is presented as $\log_{10}(\text{volume (cm}^3) + 1)$, abbreviated to $\log(v + 1)$.

The suction trap catches probably give a reliable estimate of the quantity of resources available to breeding sand martins, which often forage at about trap height (Waugh, 1978). Since the swallow, and in poor conditions the sand martin, commonly feed closer to the ground than the level sampled by the suction trap (Waugh, 1978), an alternative method of insect capture was also employed, namely hand-net sampling.

Hand-net sampling

A 'butterfly' net with mesh of less than 1 mm diameter was used to sample insects by sweep netting in areas where swallows were feeding. Three arable farmland sites were sampled daily on the Carse of Lecropt (G.R. NS 770970) in May-September 1982 and 1983, and in June and July 1984. One hundred sweeps were made at 0.3-2m at each site, this being the most frequent feeding height for swallows (Waugh, 1978). Most samples were taken between 13.00h and 16.00h, a time when many larger Brachyceran and Cyclorrhapan Diptera have their main flight periods (Lewis and Taylor, 1965).

The captured insects were killed in a killing jar by ethyl acetate or chloroform, and were deep frozen until analysis. Each site's sample was freeze-dried for a week, weighed by a four-figure electronic balance, and insects then counted. The number of large items (> 1.5 mg dry mass) in the samples were also ranked, since these are preferred prey items of swallows (Waugh, 1978; Turner, 1980). The mean values of biomass and numbers from the three sites were used in analysis.

From the hand-net samples, Diptera, small Hymenoptera, Ephemeroptera, Neuroptera, Trichoptera, and small Lepidoptera were retained. Excluded insects were large bees and wasps, large Lepidoptera, flightless lepidopteran larvae and large Arachnida, and the infrequently flying Hemiptera and Coleoptera. Although the excluded invertebrates are occasionally eaten or collected by swallows, Turner (1980) found that Diptera contributed 81.3% of the food items fed to first brood and 69.4% to second brood swallows, so the major prey items were probably accurately sampled. Hand-net sampling did involve striking the tops of vegetation, so not all insects captured were actually flying. Such a technique was necessary if a large sample of insects were to be obtained, and is likely to be representative of flying insects available since the hand-net samples correlate significantly with suction trap volumes (see Results).

The two insect sampling methods employed each had its own merits and drawbacks. The suction trap caught insects more likely to be taken by sand martins, and sampled over a 24h period. Daytime catches overwhelm night catches in suction trap catches (Lewis and Taylor 1965), so suction trap volumes probably reliably reflected resources available for breeding hirundines over an entire day's foraging. The results from this technique may be useful in interpreting body mass changes of both sand martins and swallows, since the birds' body condition will probably reflect relatively long term changes in food abundance.

Hand-net sampling catches the larger, low flying insects more likely to be eaten by swallows, and sampling also occurs at actual feeding stations. The short term nature of hand-net sampling renders the technique very sensitive to sudden meteorological changes. Such

effects may be a drawback in interpreting daily body mass changes, but may be advantageous in studying food delivery rates and foraging ecology which would be most dependent on immediate conditions in the sampling area.

Meteorological data collection was as described in Chapter 2.

3.3 RESULTS

3.3.1 Suction trap catches

(a) Seasonal changes in suction trap catch volume

Suction trap catches are shown for 1982 in Figure 3.1, and for 1983 in Figure 3.2. In both years catches were low in April, with largest catches between May and September inclusive. The catches varied greatly from day to day, emphasising the unpredictable nature of aerial insects as a food source for hirundines. The patterns of insect abundance show some major differences between the two years, suggesting that aerial insects may be unpredictable in abundance from year to year, besides being unpredictable on a daily basis. This is further discussed in Section 3.3.3. For example, in 1982 aerial insect catches fell to very low levels in June, during a spell of unseasonably cold and wet weather. However, catches from July to September 1982 are generally higher than those for the same period in 1983.

(b) Factors influencing suction trap catch volume

The correlation matrices for environmental factors and suction trap catch volume for 1982 and 1983 are given in Table 3.1. In both years, the catch was positively correlated with date and maximal daily temperature. Maximal daily temperatures were included in the analyses because swallow weighings were performed during afternoons, when daily

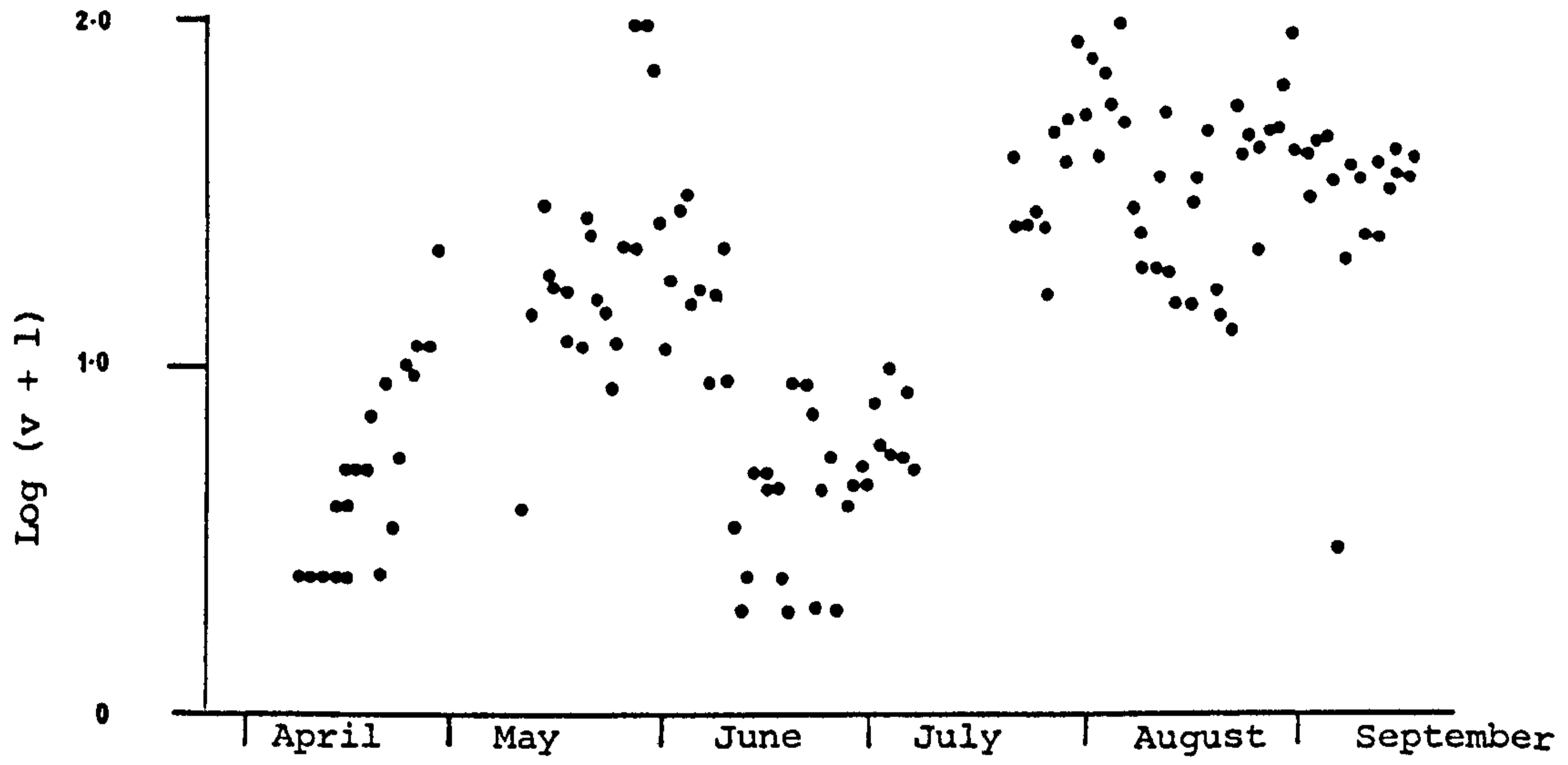


Figure 3.1

Seasonal variation in food abundance in 1982
as shown by the 12.2m suction trap.

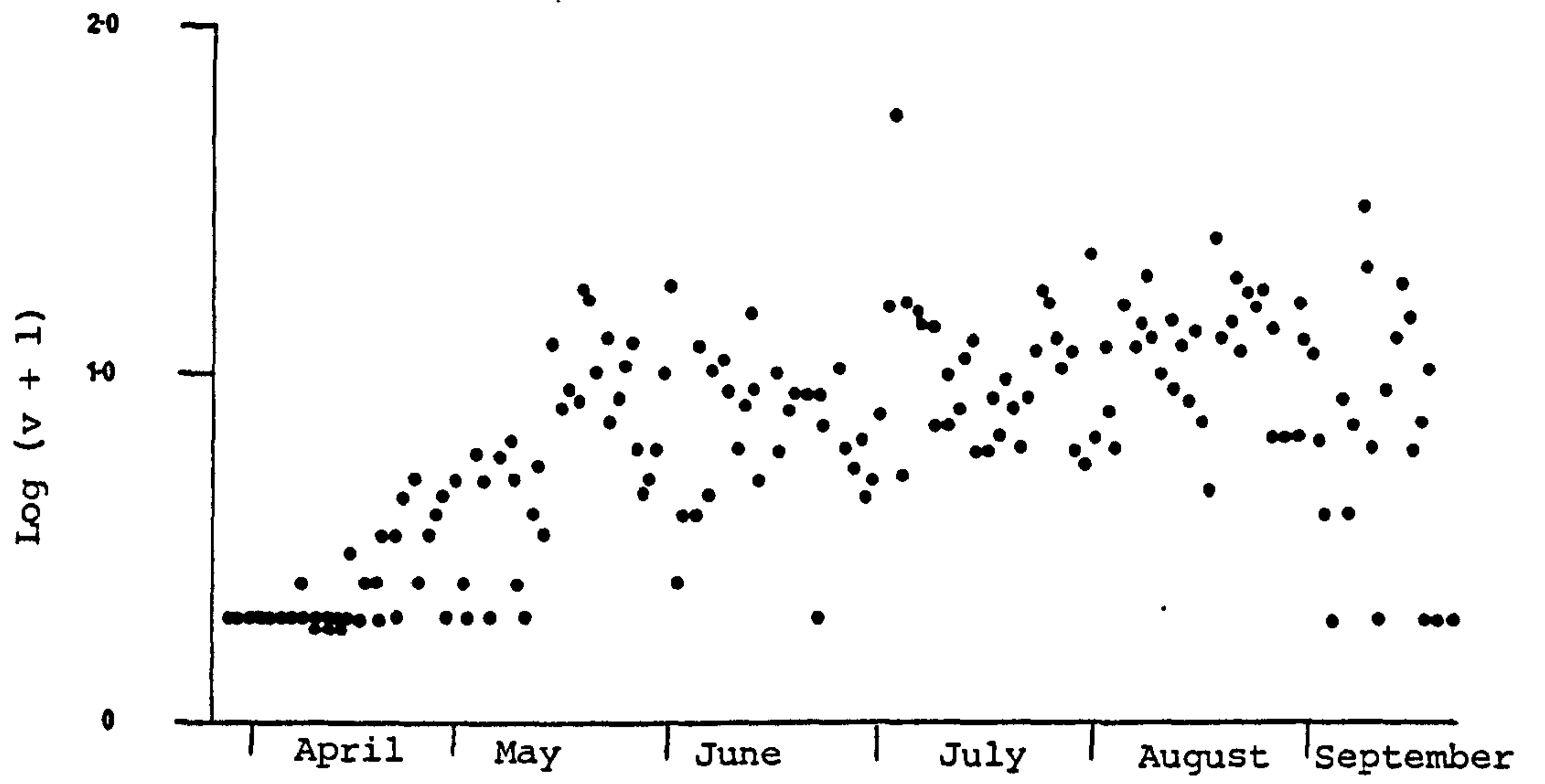


Figure 3.2

Seasonal variation in food abundance in 1983 as shown by the 12.2m suction trap.

Table 3.1

Correlation matrices of environmental factors and suction trap catch, $\log(\text{volume} + 1)$

(a) 1982 : n = 130 sampling days, April 9th - September 16th

(b) 1983 : n = 175 sampling days, March 29th - September 20th

For all correlation matrices, tabulated values are Pearson product-moment correlation coefficients, r.

*** : P < 0.001

** : P < 0.01

* : P < 0.05

ns : not statistically significant, P > 0.05

(a)

	Log (v + 1)	Date	tmax	Windspeed	Rainfall, mm
Log (v + 1) suction trap catch		0.60 ***	0.59 ***	-0.14 ns	0.06 ns
Date (days after April 8th)			0.25 **	0.20 *	0.22 *
Maximal Daily Temperature, °C (tmax)				-0.27 **	-0.06 ns
Windspeed, knots					0.01 ns

(b)

	Log (v + 1)	Date	tmax	Windspeed	Rainfall
Log (v + 1)		0.54 ***	0.63 ***	-0.19 *	-0.19 *
Date			0.68 ***	-0.02 ns	0.06 ns
tmax				-0.19 *	-0.25 ***
Windspeed					0.07 ns

temperature was generally highest. However, in both 1982 and 1983 maximal daily temperature (t_{\max}) and date were also positively correlated, so stepdown multiple regression analyses were performed to examine whether season and temperature contributed independently to variation in trap volume. In 1983, $\log(v + 1)$ was also significantly correlated with both windspeed and rainfall.

The results of the multiple regression analyses are given in Table 3.2, and the results of the abbreviated analyses will be described here. Date and maximal daily temperature each exerted influence on $\log(v + 1)$ for both 1982 and 1983. Hence, during the study period, aerial insects became more abundant later in the season, and were more abundant at higher temperatures. Although insects tended to become less abundant or windspeed and rainfall increased, neither of these variables significantly contributed to the variance in aerial insect abundance in the regression analyses.

3.3.2 Hand-net catches

(a) A comparison of sampling sites

In Table 3.3 correlated matrices are presented for insect biomass at the three sites sampled. In all cases catches between sites were significantly positively correlated except sites A and C in 1982. Hence different factors may influence catches at different sites, and 100 sweeps in only one site may not give a realistic impression of overall prey availability.

Lewis (1965) and Lewis and Stephenson (1966) showed that flying insects tended to congregate behind shelter belts, such as hedgerows, during strong winds, and swallows selectively exploit such sites on windy days (Waugh, 1978). One of the sampling sites (site C) was adjacent to a hedgerow, whilst B and C were exposed. Hence biases

Table 3.2 Stepdown regression analyses of determinants of suction trap catch, log (v + 1)

(a) 1982; (b) 1983 ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

Independent variable	Multiple r ² x 100	Degrees of Freedom	Full analysis		Abbreviated analysis	
			Regression Equation	t-value	Regression Equation	t-value
(a)						
Date, days after April 8th	35.5	1,128	0.005x ₁ +	8.03***	0.005x ₁ +	7.88***
Maximal daily temperature, °C (t max)	56.5	2,127	0.052x ₂ -	6.61***	0.059x ₂ + 0.058	7.81***
Windspeed, knots	57.8	3,126	0.012x ₃ -	-1.97 ns		
Rainfall, mm	57.8	4,125	0.003x ₄ - 0.094	-0.55 ns		
						F = 82.2 P < 0.001***
(b)						
Date	29.3	1,173	0.002x ₁ +	3.22**	0.001x ₁ +	2.67**
tmax	42.3	2,172	0.025x ₂ -	4.71***	0.030x ₂ + 0.231	6.24***
Windspeed	43.0	3,171	0.006x ₃ -	-1.71 ns		
Rainfall	44.0	4,170	0.007x ₄ + 0.321	-1.46 ns		
						F = 63.2 P < 0.001***

Table 3.3

Correlation matrices of hand-net biomass from the three sampling sites.

(a) 1982, n = 81 sampling sessions

(b) 1983, n = 101 sampling sessions.

Tabulated values are correlation coefficients, r.

ns : not significant

** : P < 0.01

***: P < 0.001

(a)		Site A	Site B
	Site B	0.32**	
	Site C	0.14 ns	0.34**
(b)		Site A	Site B
	Site B	0.40***	
	Site C	0.40***	0.39***

associated with sampling on windy days may have been reduced to some extent by including a sheltered site in the sampling programme.

(b) Seasonal changes in hand-net catches

Hand-net catches for the summers of 1982 and 1983 are plotted as a function of season in Figures 3.3 and 3.4 respectively. Plots are presented for hand-net biomass (mg dry mass), number of items in the catch, and the number of large items (≥ 1.5 mg dry mass) sampled.

Little sampling occurred in July 1982, so seasonal trends for that year are difficult to elucidate. Nevertheless, biomass, number of items, and number of large items all follow similar patterns. In 1983 a distinct pattern for all parameters is apparent (Figure 3.4). Each parameter takes low values for early in the season (late May/early June) with a progressive increase to highest values in mid-season, early July. Thereafter declines in insect abundance occur during late July/August to low values in September.

The pattern of insect abundance during 1983 and illustrated in Figure 3.4, is clearly different from aerial insect abundance during the same year as measured by the suction trap (Figure 3.2), which rises to a May-September plateau, although the peak in hand-net catch biomass would be reduced if the data was transformed logarithmically, as were the suction trap data.

(c) Factors influencing hand-net catches

Hand-net catches were analysed according to dry mass biomass, number of items, and the number of large items in the catch. Environmental factors influencing these parameters will now be described. Correlation matrices of environmental factors and hand-net catch parameters in 1982 and 1983 are presented in Table 3.4, and stepdown regression analyses for all parameters in Tables 3.5-3.7.

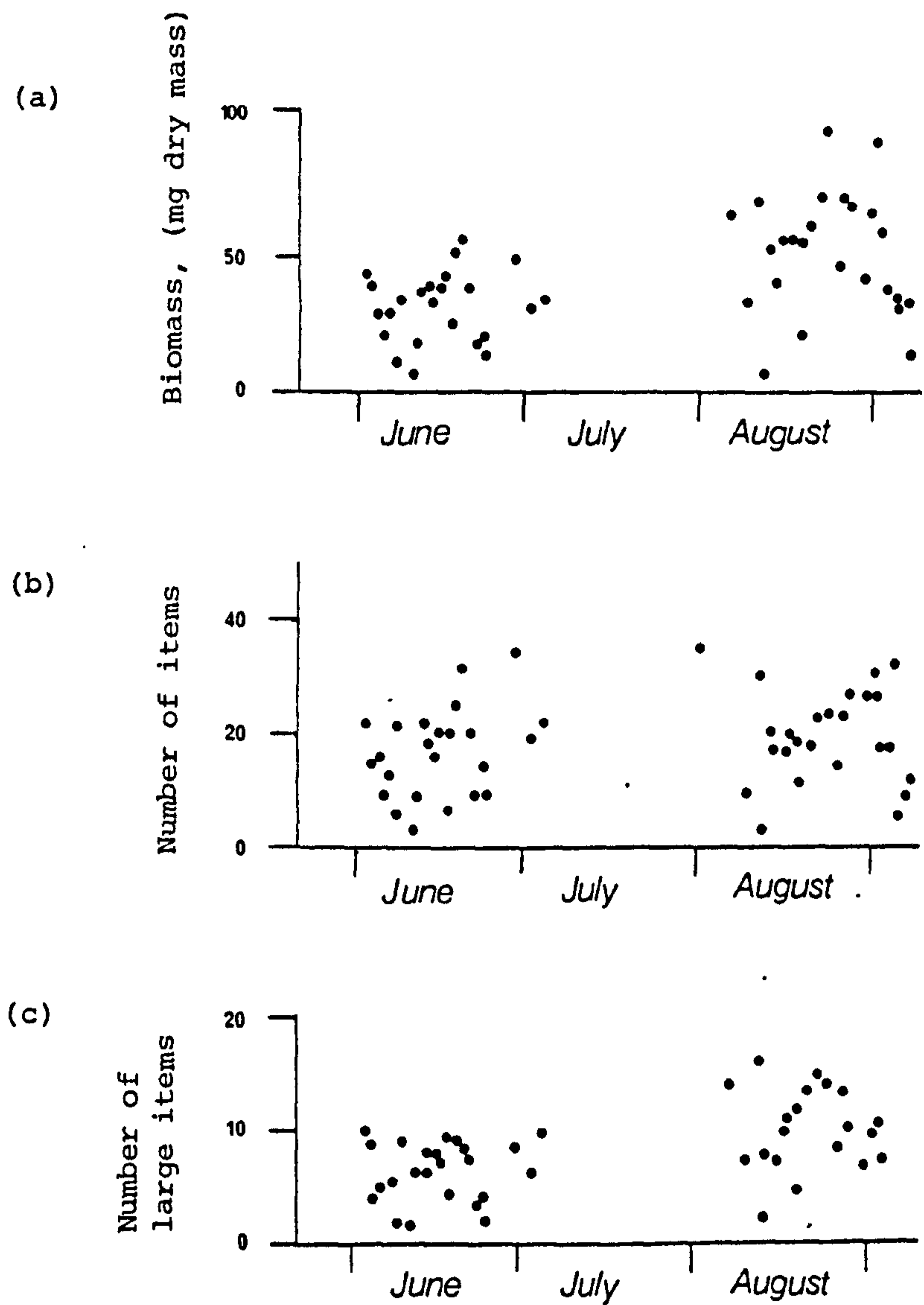


Figure 3.3

Seasonal variation in food abundance in 1982
as measured by hand-net sampling.

(a) Biomass, mg dry mass

(b) Number of items

(c) Number of large items (> 1.5 mg dry mass).

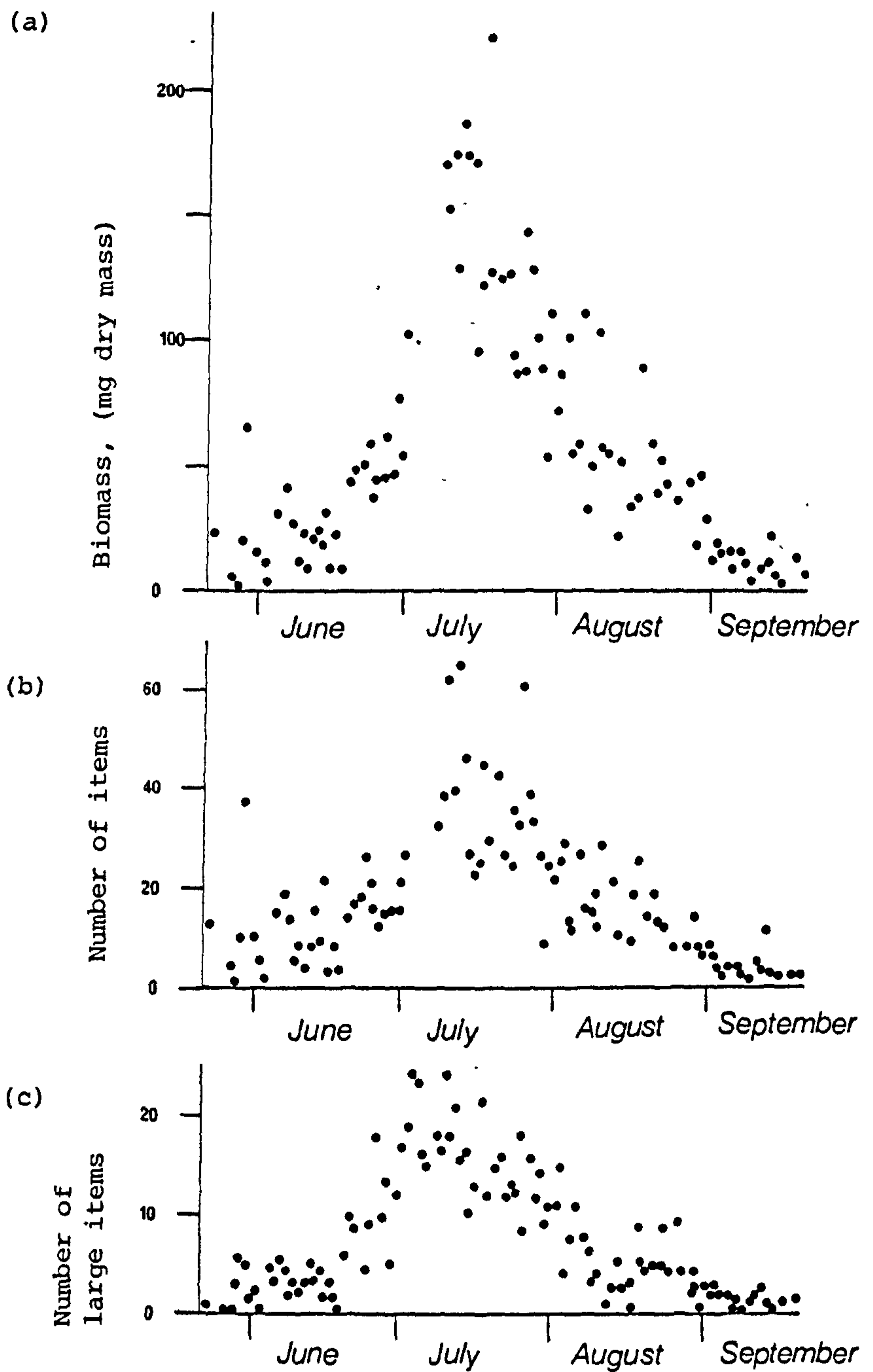


Figure 3.4

Seasonal variation in food abundance in 1983 as measured by hand-net sampling.

(a) Biomass, mg dry mass

(b) Number of items

(c) Number of large items (≥ 1.5 mg dry mass).

Table 3.4 Correlation matrices of environmental factors and hand-net catch parameters

(a) 1982, n = 49 sampling days
 (b) 1983, n = 95 sampling days

Tabulated values are correlation coefficients, r. ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

	Biomass	Number of items	Number of large items ($\geq 1.5\text{mg dry mass}$)	Date	Maximal Daily Temperature t max	Windspeed	Rainfall mm
(a)							
Biomass, mg dry mass		0.70***	0.87***	0.45**	0.15 ns	0.18 ns	-0.05 ns
Number of items			0.70***	0.18 ns	0.17 ns	-0.06 ns	-0.003 ns
Number of large items				0.32*	0.16 ns	0.08 ns	-0.06 ns
Date, days after June 1st					-0.18 ns	0.14 ns	0.35*
Maximal daily temperature, °C (t max)						-0.39	-0.09 ns
Windspeed, knots							0.01 ns
(b)							
Biomass		0.88***	0.92***	-0.07 ns	0.57***	-0.22*	-0.31**
Number of items			0.79***	-0.16 ns	0.52***	-0.23*	-0.30**
Number of large items				-0.15 ns	-0.49***	-0.15 ns	-0.28**
Date					0.28**	-0.12 ns	0.07 ns
t max						-0.32**	-0.42***
Windspeed							0.13 ns

Table 3.5 Stepdown regression analyses of determinants of hand-net biomass (mg dry mass)

(a) 1982 (b) 1983 ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

Independent Variable	Multiple r ² x 100	Degrees of Freedom	Full analysis		Abbreviated analysis	
			Regression Equation	t-value	Regression Equation	t-value
(a) Date, days after June 1st	20.1	1,47	0.306x ₁ +	4.14***	0.247x ₁ + 26.1	3.44**
Maximal daily temperature °C (t max)	25.7	2,46	1.727x ₂ +	2.14*		
Windspeed, knots	27.7	3,45	0.627x ₃ -	-1.66 ns		
Rainfall, mm	32.3	4,44	0.722x ₄ - 7.08	1.15 ns		
			F = 5.3 P < 0.01**		F = 11.85 P < 0.01**	
(b) Date	0.5	1,93	-0.372x ₁ +	-2.80**	-0.379x ₁ +	-2.95**
t max	38.1	2,92	6.94x ₂ -	6.13***	7.27x ₂ - 59.9	7.55***
Windspeed	38.8	3,91	0.417x ₃ -	-0.56 ns		
Rainfall	38.9	4,90	0.450x ₄ - 51.5	-0.33 ns		
			F = 14.3 P < 0.001***		F = 28.9 P < 0.001***	

Table 3.6 Stepdown regression analyses of determinants of the number of items in hand-net catches,

(a) 1982 (b) 1983 ns : not significant; * : P < 0.05; ** : P < 0.01 *** : P < 0.001

Independent Variable	Multiple r^2 x 100	Degrees of Freedom	Full analysis		Abbreviated analysis	
			Regression Equation	t-value	Regression Equation	t-value
(a)						
Date, days after June 1st	3.0	1,47	$0.054x_1 +$	1.50 ns	no significant variables	
Maximal daily temperature °C (t max)	7.2	2,46	$0.497x_2 -$	1.28 ns		
Windspeed, knots	7.2	3,45	$0.015x_3 -$	-0.06 ns		
Rainfall, mm	7.6	4,44	$0.090x_4 + 6.78$	-0.43 ns		
				F = 0.9		
				P = n.s.		
(b)						
Date	2.6	1,93	$-0.137x_1 +$	-3.74***	$-0.138x_1 +$	-3.89***
t max	37.2	2,92	$1.770x_2 -$	5.69***	$1.890x_2 - 10.7$	7.12***
Windspeed	37.7	3,91	$0.190x_3 -$	-0.93 ns		
Rainfall	37.8	4,90	$0.110x_4 - 7.54$	-0.29 ns		

F = 13.7

P < 0.001***

F = 27.2

P < 0.001***

Table 3.7 Stepdown regression analyses of determinants of the number of large items (≥ 1.5 mg dry mass) in hand-net catches

Independent Variable	Multiple r^2 $\times 100$	Degrees of Freedom	Full analysis		Abbreviated analysis	
			Regression Equation	t-value	Regression Equation	t-value
(a)						
Date, days after June 1st	10.2	1,47	$0.040x_1 +$	2.84**	$0.031x_1 + 5.85$	2.32*
Maximal daily temperature °C, (t max)	15.1	2,46	$0.280x_2 +$	1.79 ns		
Windspeed, knots	18.2	3,45	$0.088x_3 -$	-1.25 ns		
Rainfall, mm	19.5	4,44	$0.105x_4 + 0.53$	0.84 ns		
				F = 2.7		F = 5.4
				P < 0.05*		P < 0.05*
(b)						
Date	2.2	1,93	$-0.055x_1 +$	-3.31**	$-0.055x_1 +$	-3.47***
t max	30.7	2,92	$0.758x_2 -$	5.37***	$0.771x_2 - 4.66$	6.45***
Windspeed	30.7	3,91	$0.002x_3 -$	-0.03 ns		
Rainfall	30.7	4,90	$0.036x_4 - 4.37$	-0.21 ns		
				F = 9.48		F = 22.3
				P < 0.001***		P < 0.001***

(i) Factors influencing hand-net catch biomass

For 1982 hand-net biomass was significantly positively correlated with date. For the larger sample of 1983, date had no significant effect, but biomass was significantly positively correlated with maximal daily temperature, and significantly negatively correlated with windspeed and rainfall.

A stepdown multiple regression analysis of hand-net catch biomass for each of the two seasons is given in Table 3.5. For the abbreviated analysis in 1982, only date contributed significantly to the biomass variance: biomass became heavier later in the season. Maximal daily temperature entered as a significant variable in the full analysis with greater biomass occurring at higher temperatures, but was not significant in the abbreviated analysis.

In 1983 the seasonal trend was reversed, and biomass became smaller later in the season, though, as Figure 3.4 shows, biomass and season were not related in a simple linear fashion, rather biomass peaked during mid-season. For the abbreviated analysis biomass was greater at higher maximal daily temperatures in 1983.

(ii) Factors influencing the number of items in hand-net catches

For 1982 no measured environmental variables correlated significantly with the number of items in hand-net catches (Table 3.4). In 1983, the number of items was significantly positively correlated with maximal daily temperature, and significantly negatively correlated with windspeed and rainfall.

A stepdown regression analysis of number of items in hand-net catches is presented in Table 3.6. No independent variables entered the analysis significantly in 1982. Fewer items were present later

in the season in 1983, and more items occurred at higher maximal daily temperatures.

(iii) Factors influencing the number of large items in hand-net catches

In 1982 the number of large items in hand-net catches was positively correlated with date. In 1983 number of large items was positively correlated with maximal daily temperature, and negatively correlated with rainfall (Table 3.4). Stepdown regression analyses of the number of large items in hand-net catches in 1982 and 1983 are presented in Table 3.7.

In 1982 more large items were present later in the season. In 1983 fewer large items were present as the season progressed, and more large items were captured at higher maximal daily temperatures.

(iv) Mean insect mass in hand-net samples

A correlation matrix of environmental parameters and mean insect mass in the hand-net samples (mg dry mass) for 1982 and 1983 is given in Table 3.8. Mean insect mass was significantly positively correlated with date and windspeed in 1982, significantly positively correlated with date and maximal daily temperature and negatively correlated with rainfall in 1983.

In the stepdown regression analysis (Table 3.9), date had a significant positive influence on mean insect mass in both years, and maximal daily temperature had a significant positive effect in 1983.

Table 3.8

Correlation matrices of environmental factors and mean insect dry mass (mg) in hand-net catches

(a) 1982, n = 49 sampling days

(b) 1983, n = 95 sampling days.

Tabulated values are correlation coefficients, r.

ns : not significant

* : P < 0.05

** : P < 0.001

***: P < 0.001

		Date days after June 1st	Maximal daily Temperature °C	Windspeed knots	Rainfall mm
1982	Mean insect mass, mg dry mass	0.43**	-0.16 ns	0.29*	0.01 ns
1983	Mean insect mass, mg dry mass	0.31**	0.41***	-0.11 ns	-0.26*

Table 3.9 Stepdown regression analyses of determinants of mean insect dry mass (mg) in hand-net catches

(a) 1982; (b) 1983 ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

Independent variable	Multiple r^2 x 100	Degrees of Freedom	Full analysis		Abbreviated analysis	
			Regression Equation	t-value	Regression Equation	t-value
(a)						
Date, days after June 1st	18.1	1,47	$0.012x_1 -$	3.15**	$0.011x_1 + 1.76$	3.22**
Maximal daily temperature °C (t max)	18.8	2,46	$0.001x_2 +$	-0.03 ns		
Windspeed, knots	21.1	3,45	$0.043x_3 -$	1.59 ns		
Rainfall, mm	25.4	4,44	$0.023x_4 + 1.58$	-1.07 ns		
			F = 3.7		F = 10.4	
			P < 0.05*		P < 0.01**	
(b)						
Date	9.7	1,93	$0.009x_1 +$	2.50*	$0.008x_1 +$	2.21*
t max	20.8	2,92	$0.078x_2 +$	2.51*	$0.096x_2 + 0.907$	3.59**
Windspeed	20.9	3,91	$0.007x_3 -$	0.35 ns		
Rainfall	22.9	4,90	$0.058x_4 + 1.24$	-1.52 ns		
			F = 6.7		F = 12.1	
			P < 0.001***		P < 0.001***	

3.3.3 Differences in insect abundance between years

(a) Suction trap catches

Suction trap catches ($\log (v + 1)$) were averaged for each month and plotted in Figure 3.5. Aerial insect abundance was compared across the same months of each year by t-tests.

Aerial insect abundance was significantly higher in each month sampled during 1982 than during 1983, except for June where no significant difference occurred between the years.

June 1982 was an unseasonably cold and wet month. Hence even over the two years of the study, aerial insect abundance was found to be higher for five out of six months in one summer than in another.

(b) Hand-net catches

An overall comparison of hand-net catches in 1982 and 1983 was not considered valid because of the sampling gap in 1982. Hence parameters for the two years were compared for the months of June and August, when samples were taken for most days during each year. The results are presented in Table 3.10.

There was no significant difference for means of June biomass, August biomass, number of items in June, number of items in August, and number of large items in June between 1982 and 1983. However, significantly more large items were present in the hand-net sample for August 1982 compared with 1983, although mean prey mass was significantly higher in June and August 1983 compared with 1982.

3.3.4 A comparison of suction trap and hand-net catches

The seasonal trend in aerial insect abundance during 1983 (Figure 3.2) followed a different pattern from insect abundance determined by hand-net sampling during the same period (Figure 3.4). Suction trap

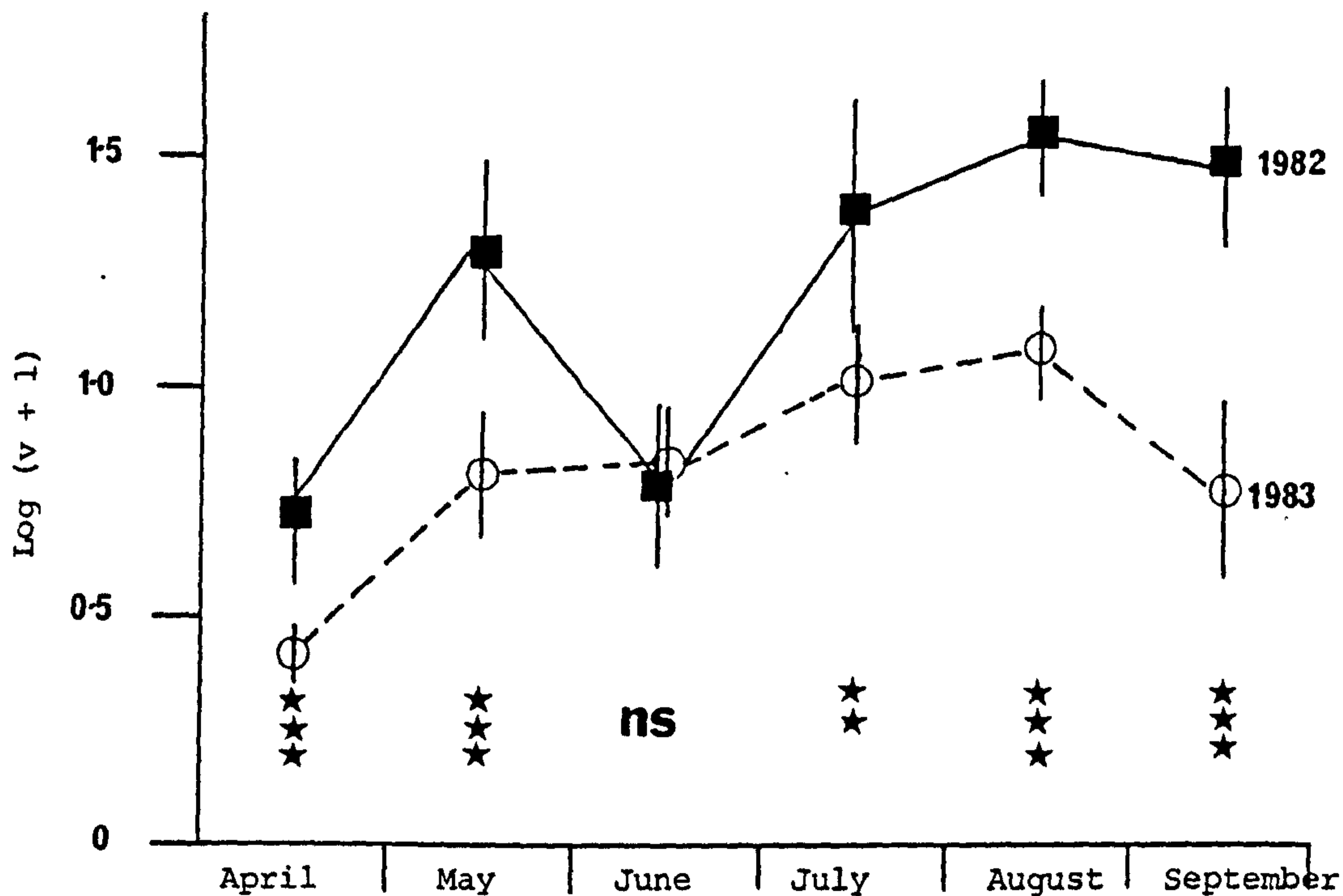


Figure 3.5

Aerial insect abundance as measured by the 12.2m suction trap during 1982 and 1983. Values plotted are means for each month \pm s.d. Asterisks denoted the significance levels of t-tests across months between 1982 and 1982 (ns: not significant; **: $P < 0.01$; ***: $P < 0.001$). 1982 values are represented by closed squares, 1983 values by open circles. Sampling dates were 9th April - 16th September 1982, and 1st April - 20th September 1983.

Table 3.10

A comparison of hand-net catch parameters in 1982 and 1983

Note: ¹A large item is one of ≥ 1.5 mg dry mass.

<u>Parameter</u>	<u>Mean</u>	<u>s.d.</u>	<u>n</u>	<u>t</u>	<u>significance</u>
Biomass (mg dry mass)					
June 1982	29.07	12.99	22	0.72	n.s.
1983	32.28	18.32	27		
August 1982	50.44	19.99	18	0.34	n.s.
1983	52.88	26.74	25		
Number of items					
June 1982	15.83	8.20	22	1.38	n.s.
1983	12.91	6.26	27		
August 1982	19.39	7.91	18	1.53	n.s.
1983	15.85	6.82	25		
Number of large items ¹					
June 1982	5.93	2.54	22	0.46	n.s.
1983	5.48	4.21	27		
August 1982	9.69	3.77	18	4.16	P < 0.001***
1983	5.07	3.33	25		
Mean insect mass, (mg dry mass)					
June 1982	1.93	0.50	22	3.08	P < 0.01**
1983	2.50	0.75	27		
August 1982	2.65	0.71	14	2.76	P < 0.01**
1983	3.52	1.34	25		

catches tended to stabilise at a high level between May and mid-September, while the hand-net catches peaked during mid-July (although suction trap data were transformed, hand-net data were not - see section 3.3.2). Nevertheless, $\log (v + 1)$ and the log of hand-net biomass for afternoon samples on the same day were significantly positively correlated in both 1982 and 1983 (Figure 3.6).

Both suction trap and hand-net catches tended to be greater as maximal daily temperature increased, and this may be partly responsible for the correlation. Both methods yielded larger catches as the season progressed in 1982 (Tables 3.2 - 3.5) probably explaining why the 1982 correlation coefficient is higher than the 1983 value. In 1983 suction trap catches tended to remain relatively stable from June to September, while hand-net catches decreased after mid-July.

A few points on each graph in Figure 3.6 deviate substantially from the line of best fit (for example the three points at the top-left of Figure 3.6a). The hand-net catches were made over a short time period of about twenty minutes, while the suction trap sampled over twenty-four hours. Hence the hand-net catches may be strongly influenced by short-term meteorological changes which may be insignificant over the course of the whole day.

Moreover aerial insects sampled by the suction trap may respond to high temperatures in a different manner from lower-flying forms. On very warm days insects may remain abundant at low levels, but those individuals normally sampled by the suction trap may drift to high altitudes. On very cold days small insects may not rise to the level of the suction trap, whilst hand-net sampling, because of its reliance on striking the tips of vegetation, may have sampled some sluggish insects not available to feeding swallows.

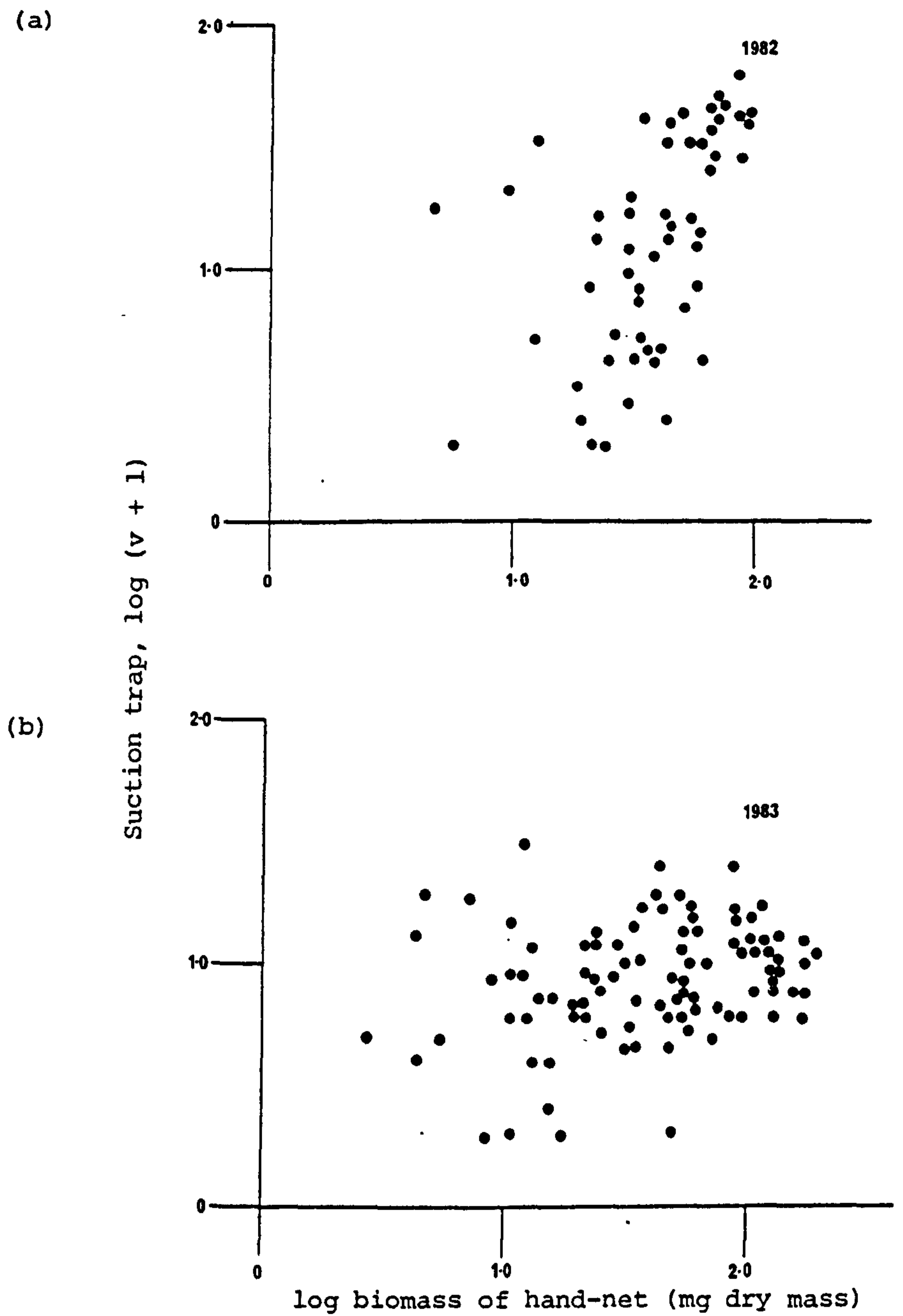


Figure 3.6

Comparison of afternoon hand-net catches and suction trap catches.

(a) 1982 : $r = 0.61$, $n = 54$, $P < 0.001$.

(b) 1983 : $r = 0.21$, $n = 95$, $P < 0.05$.

3.3.5 A summary of factors influencing the resources available for breeding hirundines

Both suction trap volumes and hand-net catches differed in their response to environmental conditions between 1982 and 1983, and it would therefore be difficult to generalise about factors influencing insect availability.

Nevertheless, suction trap catches in both years were greater later in the season and at higher maximal daily temperatures (Tables 3.1, 3.2). Hand-net catches were influenced by environmental conditions in a less consistent manner between years than were the suction trap catches. Seasonal effects may have been different in the two years of study (Figures 3.3, 3.4). However, increasing maximal daily temperature tended to increase the biomass of, the number of items in, and number of large items in the catches, while increasing windspeed and rainfall tended to reduce these parameters (Tables 3.4 to 3.7). Mean available insect mass in the hand-net catches tended to increase over the season in both 1982 and 1983 (Tables 3.8, 3.9).

3.4 DISCUSSION

Both suction trap (Figures 3.1, 3.2, 3.5) and hand-net catches (Figures 3.3, 3.4, Table 3.10) show considerable variation from day to day and between the two years of the study. Hence both martins and swallows are likely to encounter an unpredictable food supply both in the long-term and in the short-term. Williams (1962) found that night-flying Diptera catches in suction traps were influenced by minimal temperature and windspeed, and that annual catches were influenced by long-term variation in minimal temperature and rainfall over the previous three months.

Martins are likely to encounter more unpredictable feeding conditions than swallows since insects sampled at the height of the suction trap are more sensitive to weather changes than lower-flying insects sampled by the hand-net, and aerial insect density is generally higher closer to the ground (Waugh, 1978).

Although both methods of insect sampling probably reliably quantify the amount of insect prey available to breeding hirundines, prey nutrient content may sometimes be more important than overall prey abundance at certain stages of the nesting cycle. For example, specific amino-acids (Jones and Ward, 1976) or calcium (Jones, 1976; Schifferli, 1976) may be important constituents of a female bird's diet during the laying period, and hirundines may actively search for prey containing large quantities of such nutrients for egg formation. Female pheasants, Phasianus colchicus, select calcareous grit for ingestion during laying (Kopischke, 1966), and North American barn swallows supply calcium rich grit to young nestlings (Barrentine, 1980).

Below, two aspects of the nature of the unpredictable food supply for swallows and martins are discussed. Firstly some implications of low levels of food abundance on hirundine feeding behaviour and body condition are covered. Secondly the implications of short and long-term fluctuations in food supply for hirundine breeding biology is investigated.

3.4.1 The implications of low levels of food abundance on hirundine feeding behaviour and body condition

In poor weather, when aerial insects are scarce, swallows and martins modify their feeding behaviour to exploit profitable food patches. On days of low food abundance martins tend to feed at lower levels where aerial insect density may be higher, and hirundines

frequently feed in areas where most insects still fly in poor weather, for example, behind shelter belts, over fresh water, or near to domestic stock, where sluggish insects may get disturbed (Waugh, 1978).

During poor weather the rates of energy gain by hirundines are reduced (Turner, 1982a), so several days of low insect availability would be expected to reduce adult body reserves, and maybe jeopardise clutch or brood survival. This problem is discussed in more detail in Chapters 7 and 8 for incubating and nestling rearing swallows. There are several lines of evidence showing that prolonged bad weather severely affects hirundine fitness through affecting brood or adult condition and survival.

Body mass of incubating and nestling-feeding swallows is positively correlated with temperature and insect abundance, birds becoming lighter at low temperatures when insects are scarce (Chapter 7). Low body mass in incubation may lead to clutch desertion, and indeed, three swallow clutches (under 5% of total clutches recorded) were deserted in bad weather during the study.

The level of insect abundance also affects the timing of laying in British hirundines (Bryant, 1975b; Turner, 1982a), and house martins may suspend or interrupt laying in poor weather (Bryant, 1979). If bad weather persists, house martins and swallows sometimes lay fewer eggs than usual, and such small clutches can later be deserted (D. M. Bryant, pers. comm., pers. obs.). Most hirundine mortality in the breeding season is associated with poor weather (Rheinwald, 1970; Bryant, 1975b, 1979), and a female swallow found dead with an incomplete clutch during the study was discovered during a cold spell when a nearby pair deserted a newly hatched brood. Although most mortality of sand martins nesting in Britain occurs outside of the breeding

season, the highest mortality of summering birds appears to be in spring and early summer (Mead, 1979), before aerial insect levels have reached relatively high, stable levels. Early arriving sand martins may have large fat reserves to buffer against bad weather (Chapter 5), but the birds run a high risk of encountering food shortages in the early season (Turner, 1982a).

Hence low levels of food abundance may influence hirundine fitness through reducing fecundity (time costs of suspended layings, clutch desertions, brood deaths), or by directly affecting adult survival.

3.4.2 The implications of short and long term fluctuations in food availability for hirundine breeding biology

If available resources vary from day to day, it will pay for adult hirundines to carry substantial fat reserves to buffer against periods of food shortage. However, carrying large quantities of fat will increase the flight costs of birds by increasing their wing loadings, so the insurance benefits of fat reserves must be weighed against the energetic costs of carrying the fat (Chapter 8).

Chicks will also be expected to show adaptations to overcome temporary food shortages. Another aerial insectivore, the swift, Apus apus, which forages at greater heights than swallows and martins, and is hence subjected to an even more unpredictable food supply, has chicks which can reduce their metabolic rate during food shortages, and become torpid (Koskimies, 1950). The amount of fat carried by chicks of British hirundines and the swift increases with parental foraging height (Bryant and Hails, 1983).

The annual fluctuations in aerial insect abundance will also have implications for resource allocation in aerial insectivores. If

year to year environmental conditions are unpredictable at the time of reproduction, making too early or too large a reproductive effort may result in a complete failure, whereas laying a smaller clutch later on would result in some young being produced. Such restrained reproductive effort, or hedging bets in the face of uncertainty, has been expounded by Cohen (1967), Boer (1968), and Mountford (1973), and may explain why tree swallows given enlarged broods do not suffer an increased mortality cost (De Steven, 1980).

CHAPTER · 4

4. PHYSIOLOGICAL ASPECTS OF SHORT-TERM

BODY MASS CHANGES IN BIRDS

4.1 INTRODUCTION

Wild birds normally undergo characteristic changes in body mass over the course of the annual cycle. Published studies include those of Newton (1972) on bullfinches, Pyrrhulla pyrrhulla, Owen and Cook (1977) on mallards, Anas platyrhynchos, Coulson et al., (1983) on herring gulls, Larus argentatus, Wijnandts (1984) on long-eared owls, Asio otus, and the work of Newton, Marquiss and Village (1983) on sparrowhawks, Accipiter nisus.

Breeding birds also tend to follow characteristic patterns of mass change (e.g. house martins (Bryant, 1975a), pied flycatchers (Silverin, 1981), house wrens, Troglodytes aedon, (Freed, 1981), kestrels (Village, 1983), and sparrowhawks (Newton et al., 1983).

Long-term changes in body mass within individual birds during breeding mainly reflect changes in fat and protein reserves (Jones and Ward, 1976), Fogden and Fogden, 1979), and changes in the mass of reproductive structures (Petersen, 1955). Little work has been performed on how such coarse variation over the long-term relates to short-term variation caused by changes in rates of food consumption, defaecation, metabolic water loss, and gaseous exchange. If birds are to optimise their behaviour with respect to long-term interests of surviving and reproducing, they can be expected to make behavioural decisions over changes in their condition manifested by short-term body mass changes (Drent and Daan, 1980). Hence, a detailed knowledge of the nature and mechanisms of short-term body mass changes in birds may provide a useful background for interpreting behavioural decisions which may contribute towards a bird's fitness (Chapters 7, 8, 9).

The aim of this Chapter is to analyse the factors responsible for short-term body mass changes in canaries, Serinus canarius, in laboratory conditions, and to provide a scale for the relative importance of the pathways of mass intake and output. A model of diurnal mass changes in canaries is developed, and some comparative laboratory work on short-term mass changes in sand martins is also presented.

The understanding of short-term mass changes developed from laboratory studies is applied to the study of a free-living, breeding bird, the swallow. A knowledge of the factors responsible for short-term mass changes allows energy balance data to be collected from breeding birds by the use of precision automated nest balances.

4.2 MATERIALS AND METHODS

4.2.1 Laboratory studies

(a) The balances

Two Mettler PK2000 electronic balances were used in the study. The balances have an accuracy of $\pm 0.01\text{g}$ and a capacity of 2000g. They incorporate an animal weighing function which averages weighings taken over an adjustable interval of 0.8 to 6 seconds, minimising mass fluctuations caused by movements. In all cases the balances were operated from a mains supply.

The accuracy and consistency of the balances was tested in the laboratory. Twenty swallow carcasses were individually thrown onto a pan placed on a Mettler balance, and weighings were recorded after five seconds, the minimum interval normally used in the field and laboratory. The same carcasses were then weighed on an Oertling electronic balance accurate to 0.0001g, underneath a draught shield.

The Mettler weighings differed on average by $0.0076 \pm 0.00005g$ from the Oertling weighings, despite being made only 5s after being thrown onto the Mettler pan.

Several accessories were used with the balances. A manual control button prompted the animal weighing function from a distance. This was later incorporated into an automatic timer built by Stirling University Shared Technical Services, allowing automatic remote prompting of the animal weighing function on a timescale ranging from five seconds to ten minutes. A remote taring foot pedal was also used. Data were collected on Mettler GA40 Thermal Printers. The apparatus is illustrated in Plate 4.1.

(b) Laboratory studies of canaries

Canaries were kept individually in a $3m^3$ aviary in a constant temperature room where temperature and photoperiod could be accurately controlled, and were trained to perch on a metal ring suspended from a Mettler balance. Photoperiod was kept constant at 12h light/12h dark throughout the study, and dark period temperature was always $10^\circ C$. Light period temperature was maintained at either $15^\circ C$ or $30^\circ C$. Canary seed and water were supplied ad libitum. A total of seven different canaries were used in the laboratory studies.

(c) Incubator studies

Rate of mass loss was recorded for post-absorptive canaries and sand martins maintained at constant temperature in a darkened incubator. The configuration of the apparatus is illustrated in Figure 4.1. Birds were allowed to equilibrate for one hour, except at extreme temperatures where prolonged exposure may harm the birds. Hence at $0^\circ C$, and temperatures above $35^\circ C$, only 30 minutes equilibration time was allowed. Rate of mass loss reached constant levels



Plate 4.1

Precision automated Mettler electronic balance (PK2000) and accessories used in the study.

A : Mettler PK2000 electronic balance

B : Mettler GA40 data printer

C : Remote animal weighing activation button

D : Remote taring pedal

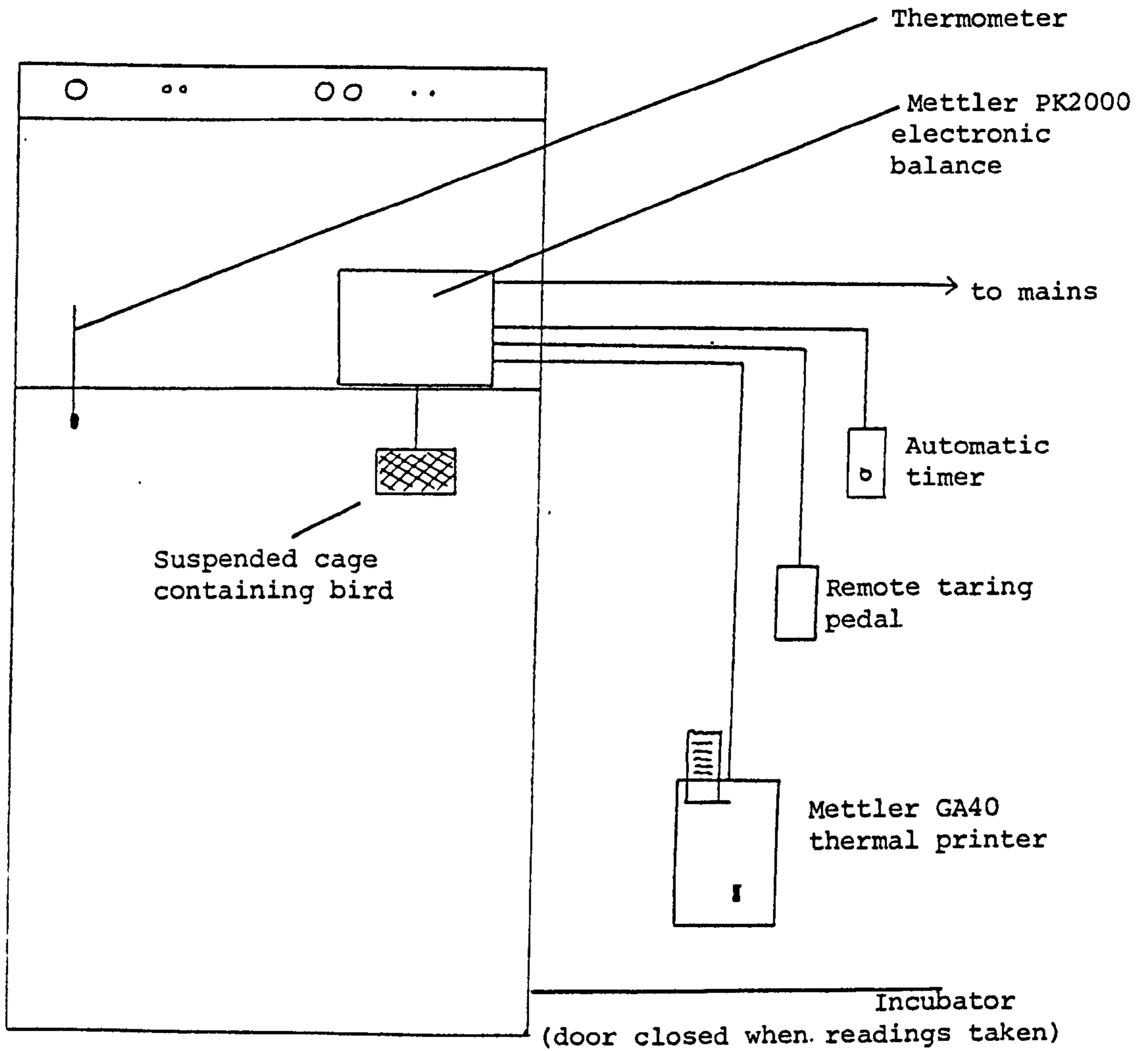


Figure 4.1

Apparatus for measuring mass loss of birds in laboratory conditions.

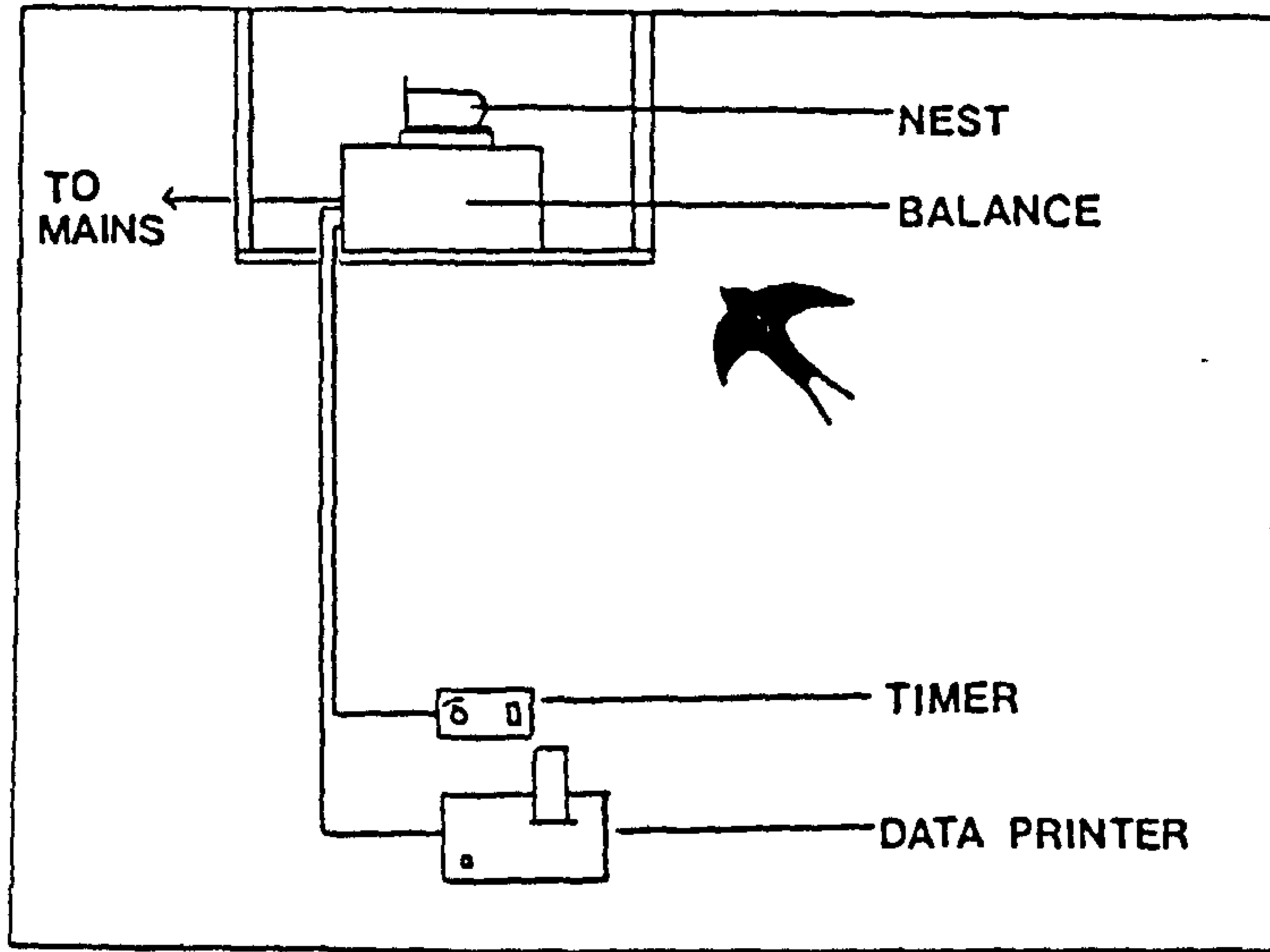
after 30 minutes for all temperatures considered.. Sand martins were brought to the laboratory after being captured at dawn, and were kept at room temperature until equilibration.

(d) Field techniques

Swallow nests were removed from beams in barn roofs, and placed on the balances during the incubation period. The apparatus was supported by planks, and the nests were attached to the balance pan by cementing them to hardboard platforms with evo-stick adhesive and moistened plaster of paris. Nests were chosen to be near to an electricity supply, to be sheltered from draughts, and to be observable from a concealed position. The configuration of the field apparatus is shown in Figure 4.2 and a nest balance is illustrated in operation in Plates 4.2 and 4.3.

Nests were observed from a hide some 10 metres distant, and parent birds were colour marked and ringed when captured. Wing-length (maximum chord, measured to the nearest 0.5 mm), and keel-length (measured to the nearest 0.1 mm) were recorded. Birds were sexed by plumage and brood patch criteria (Svensson, 1975), and their fat reserves were quantified using a 12 point scoring system on fat deposits in the tracheal pit and on the bottom edge of the keel (modified from Bryant and Westerterp, 1983a, elaborated in Chapter 2).

Only the female swallow has a well developed brood patch, and the female was the only sex seen to perform functional incubation during the study. However, barn swallows in North American often show functional incubation by the male (Ball, 1983a, b), and male swallows in the study area occasionally stood over the nests for several minutes (pers. obs.).



AUTOMATED NEST BALANCE SYSTEM

Figure 4.2

Automated nest balance in position in the field.

Plates 4.2 and 4.3

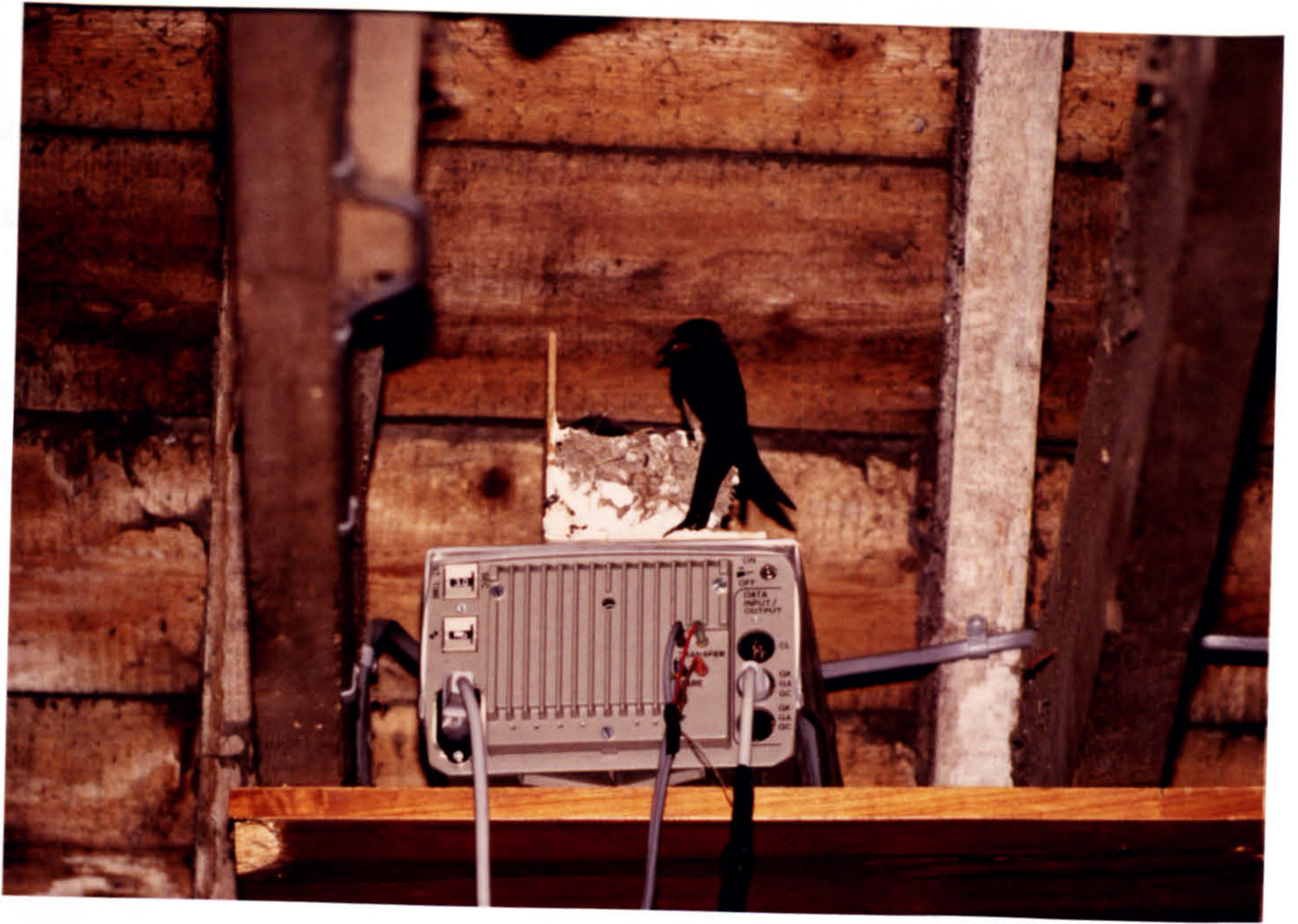
Automated nest balances in operation in the field.

Plate 4.2

Female swallow feeding small chicks.

Plate 4.3

Brood of five c. 16 day old chicks awaiting feeding.



During the incubation and brooding phases of the nesting cycle, female swallows have a limited behavioural repertoire of nest attendance and foraging, though they may spend some time perching at high temperatures (pers. obs.). Hence time budgets of birds during incubation were obtained from direct observation at nests, and from data collected by the automated timer, when incubation and flying were assumed to be the only activities performed by females. Observation periods lasted for at least one hour (range 1h - 4h).

The limited behavioural repertoire of swallows, their nesting in sheltered situations, their tolerance of disturbance, and their discrete nest cups make them amenable birds to study with nest balances. Because the birds deliver food to their nestlings in discrete boluses, and because swallow insect prey can readily be sampled (Chapter 3), precision nest balances can also give an insight into the birds' foraging behaviour over the breeding season (Chapter 8). The accuracy of the balances allows data to be accumulated on short-term body mass changes of adults, changes in brood mass, and allows measurement of bolus masses delivered to and faecal masses removed from the chicks.

Although adult masses were easily obtained when the chicks were young, because the adults tended to spend considerable time at the nest, body mass on later visits was difficult to monitor because food was often delivered to the brood fractionally before the parents landed. Adult masses were only recorded if two consecutive animal weighings within 0.02g of one another were obtained within 10s or if five consecutive masses within 0.02g of one another were recorded in 10s when the animal weighing system was not in use.

Body mass of adult birds tends to increase over the course of a day, as the birds feed to accumulate reserves which are metabolised overnight (Clark, 1979, results this chapter). Hence weighings and observations were made at a standardised time of day, between 14.00h and 16.00h B.S.T.

Balances were placed underneath 17 different swallow nests for a total of 368 nest days. Of these, 104 days of incubation data were collected (86 control, 18 experimental days), 110 days of nestling feeding to control broods, and 154 days of nestling feeding to experimentally manipulated broods.

4.3 THEORY AND RESULTS

4.3.1 A model of canary body mass changes : theory

Changes in a bird's body mass should be predictable if the routes and quantities of mass inputs and output are known. The theory is based on the Principle of the Conservation of Matter.

1. Mass inputs are:

- (a) Food consumption (C)
- (b) Water ingestion (D_r)
- (c) Oxygen consumption (O_2)

2. Mass outputs are:

- (a) Faecal and urinary output (FU)
- (b) Evaporative water loss (EWL)
- (c) Carbon dioxide output (CO_2).

A schematic representation of the routes of mass input and output through a bird is presented in Figure 4.3. Oxygen is consumed for metabolism, and in birds the commonest metabolic substrate is fat, because of its high energy yield per unit mass (Pond, 1981). A high

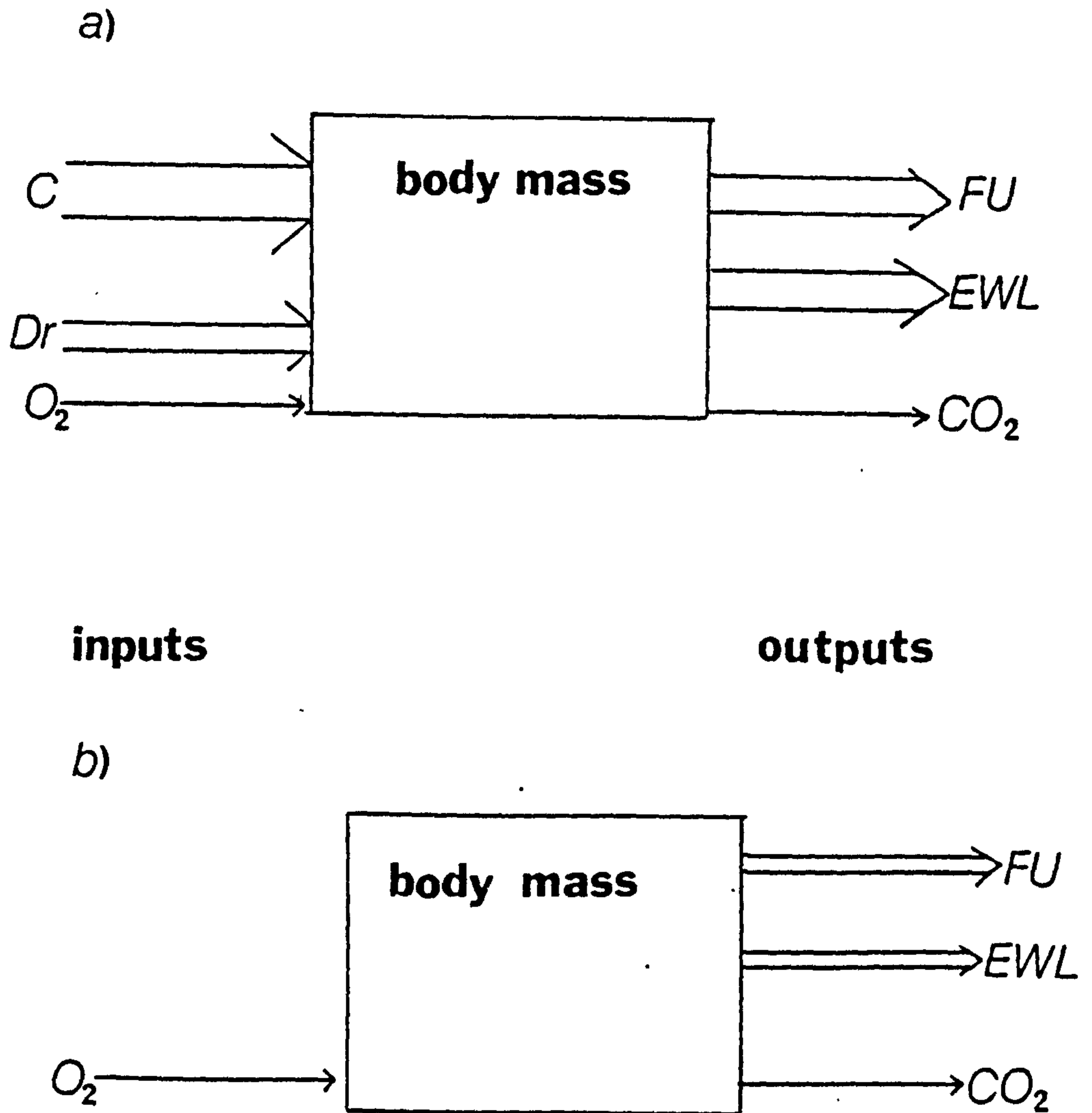


Figure 4.3

Schematic representation of the routes of mass input and mass output through a bird.

(a) during the active period

(b) during roosting.

inputs: C - food consumption
 Dr - water intake
 O_2 - oxygen consumption

Outputs: FU - defaecations
 EWL - evaporative water loss
 CO_2 - carbon dioxide production

energy substrate with low mass is especially important for flying organisms, since increased body mass can result in increased power requirements for flight (Norberg, 1981).

Carbon dioxide and water occur as by-products of fat metabolism, and evaporative water losses may occur either cutaneously or through the respiratory tract (Dawson, 1982). Water may be lost either evaporatively, or through faecal output, and most food consumed was assumed to be converted to fat rather than being catabolised directly (R.Q. assumed to be 0.73, section 4.3.2).

If a bird has an R.Q. of 0.73, typical of fat metabolism, the mass of oxygen consumed is balanced by the mass of carbon dioxide produced, so 1(c) cancels out 2(c) in the list of mass inputs and outputs (Lasiewski, Acosta and Bernstein, 1966).

Therefore, assuming a bird has an empty gut in the morning, as was found from sand martin carcass analysis, its body mass at roosting time (M_R) should be predictable by equation 4(1).

$$\frac{M_R}{\text{Mass Inputs}} = \frac{(C + Dr) - (FU + EWL)}{\text{Mass Outputs}} \quad \text{Equation 4(1)}$$

where C, Dr, FU and EWL are summed values for the active period.

The factors in equation 4(1) were quantified as below:

(a) Rate of mass increase while foraging

This was determined by time budgeting the bird in the aviary, behaviours being monitored every minute. Hence the percentage time during each hour's observation period spent foraging (%F) could be calculated. The intake rate of husked seeds (I) was also recorded by direct observation. Since canaries husk seeds before eating them, the average mass of 100 husked seeds was determined as 0.0073g.

Thus hourly mass intake through foraging (Ch^{-1}) could be calculated by equation 4(2).

$$Ch^{-1} = \%F \times I \times 0.0073g \quad \text{Equation 4(2)}$$

(b) Rate of mass increase through drinking

This was not measured directly, but calculated as below.

At 15°C a linear relationship between length of foraging period and mass increase while foraging was obtained for foraging periods when the bird was not seen to drink. A linear relationship with a steeper slope was obtained for length of foraging period, including drinking bouts plotted against mass increase through foraging and drinking. Regression lines for both relationships were highly significant ($P < 0.01$). EWL was assumed to be the same in foraging bouts of defined length regardless of whether or not drinking occurred. Mass increase through drinking was calculated as the difference between the predicted values from the two regression lines at the mean length of foraging period when drinking occurred.

(c) Rate of mass decrease through defaecation was measured directly. Fortunately almost all defaecations occurred when canaries were perched. Mass loss through defaecation corresponded exactly with the mass of faeces voided for five droppings weighed within one minute of defaecating. Hourly defaecation rate (FUh^{-1}) was calculated from recording the mean number of defaecations per hour, and multiplying this by mean faecal mass. Mean faecal mass was significantly heavier at 15°C than at 30°C (15°C : $0.0599 \pm 0.0188g$, 30°C ; $0.0536 \pm 0.020g$, $n = 133$, $t = 1.91$, $P < 0.05$) though there was no significant difference in defaecation rate between the two temperatures ($3.75 \pm 1.18 h^{-1}$ at 15°C, $3.34 \pm h^{-1}$ at 30°C, $P > 0.1$).

(d) Rate of mass loss through evaporative water loss was recorded directly when the birds were perched. Regression equations were calculated to obtain values of EWL $\text{mg}\cdot\text{min}^{-1}$. Evaporative water loss while foraging was calculated as (observed mass increase while foraging - predicted mass increase through seed intake) for foraging bouts which did not include drinking bouts or defaecations.

4.3.2 Laboratory studies: short term body mass changes in canaries and sand martins

(a) Diurnal body mass changes in canaries

The pattern of diurnal body mass change for two canaries over three temperatures is shown in Figure 4.4. Body mass tends to increase relatively rapidly over the first four hours of the light period, thereafter the rate of increase is less rapid. The best fit line describing average diurnal mass changes at both 15°C and 30°C was one where both mass and time were transformed to \log_e . Equations are given in the legend to Figure 4.4.

Figure 4.5 shows that this initial rapid increase in mass can be accounted for by an initially high rate of food consumption. At both 15°C and 30°C intake rates were highest during the first two hours of the light period. This was due to a higher seed intake rate rather than an increase in foraging time during the early period, since percentage of time spent foraging was not correlated with time of day ($r = 0.15$, $n = 24$, $P > 0.2$). The mean percentage diurnal mass gain (\pm sd) at 15°C was $5.45 \pm 2.20\%$ ($n = 8$), and $5.49 \pm 0.32\%$ ($n = 3$) at 30°C.

(b) Short-term body mass changes in captive canaries

Although the trend over a day is for birds to increase in mass, the overall net increase is composed of a series of short-term mass changes, as illustrated in Figure 4.6. Birds increase in mass

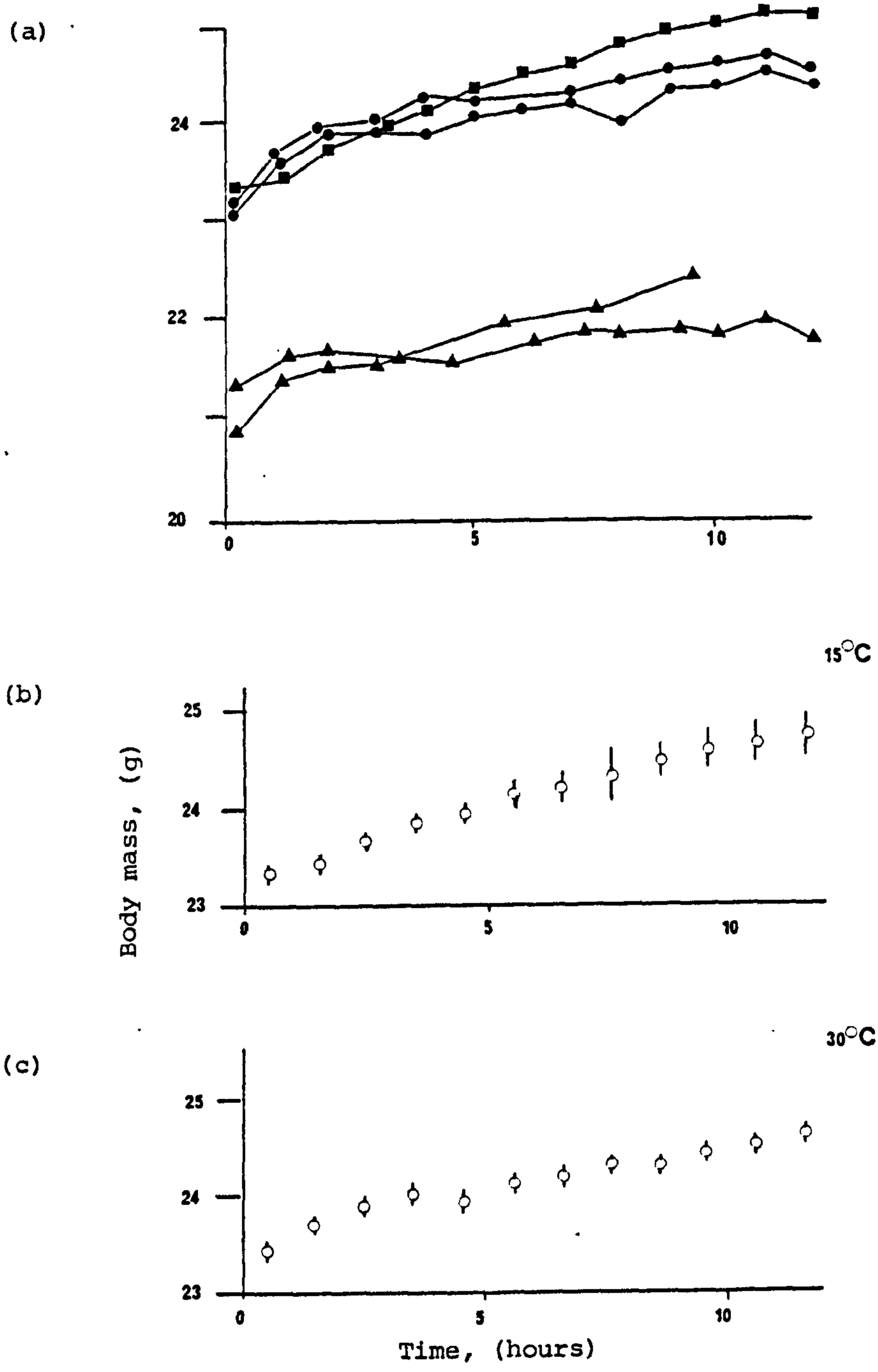


Figure 4.4

Diurnal body mass changes of two captive canaries.

(a) Data for individuals:

circles; canary 1, 30°C
squares; canary 1, 15°C
triangles; canary 2, 10°C

(b) Averages for hourly periods (\pm sd) at 15°C.

The data is described by
 $\ln y = 3.01 + 0.07 \ln x$, $F = 121$, $n = 53$, $P < 0.001$.

(c) Averages for hourly periods (\pm sd) at 30°C.

The data is described by
 $\ln y = 3.04 + 0.06 \ln x$, $F = 218$, $n = 36$, $P < 0.001$.

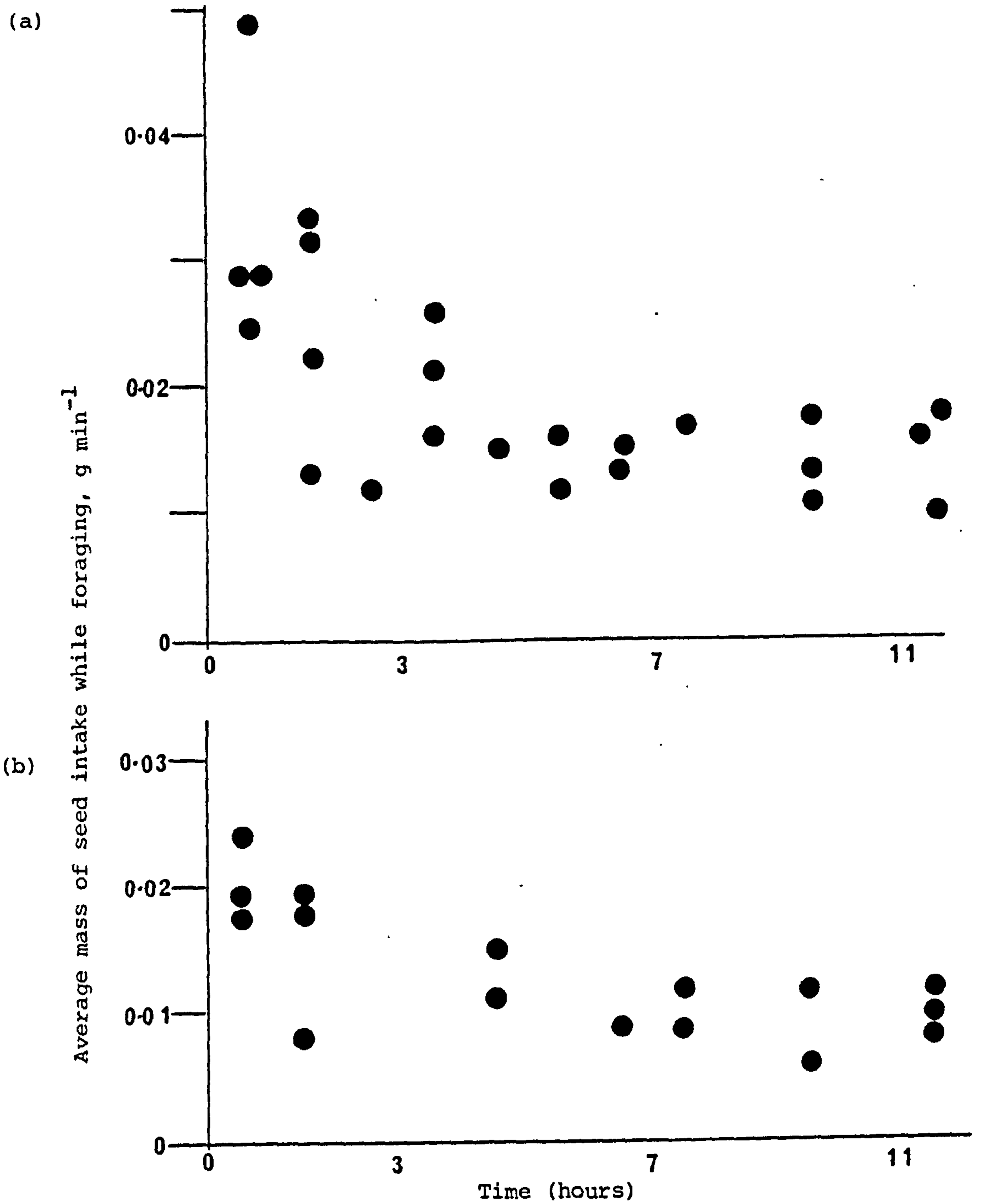


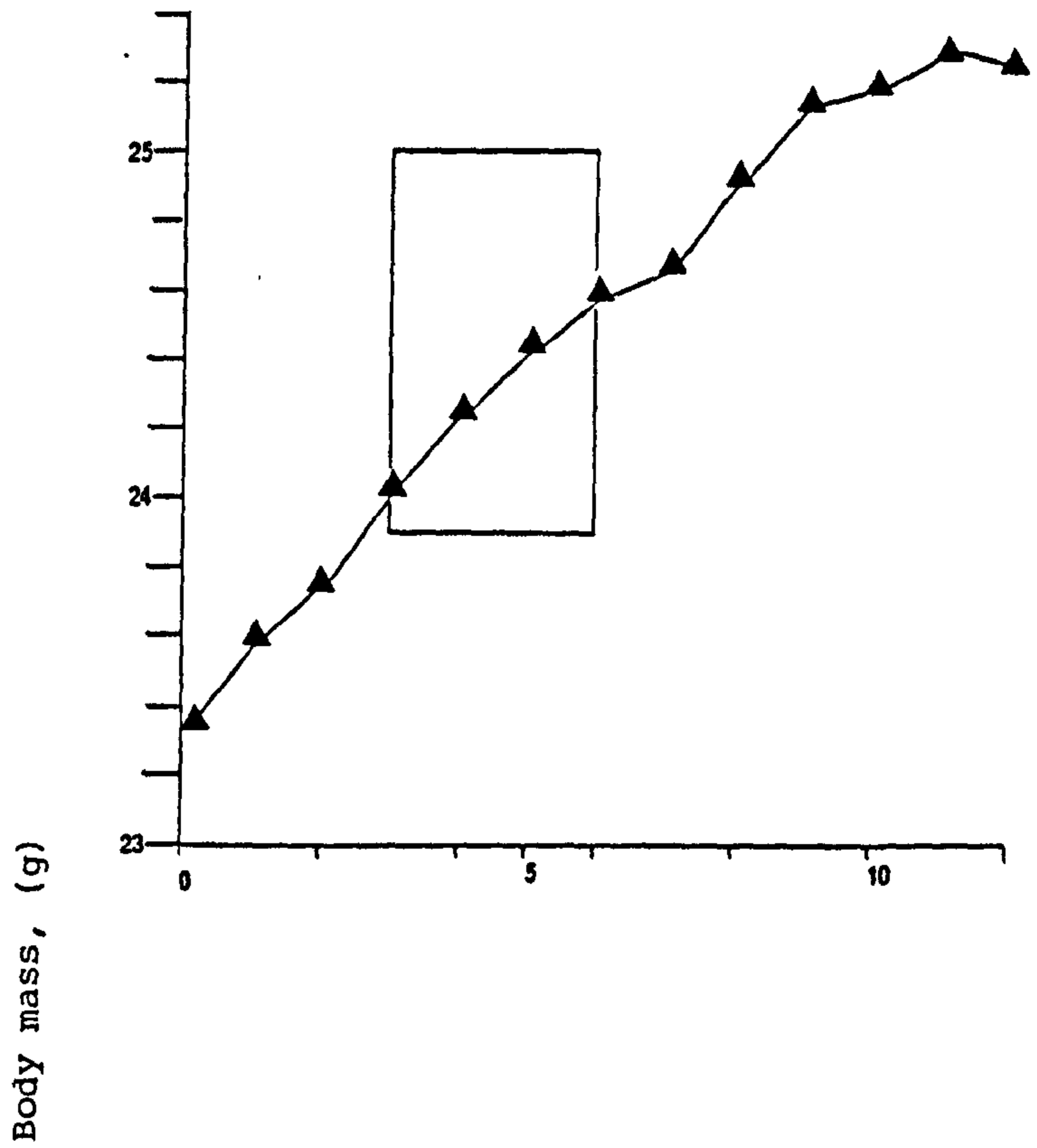
Figure 4.5

Seed intake rates for canary 1 over the active period.

(a) 15°C : $\ln y = -1.86 - 0.87 \ln x$; $F = 20.1$, $n = 24$, $P < 0.001$.

(b) 30°C : $\ln y = -2.75 - 0.66 \ln x$; $F = 8.2$, $n = 16$, $P < 0.01$.

(a)



(b)

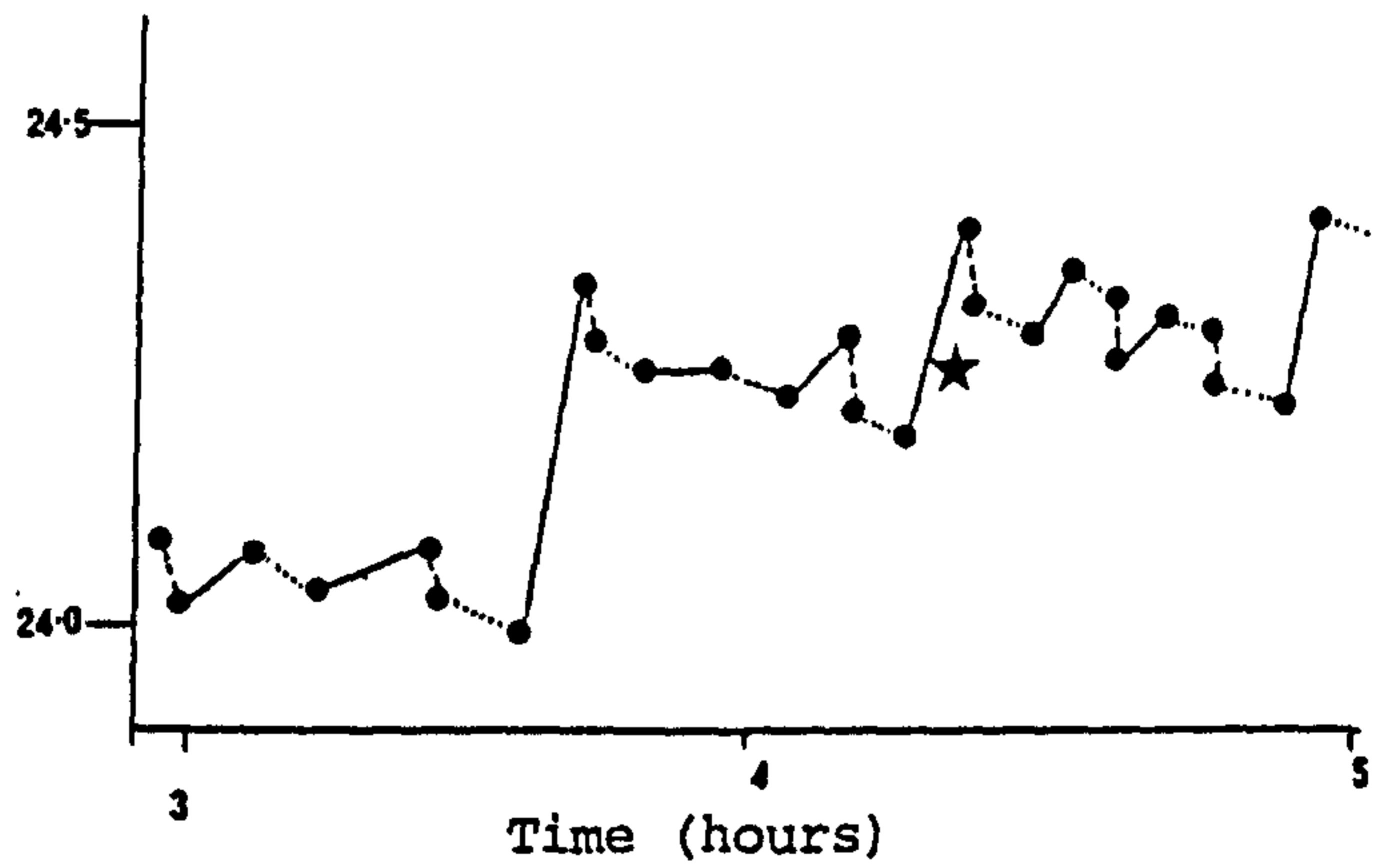


Figure 4.6

(a) Diurnal body mass changes of canary 1, 15°C

(b) Inset (box on Figure 4.6a).

Short term body mass changes over a two hour period.

..... evaporative water loss while perched.

———— mass increase while foraging. Drinking bout represented by asterisk.

----- mass loss through defaecating.

through feeding and drinking, lose mass at all times through evaporative water loss, and lose mass instantaneously through defaecating.

(c) Overnight body mass changes in canaries

Birds lose mass continuously while roosting through evaporative water loss, and may also defaecate. The mean overnight mass loss (\pm s.d.) of seven canaries at 10°C was $5.02 \pm 1.82\%$ ($n = 29$). Hence the birds lost almost as much mass roosting at 10°C as they gained during the day at 15°C or 30°C .

The pattern of overnight mass loss for three birds is shown in Figure 4.7, and the mass losses while perched and through defaecating are illustrated.

(d) Short-term continuous mass losses

When canaries are perched, either during the light period or when roosting at night, they continuously lose mass. Such mass loss could either be metabolic, whereby the mass of carbon dioxide expired exceeds the mass of oxygen inspired, or could represent evaporative water loss, the water being a by-product of metabolism. Both rates of mass loss may be operative, and the observed mass loss a balance between the two processes. However, as mentioned in Section 4.3.1, if the canaries are functioning with a respiratory quotient of 0.73, the mass of carbon dioxide expired should balance the mass of oxygen inspired, and any mass loss should represent evaporative water loss. The mean R.Q. of canaries studied by Benedict and Fox (1933) was 0.79 ± 0.01 ($n = 22$), that of yellow buntings, Emberiza citrinella, fed on canary seed 0.69 (Wallgren, 1954). Hence an assumption of an R.Q. near to 0.73 in this study seems reasonable.

To investigate the nature of continuous short-term mass losses

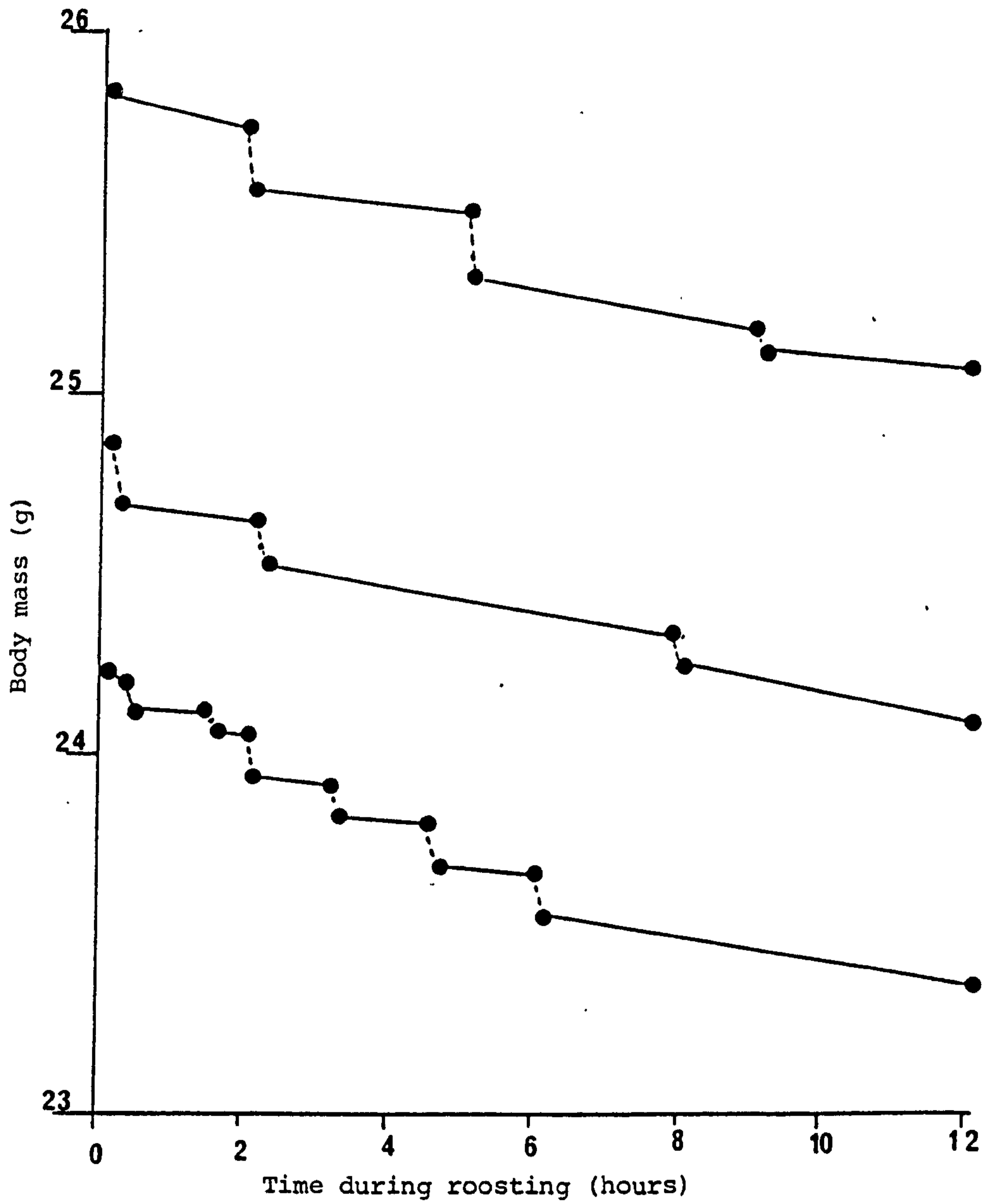


Figure 4.7

Overnight body mass losses of three roosting, perched canaries at 10°C.

— : mass loss while perched.

- - - : mass loss through defaecating.

in more detail, post-absorptive canaries were placed in an incubator at constant temperature and rate of mass loss recorded, defaecations being excluded. Rate of mass loss as a function of temperature in canaries is illustrated in Figure 4.8.

The plot follows a characteristic evaporative water loss/temperature plot (Lasiewski et al., 1966; Moldenhauer, 1970), with little variation in the rate of mass loss below the thermoneutral zone. Above the thermoneutral zone, rate of mass loss increases rapidly with increasing temperature as the birds attempt to maintain body temperature by dissipating heat through cutaneous and respiratory water loss.

A similar plot of rate of mass loss as a function of temperature is shown for post-absorptive sand martins in Figure 4.9, and again a characteristic evaporative water loss/temperature plot is generated, with a sharp rise in the rate of mass loss at temperatures above 28-34°C.

(e) Continuous mass losses and activity

In Figure 4.10(a), rate of mass loss is plotted for a range of activities in canaries. Roosting and post-absorptive data were collected in an incubator maintained at constant temperature, whilst the data for active, perched canaries comes from the aviary birds in a constant temperature room.

A t-test matrix for mean rates of mass loss in canaries performing a range of activities is presented in Table 4.1. All differences between means were significantly different, except for the difference between mean rates of mass loss while roosting at 10°C and 25°C, where the sample size was small. Mean rate of mass loss while

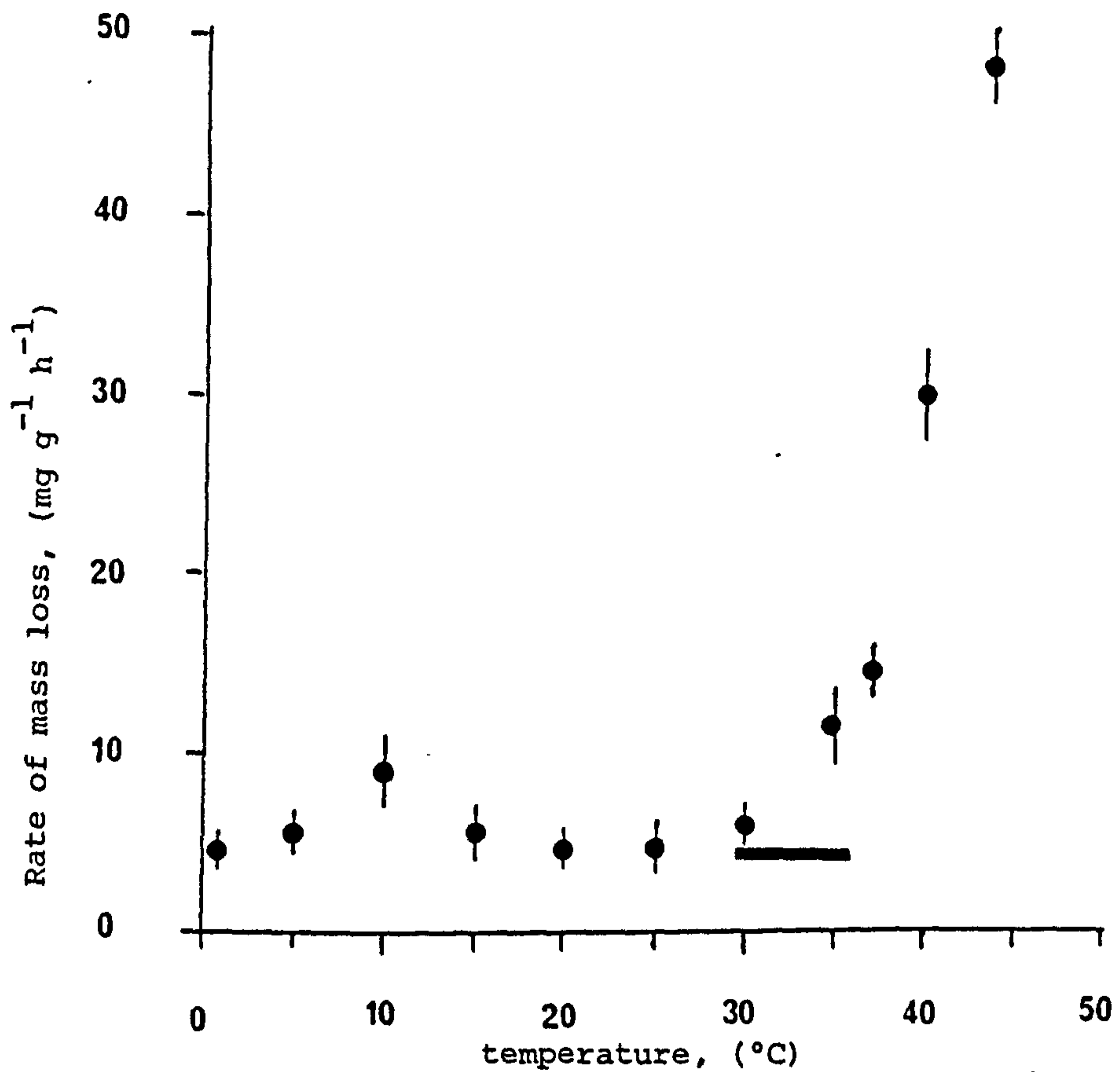


Figure 4.8

Rate of mass loss as a function of temperature for seven post-absorptive canaries maintained at constant temperature in an incubator.

Means \pm sd illustrated. The thick black line represents the thermoneutral zone (from Whitlock, 1979).

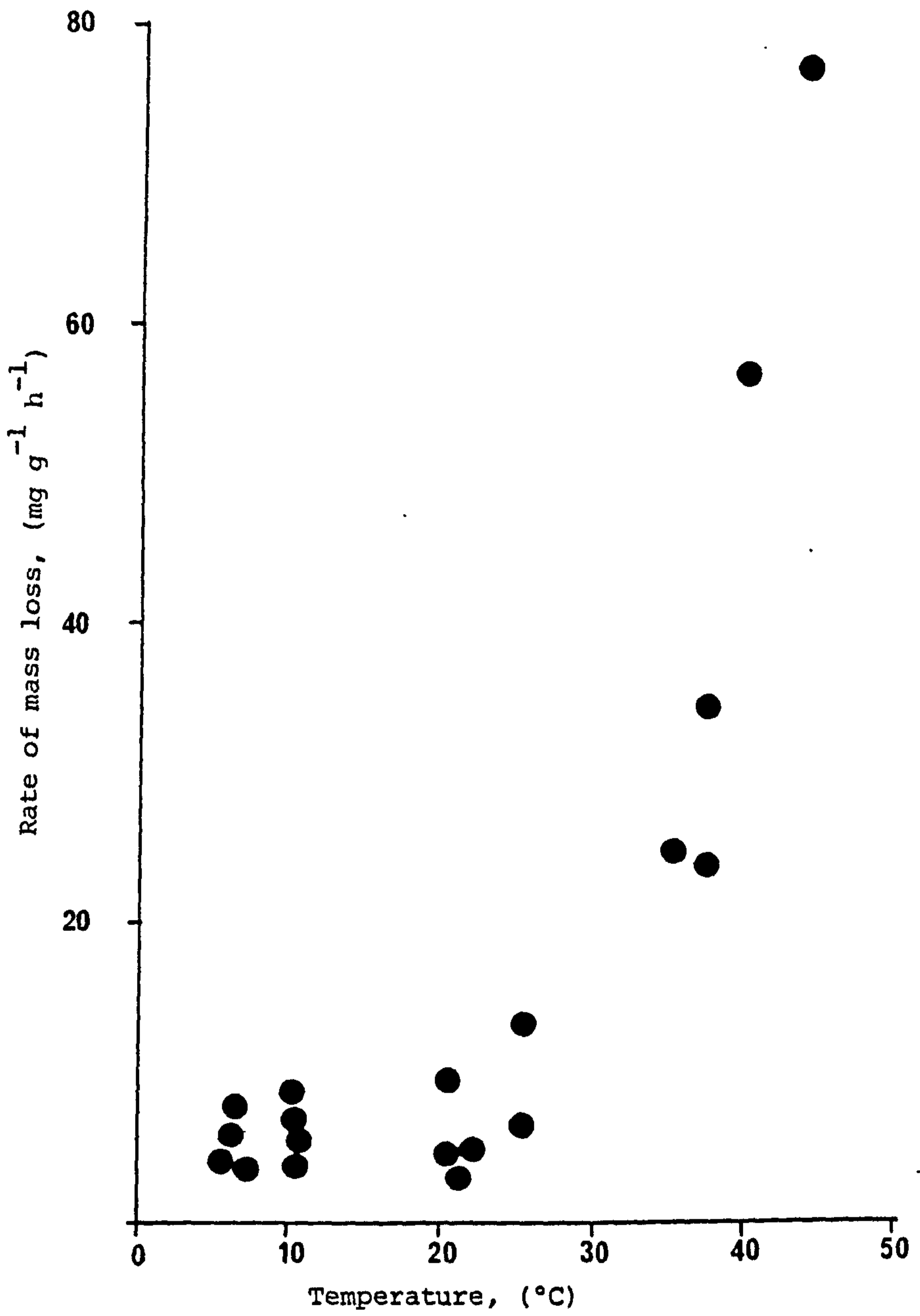
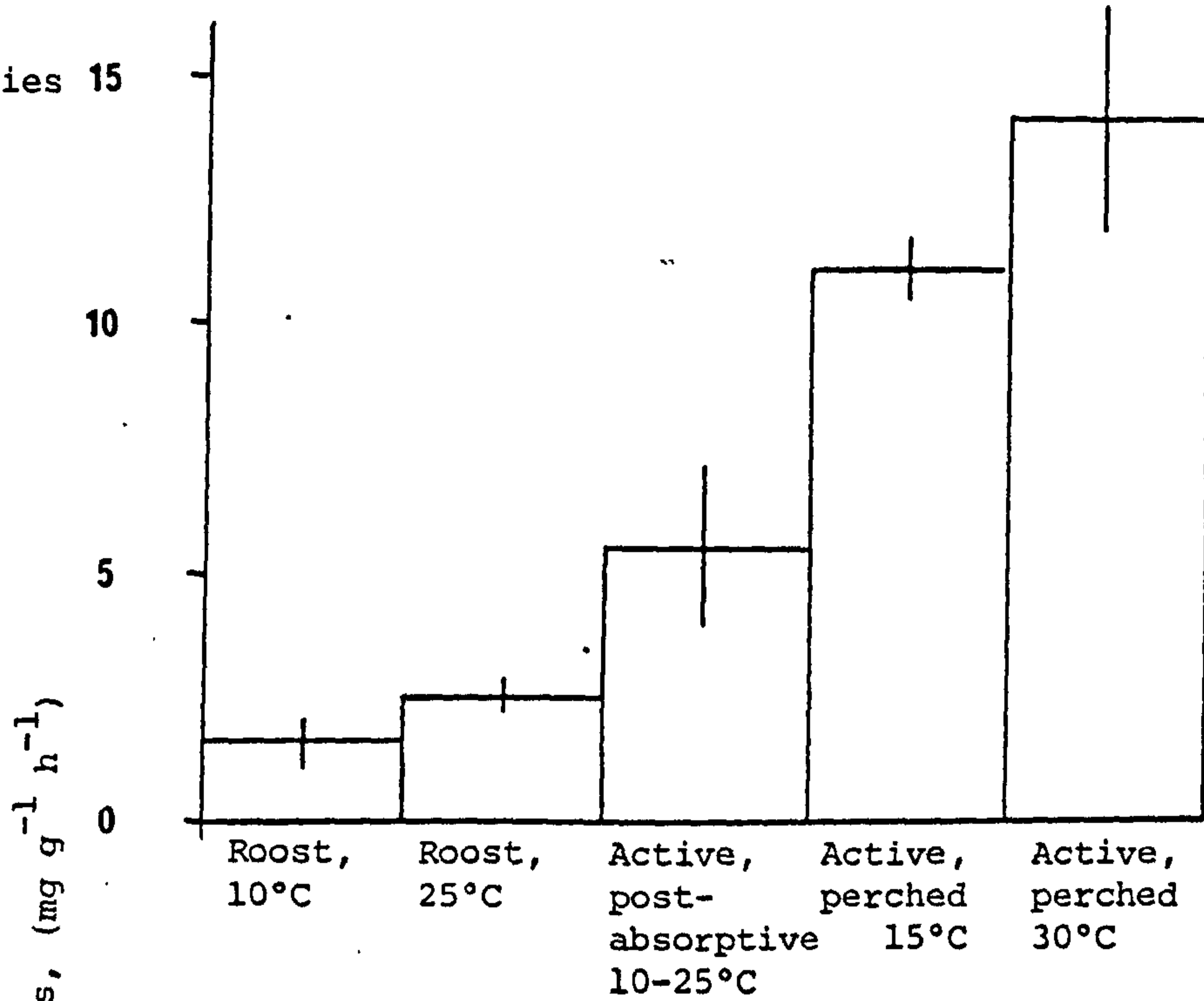


Figure 4.9

Rate of mass loss as a function of temperature for post-absorptive sand martins maintained at constant temperature in an incubator.

(a)
Canaries 15



(b)
Swallows

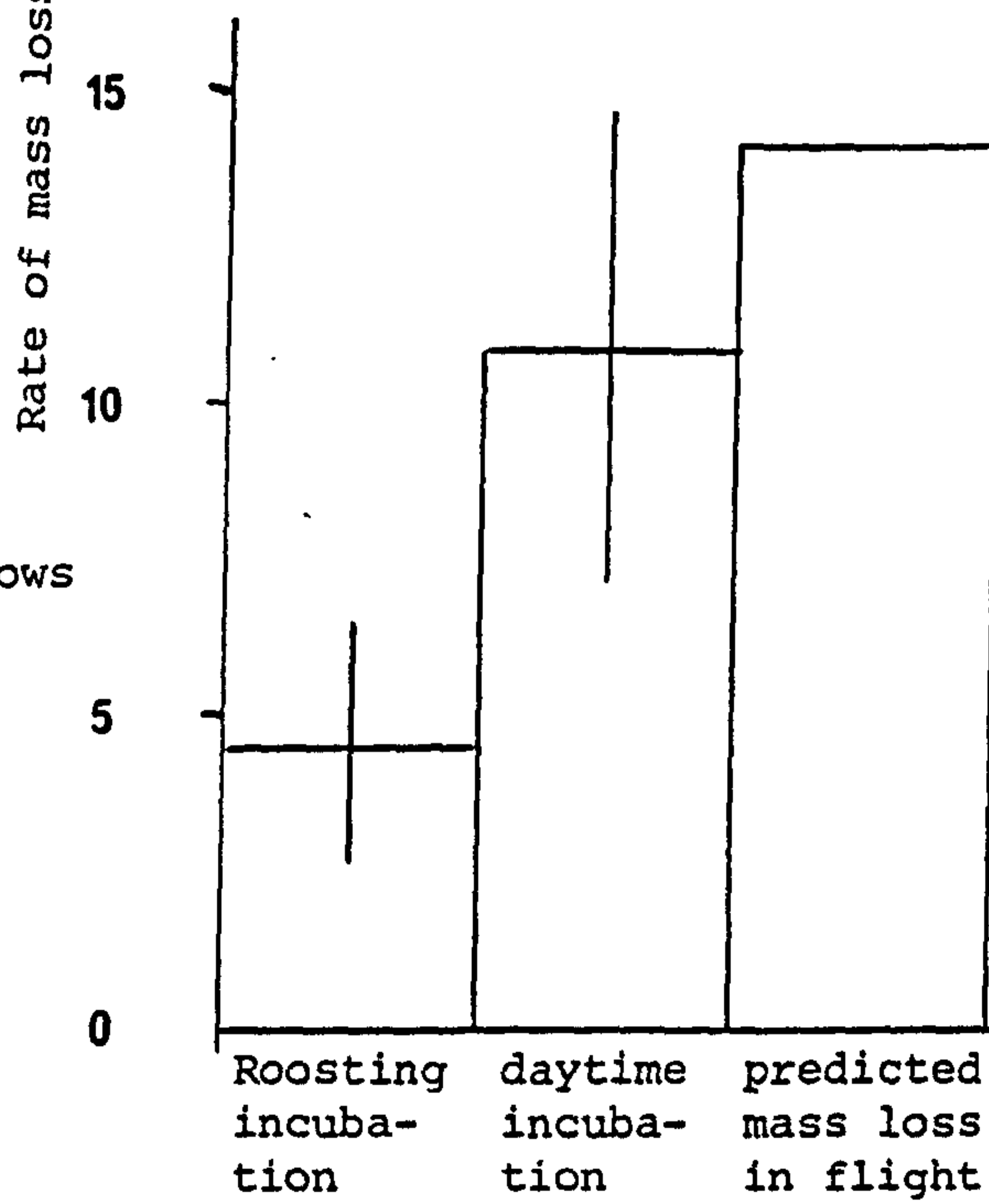


Figure 4.10

Rates of mass loss for different activities in

(a) Canaries

(b) Swallows

Means \pm sd illustrated.

Table 4.1

t-test matrix for mean rates of mass loss in canaries
performing a range of activities (data from Fig. 4.10)

Activity	Roost 25°C	Active, post-absorptive 10-25°C	Active, perched 15°C	Active, perched 30°C
Roost, 10°C	1.6 ns	2.32*	23.8***	6.8***
Roost, 25°C	-	2.53*	30.9***	8.9***
Active, post-absorptive 10-25°C	-	-	15.8***	10.9***
Active, perched 15°C	-	-	-	7.06***

ns : not significant

* : P < 0.05

** : P < 0.01

*** : P < 0.001

roosting was significantly lower than that of active birds. Data for post-absorptive birds was lumped for the temperature range 10°C-25°C, since no substantial influence of temperature on rate of mass loss was apparent over this portion of Figure 4.8. Rate of mass loss was on average significantly higher in active, perched canaries than in post-absorptive birds, and was significantly higher at 30°C than at 15°C, for active, perched canaries.

In Figure 4.10(b) rate of mass loss is plotted for a range of activities in free-living swallows. Roosting incubation and daytime rate of mass loss in flight was calculated using the following assumptions:

- (a) Flight costs of swallows = $0.3063 \text{ kJ g}^{-1} \text{ h}^{-1}$ (Turner, 1980).
- (b) The birds are flying with an R.Q. of 0.78, as observed in budgerigars, Melopsittacus undulatus, (Tucker, 1968). This R.Q. corresponds to a calorific equivalent of 20.08 J/ml O_2 (Tucker, 1968).
- (c) Swallows lose 0.93 mg of water for every ml of O_2 consumed, as occurs in flying budgerigars at 18=20°C. (Tucker, 1968).

Through multiplication, these assumptions predict that swallows should lose $14.186 \text{ mg g}^{-1} \text{ h}^{-1}$ of water during flight. The estimate is intermediate between directly measured values of $9.9 \text{ mg g}^{-1} \text{ h}^{-1}$ in pigeons Columba livia (Le Febvre 1964), and $20.4 \text{ mg g}^{-1} \text{ h}^{-1}$ in budgerigars flying at 19°C (Tucker, 1968).

Swallows lose mass at a higher rate in daytime incubation than during nighttime incubation ($t = 2.6$, $n = 119$, $P < 0.05$), and would be expected to lose mass more rapidly in flight than during incubation. The relatively small difference between rates of mass loss during

flight and while incubating is surprising, given that energy expenditure is considerably higher in flight than during incubation in swallows (Turner, 1980). However, more water may in practice be lost through defaecations in a continuously flying bird than in an incubating individual.

4.3.3 A model of canary body mass changes : results

The routes of mass intake and output for a canary maintained in an aviary at 15°C for a 12 hour light period are quantified in Table 4.2, and plotted in Figure 4.11 as a function of time during the light period. EWL while perched was measured as $0.270 \pm 0.080 \text{ gh}^{-1}$ (n = 65 perching bouts). EWL while foraging was estimated as $0.410 \pm 0.170 \text{ gh}^{-1}$ (n = 41 foraging bouts), and since on average 35.69% of the bird's time was spent perching, total EWL for a one-hour period could be calculated as 0.319 gh^{-1} .

The largest factor contributing to mass input was food consumption, whereas mass loss through evaporative water loss exceeded mass loss through defaecation in this instance. Total mass gain rate exceeded total mass loss rate, so the canary increased in body mass over the day. The predicted net rate of mass gain is shown by line (a) in Figure 4.11, whereas the actual mean rate of mass gain at 15°C for the study bird is depicted by line (b) on the graph.

The predicted rate of mass gain corresponded closely with that observed ($+ 0.057 \text{ gh}^{-1}$ predicted, $+ 0.087 \pm 0.017 \text{ gh}^{-1}$ (n = 52) observed), and the difference between predicted and observed was not statistically significant as judged by a normal approximation for the sign test ($z = 0.35$, $n = 52$, $P > 0.5$). Hence it appears that quantification of consumption, drinking, defaecation, and evaporative

Table 4.2

Short-term body mass changes of a canary kept at 15°C,
in a 12 hour light period

	<u>Mean</u>	<u>Standard Deviation</u>	<u>n</u>
MASS INTAKE			
(a) FORAGING			
(i) seed intake rate (n seeds min ⁻¹ foraging)	0.020	0.009	157 mins
(ii) % time foraging	35.69	13.37	257 mins
(iii) mass intake of husked seeds (gh ⁻¹)	0.433	0.132	24 hours
(b) DRINKING			
Mass intake through drinking (gh ⁻¹)	0.168		16 drinking bouts
TOTAL MASS INTAKE (gh⁻¹)	0.601		
MASS LOSS			
(a) DEFAECATIONS			
(i) number of defaecations (h ⁻¹)	3.750	1.175	28 hours
(ii) faecal mass (g)	0.060	0.019	78 faeces
(iii) faecal output (gh ⁻¹)	0.225	0.063	24 hours
(b) EWL			
(i) EWL while perched (gh ⁻¹)	0.270	0.080	65 perching bouts
(ii) EWL while foraging (gh ⁻¹)	0.410	0.170	41 foraging bouts
(iii) EWL while perched for 64.31% of time (gh ⁻¹)	0.173		
(iv) EWL while foraging for 35.69% of time (gh ⁻¹)	0.146		
Total EWL (gh ⁻¹)	0.319		
TOTAL MASS LOSS (gh⁻¹)	0.544		
PREDICTED MASS CHANGE (gh⁻¹)	+0.057		
ACTUAL MASS CHANGE (gh⁻¹)	+0.087	0.017	52

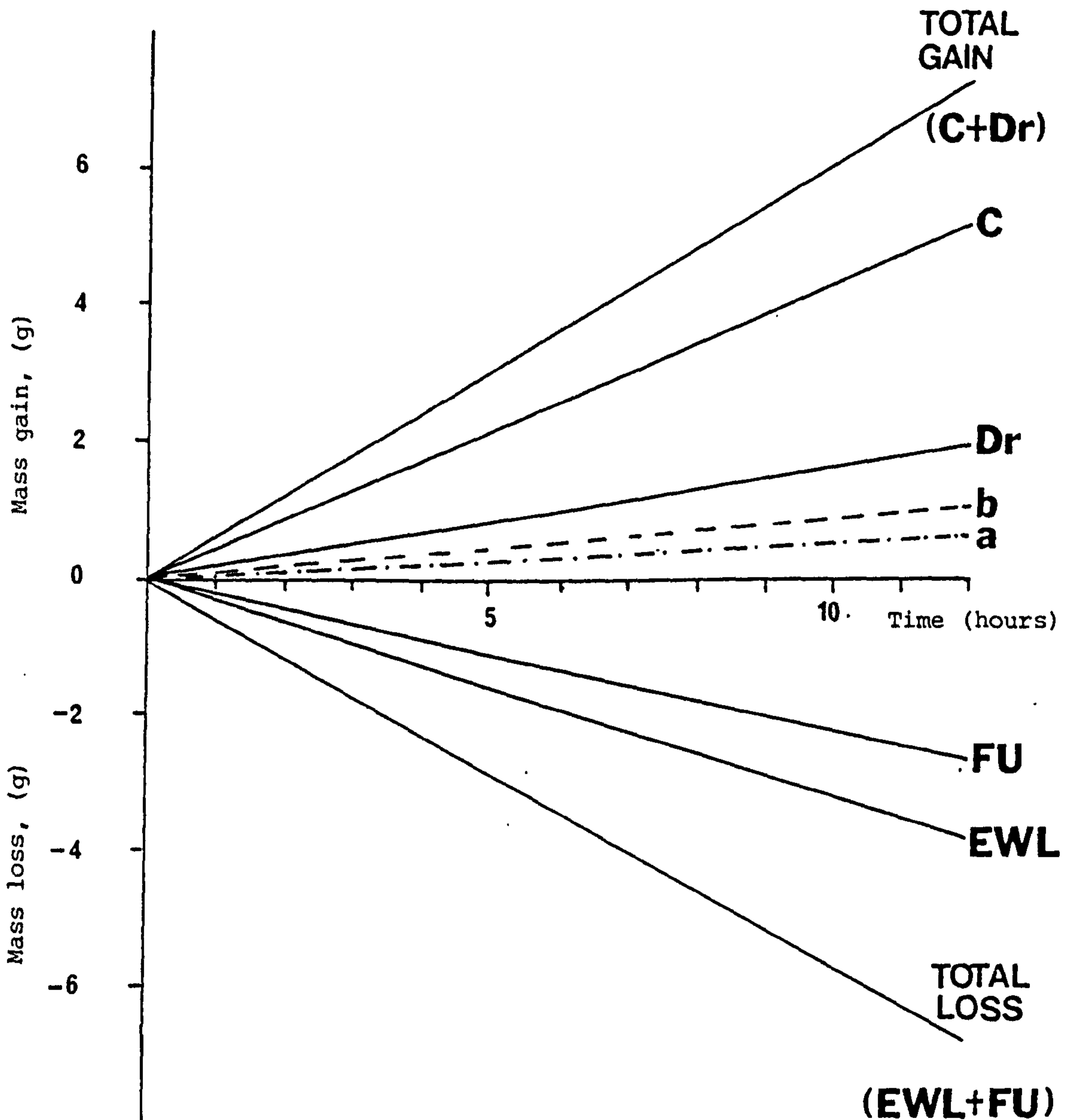


Figure 4.11

Predicted short term body mass changes of a canary at 15°C over a twelve hour light period.

a = predicted mass change; b = actual mass change.

C = mass intake while foraging; Dr = water intake;

FU = mass loss through defaecating;

EWL = evaporative water loss.

See text for explanation.

water loss can accurately predict the diurnal pattern of body mass changes of a canary in controlled laboratory conditions.

4.3.4 Short-term body mass changes in breeding swallows

Having established an understanding of the factors responsible for short-term body mass changes in birds under laboratory conditions, an investigation is now made into the factors responsible for instantaneous mass changes of free-living breeding swallows.

(a) Diurnal body mass changes

Diurnal body mass changes for three incubating female swallows are illustrated in Figure 4.12. The line of best fit to the data was a linear regression equation ($P < 0.001$), with birds on average increasing in mass by 0.113 gh^{-1} .

The mean percentage overnight mass loss \pm s.d. of seven roosting incubating female swallows was $4.97 \pm 2.05\%$.

(b) Instantaneous body mass changes in swallows

An understanding of the factors responsible for instantaneous body mass changes in breeding swallows would enable mass changes to be related to energy currency in some instances. For example, if swallows gain mass through feeding and the expected mass loss through flying can be calculated, mass gains can be transformed to energy values if the calorific value of prey is known, assuming no defaecations to have occurred.

The short-term body mass changes associated with one typical incubating female swallow are shown in Figure 4.13. The mass changes can be interpreted as follows:

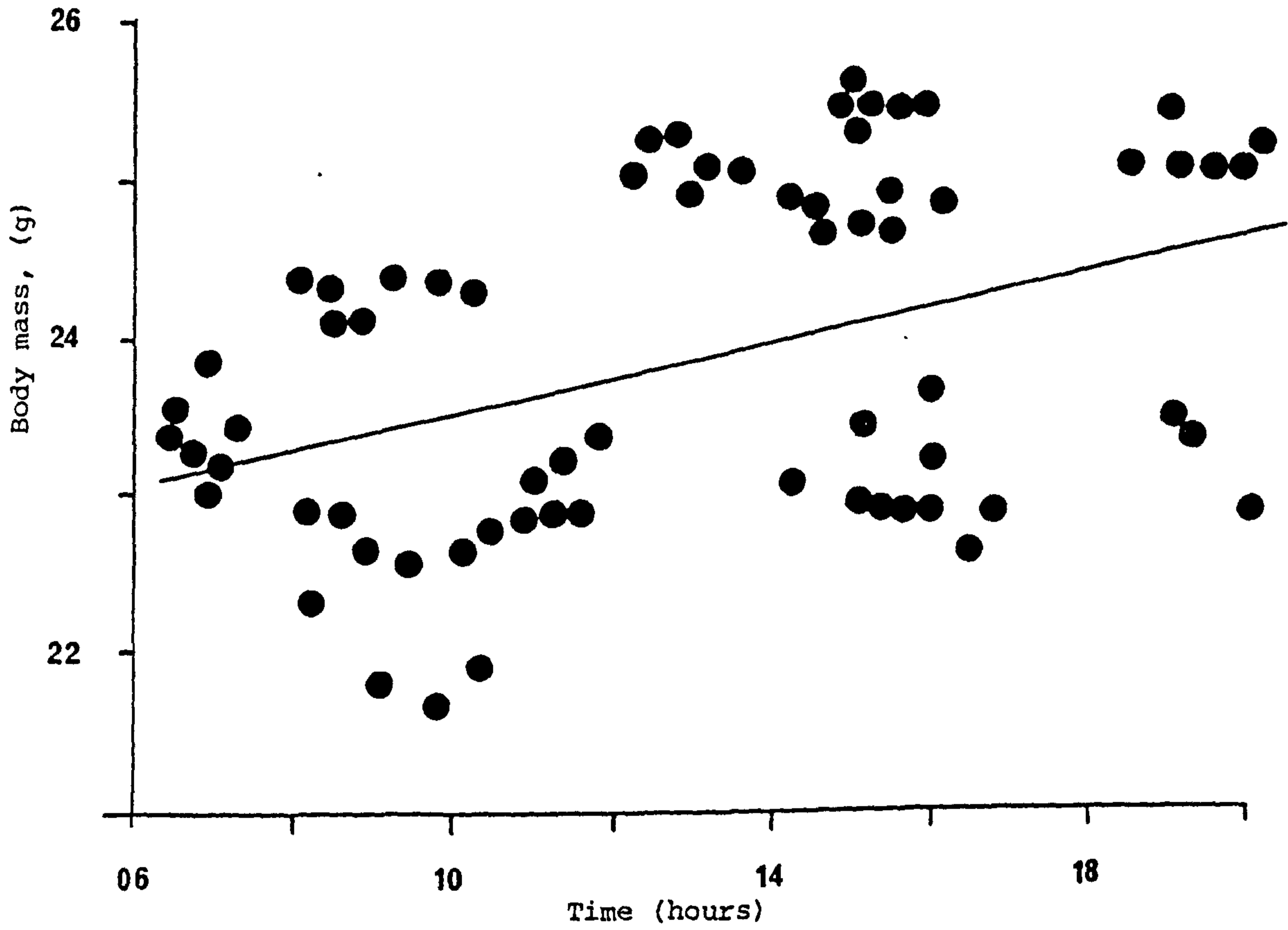


Figure 4.12

Diurnal body mass changes of incubating female swallows.

The regression equation is:

$$y = 22.4 + 0.113x$$

$$F = 14.0, n = 70, P < 0.001.$$

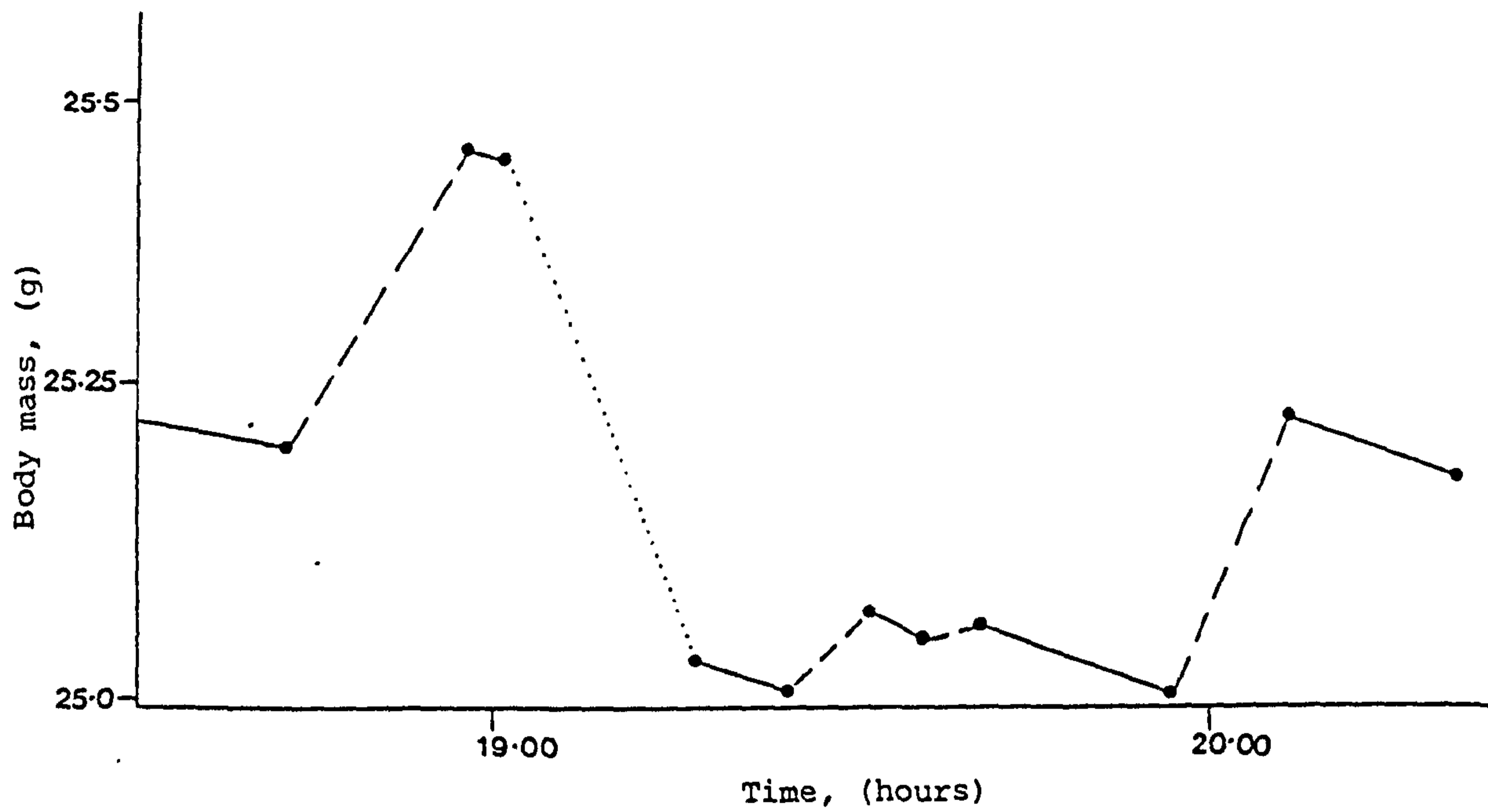


Figure 4.13

Short term body mass changes in a typical incubating female swallow.

- incubation mass loss
- assumed defaecation
- foraging mass change

- (i) mass loss while incubating. This will represent EWL whilst sitting on eggs. No defaecations occurred while birds were on the nest. Some mass may also be lost to parasites such as hippoboscids, but since only two hippoboscids were found on adult swallows during this study, such mass losses were assumed to be negligible. The mean rate of mass loss during incubation over the temperature range 12°C-28°C was $-0.180 \pm 0.115 \text{ mg g}^{-1} \text{ min}^{-1}$ ($n = 111$).
- (ii) mass changes while foraging. On feeding trips, swallows may gain mass by drinking or by consuming prey, and may lose mass through defaecating and from EWL while flying (EWL_{fly}). The body mass dynamics of female swallows feeding between incubation bouts is therefore described by equation 4(3)

$$\text{Mass change while foraging} = \frac{(\text{C} + \text{DR}) - (\text{FU} + \text{EWL}_{\text{fly}})}{\text{Mass inputs} \quad \text{Mass outputs}}$$

Equation 4(3)

No drinking was observed by breeding swallows at any of the study sites, although it is the case that migrating swallows may often be observed drinking. Insects present in the study area contained on average $72.94 \pm 2.30\%$ water (Turner, 1980), so it is likely that the birds obtained all of their water requirements from their succulent insect prey. The average rate of mass change during inattentive periods was $+ 0.241 \pm 2.908 \text{ mg g}^{-1} \text{ min}^{-1}$ ($n = 266$), so incubating female swallows on average make a net mass gain while foraging between incubation bouts.

Water loss while flying can be estimated as described in Section 4.3.3. Hence if foraging trips where defaecations did not occur

could be identified, mass gains through foraging could be calculated and related to net energy gains.

To minimise the chances of including defaecations on foraging trips when relating mass changes to energy gains, the following rationale was used unless otherwise stated. The mean inattentive period during incubation was 4.107 ± 2.624 mins ($n = 293$) during which time a female swallow of average mass (22.48g) would be expected to lose 0.02g through water loss in flight using the assumptions developed in Section 4.3.3. Mean faecal mass was $0.3973 \pm .1601$ g ($n = 9$), and hence a defaecating swallow should lose 0.4173g at the mean inattentive period if no feeding occurred. To achieve a mass gain, prey equivalent to 3.1 times the mean load mass (0.137 ± 0.006 g, (Chapter 8)) delivered to chicks during the period of maximum food demand from the young would need to be consumed. Since foraging periods during food collection for young are on average 36 seconds shorter than those during incubation (Chapter 8), it was considered that incubating females could not collect sufficient food during the inattentive period to return to the nest with increased mass if they had defaecated. Hence inattentive periods whereby females increased in mass were considered not to have involved defaecations.

4.4 DISCUSSION

4.4.1 The use of precision automated balances in studies of avian body mass changes

Most studies of mass changes in birds have involved frequent trapping of individuals throughout the annual or breeding cycle. Such studies have been performed on robins (Erithacus rubecula) (Lees, 1949), bank swallows (Petersen, 1955), house martins (Bryant, 1975), and tawny owls (Strix aluco) (Hirons, Hardy and Stanley, 1984).

This method has a disadvantage in that frequent trapping may stress the birds, causing unnatural mass changes to occur. Trapping studies also tend to consider mean masses of different individuals at given times in the annual cycle, because of the problems involved in repeated trappings of the same individual. Hence much variation about mean masses is often observed, and factors affecting body mass such as time of day, body size and bird age are rarely considered.

If individual birds are weighed at habitual perches or at nests, these two problems may be overcome. Recent work with balances placed underneath or near to birds' nests includes studies on barnacle geese, Anser leucopsis, (Lessells, Sibly, Owen and Ellis, 1979), ospreys, Pandion haliaetus, (Poole, 1982), herring gulls, Larus argentatus, (Sibly and McCleery, 1983), starlings, Sturnus vulgaris, (Westerterp et al., 1983), red-throated bee-eaters, Merops bulocki; (Crick, 1984), hummingbirds, Selasphorus rufus, (Carpenter, Paton, and Hixon, 1983). In the last mentioned example, Mettler electronic balances were also used to determine daily mass changes of individually marked birds in the field. Weighing of birds at habitual perches or nests probably does not repeatedly stress the birds being weighed and allows several weighings to be performed on the same individuals. If the balances are attached to a power source, and linked to a data logger or printer, continuous recording of adult mass changes can be made (e.g. Sibly and McCleery, 1983).

Precision balances also allow accurate measurements of load masses to be made without collaring nestlings. Since collaring nestlings to prevent them swallowing food loads may affect begging behaviour and hence the parents' food delivery rates (Johnson, Best and Heagy, 1980), accurate balances can be useful in studies of foraging behaviour.

Measurements of evaporative water loss can also be made with precision balances. Indeed, Lasiewski et al., (1966) considered the direct weighing method of determining EWL to be advantageous over the conventional open flow technique, since measurements in the laboratory could be made under controlled conditions with temperatures and relative humidities varied independently.

4.4.2 Short-term body mass changes in birds

(a) Diurnal body mass changes

(i) Canaries

Body mass increased most rapidly during the early stages of the light period, and thereafter increased at a slower rate (Figure 4.4). Presumably either a satiation effect or a digestive bottleneck effect was operating (Kenward and Sibly, 1977). The canaries' guts were probably empty by morning (as seen in sand martins' carcasses taken at dawn), and were filled rapidly in the early morning when intake rates were high (Figure 4.5). The seed was presumably digested relatively slowly, and lack of space in the digestive system would have limited the rate of food intake during the afternoon and evening if a digestive bottleneck was operating. Rate of mass increase was also greatest during the first two and a half hours of light in captive white-throated sparrows, Zonotrichia albicollis, (Kontogiannis, 1967). If gut volume was optimised in relation to normal demands (Sibly, 1981), reduced intake rates later in the day may occur because the canaries were satiated, and gut capacities may not necessarily be filled to capacity.

(ii) Swallows

There was no evidence of a digestive bottleneck effect shaping the diurnal body mass changes of incubating female swallows (Figure 4.12) since body mass increased in a linear fashion over the day. Insect material is probably more easily digested than seeds, and passes through the gut more rapidly. The first identifiable prey remains in the faeces of a food-deprived swallow nestling appeared two hours after ingestion, with 90% of identifiable prey remains appearing in the faeces after 5-7 hours (Waugh, 1978).

(b) Overnight body mass changes

The rate of mass loss in roosting canaries was higher at 25°C than at 10°C, although the difference between means was not statistically significant. Kontogiannis (1967) studied overnight mass losses in captive white-throated sparrows at -5°C, 22°C and 30°C. Birds lost most mass overnight at -5°C, least at 22°C, and an intermediate amount at 30°C.

Overnight mass losses in birds should be viewed as having two components: evaporative water loss while roosting (EWL_{roost}), and mass loss through defaecations. If EWL_{roost} were the only route of mass loss at night, it would be expected that birds lose most mass on warm nights, since EWL increases with increasing temperature. However, during cold days, birds often have a higher food intake rate than on warmer days (e.g. goldcrests, Regulus regulus, Gibb, 1954), or may increase overall food intake by spending more time feeding on cold days (e.g. grey plovers, Pluvialis squatarola, Pienkowski, 1982). A higher food intake allows fat reserves to be accumulated to meet the metabolic cost of maintaining constant body temperature as ambient temperature falls (King and Farner, 1966; Evans, 1969). Hence a

higher diurnal food intake in cold conditions will result in more mass being lost through defaecations on cold nights, since more reserves need to be metabolised overnight in response to falling ambient temperatures. Kontogiannis (1967) showed that white-throated sparrows indeed lost more mass through defaecating on cold nights than on warm nights, and that this increasing rate of mass loss through defaecation overrode the reduced EWL_{roost} to result in the greatest total mass loss overnight at the coldest temperature studied. Hence overnight mass losses are caused by an interaction of EWL_{roost} and defaecation mass loss, both following opposing trends with temperature.

Overnight body mass losses seem to be highest during the first few hours of darkness, when defaecation rates are highest (Figure 4.7). Presumably defaecation rate declines overnight as the gut becomes emptied. Similar high initial overnight rates of mass loss have been shown in the white-throated sparrow (Kontogiannis, 1967), and in yellow-vented bulbuls, Pycnonotus goiavier, (Ward, 1969a).

(c) Short-term continuous mass losses

Lasiewski et al. (1966) showed that recording mass losses in birds using accurate balances gave measures of EWL that were comparable with results from the conventional open-flow technique, and indeed overcome some of the errors inherent in that technique. The values of EWL for canaries at 25°C are close to those predicted by Crawford and Lasiewski (1968) from the equation:

$$M_{we} = 24.6 M^{0.585}$$

where

M_{we} is total evaporative water loss, $g\ 24h^{-1}$ at 25°C

M is body mass, kg.

Dawson's predicted value for a 23.28g bird (mean canary body mass) is 0.114 gh^{-1} , that measured in the incubator at 25°C was 0.105 gh^{-1} .

The shape of the EWL/temperature plots for both canaries (Figure 4.8) and sand martins (Figure 4.9) are similar. Rate of mass loss was relatively low and more or less constant until the thermoneutral zone was reached (assumed to be similar in sand martins and canaries), thereafter rate of mass loss increased rapidly with increasing temperature. Most studies of EWL show a slight and gradual increase in EWL with increasing temperature below the thermoneutral zone (e.g. painted quails, Excalfactoria chinensis, house sparrows, Passer domesticus, Lasiewski et al. 1966), though no such trend was apparent in this study for canaries, as also seen in sage sparrows, Amphispiza belli nevadensis (Moldenhauer, 1970).

(d) Evaporative water loss and activity

At any temperature, the rate at which a bird loses mass through evaporative water loss is likely to vary with the bird's activity. In Figure 4.10 it was shown that roosting canaries lost mass at a rate 2-3 times lower than that of active birds at similar temperatures. Moreover, active feeding birds in an aviary lost mass more rapidly than post-absorptive birds in an incubator at the same temperature. Flying swallows will also lose mass more rapidly than incubating birds.

The differences in the rates of mass loss with activity will result from differences in the metabolic costs of activities. For example, since flight is energetically more expensive than resting (e.g. Tucker, 1968), flying birds will produce more metabolic water than resting individuals, hence their rate of EWL and rate of mass loss should be higher during flight.

Active birds typically have a basal metabolic rate some 24% greater than that of roosting birds (Aschoff and Pohl, 1970), and body temperature typically drops by 1°C-3°C during roosting (Walsberg, 1983). These factors presumably explain why roosting canaries and swallows lost mass at a 38-47% lower rate than birds in comparable temperatures during the active period.

Active canaries perched in a constant temperature aviary may lose mass more rapidly than post-absorptive birds in an incubator at the same temperature for two reasons. Firstly, in the aviary, mass changes were recorded in perching birds. Between perching bouts birds foraged actively, presumably at a higher metabolic rate and body temperature than when perched. This increase in metabolic rate during foraging could take a considerable time to fall to the typical resting metabolic rate, and could be in operation during the early stages of a perching bout. Secondly, aviary birds were actively processing food, while incubator birds were post-absorptive. Aviary birds may therefore have functioned at a higher metabolic rate than post-absorptive canaries because of the influence of specific dynamic action (SDA). SDA is a post-feeding increase in resting metabolism due to deamination and digestion costs (Brody, 1945; Kleiber, 1975), and in some mammals, SDA may increase resting heat production by 30% (Kleiber, 1975). Costa and Kooyman (1984) measured SDA in sea otters, Enhydra lutris, and found a mean peak increase in resting oxygen consumption of 54%, peaking on average 82 minutes after feeding. The ratio of SDA/BMR in birds varies from 15-60% (Ricklefs, 1974).

Incubating female swallows lost mass at an average of 10.8 mg. $g^{-1} h^{-1}$ (Figure 4.10b), while the prediction of Crawford and Lasiewski

(1968) for a resting bird at 25°C is $5.0 \text{ mg g}^{-1} \text{ h}^{-1}$. The increased rate of mass loss observed in the field may reflect the metabolic cost of reheating eggs during incubation.

Swallows are predicted to lose mass more rapidly when flying than during incubation (Figure 4.10b). Several studies have shown an increased rate of evaporative water loss during locomotion. Brackenbery, Gleeson and Avery (1981) found that EWL increased during walking in domestic fowl, G. gallus, and Pearson (1964) demonstrated an increase in the rate of mass loss of flying pigeons, Columba livia, with sealed cloacas, when compared with resting birds. Tucker (1968) found that flying budgerigars, Melópsittacus undulatus, lost mass five times as rapidly as when resting at 20°C and twelve times as rapidly when flying at 35°C compared with resting birds. Torre-Bueno (1978) has suggested that starlings may dehydrate during flights in air temperatures above 7°C.

Caution must be exercised when relating evaporative water losses to the metabolic costs of activities however. Although the production of metabolic water will undoubtedly increase as metabolic rate increases, the fate of the water may be difficult to ascertain. Birds may lose water either as reflected in continuous mass losses, or water may be excreted with faecal losses. No study appears to have attempted to partition water loss in birds into these components in relation to the birds' activity (Skadhauge, 1981), although five times as much water is lost by evaporation compared with faecal water losses in flying budgerigars (Tucker, 1968).

4.4.3 Modelling avian body mass changes in the laboratory

The model of canary diurnal mass changes (Table 4.2, Figure 4.11), closely predicts the mass changes actually observed. Two sources of error are likely to contribute significantly to the deviation between observed and predicted mass changes.

The model fails to consider any size-selection of seeds in its estimate of food consumption (equation 4(2)), so mass intake through foraging may be subject to error. Since the estimate of EWL while foraging depends on estimates of mass intake through foraging, it too may introduce inaccuracy into the model.

The linear prediction of body mass increase over the daytime period is a simplification as shown in Figure 4.4, body mass increases in a non-linear fashion over the light period, presumably because of a digestive bottleneck effect. A more precise model would consider this in greater detail.

The components of a bird's daily mass budget are all likely to vary with temperature. For example, as temperature decreases, C and FU are likely to increase, while Dr and EWL should decrease. The modelling of avian mass changes in relation to changing temperature would make a profitable study.

CHAPTER 5

5. THE BODY CONDITION OF BREEDING HIRUNDINES

5.1 INTRODUCTION

Parent birds may be expected to evaluate their long term survival prospects through monitoring short term increments in energy balance (Drent and Daan, 1980). An understanding of adult body condition changes during breeding may therefore produce a rigorous background for interpreting decisions concerning the allocation of resources between parent and offspring. Body mass changes may be related to energy expenditure (Ryer and Westerterp in prep.), or to the level of work involved in feeding nestlings (Tinbergen et al. in Drent and Daan, 1980; Nur, 1984b, Chapter 8), and the increased time spent at high activity levels may be an important stress factor (Priede, 1977) by which parents could judge their future survival prospects.

Although considerable work has been performed on the energetics of growth of nestlings (Ricklefs, 1967; O'Connor, 1975, 1977; Bryant and Gardiner, 1979; Turner and Bryant, 1979; Bryant and Hails, 1983; Tatner, 1984), most studies of changes in adult body condition have considered the entire annual cycle (Hirons et al., 1984) or winter fattening (Farner and King, 1965; Evans, 1969; Newton, 1972). Work on adult body condition changes during breeding has focussed on changes in fat and protein reserves during laying (Jones and Ward, 1976; Fogden and Fogden, 1979; Hails and Turner, in prep.).

In this chapter the body condition of adult sand martins over the breeding cycle is described, and changes in body condition are related to body mass changes. The relationship of a bird's energy reserves to its overall body mass is important for the interpretation of

swallow adult mass changes (Chapters 7, 8) and a small sample of swallow carcasses was analysed for comparison with the more intensively studied sand martin.

Changes in nestling body condition over the rearing period are also described for sand martins, so that adult condition changes during nestling rearing could be related to the energy reserves of the brood. The significance of a nestling's position within the brood hierarchy for its body composition is also investigated in sand martins, and the implications of changes in adult and nestling body condition for parent:offspring resource allocation strategies are discussed.

5.2 MATERIALS AND METHODS

A sample of 33 adult sand martins at different stages of the breeding cycle was killed under license for carcass analysis. Six fledglings were also taken, and when nestling-rearing adults were sacrificed, their brood was also killed for carcass analysis. Thirty-seven chicks from 10 broods were taken in total. All birds except for three adults were taken at dusk, and although most birds were killed through license from the Nature Conservancy Council, supplementary carcasses were collected after sand cliff collapses.

Nine swallows (six adults, three fledglings) were also killed under license for carcass analysis.

All birds were killed by chloroform inhalation. Carcasses were then dissected, freeze dried for seven days, weighed to the nearest 0.0001g, and then underwent lipid extraction in soxhlet apparatus, with five parts diethyl ether:one part chloroform used as the lipid solvent. The carcasses were then freeze-dried for a further week, and weighed to determine lipid-free dry masses.

Dissected components were tail feathers, wing feathers, skin and contour feathers, legs (cut at hip), wings (cut at shoulder), pectoralis major, pectoralis minor, body shell, head, neck, oesophagus and gizzard (gizzard emptied), lungs, heart, liver, gut, kidneys, gonads, and major lipid deposits.

Lipid indices were calculated on fat content/lean dry mass, water indices as water content/lean dry mass, with all masses in grams.

Wing areas were determined by tracing outlines of the right wings of carcasses of 29 adult and five fledgling sand martins and multiplying by two. The mass of tracing paper accurately reflected wing area, with a correlation coefficient of 1.0 between paper mass and area. The wing area of six birds was calculated from 1 mm² graph paper and compared with the results from weighing tracing paper. Wing area determined by weighing tracing paper gave results that were on average $100.06 \pm 0.71\%$ of those obtained from direct measurement on graph paper. Wing loadings were calculated on body mass/wing area, g cm⁻².

5.3 RESULTS

In order to understand body mass changes in breeding sand martins in greater detail, carcass analysis was performed on 33 adult birds, and comparisons made with six fledgling carcasses.

5.3.1 Lipid reserves of adult and fledgling sand martins

(a) The distribution of lipid reserves

On dissection, large quantities of subcutaneous lipid were noted in heavy adults. The distribution of this lipid is illustrated in Figure 5.1, the nomenclature of lipid deposits based on that of King

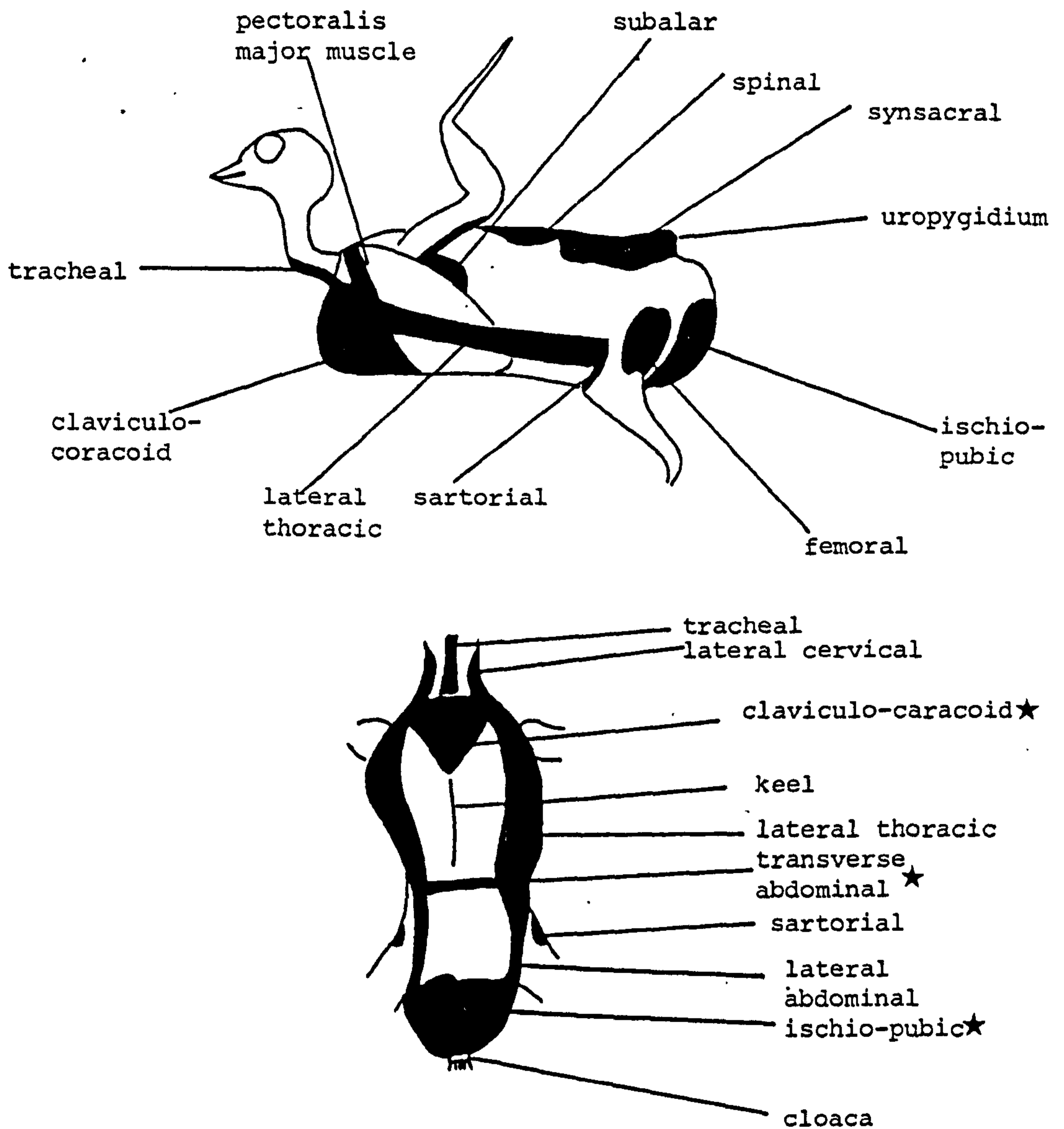


Figure 5.1

Major lipid storage sites visible in a skinned sand martin with large lipid deposits.

Terminology from King and Farner (1965).

*: quantified in live birds by fat scoring.

and Farner (1965). The subcutaneous lipid deposits in the claviculo-coracoid area, transverse abdominal lipid, and the ischio-pubic deposits were normally visible in live birds and formed the basis of the fat scoring system for tracheal fat, fat on the posterior edge of the keel, and abdominal fat respectively (Chapter 2).

Scoring of the lipid deposits of live birds was easier for individuals with well developed brood patches. The ischio-pubic deposit was often obscured by feathers in males, whose brood patches were never as extensively developed as those of incubating or nestling rearing females.

A fat scoring system including claviculo-coracoid, transverse abdominal, and ischio-pubic deposits gave a higher correlation coefficient when plotted against body mass in females ($r = 0.59$, $n = 95$, $P < 0.001$), than when only claviculo-coracoid and transverse abdominal deposits were correlated with body mass ($r = 0.52$, $n = 59$, $P < 0.001$). Moreover, for eight carcasses examined, the three deposits fat score gave a higher correlation coefficient when plotted against lipid index than did the two deposit score (two deposits: $r = 0.80$, $n = 8$, $P < 0.05$; three deposits: $r = 0.84$, $n = 8$, $P < 0.01$). However, because of the difficulty in quantifying the ischio-pubic deposit in males, and because a larger sample of females was available scored with the two deposit system, only claviculo-coracoid and transverse abdominal deposits are incorporated in the fat-scoring system in the subsequent analysis.

The dry masses (DMs), lean dry masses (LDMs), and lipid indices of the dissected components of adults and fledglings are presented in Appendix II(a). Appendix II(b) shows a table of 't' tests comparing mean masses of male and female body components before and after lipid

extraction. There were no significant differences between mean male and female component DMs or LDMS, except that mean female head LDM in the sample was significantly lighter than mean male head LDM. In view of the general similarity between male and female body component masses, data from both sexes were lumped for a comparison with fledgling body component masses. In Appendix II(c), mean adult component DMs and LDMS are compared with those of fledglings. There was no significant difference between either mean DM or mean LDM of adult and fledgling components for pectoralis muscles, neck, oesophagus and gizzard, lungs, gut, kidneys, and dissectable tracheal fat, suggesting that these components are fully developed at fledging, and that there is no difference in the components' mean lipid content between fledglings and adults.

Fledglings had significantly heavier mean heart masses (DM and LDM) than did adults in the sample. Adults had significantly heavier mean LDMS than fledglings for tail feathers, wing feathers, legs, wings, body shell, head, liver and gonads (not discernable in fledglings).

When mean DMs of adult and fledgling components are not significantly different, but mean LDMS for the components do differ significantly, a difference in the percentage lipid content of the component between adults and fledglings is suggested. When significant differences occurred between mean LDMS of adult and fledgling components, it was always the fledgling value which was smaller (except for heart). Therefore, when fledgling and adult mean component DMs are not significantly different, but mean component LDMS are, a greater percentage lipid content in the fledgling component is implied. This situation indeed exists for skin and contour

feathers (mean lipid index of adults = 39.1, fledglings 57.5), legs (56.1 adults, 73.6 fledglings), and body shell (54.1 adults, 67.1 fledglings). These differences probably reflect relatively more subcutaneous lipid being deposited in fledglings than in adults.

When differences occur in component DMs and LDMs of adults and fledglings, a difference in the percentage lipid content of the two classes may still exist. In such instances, 't' tests were performed on the mean values of component lipid indices of adults and fledglings. This analysis was performed for wings (mean lipid index of adults = 42.8, fledglings 40.5, $t = 0.85$, ns), head (29.3 adults, 28.9 fledglings, $t = 0.20$ ns), and liver (38.6 adults, 29.5 fledglings, $t = 1.41$ ns).

Hence fledglings sampled had 9/17 body components which were on average lighter in LDM than adult values, while only one component was on average heavier in fledglings (Appendix II). Fledglings were thus structurally smaller than adults in most body components. Fledglings on average appeared to store more subcutaneous fat than did adults.

In Table 5.1, mean wet body mass, keel-length, wing-length, total DM, total LDM, water content, water index, percentage water content, lipid content and lipid index formation for adult males, adult females, adults of both sexes and fledglings are presented. In Table 5.2(a) the mean measurements of males and females are compared by 't' tests. None of the values was significantly different between sexes for the individuals sampled, so male and female values were combined for a comparison with fledglings (Table 5.2(b)).

Mean adult lean dry mass was significantly greater than that of fledglings, and adults also had significantly longer wings.

Table 5.1 Carcass analysis information for sand martins

	<u>Males</u>		<u>Females</u>		<u>All Adults</u>		<u>Fledglings</u>	
Wet mass (g)	13.35	+ 1.04 (13)	13.82	+ 1.36 (19)	13.63	+ 1.25 (32)	12.58	+ 0.48 (5)
Keel-length (mm)	18.67	+ 0.46 (13)	18.74	+ 0.53 (19)	18.71	+ 0.49 (32)	18.53	+ 0.75 (4)
Wing-length (mm)	105.81	+ 3.19 (13)	104.55	+ 2.80 (19)	105.06	+ 2.98 (32)	97.75	+ 4.45 (6)
Dry mass (g)	5.2453	+ 0.5840 (13)	5.4257	+ 0.7858 (19)	5.3205	+ 0.7187 (33)	4.8686	+ 0.4411 (6)
Lean dry mass (g)	3.9066	+ 0.2568 (13)	3.9940	+ 0.3241 (19)	3.9458	+ 0.3016 (33)	3.4035	+ 0.1902 (6)
Water content (g)	8.0876	+ 0.4814 (13)	8.4347	+ 0.7783 (18)	8.2891	+ 0.6828 (31)	7.8535	+ 0.2901 (5)
Water index	207.23	+ 7.40 (13)	211.50	+ 10.41 (19)	209.79	+ 9.42 (32)	232.5	+ 9.69 (5)
% Water content	60.65	+ 1.48 (13)	61.19	+ 1.95 (18)	60.96	+ 1.76 (31)	62.45	+ 0.58 (5)
Lipid content (g)	1.3387	+ 0.3930 (13)	1.4317	+ 0.5581 (19)	1.3748	+ 0.4973 (33)	1.4651	+ 0.3565 (6)
Lipid index	34.04	+ 8.65 (13)	35.49	+ 12.67 (19)	34.49	+ 11.15 (33)	43.04	+ 9.88 (6)

Mean values ± sd, (n) are tabulated.

Table 5.2

(a) Comparison of male and female carcass analysis measurements in sand martins.

Tabulated values are t, ns = no significant difference between means. Data from Table 5.1

<u>Measurement</u>	<u>t</u>	<u>P</u>
Wet mass (g)	1.05	ns
Keel-length (mm)	0.39	ns
Wing-length (mm)	1.18	ns
Dry mass (g)	0.70	ns
Lean dry mass (g)	0.81	ns
Water content (g)	1.42	ns
Water index	1.27	ns
% water content	0.84	ns
Lipid content (g)	0.52	ns
Lipid index	0.36	ns

(b) Comparison of adult and fledgling carcass analysis measurements in sand martins

Tabulated values are t, ns = no significant difference between means, ***, $P < 0.001$. Data from Table 5.1

<u>Measurement</u>	<u>t</u>	<u>P</u>
Wet mass (g)	1.81	ns
Keel-length (mm)	0.65	ns
Wing-length (mm)	5.10	***
Dry mass (g)	1.48	ns
Lean dry mass (g)	4.23	***
Water content (g)	1.39	ns
Water index	5.00	***
% water content	1.86	ns
Lipid content (g)	0.42	ns
Lipid index	1.75	ns

Fledglings had a significantly higher mean water index than adults sampled.

To show where most lipid was stored in the body, pie-diagrams breaking down total body lipid in adults and fledglings into component lipid contents is presented in Figure 5.2. In adults 66.7% of total body lipid was found in the body shell, skin and contour feathers, wings, legs and tracheal lipid deposit. This is probably predominantly subcutaneous lipid, most of which will be potentially mobilisable as an energy reserve. In fledglings on average 70.5% of total body lipid was stored in these places.

In Table 5.3 a correlation matrix of the measurements made during adult carcass analysis and whose means are described in Table 5.1 is presented, along with other information from carcasses.. A high degree of intercorrelation between variables is observed and pertinent correlations will be examined below.

- (b) The role of lipid reserves in body mass changes of breeding sand martins
- (i) Component lipid content and total body lipid content

The dissection of carcasses into components, their freeze-drying and lipid extraction is both time consuming and expensive. Several workers have attempted to estimate total body lipid by relating the lipid content of one component or the mass of a single lipid deposit to total lipid, and performing analyses only on the component lipid, if component lipid is strongly correlated with total body lipid. For example, Houston (1977) found that the omental lipid of hooded crows, Corvus corone cornix, was strongly positively correlated with total body lipid, and thus used the mass of omental lipid as an index of body condition when examining large numbers of

Figure 5.2

Breakdown of total body lipid into body component

lipid in

(a) adult

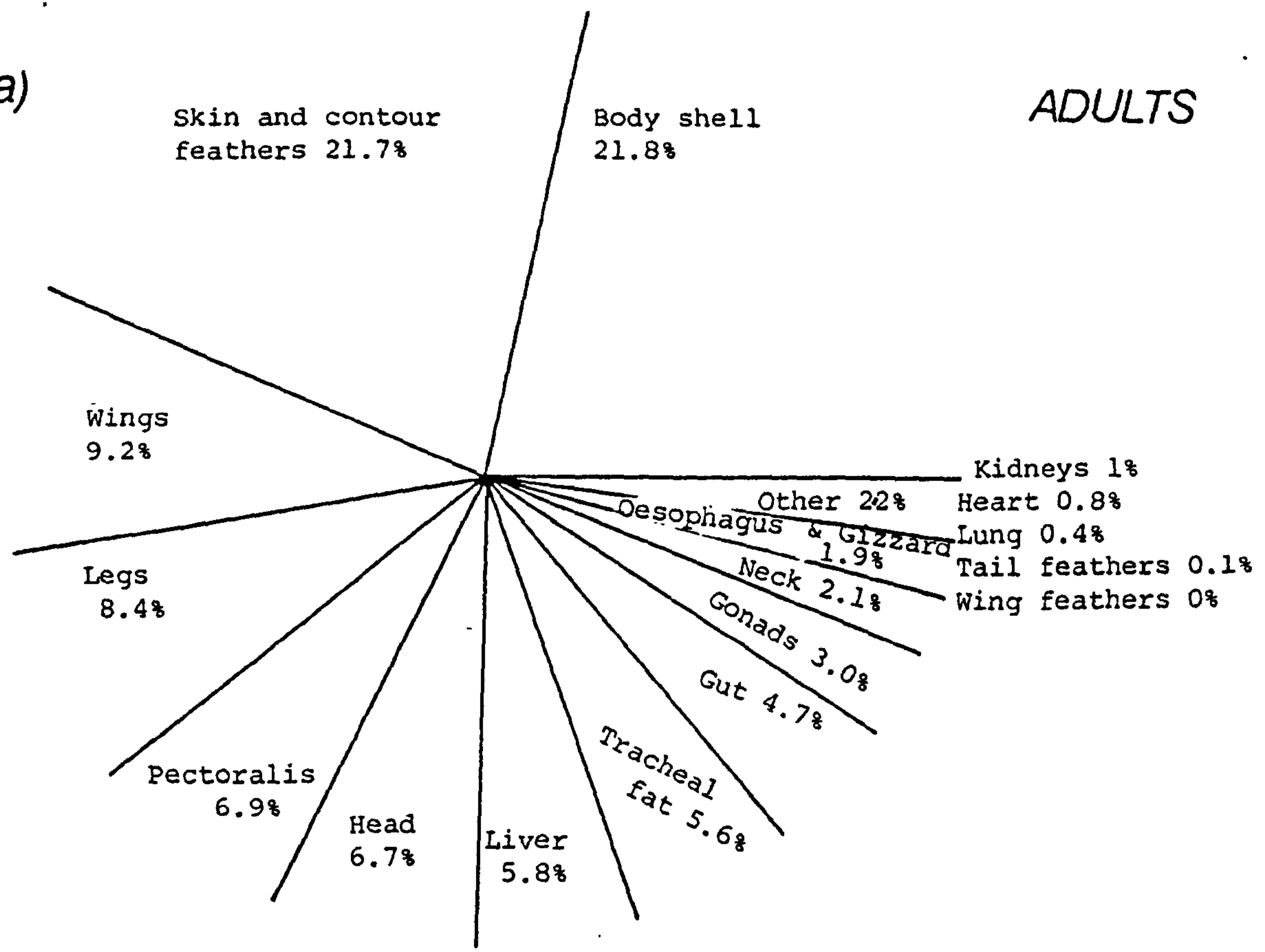
and

(b) fledgling

sand martins

a)

ADULTS



b)

FLEDGLINGS

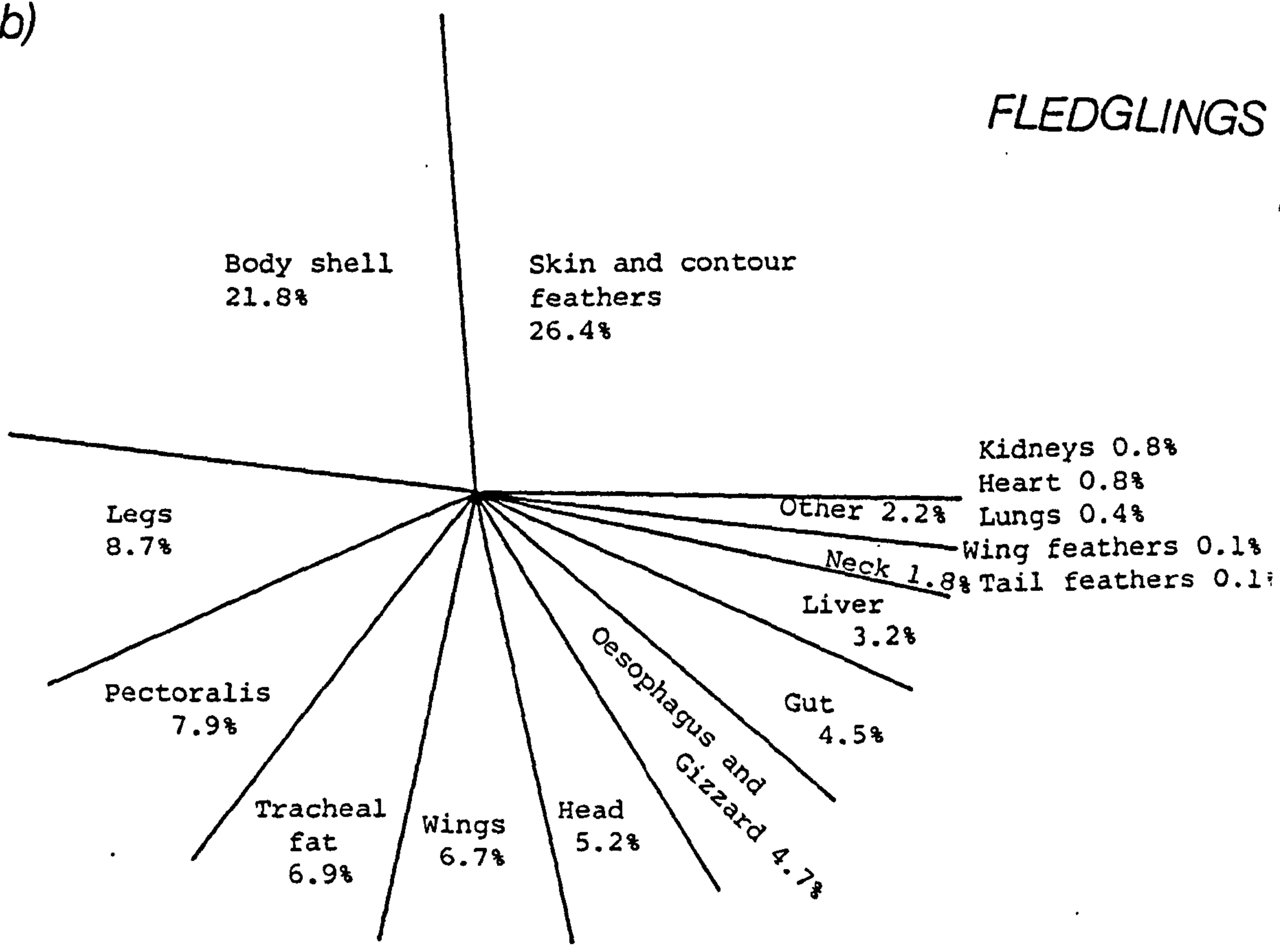


Table 5.3 Correlation matrix of measurements made during sand martin adult carcass analysis

	Fat Score	Wet Mass	Pectoralis LDM	Pectoralis DM	Water g	Fat g	Lipid Index	LDM	Keel-length	Water Index
Dry mass, g	0.761 ***	0.902 ***	0.603 ***	0.738 ***	0.778 ***	0.849 ***	0.841 ***	0.820 ***	-0.046 ns	0.061 ns
Fat score	-	0.686 ***	0.411 *	0.496 **	0.597 ***	0.787 ***	0.713 ***	0.536 **	0.155 ns	0.199 ns
Wet mass, g	-	-	0.616 ***	0.641 ***	0.949 ***	0.667 ***	0.681 ***	0.840 ***	-0.061 ns	0.319 ns
Pectoralis Lean dry mass (LDM), g	-	-	-	0.972 ***	0.522 **	0.512 **	0.419 *	0.718 ***	0.475 **	-0.231 ns
Pectoralis Dry mass (DM), g	-	-	-	-	0.540 **	0.621 ***	0.516 **	0.703 ***	0.378 *	-0.165 ns
Water content, g	-	-	-	-	-	0.498 **	0.496 **	0.833 ***	-0.074 ns	0.419 *
Extractable fat, g	-	-	-	-	-	-	0.931 ***	0.479 **	-0.25 ns	0.134 ns
Lipid index	-	-	-	-	-	-	-	0.392 *	-0.27 ns	0.267 ns
LDM, g	-	-	-	-	-	-	-	-	0.181 ns	-0.152 ns
Keel-length, mm	-	-	-	-	-	-	-	-	-	-0.430 *

n = 32 adults. Tabulated values are correlation coefficients, r.
 ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

birds. Wishart (1979) showed the mass of abdominal and skin fat to be a good predictor of total body lipid in American wigeons, Anas americana.

In sand martin adults, lipid indices for head, lung, heart, liver and kidney were calculated as

$$\frac{\text{component lipid content (g)}}{\text{component LMD (g)}} \times 100$$

Component lipid indices were then correlated with the overall lipid indices of the birds, and the results are presented in Table 5.4. Although logarithmic transformations of the data were not performed, in no instance did it seem likely that an allometric relationship better fitted the component/total lipid index comparison than did a linear relationship.

Significant positive correlations between component lipid index and total lipid index occurred for head, lung, heart and kidney, though the r^2 values were always relatively small, the highest being 29.7% for the heart lipid index/total lipid index correlation. No correlation existed between liver lipid index and total lipid index.

Total lipid index should ideally be corrected as (total lipid-component lipid)/LDM to remove any autocorrelation of component lipid. This would effectively reduce r^2 even further, though the reduction in the significance of the correlations is likely to be slight, since component lipid content is always small compared with total body lipid (Table 5.4).

The value of using body component lipid indices to estimate overall lipid indices must be questioned. Most mobilisable lipid is probably deposited subcutaneously, while much lipid in the components

Table 5.4 Correlations between body component lipid indices and total extractable lipid (g) in sand martins

	Head Lipid Index	Lung Lipid Index	Heart Lipid Index	Liver Lipid Index	Kidney Lipid Index
r	0.486	0.387	0.544	0.267	0.539
n	32	30	32	32	25
p	<0.01**	<0.05*	<0.01**	ns	<0.01**
regression equation	$y = 3.05 + 1.08x$	$y = 24.09 + 0.94x$	$y = 14.20 + 1.12x$		$y = 23.12 + 0.512x$
mean % of total body lipid in component	6.7	0.4	0.8	5.8	1.0

Total extractable lipid is represented by y in the regression equations.
 r is the correlation coefficient of the relationship of component lipid index to total body lipid.

ns : not significant; * : P < 0.05; ** P < 0.01

analysed is likely to be structural. A bird with much lipid in the lungs may have little fat available as an energy reserve, so the value of component lipid indices on an index of mobilisable lipid reserves is of doubtful value.

Conversely, dissectable tracheal lipid is likely to be largely available as an energy reserve. A strong positive correlation existed between the quantity of dissectable tracheal lipid and total extractable lipid, $r^2 = 68\%$ (Figure 5.3). Logarithmic transformation of the data increased the r^2 value, and the relationship between tracheal lipid and total extractable lipid is best described by the equation

$$\log_e \text{TCL} = -0.173 + 5.16 (\log_e \text{tracheal lipid} + 1)$$

$$(r = 0.81, n = 29, r^2 = 65.1\%, P < 0.001)$$

where TCL = total corrected lipid = (total lipid - tracheal lipid). Hence the amount of extractable tracheal lipid is a good predictor of an adult sand martin's total lipid content, and probably gives a good indication of the quantity of mobilisable lipid reserves, since the claviculo-caracoid lipid deposit presumably functions solely as an energy reserve.

(ii) The extrapolation of carcass lipid analysis to the field

In the field, female body mass and fat score (tracheal, posterior edge of the keel and abdominal deposits) were significantly positively correlated ($r = 0.59, n = 117, P < 0.001$), as were male body mass and fat score ($r = 0.28, n = 64, P < 0.05$). The data are plotted in Figure 5.4. In both cases, the relationship between the variables appears to be linear. The correlation coefficient is probably higher for females because of the greater reliability of fat scoring on females which have well developed brood patches.

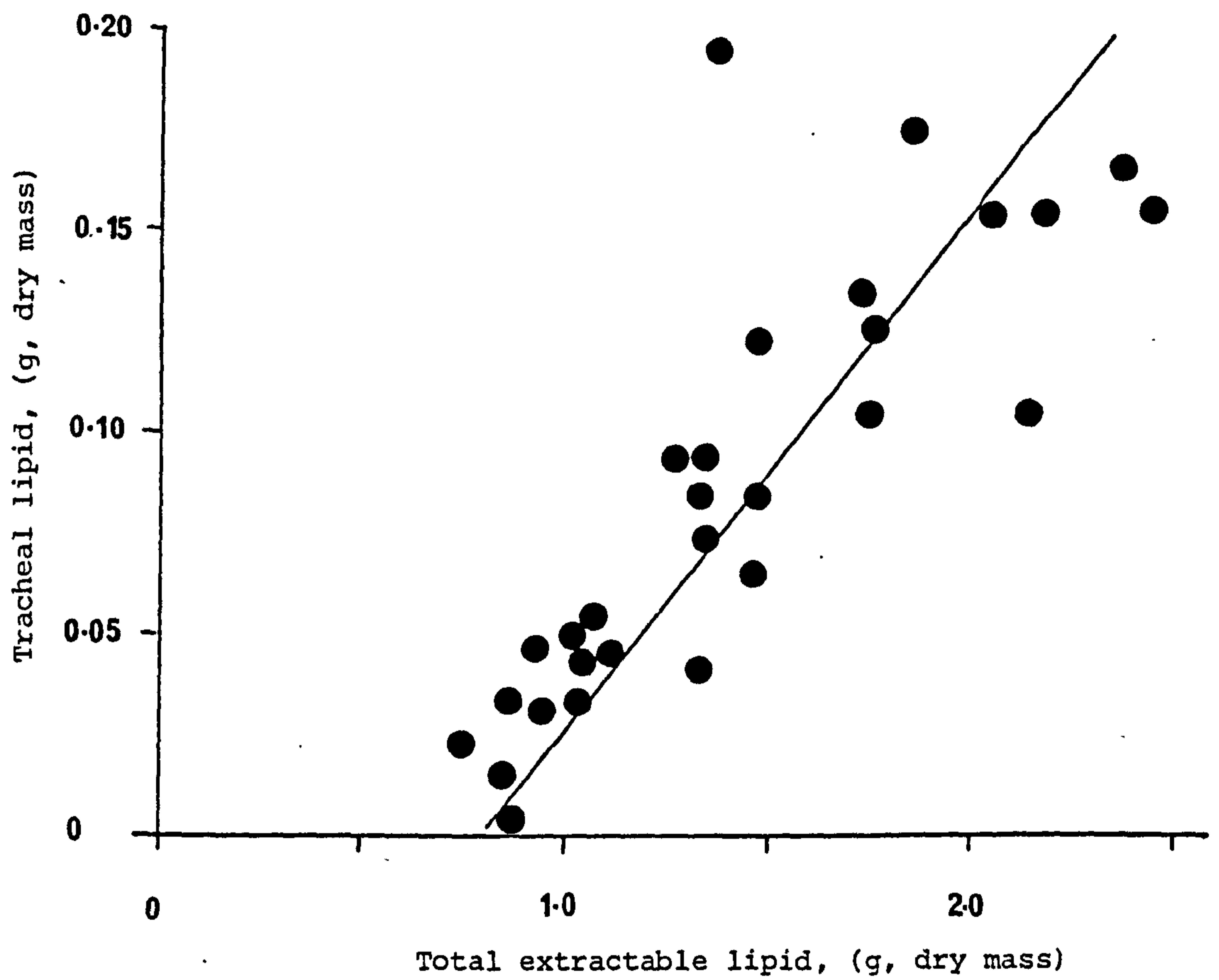


Figure 5.3

The relationship between total extractable lipid and extractable tracheal lipid in adult sand martins.

$r = 0.82$, $n = 29$, $P < 0.001$.

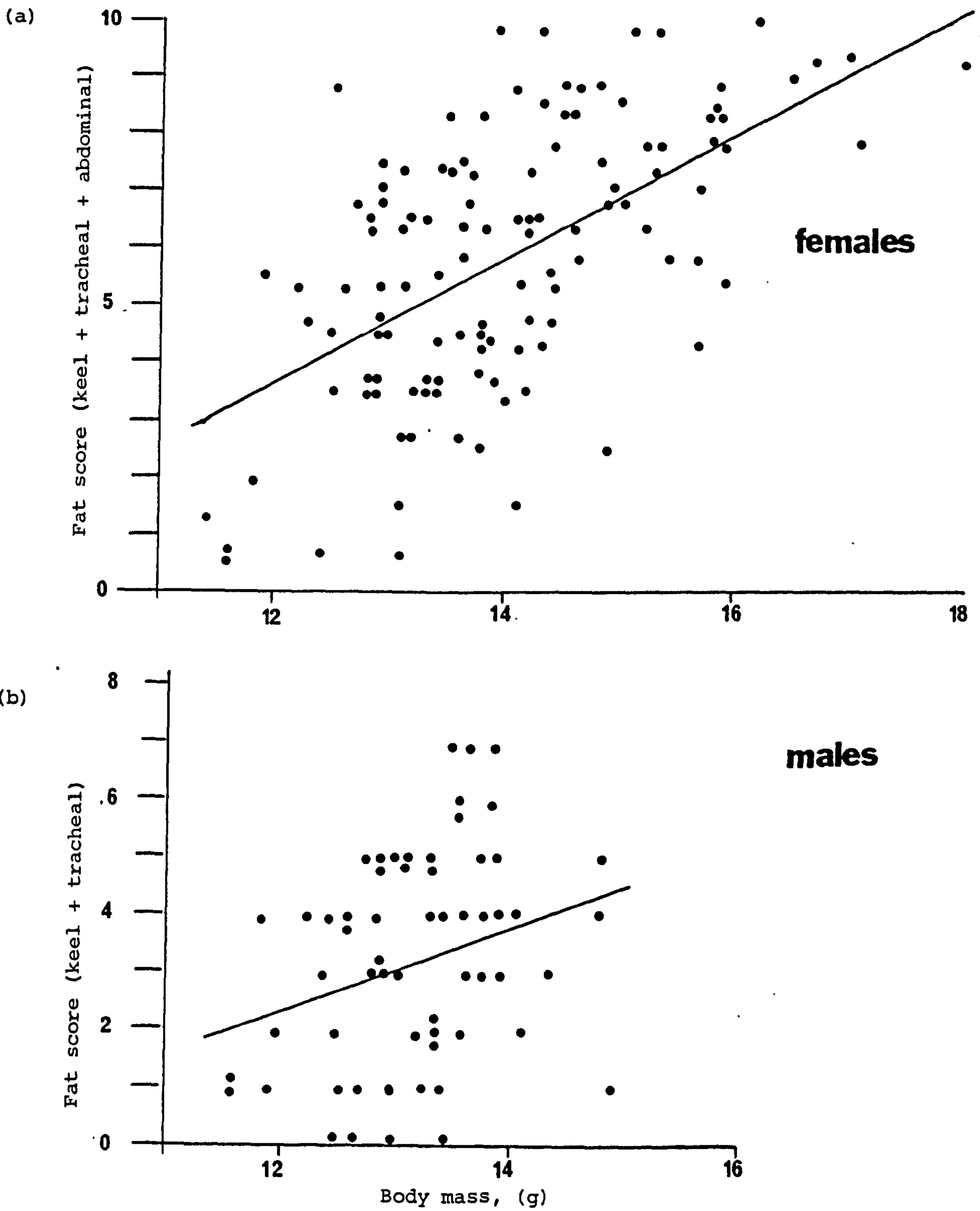


Figure 5.4

Fat score versus body mass correlations for adult sand martins.

(a) Females: $y = -7.46 + 1.09x$; $r = 0.59$, $n = 117$, $P < 0.001$

(b) Males: $y = -5.97 + 0.70x$; $r = 0.28$, $n = 64$, $P < 0.05$

In Figure 5.5a, body mass is plotted against lipid index, and a highly significant positive correlation exists ($r = 0.68$, $n = 32$, $P < 0.001$). Fledglings were omitted from the analysis because they have relatively high lipid indices for their body masses. Body mass is plotted against extractable lipid mass in Figure 5.5b, and the positive correlation is once again highly significant ($r = 0.67$, $n = 32$, $P < 0.001$). The close correlation between lipid index or content and body mass suggests that lipid mass changes closely parallel body mass changes, and that day to day mass changes in the field may largely represent changes in the size of the lipid reserve.

How accurate is the scoring estimation of lipid reserves in the field in representing actual changes in the lipid reserves of birds? In Figure 5.6a fat score is plotted against lipid index, and the correlation was positive and highly significant ($r = 0.71$, $n = 32$, $P < 0.001$). Fat score was also highly significantly correlated with total extractable lipid mass, as shown in Figure 5.6b ($r = 0.79$, $n = 32$, $P < 0.001$). In both Figures 5.6a and b, the relationship between the variables is a good fit to a straight line.

Despite the apparent accuracy of the fat scoring system as judged by linear correlation, the method is not completely reliable, especially when fat scores of intermediate value are used. For example, a fat score of five has estimated lipid indices ranging from 19 to 48. Hence the fat scoring system is subject to some error in estimating actual lipid indices or content of sand martins, probably because of its subjective scoring methodology, and because it is unable to include some subcutaneous lipid deposits not visible in live birds.

In Figure 5.7, lipid condition estimates of breeding female sand martins are compared with lipid condition as determined by carcass

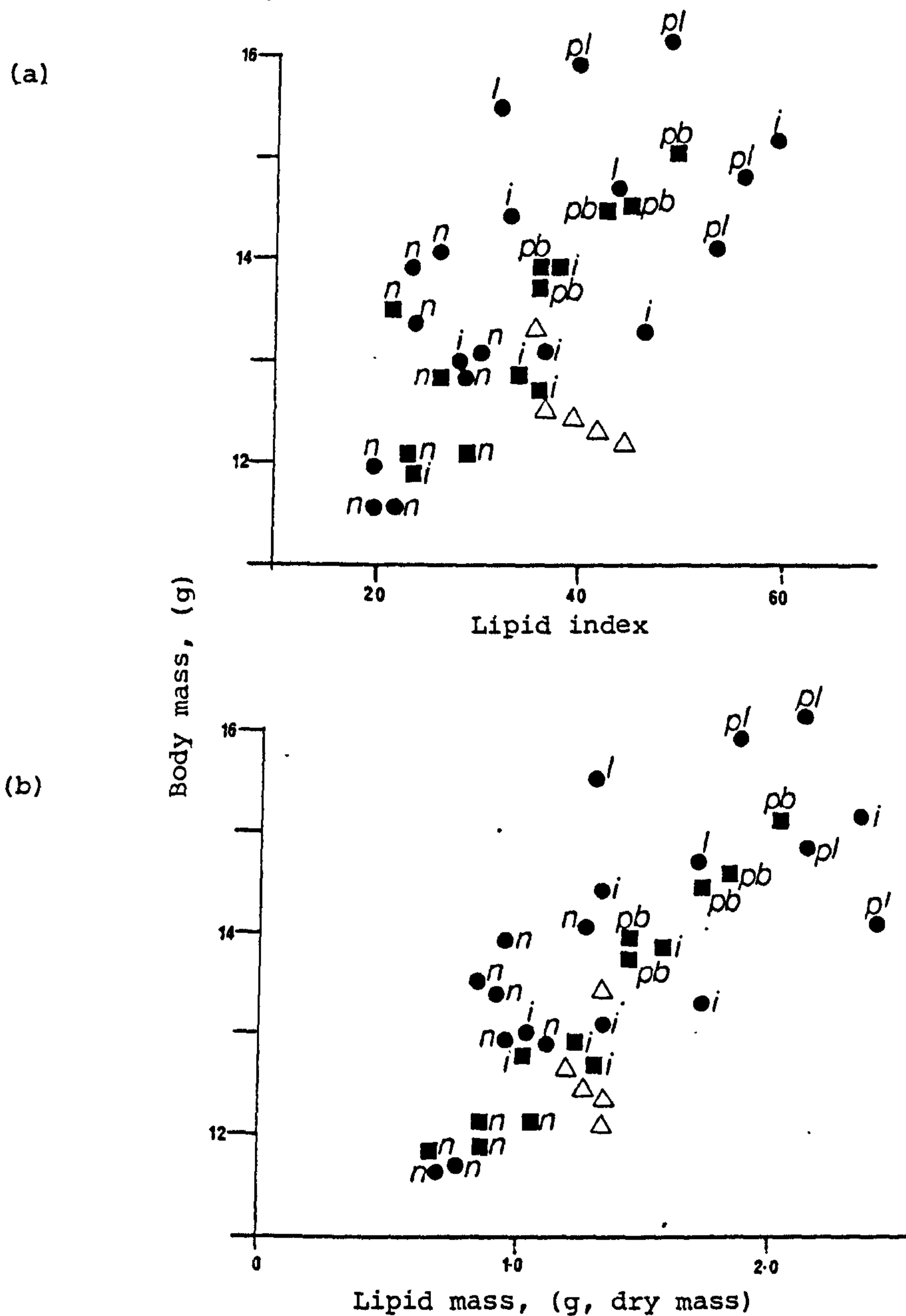


Figure 5.5

(a) Body mass versus lipid index plot for sand martins.
 $r = 0.68$, $n = 32$, $P < 0.001$.

(b) Body mass versus extractable lipid plot for sand martins.
 $r = 0.67$, $n = 32$, $P < 0.001$.

Squares: males; circles: females.

n: nestling rearing; i: incubating; pb: pre-breeding
 pl: pre-laying; l: laying.

Triangles: fledglings, excluded from correlations.

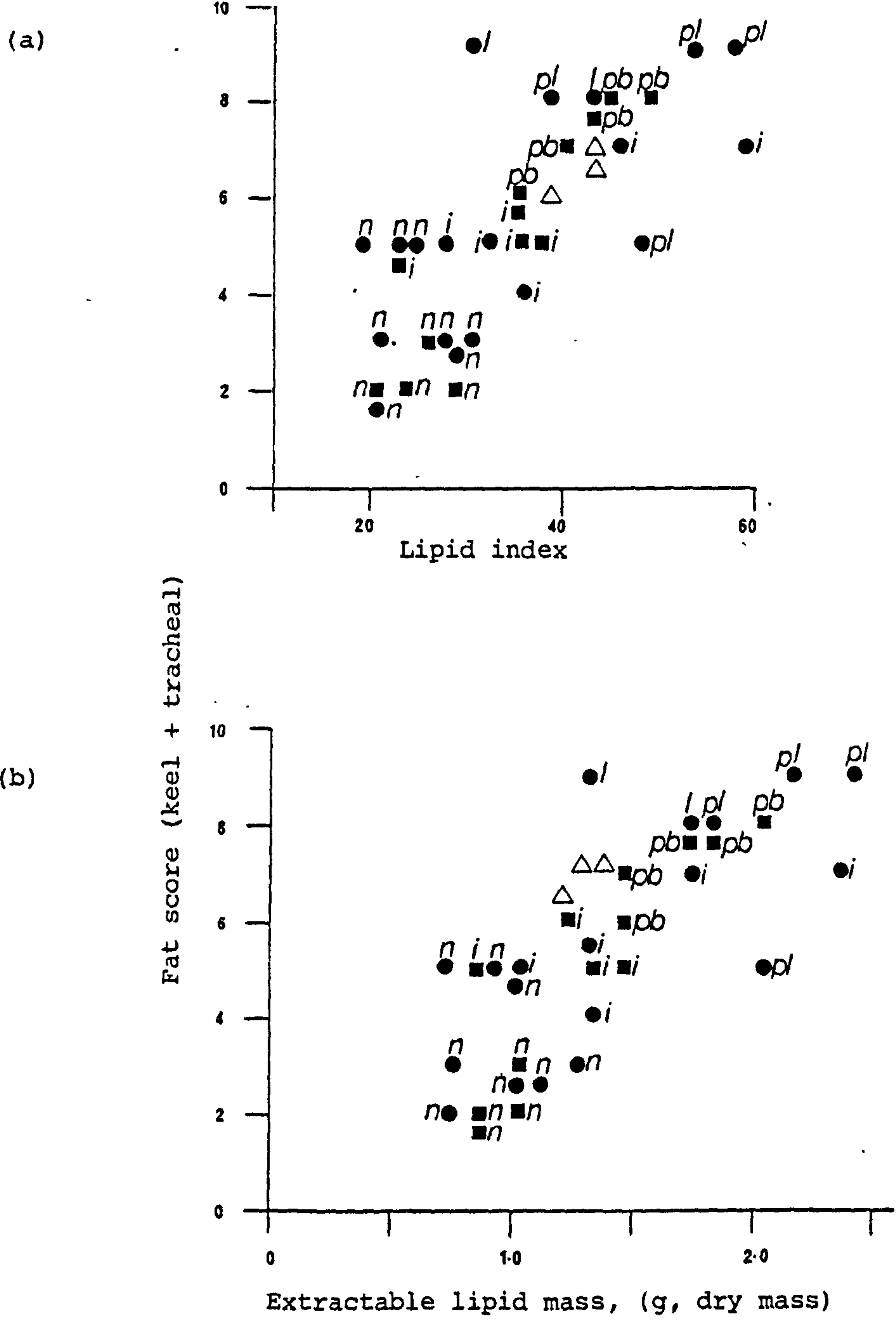


Figure 5.6

(a) Correlation of fat score and lipid index in sand martins. For adults, $r = 0.71$; $n = 32$, $P < 0.001$.

(b) Correlation of fat score and extractable lipid mass in sand martins. For adults, $r = 0.79$, $n = 32$, $P < 0.001$.

Symbols as in Figure 5.5

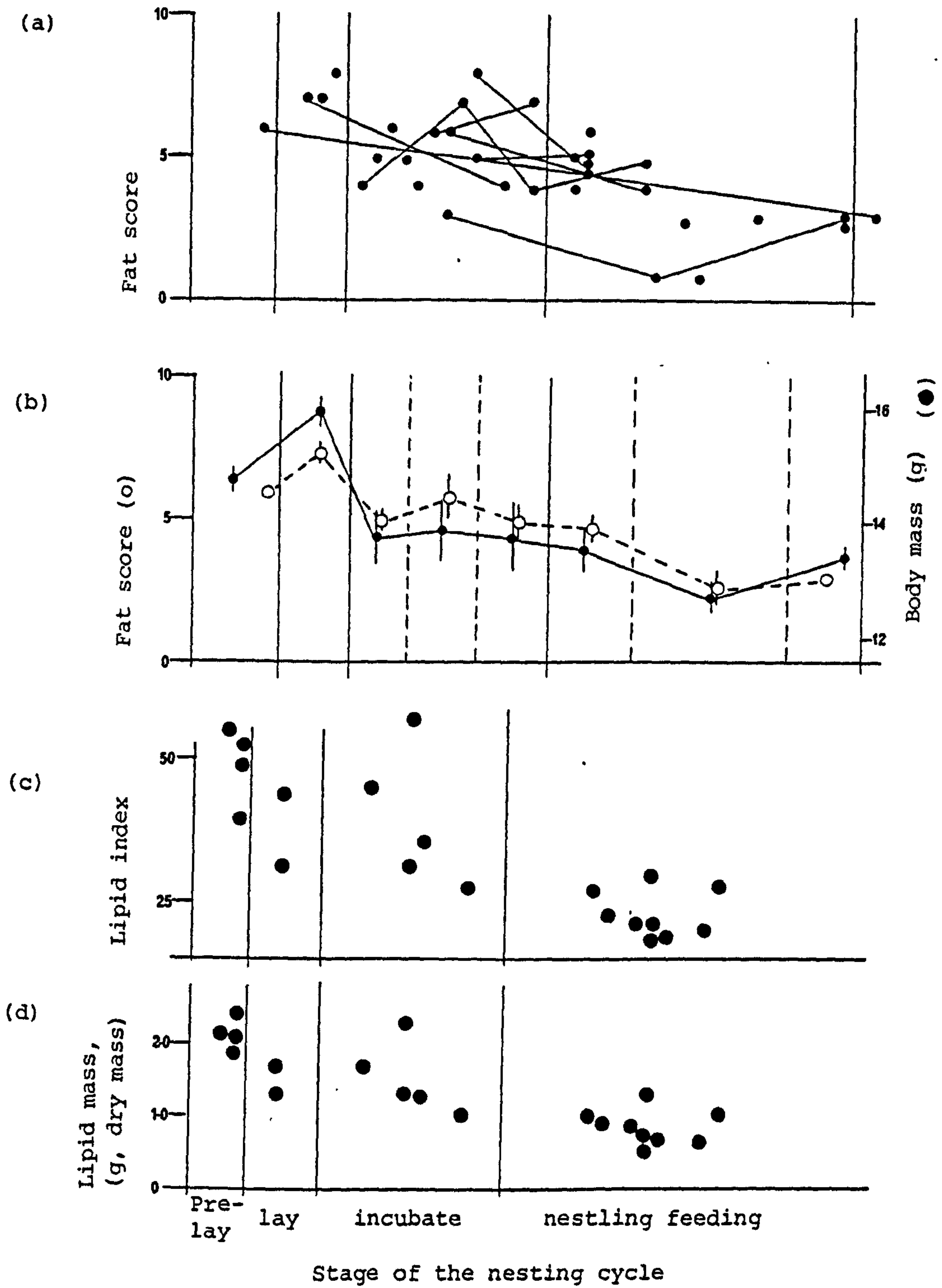


Figure 5.7

Lipid condition of breeding female sand martins.

- (a) Fat scores of individual females. Lines join successive recaptures of the same bird.
- (b) Mean fat scores (pecked line) and mean body masses (solid line) of females over the breeding cycle.
- (c) Lipid indices of breeding females, as determined by carcass analysis.
- (d) Extractable lipid of breeding females, as determined by carcass analysis.

analysis. In Figure 5.7a fat scores of individual females over the nesting period are plotted, lines joining successive recaptures of the same female. Mean fat scores over the breeding period are presented in Figure 5.7b, and compared with mean body mass changes as presented in Chapter 6. Changes in fat score closely parallel body mass changes, with greatest discrepancy occurring during the pre-laying and laying periods, when body mass is greater than expected through the fat-scoring system, since mass at this time includes considerable reproductive material (see below). In Figure 5.7c and d, lipid indices and extractable lipid of female sand martins are plotted over the breeding cycle.

Female lipid condition was seen to be relatively high during the pre-laying period, fell during laying (as determined by carcass analysis), increased or remained stable during incubation, and reached lowest values during nestling rearing. The fat-scoring results suggested some tendency for lipid reserves to recover during the later stages of the nestling rearing period.

Male lipid condition over the breeding cycle is presented in Figure 5.8 from fat scoring and carcass analysis. Lipid reserves were highest in pre-breeders, fell during the female laying period (when males were mate-guarding) and during incubation, reaching lowest values during nestling rearing, again with a tendency for lipid reserves to recover towards the end of the rearing period.

Mean lipid indices of both males and females at different stages of the breeding cycle are plotted on histograms in Figure 5.9. Fledgling values are also included for comparison. An analysis of variance of these data is presented in Table 5.5, and means are compared in a 't' test matrix. The mean lipid index of pre-laying

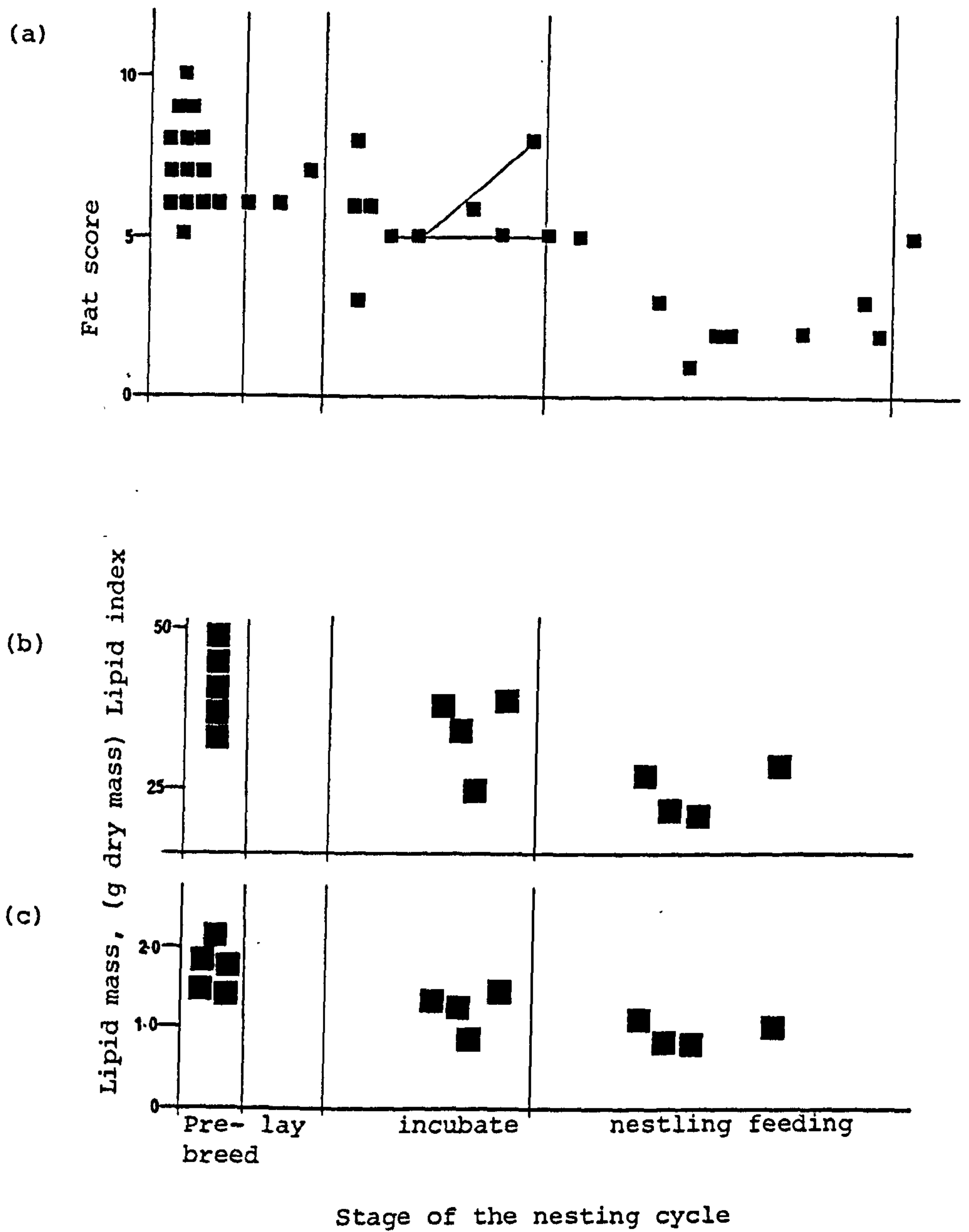


Figure 5.8

Lipid condition of male sand martins over the breeding cycle.

- (a) Fat scores. Lines join successive recaptures of the same bird.
- (b) Lipid indices, and
- (c) Extractable lipid, as determined by carcass analysis.

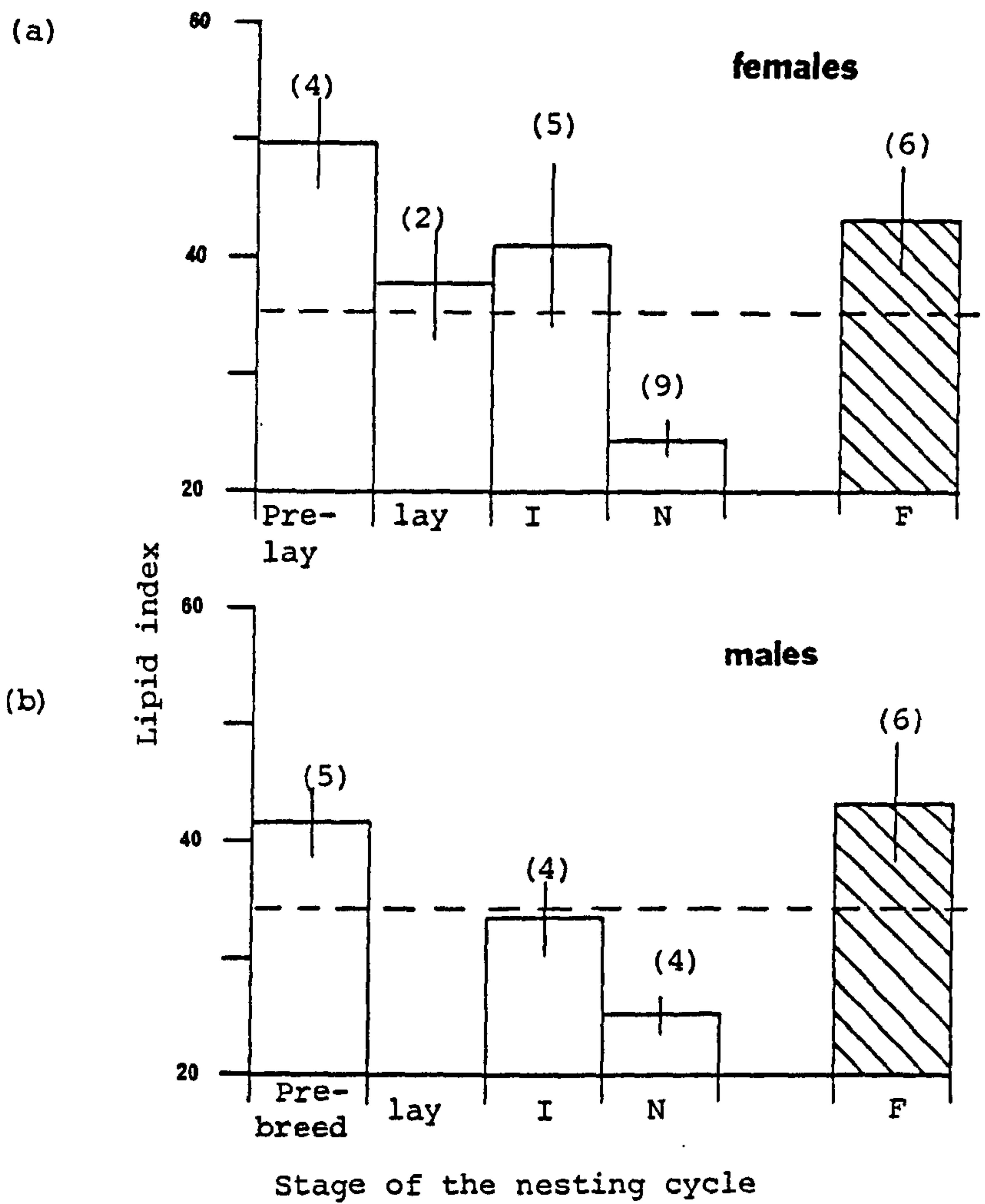


Figure 5.9

Mean lipid indices of male and female sand martins at different stages of the breeding cycle. Values plotted are means \pm sd, sample size in brackets.

Pecked lines represent overall means for males and females. Fledgling values (F) are also included for comparison.

(a) Females
 (b) Males

I = incubation;
 N = nestling rearing.

Table 5.5 Analysis of Variance of Lipid indices according to stage of the nesting cycle

Source	df	SS	MS	F
Factor	7	3061.8	437.4	7.64 P < 0.001***
Error	31	1774.6	57.2	
Total	38	4836.4		

t-test matrix

Stage	Lipid Index(mean + sd(n))											
	PB♂	I♀	L♀	I♂	NF♂	NF♀	PB♂	I♀	L♀	I♂	NF♂	NF♀
Pre-lay ♀ (PL♀)	1.74 ns	1.36 ns	1.68 ns	3.32*	5.67**	6.26**	1.74 ns	1.36 ns	1.68 ns	3.32*	5.67**	6.26**
Fledglings (F)	0.28 ns	0.36 ns	0.74 ns	1.92 ns	3.98**	4.44**	0.28 ns	0.36 ns	0.74 ns	1.92 ns	3.98**	4.44**
Pre-breeders ♂ (PB♂)	-	0.18 ns	0.61 ns	2.08 ns	5.12**	6.08***	-	0.18 ns	0.61 ns	2.08 ns	5.12**	6.08***
Incubating ♀ (I♀)	-	-	0.36 ns	1.15 ns	2.60 ns	2.86*	-	-	0.36 ns	1.15 ns	2.60 ns	2.86*
Laying ♀ (L♀)	-	-	-	0.64 ns	1.93 ns	2.14 ns	-	-	-	0.64 ns	1.93 ns	2.14 ns
Incubating ♂ (I♂)	-	-	-	-	2.16 ns	2.65 ns	-	-	-	-	2.16 ns	2.65 ns
Nestling-feeding ♂ (NF♂)	-	-	-	-	-	0.45 ns	-	-	-	-	-	0.45 ns
Nestling-feeding ♀ (NF♀)	-	-	-	-	-	-	-	-	-	-	-	-

ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

females was the highest value recorded, and was significantly greater than that of nestling rearing birds of both sexes, and greater than the mean lipid index of incubating males. Incubating females had significantly higher lipid indices than nestling-feeding females.

Pre-breeding males had a significantly higher mean lipid index than that of nestling rearing birds of both sexes, though no significant difference existed between pre-breeding males and incubating males, or between incubating and nestling rearing males. The lack of a significant difference between mean lipid indices of incubating and nestling rearing males which was seen in females suggests that females utilised more lipid between incubation and rearing than did males.

Fledglings had significantly higher mean lipid indices than did nestling rearing adults of both sexes.

5.3.2 The role of protein reserves in body mass changes of breeding sand martins

Protein reserves in birds are believed to occur primarily in the flight muscles (Kendall, Ward and Bacchus, 1973), and conditions of high protein demand often coincide with a reduction in the LDM of pectoralis muscles (e.g. egg laying (Jones and Ward, 1976; Fogden and Fogden, 1979), moult (Ward, 1969b)). Hence the analysis of changes in protein reserves in breeding sand martins will be concerned with changes in the LDM of the pectoralis major and pectoralis minor flight muscles.

Pectoralis LDM in breeding sand martins was significantly positively correlated with body size as measured by keel-length ($r = 0.48$, $n = 32$, $P < 0.01$, Figure 5.10a). Similar tendencies for flight muscles to increase in mass as body size increases have been recorded in yellow-vented bulbuls (Ward, 1969b), hooded crows

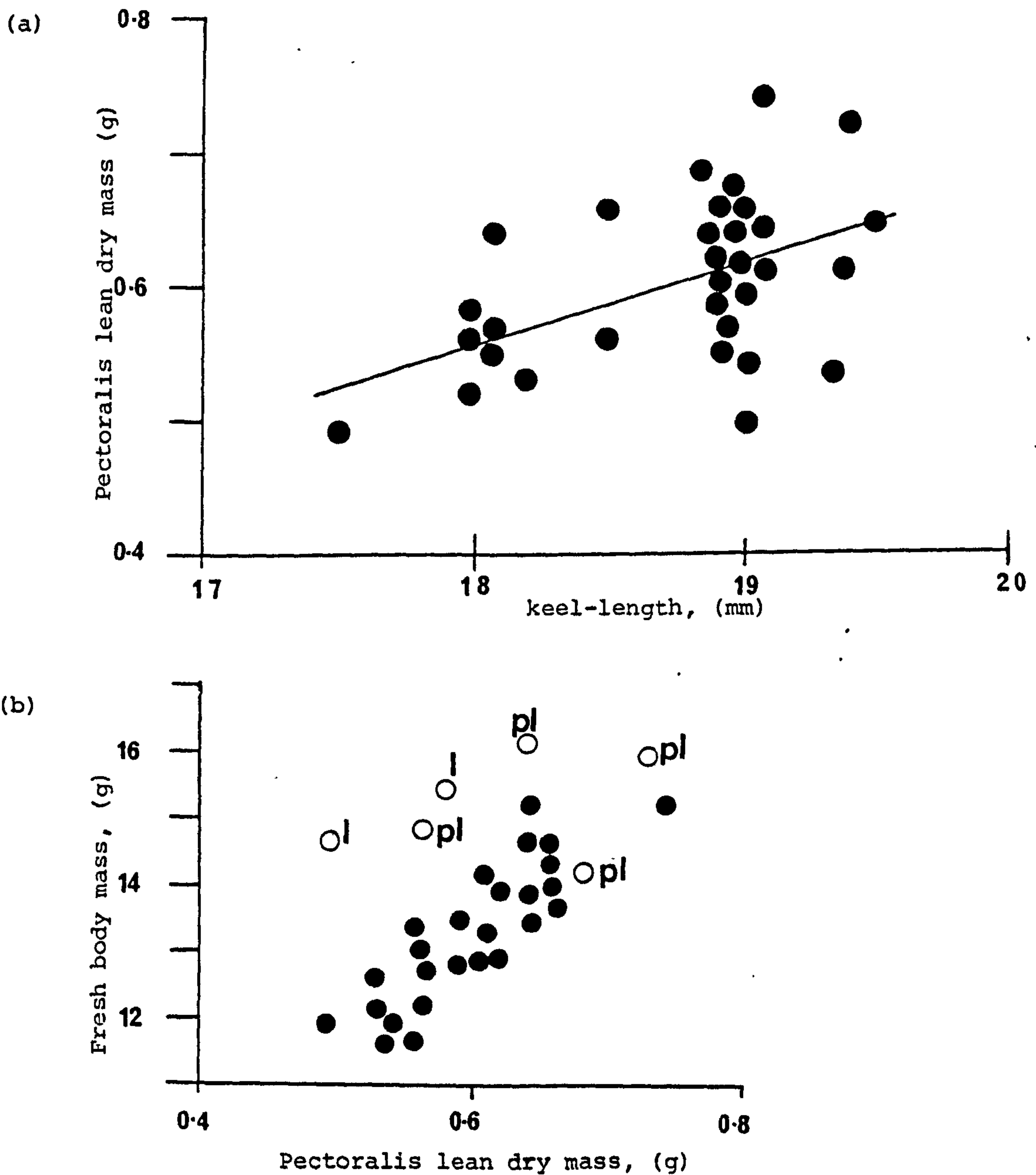


Figure 5.10

(a) The relationship between pectoralis lean dry mass and keel-length in sand martins.

$$r = 0.48, n = 32, P < 0.001: y = -0.541 + 0.061x$$

(b) The relationship between fresh body mass and pectoralis lean dry mass in sand martins.

$$r = 0.62, n = 32, P < 0.001$$

pl = prelaying female, l = laying female, excluding these from the correlation, $r = 0.86, n = 26, P < 0.001$.

(Houston, 1977), Cooper's hawks, Accipiter cooperi, (Marsh and Storer, 1981), house martins (Bryant and Westerterp, 1982), gray catbirds, Dumetella carolinensis, (Marsh, 1984) and white-bellied swiftlets, Collocalia esculenta (Hails and Turner, in prep.). To standardise for differences in keel-length between birds, the relative size of the flight muscles was quantified as 'pectoralis lean dry mass deviation' (PLDMD), where

$$\text{PLDMD} = \frac{\text{observed pectoralis LDM}}{\text{expected pectoralis LDM as a function of keel-length}}$$

A PLDMD of one indicates that pectoralis LDM is that expected for a bird of given size, as predicted by the regression equation for pectoralis LDM as a function of keel-length (Figure 5.10a).

Pectoralis LDM was significantly positively correlated with fresh body mass ($r = 0.62$, $n = 32$, $P < 0.001$, Figure 5.10b). The correlation coefficient increased to $r = 0.86$ ($P < 0.001$) when six laying/prelaying females were excluded from the correlation. Such birds were carrying considerably more non-metabolising reproductive material than other birds studied, and hence their body masses were not directly comparable with those of birds at other stages of the breeding cycle.

The correlation for pectoralis LDM and mass was not significant simply because birds are heavy through having large pectoral muscles, since pectoralis LDM was also significantly correlated with the residual LDM of the bird after removal of the pectoral muscles ($r = 0.59$, $n = 32$, $P < 0.001$).

PLDMD is plotted as a function of stage of the breeding cycle for males and females in Figures 5.11a, b, mean values for different stages plotted on a histogram in Figures 5.11c, d, and an analysis of

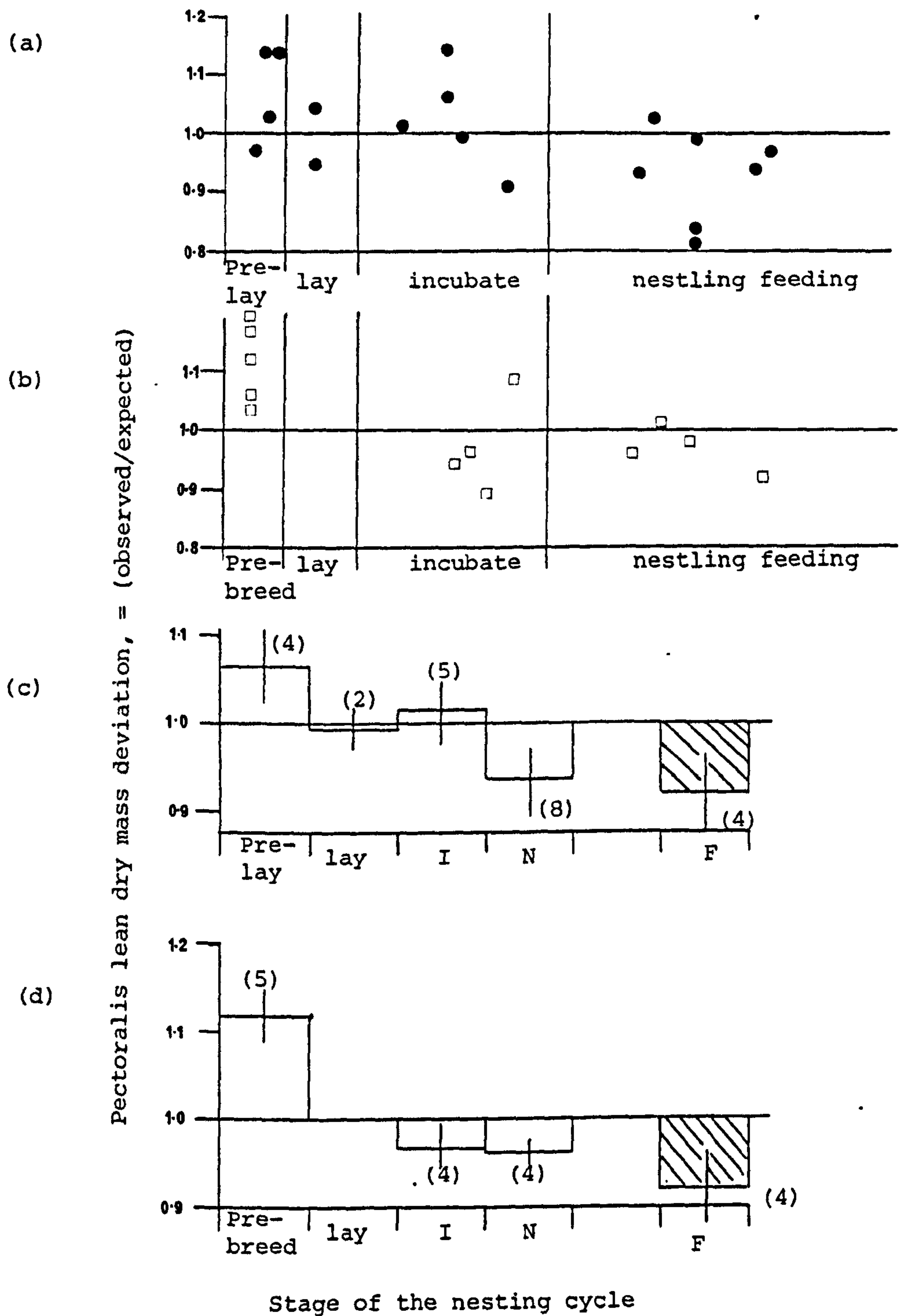


Figure 5.11

Pectoralis muscle lean dry mass changes during the breeding cycle in sand martins.

- (a) Females
- (b) Males
- (c) Females, means \pm sd, (n)
- (d) Males, means \pm sd, (n)

I = incubation; N = nestling rearing;
 F = fledgling values for comparison.

of variance of these means is presented with a 't' test matrix in Table 5.6.

Pre-breeding males had the highest values of PLDMD, and mean PLDMD of this group was significantly greater than those of nestling feeders of both sexes. Pre-laying females had a significantly greater PLDMD than that of nestling rearing females. Hence both sexes showed a decline in PLDMD over the course of the nesting cycle, as pectoral muscles became smaller relative to body size. Fledglings had the smallest pectoral muscles relative to their body size of all groups considered.

5.3.3 The role of body water in body mass changes of breeding sand martins

Water indices of male and female sand martins over the breeding season are plotted in Figure 5.12a. Mean values for the stages are plotted as histograms in Figure 5.12b and an analysis of variance of these values is presented in Table 5.7.

The highest mean water index for adults was found in laying females, the lowest in pre-breeding males. Fledglings had the highest mean water index of all groups considered. Although the sample size of laying females was only two, the birds in this group had a significantly higher mean water index than incubating birds and nestling rearers of both sexes, and than pre-breeding males. Fledglings had significantly greater mean water indices than all adult groups except for laying and prelaying females.

Table 5.6 Analysis of variance of pectoralis lean dry mass (LDM) deviation (observed/expected) in relation to stage of the nesting cycle

Source	df	SS	MS	F
Factor	7	0.1528	0.0218	3.75 P < 0.05*
Error	28	0.1631	0.0058	
Total	35	0.3159		

t-test matrix

Stage	Mean pectoralis LDM (g) + sd(n)									
	PL ♀	I ♀	L ♀	I ♂	NF ♂	NF ♀	F			
Pre-breeding ♂ (PB♂)	1.118 ± 0.060 (5)	2.06 ns	2.38 ns	3.08*	4.77**	4.72***	3.70*			
Pre-laying ♀ (PL♀)	1.064 ± 0.082 (4)	0.80 ns	1.19 ns	1.67 ns	2.25 ns	2.60*	2.30 ns			
Incubating ♀ (I♀)	1.018 ± 0.090 (5)	-	0.45 ns	0.88 ns	1.24 ns	1.69 ns	1.56 ns			
Laying ♀ (L♀)	0.991 ± 0.065 (2)	-	-	0.38 ns	0.56 ns	1.04 ns	1.04 ns			
Incubating ♂ (I♂)	0.968 ± 0.081 (4)	-	-	-	0.10 ns	0.66 ns	0.72 ns			
Nestling-feeding ♂ (NF♂)	0.963 ± 0.037 (4)	-	-	-	-	0.84 ns	0.81 ns			
Nestling-feeding ♀ (NF♀)	0.935 ± 0.079 (8)	-	-	-	-	-	0.21 ns			
Fledglings (F)	0.924 ± 0.090 (4)	-	-	-	-	-	-			

ns : not significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

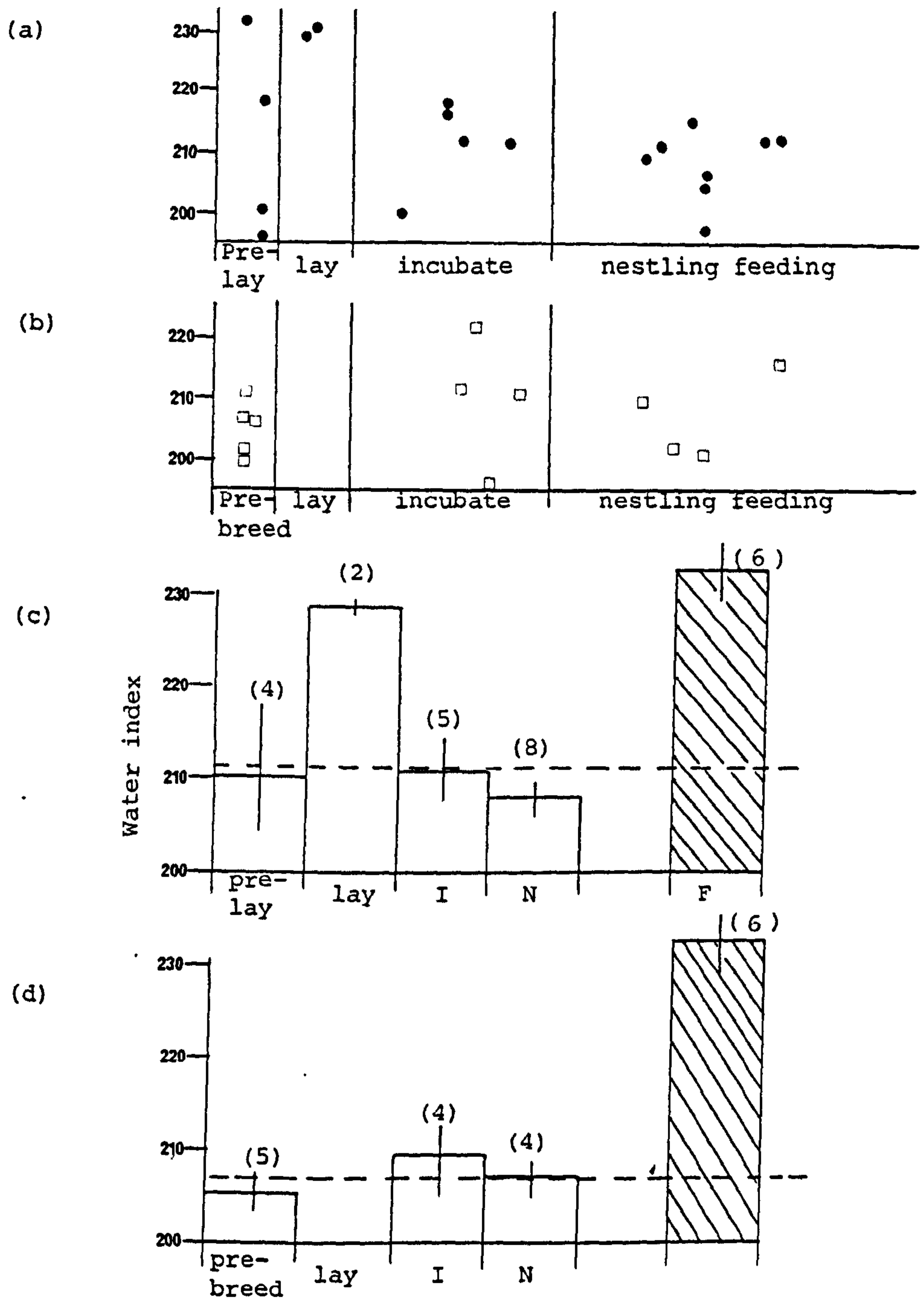


Figure 5.12

Water indices of breeding sand martins.

- (a) Females
- (b) Males
- (c) Females, means \pm sd, (n)
- (d) Males, means \pm sd, (n)

I = incubation, N = nestling feeding, F = fledgling values for comparison.

Pecked lines in (c) and (d) are overall mean values for females and males.

Table 5.7 Analysis of variance of water indices according to stage of the nesting cycle

Source	df	SS	MS	F
Factor	7	3102.1	443.2	5.69
Error	29	2259.8	77.9	
Total	36	5362.0		

P < 0.001***

t-test matrix

Stage	Mean water index + sd(n)									
	L♀	I♀	PL♀	I♂	NF♀	NF♂	PB♂	PL♀	I♀	I♂
Fledglings (F)	0.92 ns	4.00**	2.32 ns	3.17**	5.15**	4.68**	5.64**	2.32 ns	4.00**	3.17**
Laying ♀(L♀)	-	5.55**	2.13 ns	3.29*	10.72***	6.51**	10.89***	2.13 ns	5.55**	3.29*
Incubating ♀ (I♀)	-	-	0.09 ns	0.19 ns	0.80 ns	0.89 ns	1.54 ns	0.09 ns	-	0.19 ns
Pre-laying ♀(PL♀)	-	-	-	0.04 ns	0.25 ns	0.36 ns	0.57 ns	-	-	0.04 ns
Incubating ♂ (I♂)	-	-	-	-	0.29 ns	0.43 ns	0.76 ns	-	-	-
Nestling-feeding ♀ (NF♀)	-	-	-	-	-	0.29 ns	1.02 ns	-	-	-
Nestling-feeding ♂ (NF♂)	-	-	-	-	-	-	0.46 ns	-	-	-
Pre-breeding ♂ (PB♂)	-	-	-	-	-	-	-	-	-	-

ns : not significant; * : P < 0.05; ** : P < 0.01; *** P < 0.001

5.3.4 The role of reproductive structures in body mass changes of breeding sand martins

Changes in the dry mass of reproductive structures over the breeding season in male and female sand martins are illustrated in Figure 5.13.

In females, reproductive structures were heaviest during pre-laying and laying, decreased in mass rapidly after laying, reaching lowest values during nestling rearing. The mass of enlarged ova and eggs in females during late prelaying and laying contributes substantially to the total dry mass of the reproductive structures.

Testes dry mass in males was highest in pre-breeding birds, and declined through incubation to reach lowest values during nestling rearing.

In Figure 5.14 the dry masses of eggs in oviducts (which would be laid the following morning), and enlarged developing ova are plotted from four laying and immediately prelaying females. The masses of the eggs were considerably greater than any of the developing ova, suggesting further investment in egg formation on the day preceding laying. The mean lipid index of two eggs dissected from oviducts was 41.75 ± 0.52 , the mean lipid index of 15 developing ova was 138.51 ± 21.14 , the difference between means being statistically different ($t = 6.29$, $P < 0.001$). Most lipid in eggs therefore appears to be deposited several days prior to laying, and the rapid increase in the dry mass of eggs immediately before laying is due to deposition of other materials.

Yolk formation occurs in the developing ova, whilst albumen is deposited in under 24h in species that lay one egg per day (Ricklefs, 1974). Hence the rapid increase in egg dry mass on the day prior to

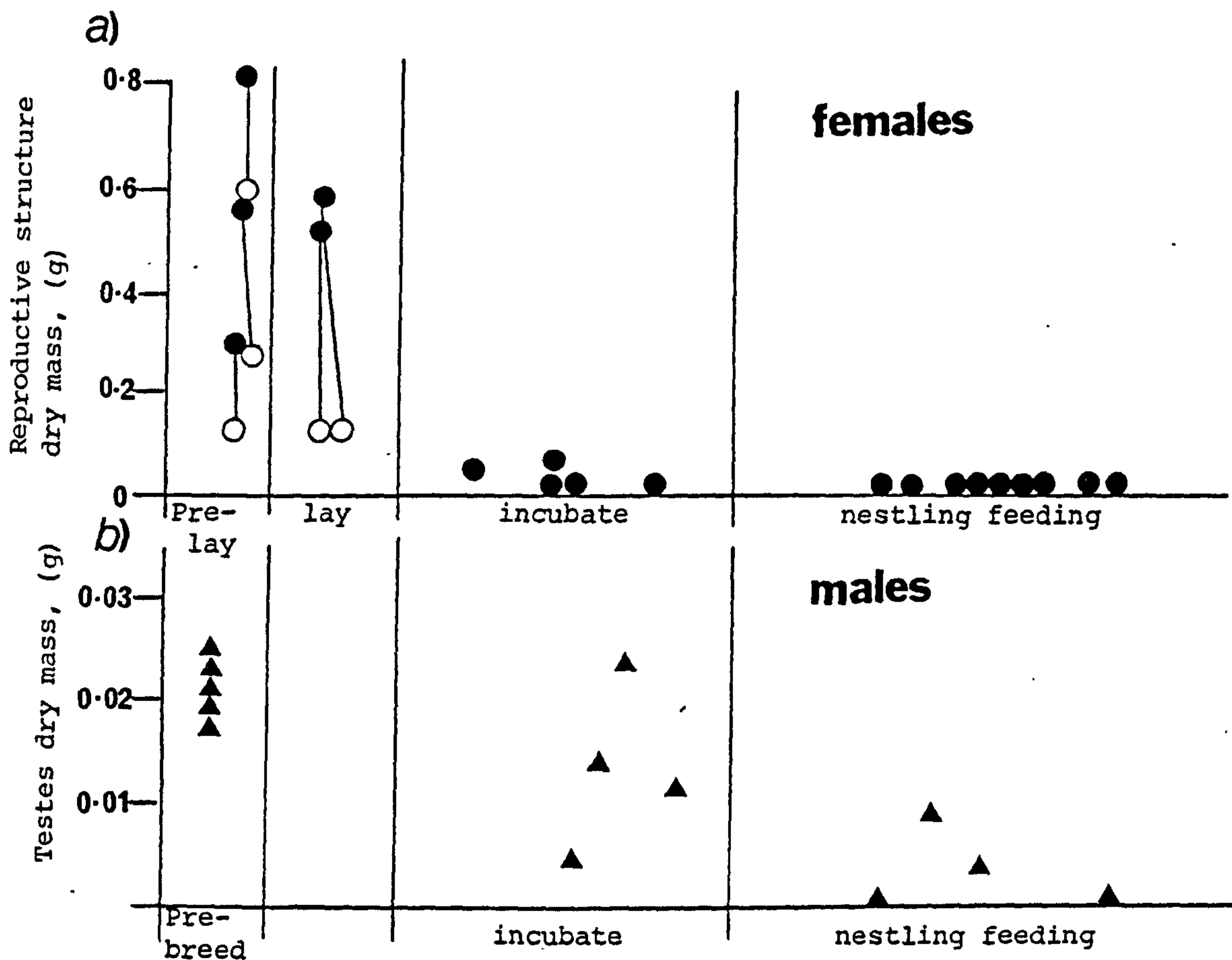
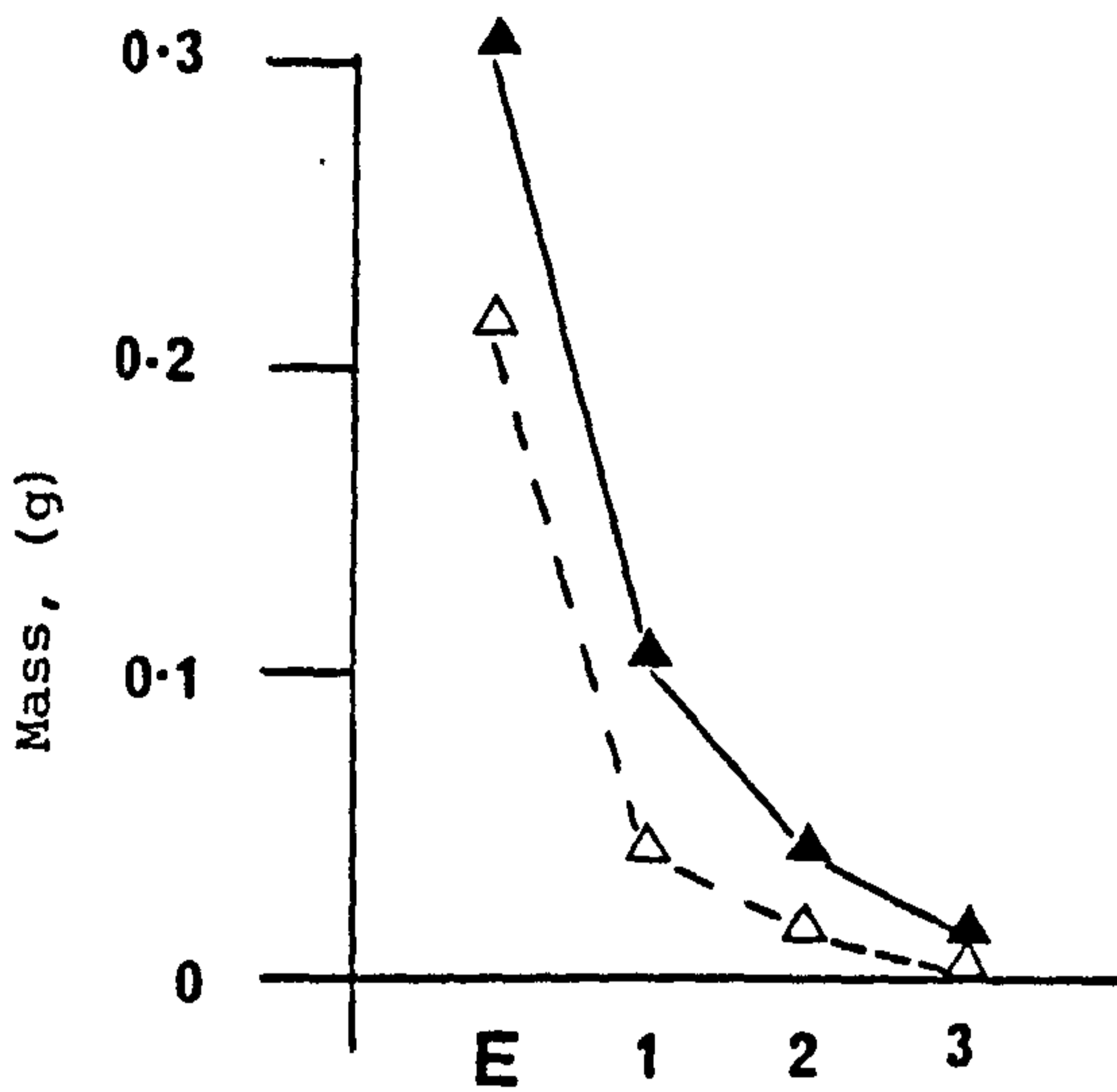


Figure 5.13

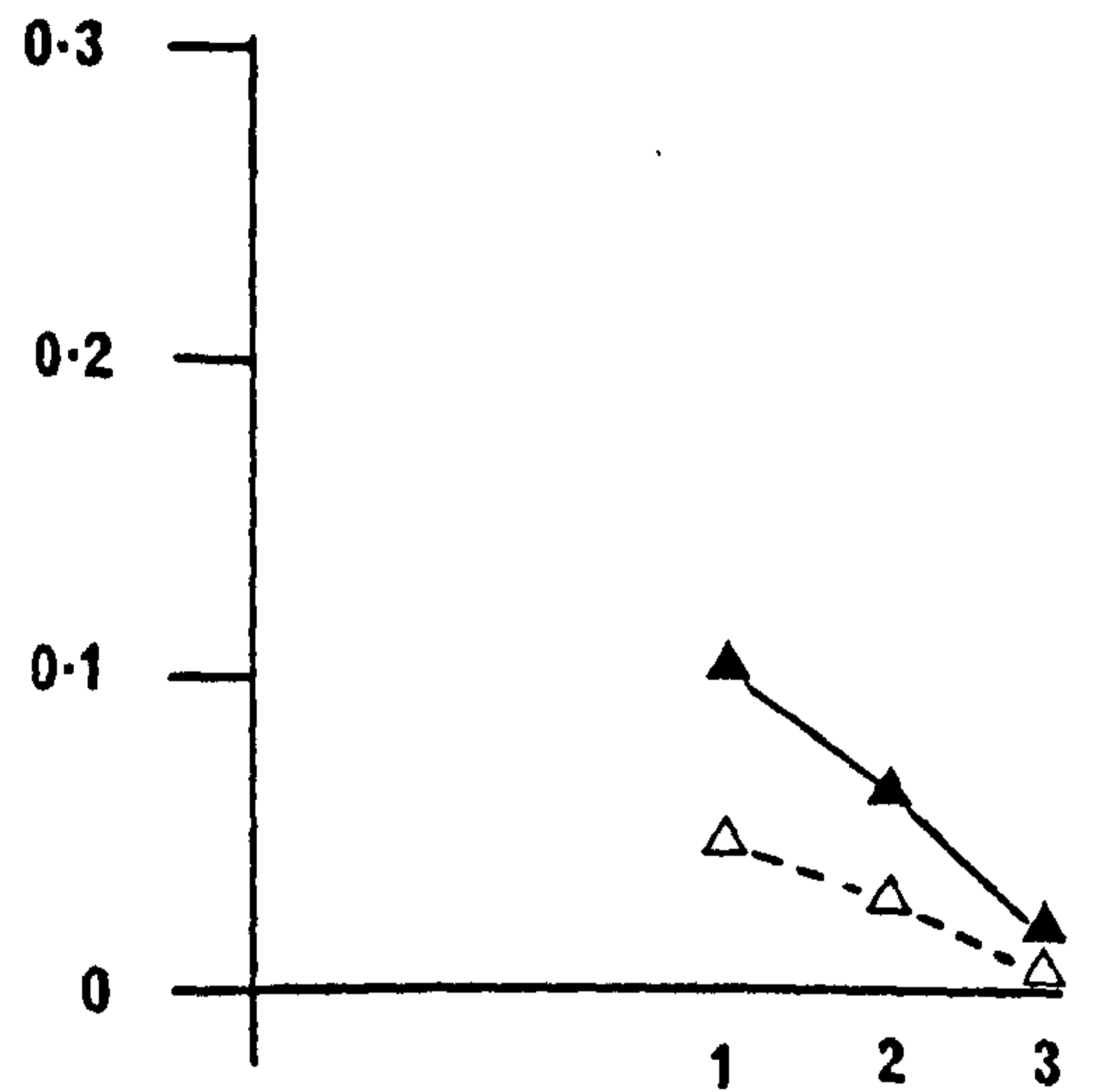
Dry masses of reproductive structures in breeding sand martins.

- (a) Females: open circles represent mass of ovary and oviduct only, after eggs and developing ova had been removed. Closed circles represent dry masses of reproductive structures and eggs. Lines connect individual female values.
- (b) Males

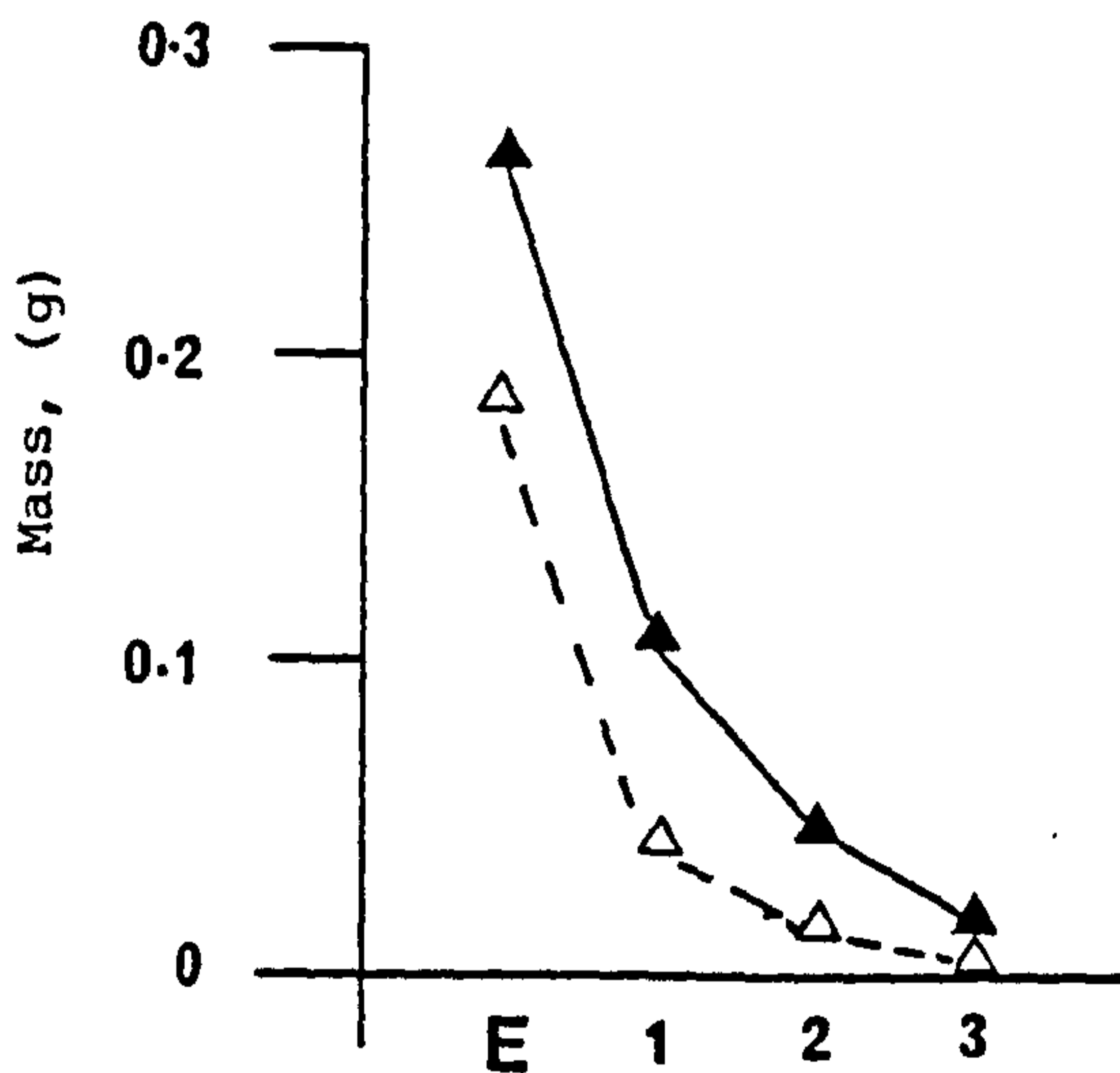
(a) B615976, early laying



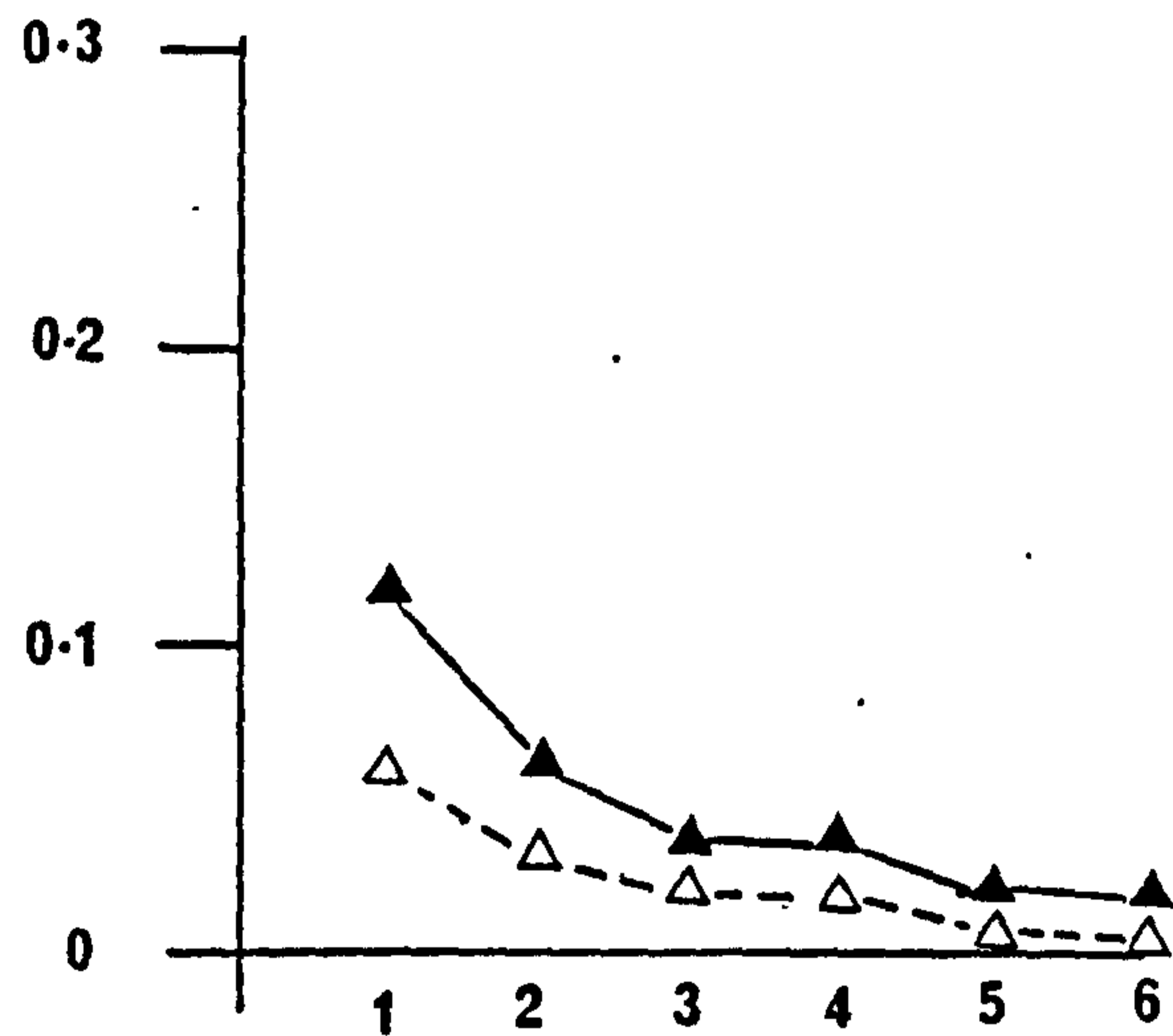
(b) RL, 1 day pre-laying



(c) B615950, early laying



(d) 5/84, 1 day pre-laying



Stage of ovarian development

Figure 5.14

Dry masses and lean dry masses of eggs and developing ova in four prelaying or laying female sand martins.

Solid triangles and solid lines represent dry masses.

Open triangles and pecked lines represent lean dry masses.

E = egg, masses include shells.

Developing ova (1-6) are numbered in sequence of descending mass.

laying is likely to be the result of calcium deposition for shell formation, and increased protein allocation for albumen formation. Most of the lipid in the egg will already have been deposited in the developing ova (Hails and Turner, in prep.).

5.3.5 Body condition of breeding adult sand martins - synthesis

FEMALES:

(a) Lipid indices:

Lipid indices were highest in pre-laying females, fell during laying, recovered slightly during incubation, and fell to their lowest values during nestling rearing. The mean lipid index of pre-laying birds was significantly greater than that of both incubating and nestling feeding females, and incubating females had significantly greater lipid indices than nestling feeders.

(b) Protein reserves:

Protein reserves in pectoralis muscle followed the same trend as lipid reserves over the breeding cycle. The heaviest pectoralis muscles occurred in pre-laying females which had a significantly higher mean PLDMD than during nestling feeding, when mean PLDMD was at its lowest.

(c) Water indices:

Laying females had a significantly higher mean water index than incubating females and nestling rearers.

(d) Reproductive structures:

Reproductive structures were heaviest during laying and pre-laying when eggs and enlarged ova were present in the hypertrophied reproductive tract. The mass of reproductive structures decreased throughout incubation to reach lowest values during nestling rearing.

Reproductive structures accounted for $8.61 \pm 3.07\%$ of total female dry mass during laying/prelaying ($n = 4$).

MALES:

(a) Lipid indices:

Lipid indices were highest in pre-breeding males, lower by incubation, and lowest in nestling rearers. Pre-breeders had a significantly greater mean lipid index than nestling rearers.

(b) Protein reserves:

These followed the same trend on lipid indices over the breeding cycle. The largest pectoral muscles occurred in pre-breeders, which had a significantly larger mean PLDMD than during nestling rearing.

(c) Water indices:

There were no significant differences in mean water index over the breeding cycle in males.

(d) Reproductive structures:

Testes DM was greatest in pre-breeders, lower in incubators, and lowest in nestling rearers. Testes accounted for a maximum of only $0.37 \pm 0.04\%$ of total dry body mass in pre-breeding males.

FLEDGLINGS:

Fledglings had a significantly higher mean lipid index than did nestling-feeding adults, and significantly smaller PLDMDs than pre-breeding males. The mean water index of fledglings was significantly greater than in incubating and nestling feeding adults. No reproductive structures were discernable for dissection.

A stepdown multiple regression analysis of adult dry mass is presented in Table 5.8, with pectoralis LDM and lipid content entered

Table 5.8

Stepdown multiple regression analysis of total dry mass
of sand martin carcasses

Independent Variable	Multiple r^2 $\times 100$	Degrees of Freedom	Regression Equation	t-value
Pectoralis lean dry mass (g)	46.6	1,31	$y = 3.87x_1 +$	3.52, $P < 0.01^{**}$
Lipid content (g)	80.4	2,30	$1.02x_2 + 1.63$	7.07, $P < 0.001^{***}$
			$F = 59.6,$	$P < 0.001^{***}$

on the independent variables. 80.4% of the variation in total dry mass was attributable to changes in the size of the flight muscles and lipid content.

5.3.6 The body condition of adult and fledgling swallows

Mean dry masses, lean dry masses, and lipid indices of the dissected body components of adult and fledgling swallows are presented in Appendix III. Measurements taken during carcass analysis are summarised in Table 5.9. The sample consisted of six adults, of which four were nestling rearers, and also included two starved birds with lipid indices of 5.35 and 15.4. Three fledglings were also killed for carcass analysis.

The mean lipid index of four nestling rearing adults (excluding the two starved birds), was 27.05 ± 6.18 . The mean wing loading of four adult swallows was $0.196 \pm 0.024 \text{ g cm}^{-2}$.

As in sand martins, the fat score of male and female swallows was positively correlated with body mass (Figure 5.15) and both lipid index and extractable lipid were correlated with body mass (Figure 5.16). Lipid index was also correlated with fat score (Figure 5.17). In all cases, as in sand martins, relationships between variables were a good fit to a straight line. Hence extrapolation from the more extensive sand martin body lipid condition data to a discussion of body condition of swallows is probably justified.

5.3.7 Nestling body masses and body condition in sand martins

Nestling body mass as a function of mean brood age is plotted in Figure 5.18. A great deal of variation in body mass occurs between mean brood ages 6-18 days. This is largely because nestlings generally hatch over 2-3 days (Turner, 1980), resulting in a range of

Table 5.9 Carcass analysis information for swallows

	<u>Adults</u> n = 6	<u>Fledglings</u> n = 3	<u>Combined sample</u> n = 9
Wet mass (g)	18.96 ± 0.89	19.17 ± 1.85	19.04 ± 1.20
Keel-length (mm)	21.33 ± 0.52	18.47 ± 1.68	20.38 ± 1.71
Wing-length (mm)	124.33 ± 3.63	107.33 ± 14.98	118.67 ± 11.69
Dry mass (g)	6.8722 ± 0.6103	7.1116 ± 0.6557	6.9520 ± 0.5955
Lean dry mass (g)	5.6581 ± 0.2263	5.2099 ± 0.2064	5.5087 ± 0.3048
Water content (g)	11.878 ± 0.7456	12.0551 ± 1.3481	11.9443 ± 0.9194
Water index	208.89 ± 7.9595	231.67 ± 27.45	217.44 ± 19.7617
% Water content	62.62 ± 1.68	62.85 ± 2.09	62.71 ± 1.70
*Lipid content (g)	1.2141 ± 0.5764	1.9017 ± 0.5331	1.4433 ± 0.6300
*Lipid index	21.49 ± 10.35	36.41 ± 9.64	26.46 ± 12.08
Wing area (cm ²)	95.15 ± 12.58	97.08 ± 11.41	95.79 ± 11.51
Wing loading (g cm ⁻²)	0.196 ± 0.024	0.200 ± 0.035	0.197 ± 0.026

Mean values ± s.d. are tabulated.

* includes two adults which starved to death.

Mean adult lipid content, excluding these starved birds = 1.5122 ± 0.3591g

Mean adult lipid indices, excluding starved birds = 27.05 ± 6.18

Starved birds had lipid indices of 5.35 and 15.4

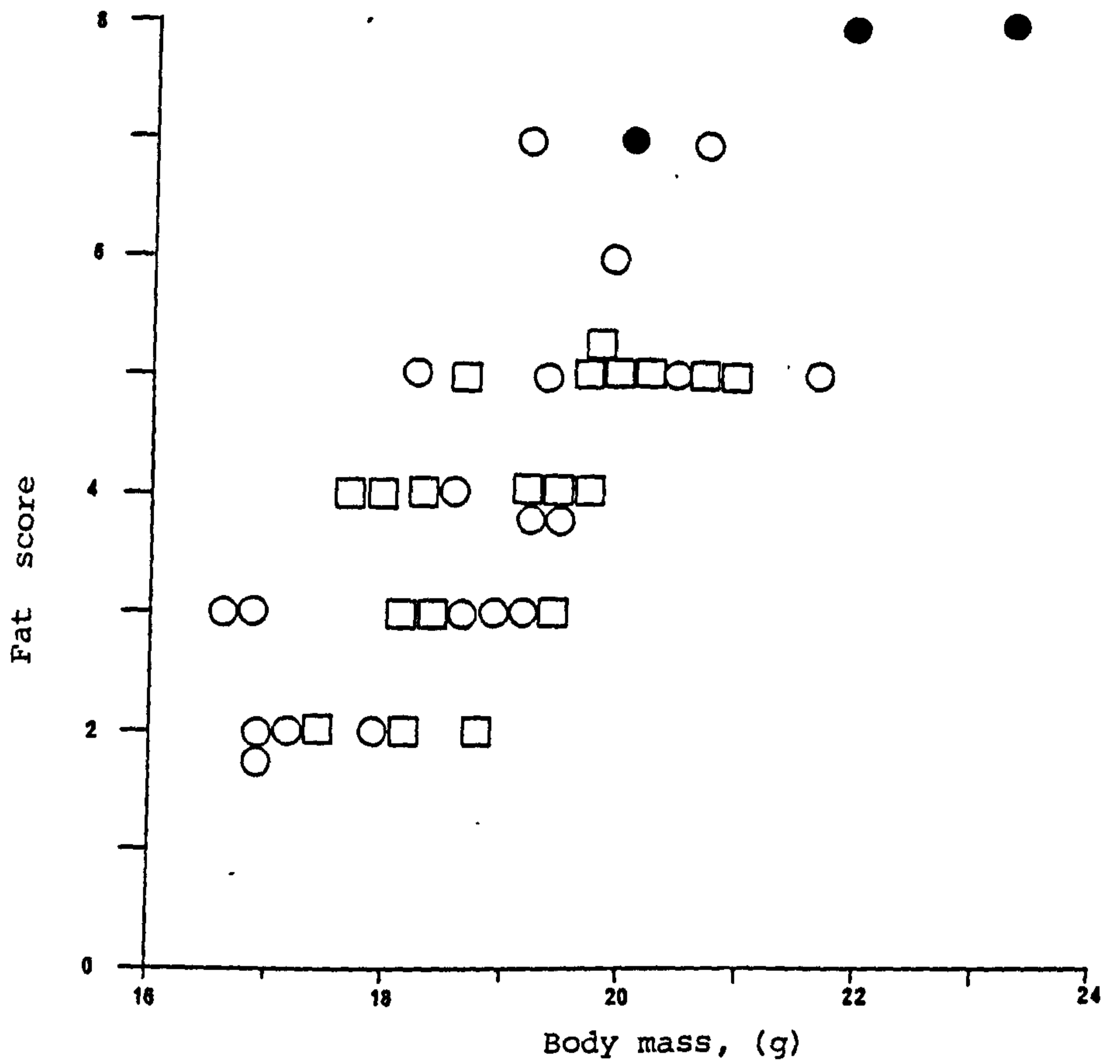


Figure 5.15

The relationship between fat score and fresh body mass in swallows.

Circles represent females, solid circles are incubating females. Squares represent males.

Females: $\text{Mass} = 17.49 + 0.33x$, $n = 22$, $r = 0.67$, $P < 0.001$

Males: $\text{Mass} = 17.79 + 0.33x$, $n = 19$, $r = 0.48$, $P < 0.05$

All data: $\text{Mass} = 17.58 + 0.34x$, $n = 41$, $r = 0.65$, $P < 0.001$

where x is fat score in regression equations.

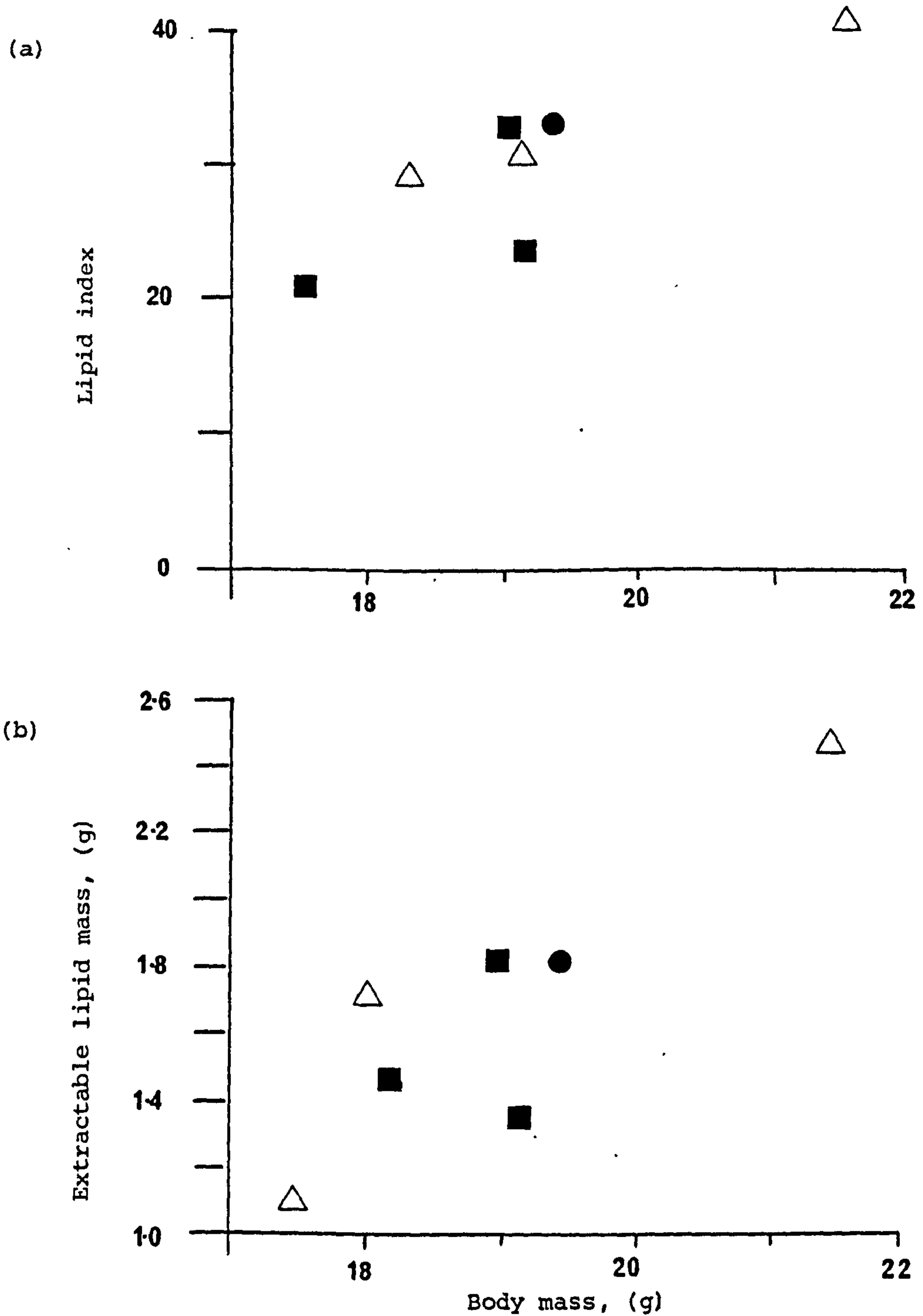


Figure 5.16

(a) The relationship between lipid index and body mass in swallows.
 $\text{lipid index} = -77.12 + 5.72 (\text{body mass})$, $n = 7$, $r = 0.82$, $P < 0.05$

(b) The relationship between extractable lipid and body mass in swallows.

$\text{extractable lipid mass} = -4.08 + 0.30 (\text{body mass})$,
 $n = 7$, $r = 0.84$, $P < 0.05$

Solid squares : males; solid circles : females;
 open triangles : fledglings.

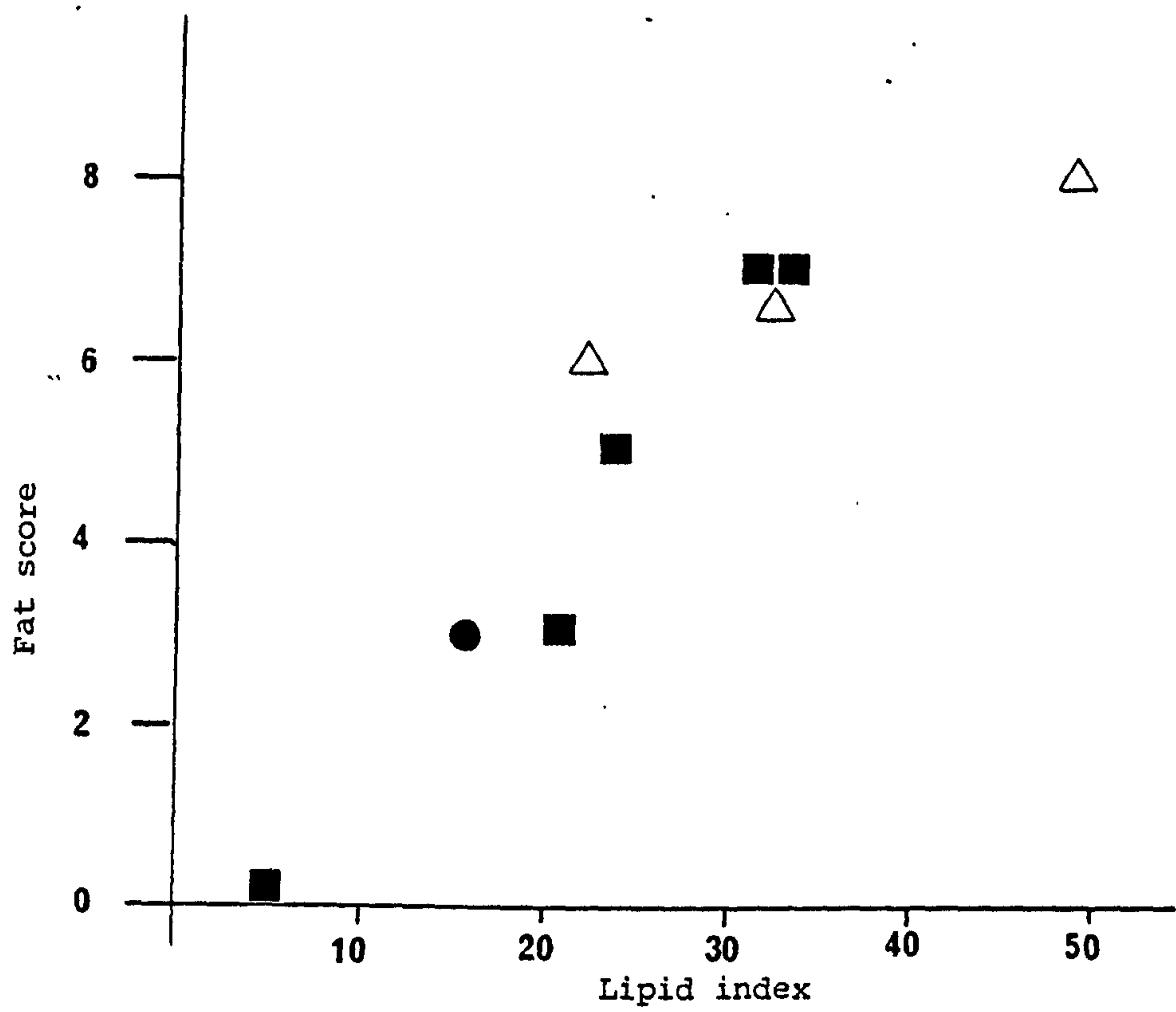


Figure 5.17

The relationship between fat score and lipid index in swallows.

$$r = 0.91, n = 9, P < 0.001$$

Symbols as in Figure 5.16

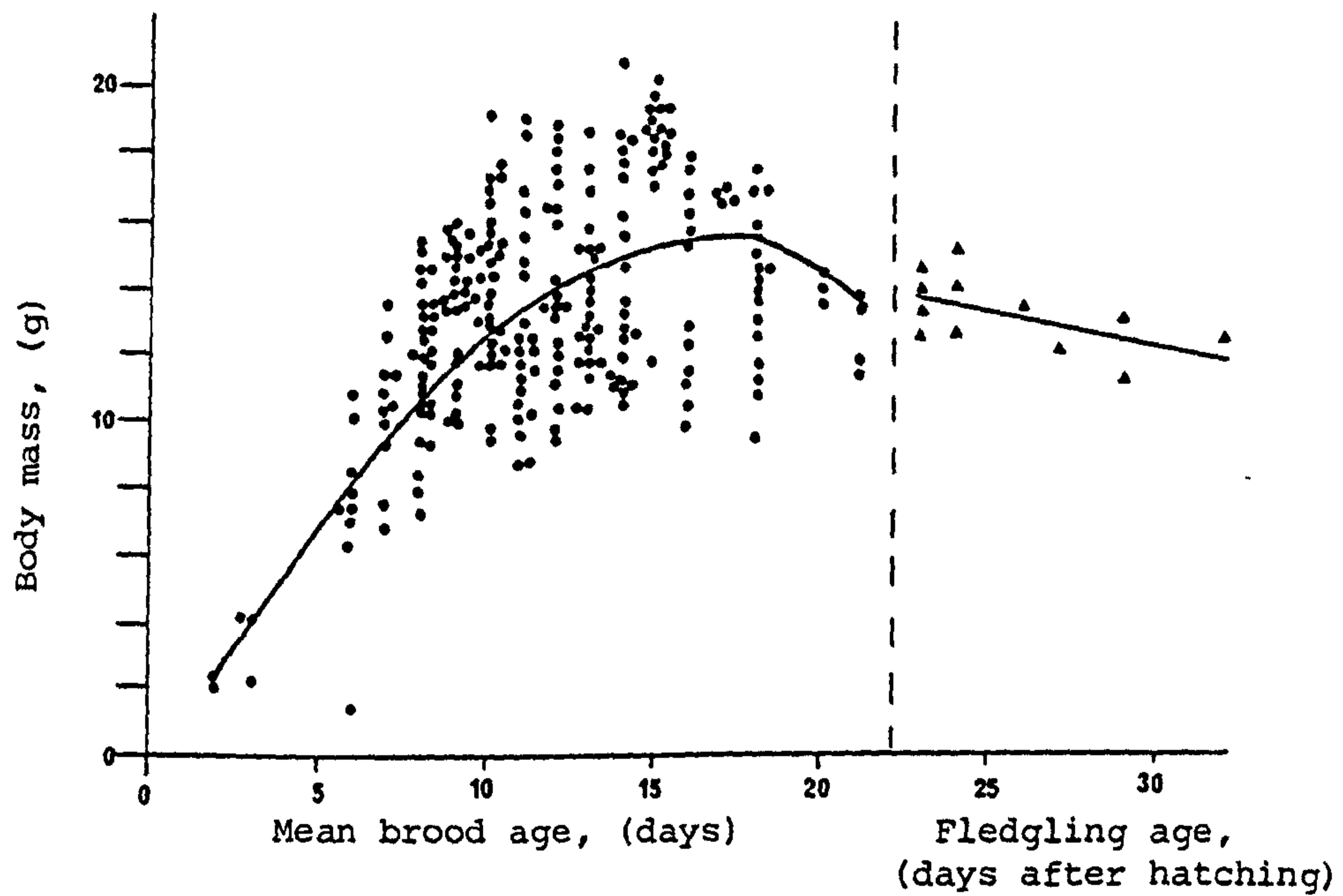


Figure 5.18

Nestling body mass as a function of mean brood age
in sand martins.

$n = 252$, curve fitted by eye.

Evening body masses of fledglings of known age are also
illustrated. After leaving the nest, fledgling body
mass (up until day 32), is described by the equation
 $y = 18.76 - 0.219x$, where $x =$ age, days after hatching.
 $r = 0.60$, $n = 12$, $P < 0.05$.

nestling ages within most broods. The consequences of this age and size hierarchy for nestling condition within a brood will be investigated in Section 5.3.10. Nestling mass is also greater when food is abundant (Turner, 1980), and hence variation in food availability will also influence the body mass of nestlings within a brood.

Turner and Bryant (1979) showed that sand martin nestlings attained peak mass at about 12d. Chicks became lighter after 12d during a period of mass recession (Edson, 1930) as loss of water occurs during tissue (especially feather) maturation (Ricklefs, 1968). Mass recession is most pronounced in birds which feed on or search for prey during long flight periods (Ricklefs, 1968), so a light mass at fledging may be adaptive in that flight costs are reduced for foraging. Hence fledglings leave the nest at a lower body mass than the maximum attained during the nestling period, and their body mass continues to decline for at least 10d following fledging (Figure 5.18). House martin fledglings also lose mass for about 5d after leaving the nest, though after this time they increase in mass (Bryant and Gardiner, 1979). The decline in mass in sand martin fledglings is probably associated with inexperience in self-feeding. To overcome this, the fledglings have relatively high lipid indices (section 5.3.1) and low wing loadings roughly equivalent to those of incubating adults, despite adults having significantly longer wings and hence larger wing areas (Discussion, Chapter 6). A relatively low wing loading may reduce flight costs in a period of foraging inexperience.

In Figure 5.19, LDM, water indices and lipid indices are plotted as a function of nestling age, and presented with comparative data for adults and fledglings. LDM increased rapidly between days 3 and 18, by which time it had reached the value attained by fledglings. Water

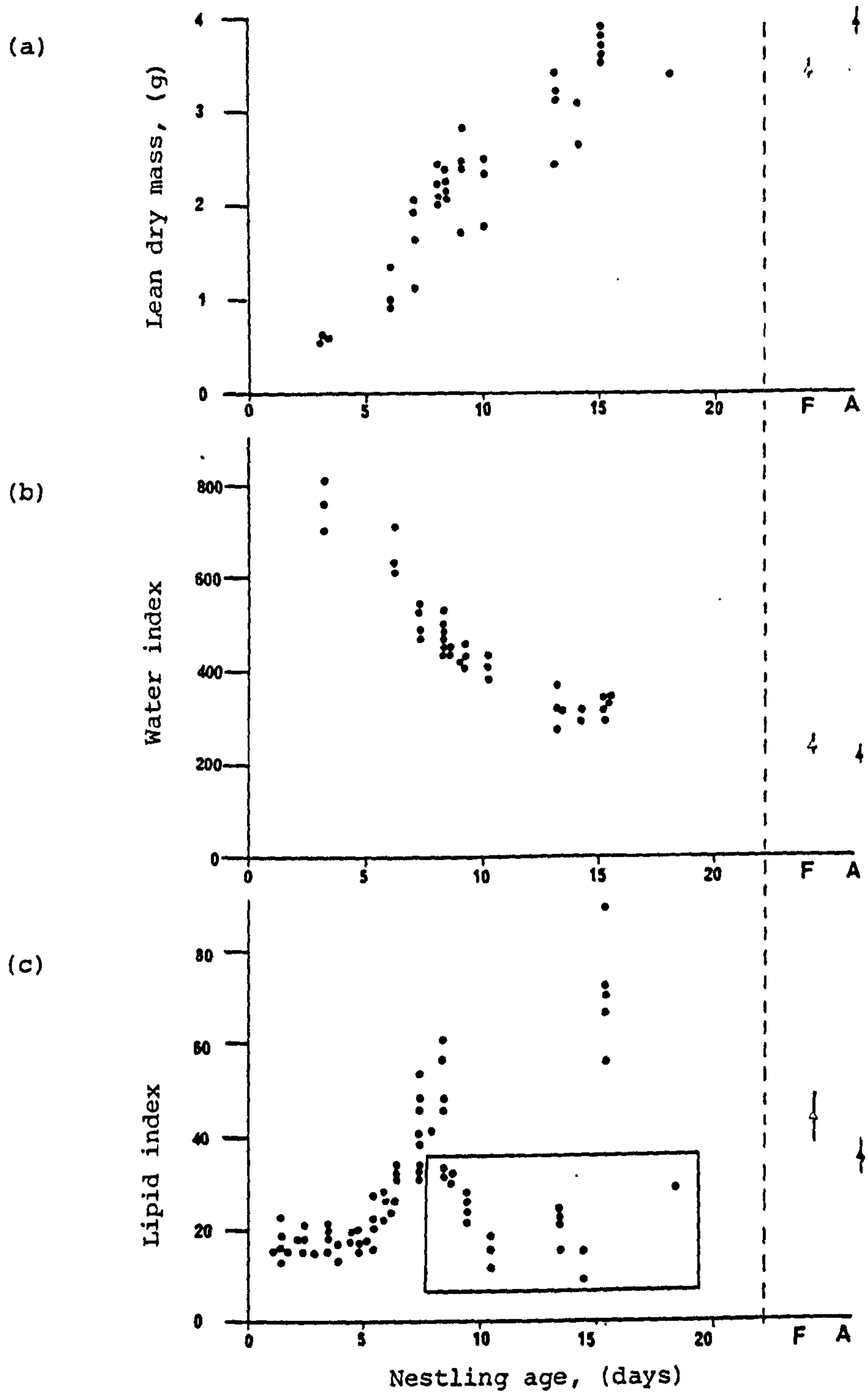


Figure 5.19

Lean dry mass, water index, and lipid index as a function of nestling age in sand martins.

Adult (A, solid triangles), and fledgling (F, open triangles) means and sds are also illustrated. Lipid indices include data of D.M. Bryant, and values in the box are for nestlings taken after 18th August.

indices declined over the nestling period as body tissues mature (O'Connor, 1977). Lipid indices increased exponentially between days 1 and 8, after which values became variable. The lipid indices enclosed in a box in Figure 5.19 are for nestlings taken late in the season (after 18th August). Although lipid content of sand martin chicks is positively correlated with food abundance (Turner, 1980), these chicks were taken on days when food was relatively abundant, and the low lipid indices may therefore reflect decreased investments in the brood in favour of self-maintenance by parents, at a time when chick or fledgling survival may be low. Observations suggested that many chicks reared after late August in 1982 were deserted. Hence the lipid index graph may be unrepresentative of the normal situation when lipid index increases with nestling age throughout the nestling period (Turner and Bryant, 1979). If this were so, fledglings would leave the nest with lipid indices lower than those maximally attained while in the nest.

5.3.8 Body component development in nestling sand martins

The growth of body components has been related to the increase in total LDM by calculating allometric equations

$$\text{LDM}_{\text{component}} = a \text{LDM}_{\text{total}}^b$$

where a is a constant, and b , the growth constant, is the slope of the log-log plot of component LDM on total LDM (e.g. Ricklefs, 1967, O'Connor, 1977, Tatner, 1984). In Table 5.10 allometric growth constants for lean dry masses of sand martin body components are presented.

Skin and feathers, wings, pectoralis muscles, kidneys, and liver had values of b greater than one, suggesting that these components grew faster than the body as a whole.

Table 5.10

Allometric growth constants for lean dry masses of
sand martin body components

Body component	Slope b	s.d. b	intercept $\log_e a$	s.d. of $\log_e a$
Skin and feathers	1.48	0.04	-1.75	0.04
Body shell	0.92	0.04	-1.94	0.04
Head	0.63	0.02	-2.27	0.02
Neck	0.61	0.04	-3.37	0.04
Legs	0.64	0.03	-2.37	0.03
Wings	1.24	0.09	-3.34	0.08
Pectoral muscles	1.60	0.07	-3.47	0.06
Oesophagus and gizzard	0.55	0.14	-2.03	0.12
Gut	0.74	0.09	-2.28	0.08
Heart	0.86	0.05	-3.86	0.04
Lungs	0.68	0.06	-3.96	0.06
Kidney	1.13	0.09	-4.62	0.08
Liver	1.60	0.07	-3.47	0.06

$$\log_e \text{LDM}_{\text{component}} = \log_e a + b \log_e \text{LDM}_{\text{total body}}$$

LDM(g)

The significance of all of the allometric growth equations

was $P < 0.001^{***}$

To illustrate the differential growth rates of body components, the relative lean dry mass of each component (RLDM) was calculated as

$$\text{RLDM}_{\text{component}} = \frac{\text{LDM}_{\text{component}}}{\text{LDM}_{\text{total}}} \times 100$$

In Figure 5.20, lean dry masses of components and their RDLMs are plotted as a function of nestling age.

All components increased in LDM over the first week of nestling life. Skin and feathers further increased in LDM until the fledgling value was attained by day 15. The LDM of wing and tail feathers is plotted separately in Figure 5.20a and they developed rapidly after the feather tips sprouted on day 9.

The relative masses of skin and feathers, wings, and pectoral muscles all increased over the nestling period though wings showed an initial drop in RLDM.

Head, neck, and legs also increased in LDM rapidly over the first two weeks of the nestling period, so that fledgling values were attained by the fifteenth day. However, unlike the skin and feathers, wings, and pectoralis muscles, the head, neck and legs declined in relative mass over the first eight days of the nestling period. The head, neck and legs are all important for food acquisition, and there will be an early premium on obtaining and assimilating food during a period of rapid growth. A well developed head in small chicks occurs partly because of the necessity of possessing a large cranial case at hatching (Portmann, 1955), and also because a large bill would facilitate food acquisition early in the nestling period. Precocial development of the neck may improve the chances of obtaining food through begging. Early growth of the legs may facilitate an upright

Figure 5.20

Lean dry masses (LDMs) and relative lean dry masses (RLDMs) of body components as a function of nestling age in sand martins.

Open circles are fledgling values (F, mean \pm sd)

Open squares are adult values (A, mean \pm sd).

(a) skin and feathers

triangles - wing and tail feathers only. The arrow denotes the nestling age when feather tips sprout (Turner and Bryant, 1979).

(b) wings

(c) pectoralis muscles

(d) head

(e) neck

(f) legs

(g) oesophagus and gizzard

(h) gut

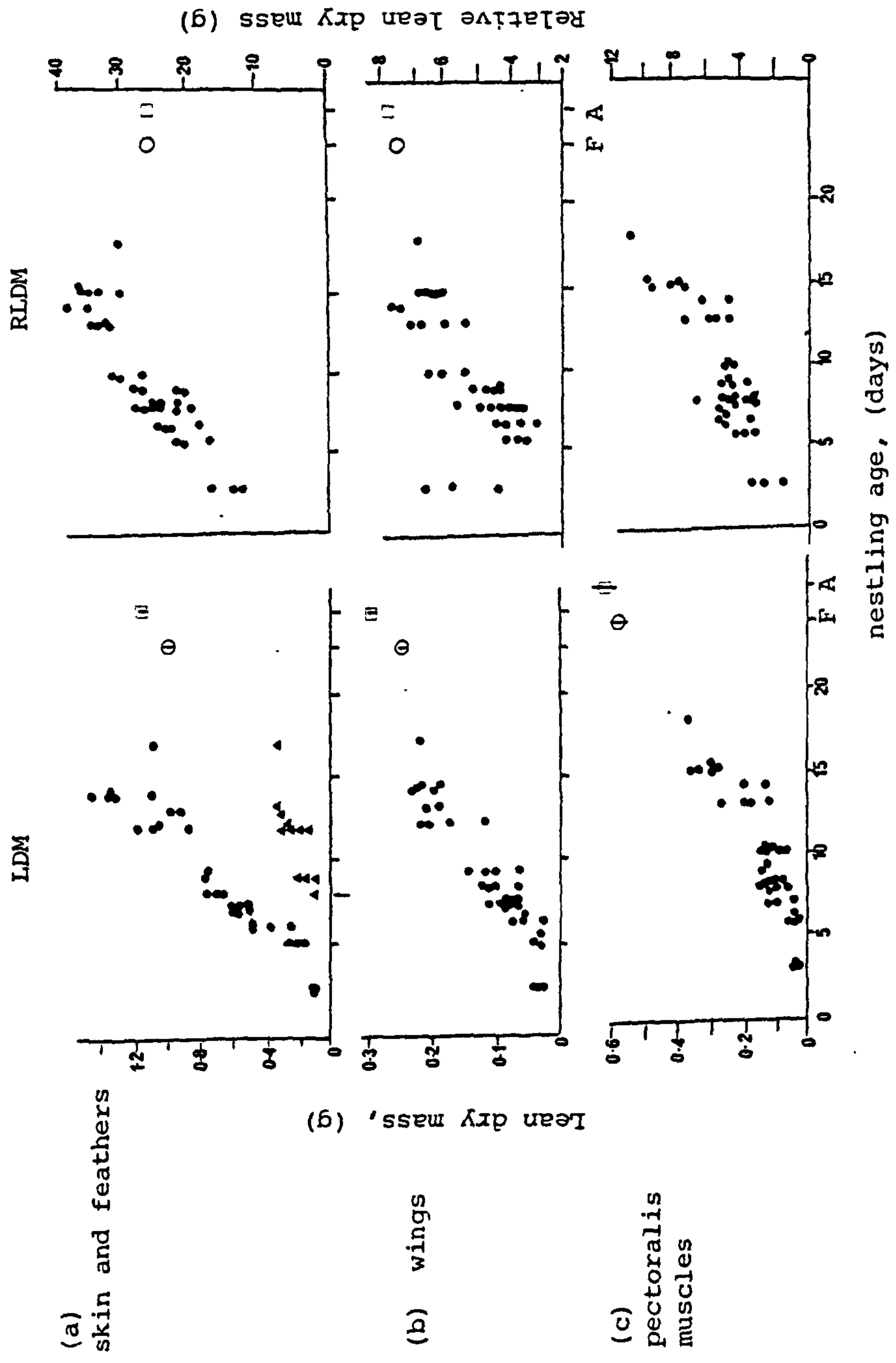
(i) liver

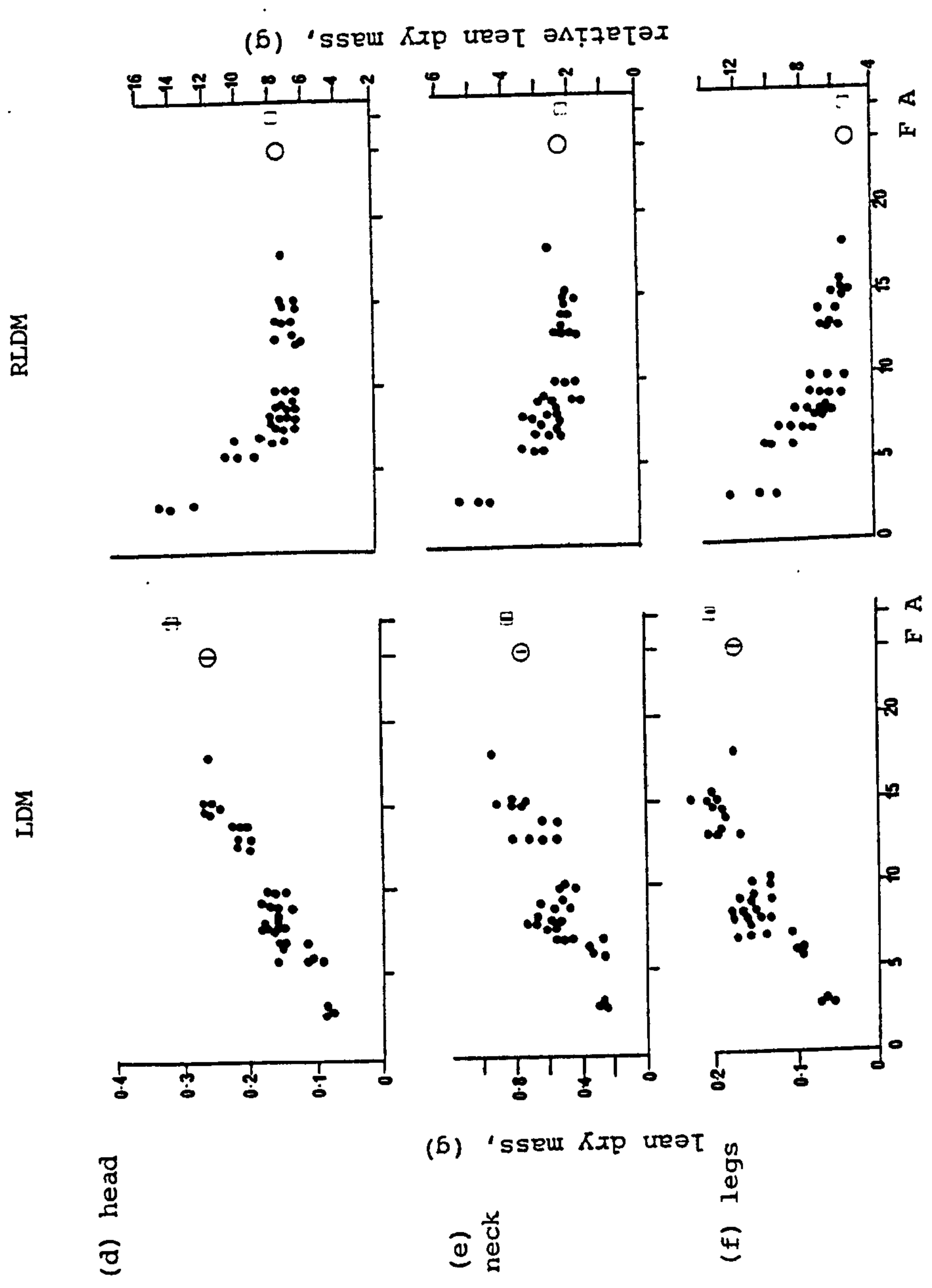
(j) heart

(k) kidneys

(l) lungs

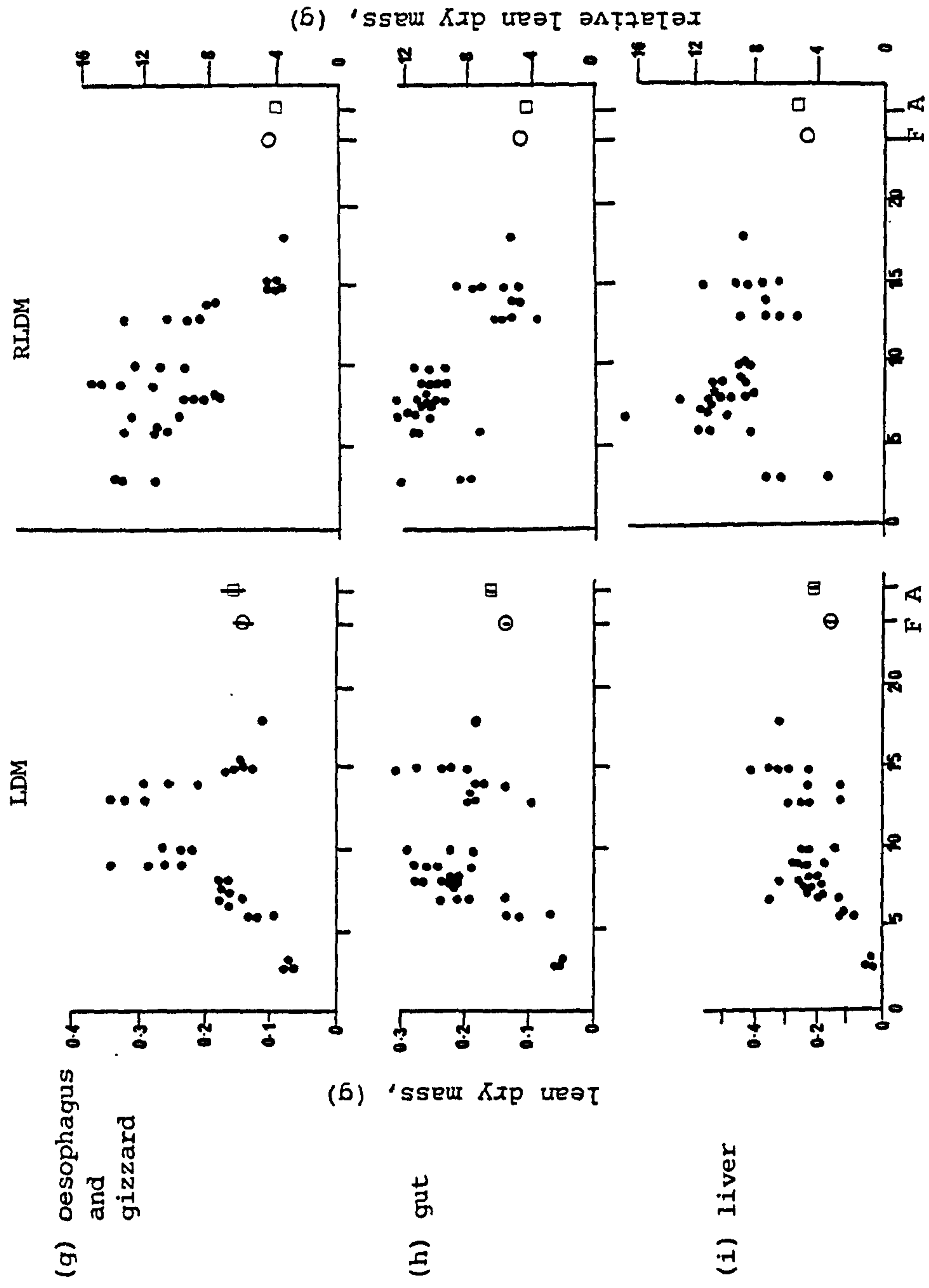
(m) body shell





nestling age, (days)

Figure 5.20 (cont.)



nestling age, (days)

Figure 5:20 (cont..)

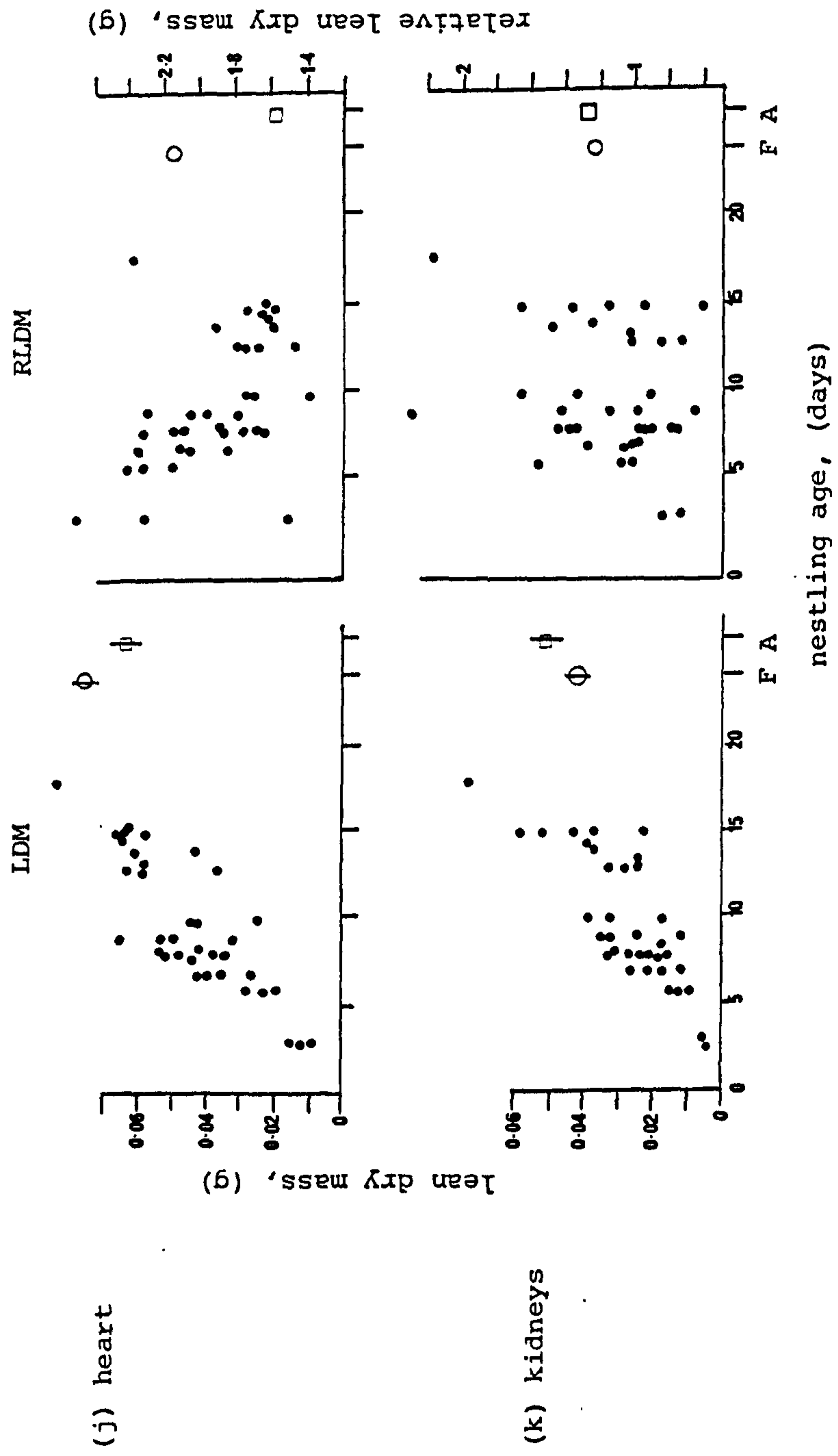
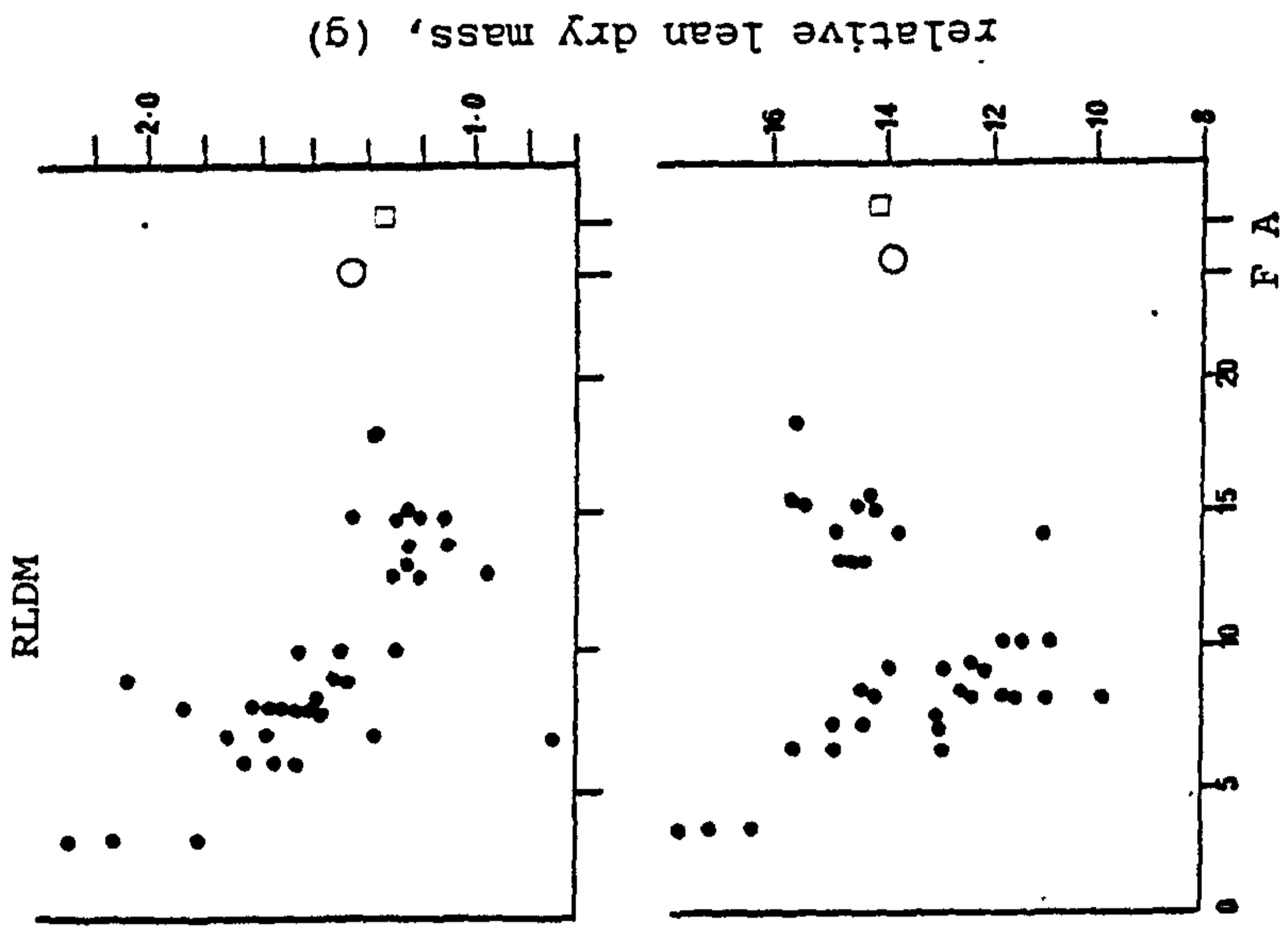
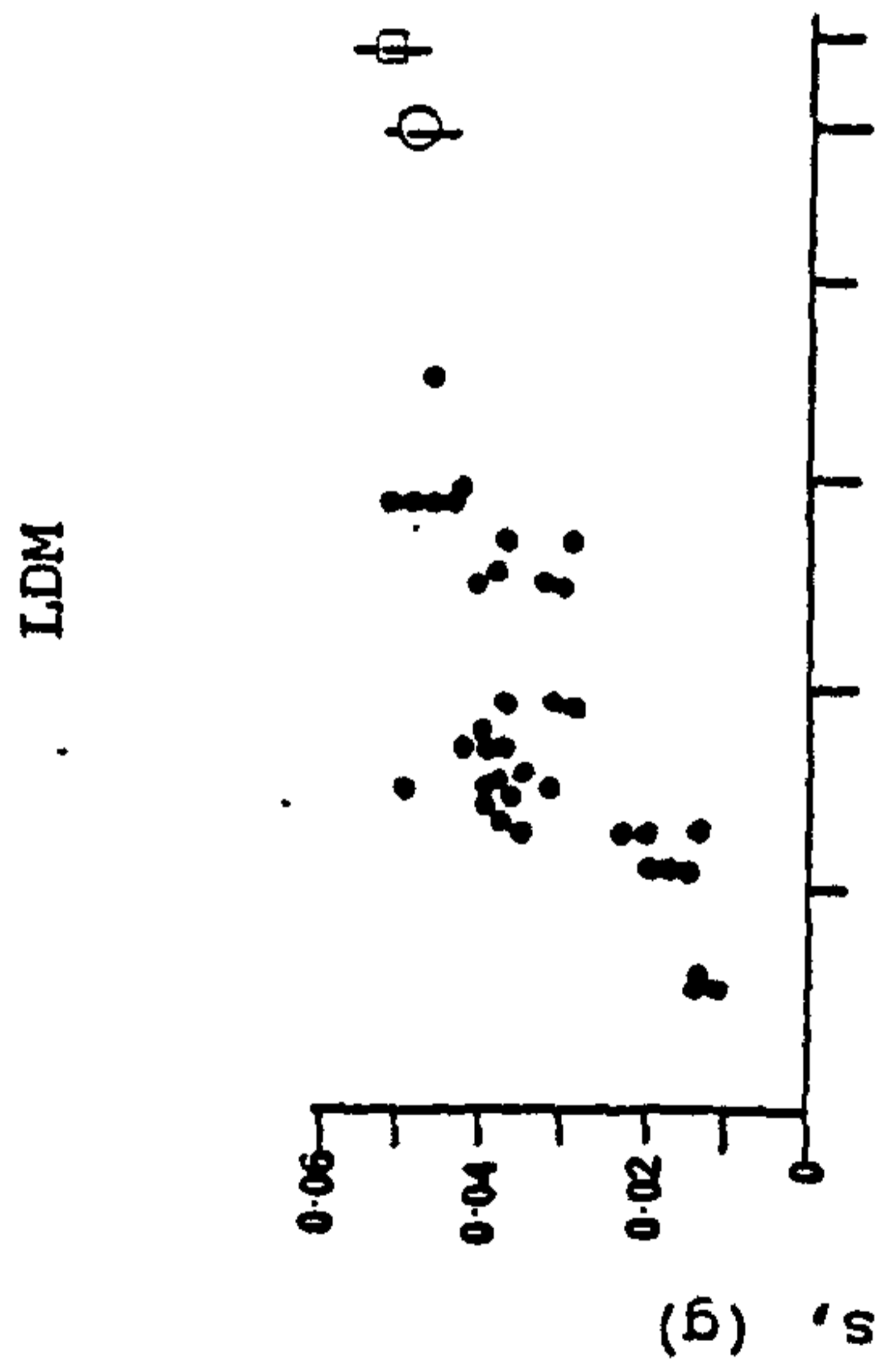
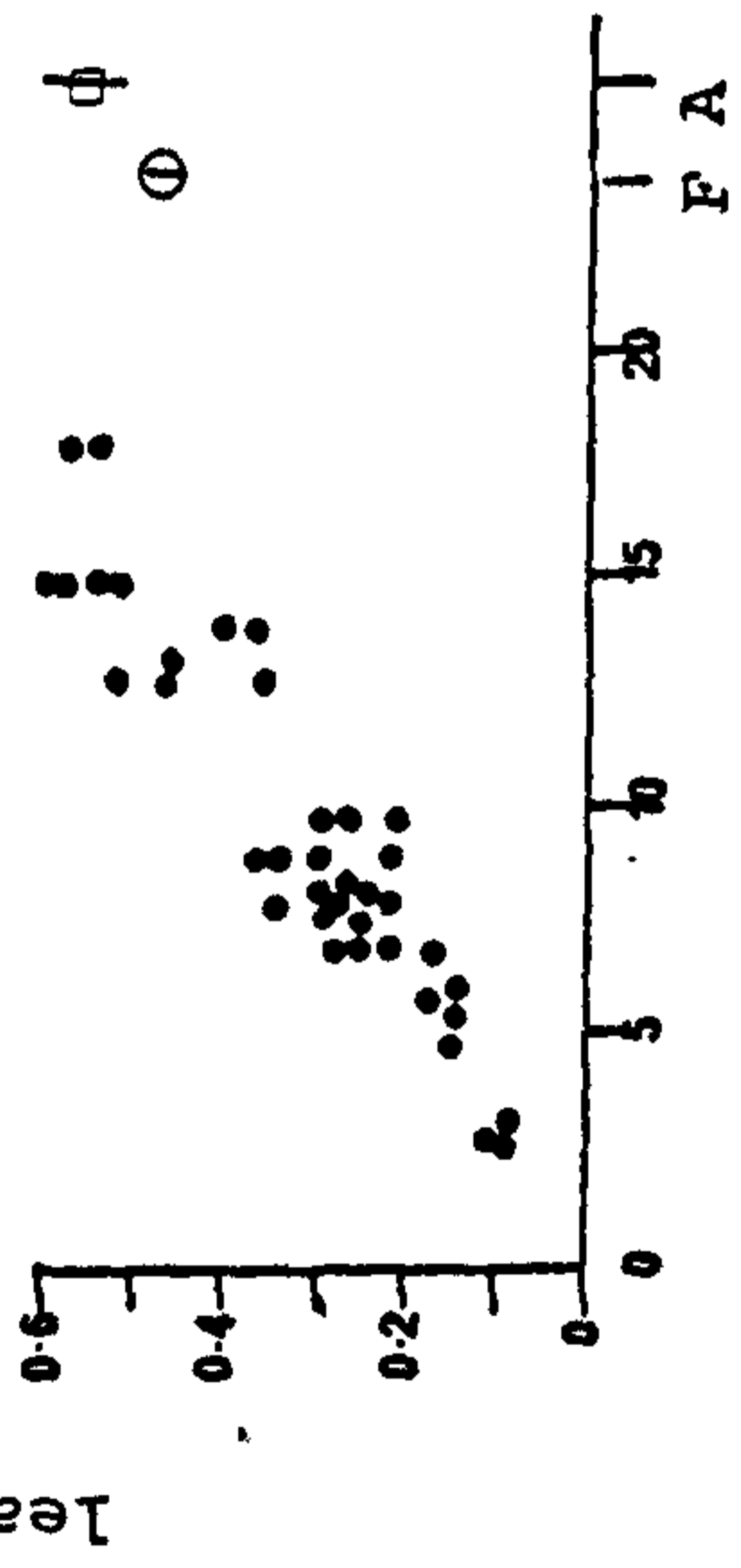


Figure 5.20 (cont.)

(l) lungs



(m) body shell



nestling age, (days)

Figure 5.20 (cont.)

position during begging, and may allow the nestlings to move along the burrow towards the parents to be fed (Turner and Bryant, 1979).

Three components of the digestive system increased in LDM early in the nestling period, and declined in LDM before fledging. Hence the RLDMs of the oesophagus and gizzard, gut and liver declined over the nestling period, although the liver showed an initial increase in RLDM. Presumably the gizzard and intestine became less important as energy processing sites when substantial lipid deposits are laid down later in the nestling period, so their relative sizes may decline.

Heart, kidneys and lungs increase in LDM until fledgling values were attained by about 15 days. Heart and lung declined in RLDM over the nestling period, though kidney increased. Body shell increased in LDM between days 3 and 15, though relative growth of the body shell showed an initial decline.

5.3.9 The lipid content of body components in nestlings

In Table 5.11 the lipid content of sand martin nestling body components is expressed as a function of total body lipid. The slope b in analysis I partitions the variation in body lipid over the whole nestling period (O'Connor, 1977; Tatner, 1984), so that the sum of the slopes is one. Hence in sand martin nestlings 36% of lipid was stored in and under the skin (feathers have a negligible lipid content - section 5.3.1), compared with 22% in adults, 27% in fledglings (Figure 5.2), 35% in the body shell (22% adults, 22% fledglings), and 10% around the legs (8% adults, 9% fledglings). So at least 71% of nestling lipid is likely to occur in subcutaneous deposits in the aforementioned areas.

When the logarithm of component lipid was plotted against the

Table 5.11

Fat content of nestling sand martin body components
expressed as a function of total body fat

Components	ANALYSIS I		ANALYSIS II			ANALYSIS III	
	Component fat as a function of total fat		log (component fat) as a function of log (total fat)			Component fat as a function of 'corrected' total fat	
	b	r	b	s.d. of b	r	b	r
Skin and feathers	0.358	0.91	1.12	0.07	0.94	0.460	0.77
Body shell	0.349	0.95	1.12	0.08	0.93	0.488	0.89
Head	0.017	0.79	0.58	0.06	0.87	0.017	0.78
Neck	0.007	0.61	0.92	0.10	0.84	0.007	0.61
Legs	0.098	0.87	0.99	0.07	0.92	0.104	0.84
Wings	0.020	0.82	1.09	0.13	0.82	0.020	0.81
Pectoral muscles	0.046	0.88	1.25	0.14	0.83	0.047	0.86
Oesophagus and gizzard	0.031	0.55	0.73	0.10	0.78	0.030	0.51
Gut	0.041	0.84	0.72	0.06	0.90	0.042	0.82
Heart	0.003	0.79	0.81	0.13	0.76	0.003	0.79
Lungs	0.001	0.48	0.54	0.14	0.56	0.001	0.48
Kidney	0.003	0.44	0.92	0.18	0.66	0.003	0.43
Liver	0.013	0.61	0.65	0.08	0.81	0.013	0.60

b = gradient of regression line

r = Pearson correlation coefficient

n = 37, P < 0.01 for all regression equations

log of total lipid (analysis II), correlation coefficients were normally higher than in the linear relationship of analysis I, indicating that allometric equations better described the relationship between component lipid and total lipid. Because the slope of the log-log relationship was greater than unity for skin and feathers, body shell, wings, and pectoralis muscles, lipid was preferentially stored in those structures.

Some degree of autocorrelation is inevitable if component lipid is plotted against total lipid, since total lipid will include the component lipid. Hence 'corrected' total lipid was calculated as (total lipid - component lipid) for all components in analysis III (Table 5.11). Although the correlation coefficients were reduced when compared with analysis I, all relationships remained highly significant, suggesting that, unlike adults (Section 5.3.1), the lipid content of nestling components can be used to accurately estimate the total lipid content of a chick.

5.3.10 Lipid index hierarchies within broods

To examine lipid index hierarchies within broods, lipid indices were calculated for each chick in 16 complete broods, one brood with a chick yet to hatch, and five incomplete broods. Data from eight complete and four incomplete broods were those of D. M. Bryant (unpubl.). Hierarchies were defined in terms of nestling age. Nestlings aged between 1 day and 7 days were aged by body mass, older chicks being aged by wing-length (Turner and Bryant, 1979).

In Figure 5.2 1, lipid index hierarchies for eight broods older than 7 days mean age are plotted. In three cases, lipid index parallels nestling age, lipid index decreasing in sequence of wing-length. For the remaining five broods, the oldest chick had the

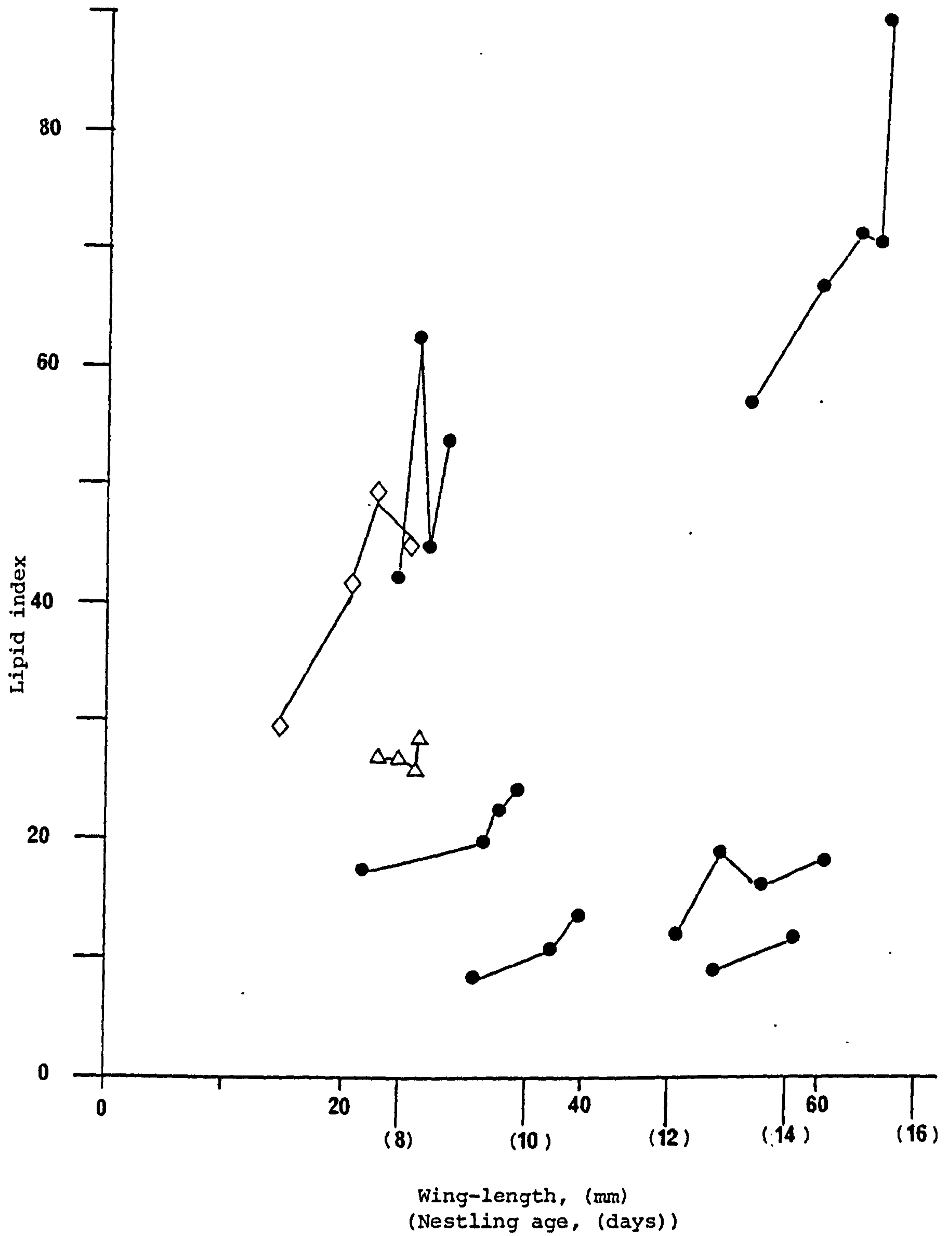


Figure 5.21

Lipid index hierarchies for eight sand martin broods aged by wing-length. Bracketed x values are nestling ages, (days).

highest lipid index in only two instances, in three cases lipid index was highest in a chick intermediate in the age hierarchy. However, in all cases, the oldest chick had a higher lipid index than the youngest, although in one instance the youngest chick did not have the lowest lipid index in the brood.

In Figure 5.22 lipid index hierarchies for eight complete broods of chicks, 7 days or younger are plotted. Once again, the oldest chick had a higher lipid index than the youngest in all but two instances, though linear lipid index hierarchies were not seen. Five young broods where one or two chicks were missing have lipid index hierarchies plotted in Figure 5.23.

Lipid index hierarchies could facilitate brood reduction during prolonged food shortages (Lack, 1968; Clark and Wilson, 1981), or could reflect a staggering of nestling demands reducing the peak food delivery rates by adults (Hussell, 1972; Bryant, 1978a; Hahn, 1981). Since the lightest chicks in house martin broods may starve in both low and high levels of food abundance (Bryant, 1978b), brood reduction is unlikely as a sole explanation for the function of lipid index hierarchies. Large brood sizes increase the difference in relative body mass and relative wing-length of the largest and smallest chicks in house martin broods, and such differences are also greater later in the season, and are dependent on the relative masses of the hatchlings (Bryant, 1978b). Hatchling masses are likely to vary according to the food supply during laying (Bryant, 1978a). Since lipid index hierarchies are not linear with respect to nestling age soon after hatching (Figures 5.22, 5.23), it seems likely that a nestling's station in the lipid index hierarchy may be at least partly governed by pre-hatching factors, and is probably modified by post-hatching factors such as the food supply during the nestling period.

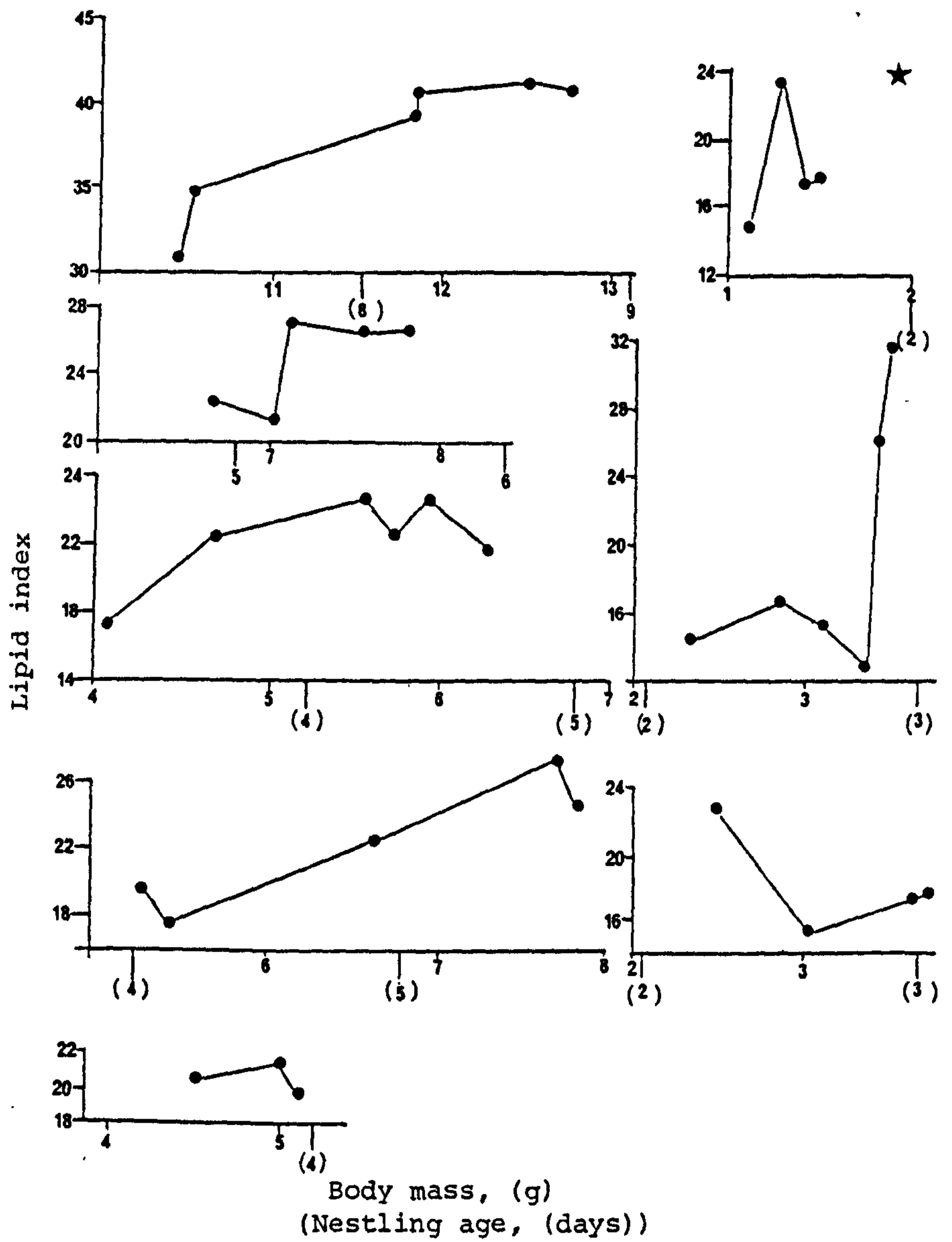


Figure 5.22

Lipid index hierarchies for eight sand martin broods aged by body mass. Data from D.M. Bryant.

One infertile egg was present in the nest marked with an asterisk.

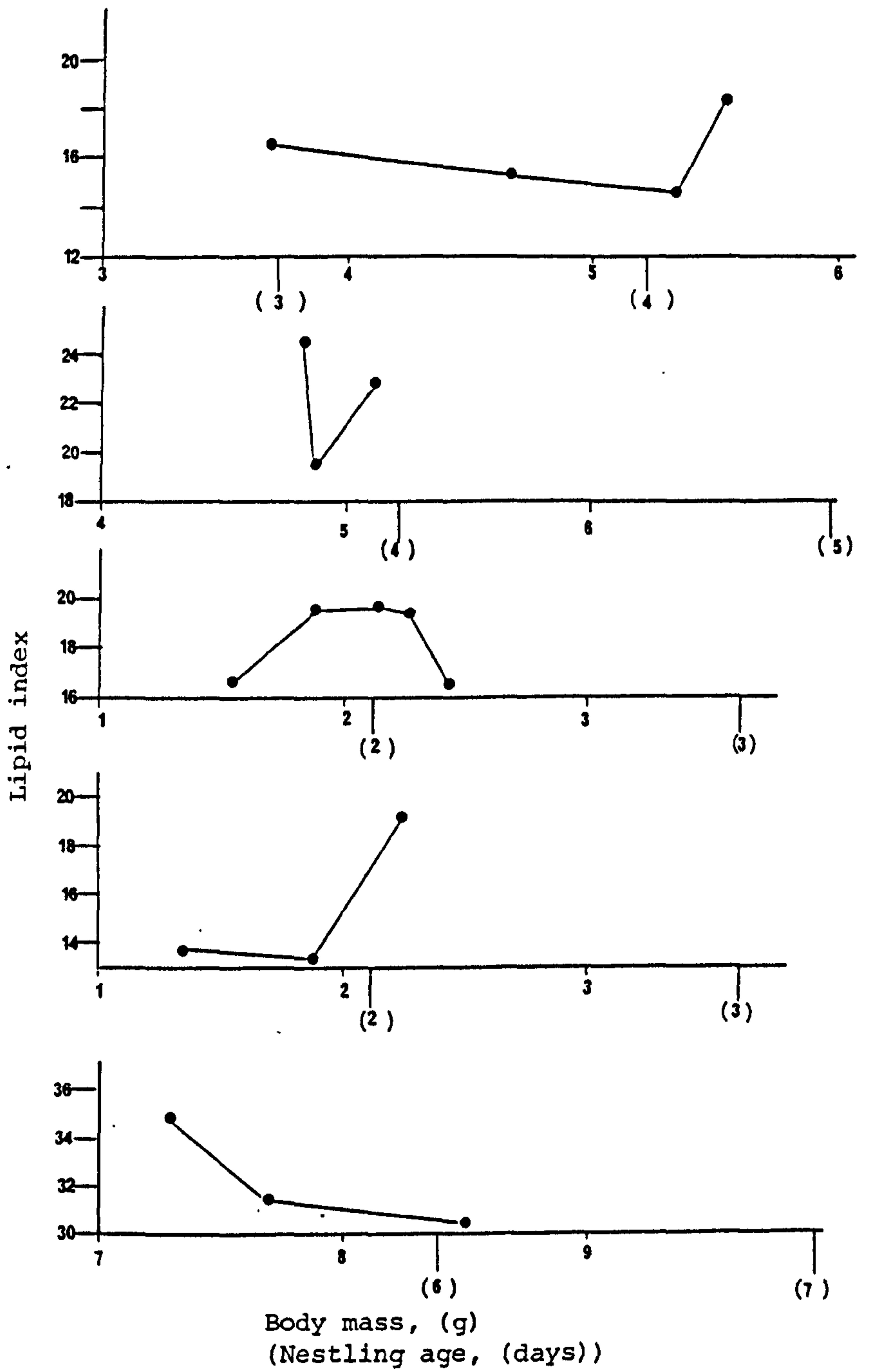


Figure 5.23

Lipid index hierarchies for five incomplete sand martin broods aged by body mass. Data for four broods from D.M. Bryant.

Nest (a) : 1 chick missing; Nest (b) : 1 chick not yet hatched.
 Nest (c) : 1 chick missing; Nest (d) : 2 chicks missing;
 Nest (e) : smallest chick missing.

Lipid index hierarchies may also be of a greater spread in sand martin broods occurring outside of the period of maximum breeding synchrony within the colony. Bank swallows breeding only a few days after the peak of synchrony had a higher incidence of starved nestlings or runts in their broods (Emlen and Demong, 1975).

5.3.11 Are the youngest or least nourished chicks in the brood age hierarchy relatively undernourished with respect to their age?

In 14 of 16 complete broods examined, the oldest chick had a higher lipid index than the youngest. The mean lipid index of 17 oldest chicks in broods was 31.93 ± 19.63 , that of 17 youngest chicks from the same broods 24.16 ± 12.97 . The difference between means is statistically significant as determined by a paired 't' test ($t = 3.64, P < 0.05$).

Between days 1 and 7, lipid index increased with nestling age, no obvious relationship being apparent between lipid index and nestling age later in the nestling period (Figure 5.19). Between days 1 and 7, nestling age is a function of nestling body mass and during this period the relationship between lipid index and body mass can be described by

$$\text{Lipid index} = 11.6 + 2.01 (\text{body mass, g}),$$

$$(r = 0.83, n = 53, P < 0.001)$$

Equation 5(1)

The tendency for lipid index to increase allometrically with body mass over this period is described by

$$\text{Log}_e \text{ lipid index} = 2.62 + 0.0803 (\text{body mass, g})$$

$$(r = 0.79, n = 53, P < 0.001)$$

Equation 5(2)

Older white-bellied swiftlets in broods of two had significantly greater lipid indices than their younger sibs, though when the lipid index of the younger sib was corrected for the difference in sib age, differences in lipid indices were insignificant between sibs (Bryant and Hails, 1983).

Hence in sand martin broods aged between 1 and 7 days, lipid

index can be related to nestling age since age is related to body mass during this period. The lipid index of the youngest chick can then be compared with that expected for a nestling of that age to determine whether the youngest chick in the brood is relatively undernourished. Between days 1 and 7 the mean lipid index of the oldest chick in nine broods was 27.38 ± 11.44 , that of the youngest sib 21.51 ± 7.41 . The difference between means is statistically significant when compared by a paired 't' test ($t = 2.48$, $P < 0.05$).

The expected mean lipid index of the youngest chick as determined by equation 5(1) was 19.73 ± 4.46 , and that expected from equation 5(2) 19.28 ± 3.52 . Neither of these values differs significantly from the mean observed in youngest chicks (equation (1), paired 't' = 0.78, ns, equation (2), paired 't' = 1.01 ns), hence there was no evidence to suggest that the youngest chick in the brood was consistently undernourished.

However, the oldest chick in the brood does not necessarily have the highest lipid index within the brood, neither does the youngest chick always have the lowest lipid index. Hence a comparison was made between the chick with the highest lipid index in a brood and the most poorly nourished sib.

The mean lipid index of the chick with the highest lipid index in 16 broods was 33.84 ± 19.60 , that of the sib with the lowest lipid index 23.26 ± 13.80 . The difference between means is statistically significant (paired 't' = 5.21, $P < 0.001$).

Between days 1 and 7 the mean lipid index of the best nourished chick was 30.20 ± 11.46 , that of the most poorly nourished sib 20.06 ± 7.95 (paired $t = 4.85$, $P < 0.01$).

Between days 1 and 7 the expected mean lipid index of the most poorly nourished chick in the nine broods examined was 21.84 ± 5.80 using equation 5(1), 21.52 ± 5.47 by equation 5(2). Neither of these values was significantly different from the observed mean lipid index of the chick with the lowest lipid index within a brood (equation 5(1), paired $t = 1.3$ ns, equation 5(2), paired $t = 1.07$ ns). Thus, although in seven cases out of nine the observed lipid index of the least nourished chick in a brood was less than that expected, on average there was no evidence to suggest that the chick with the lowest lipid index was relatively undernourished. Undernourished chicks within a brood may indeed occur during poor conditions, but this tendency is usually masked by considering data averaged over a range of feeding conditions.

5.4 DISCUSSION

The adaptive significance of body reserves in breeding sand martins and their broods: implications for parent:offspring resource allocation strategies

5.4.1 Implications for the parents

Both pectoralis LDM and lipid content of breeding sand martins were positively correlated with body mass (Table 5.3, Figures 5.5, 5.10) and 80% of the variation in adult carcass dry mass can be accounted for by changes in the size of the lipid reserves and LDM of flight muscles. Lipid reserves and flight muscle protein reserves are potentially the two most important energy stores in the bird's body. What is the potential energy storage capacity of lipid reserves and flight muscle protein, and do changes in the size of these reserves reflect changes in energetic demands placed upon the birds? For example, do the low levels of lipid and relatively small pectoralis muscles of nestling-rearing adults (Figures 5.7, 5.11) reflect the

utilization of body reserves as a result of high energetic demands by the adults?

On average, pectoralis LDM contributes 11.4% to the total dry mass of the birds, while lipid reserves on average contribute 25.8% to total dry body mass. Hence the size of a protein reserve in flight muscles is likely to be small compared with the size of the lipid reserve. Moreover, protein has a lower energy yield per gram than lipid (Ricklefs, 1974).

The coefficient of variation for pectoralis major LDM in adults was only 10.5%, suggesting little variation in the size of a protein reserve, since most of the pectoralis mass will be necessary to provide power for flight. Any utilisation of flight muscle protein beyond a certain point may present an additional cost to the bird (beyond loss of an energy store) in reducing flight performance. The coefficient of variation for extractable lipid content was 36.2%, suggesting considerably greater variation in the lipid reserve compared with flight muscle protein.

The flight muscle LDM of starved yellow-vented bulbuls was 70% of the mass considered normal for birds of their wing-length (Ward, 1969a, b). Therefore, in calculating the potential energy yield from protein in flight muscles, it was assumed that a maximum of 30% of pectoralis LDM was available for metabolism. Flight muscle protein was assumed to liberate 23.6 kJ g^{-1} (Ricklefs, 1974).

In calculating the potential energy yield from lipid reserves, 13% of fresh body mass was assumed to be structural lipid unavailable as an energy reserve (Zimmerman, 1965; Ward, 1969b). The energy yield from lipid catabolism was assumed to be 37.7 kJ g^{-1} (Ricklefs, 1974).

Table 5.12 Potential energy (P.E.) available from complete catabolism of lipid and protein reserves compared with daily energy expenditure (DEE) in sand martins

	1			2			3		
	DEE, kJ day ⁻¹	Body mass, g	n	extractable lipid, g	mean P.E. from lipid, kJ	mean protein reserve, g	mean P.E. from protein, kJ	from mean total P.E.	
Incubating females	81.7	13.80 ± 0.96	5	1.5159 ± 0.5797	50.39	0.1816	4.29	54.68	
Rearing females	90.3	12.91 ± 1.01	7	0.9768 ± 0.1869	30.5	0.1780	4.20	34.70	
Rearing males	93.7	12.63 ± 0.67	4	0.9537 ± 0.0913	29.8	0.1712	4.04	33.80	

1. Values are from doubly labelled water measurements of Westerterp and Bryant (1984).
2. Reserve lipid was calculated as (extractable lipid - 1.3/100 × body mass), assuming body mass to be 1.3% structural lipid (Ward, 1969a, b).
3. Thirty percent of flight muscle is assumed to be available for metabolism. Hence values are 30% of mean LDM of pectoralis major and minor, (Ward, 1969a, b).

In Table 5.12 the potential energy yield from the total catabolism of body reserves of lipid and protein is compared with the daily energy expenditure of sand martins during incubation and nestling rearing as determined directly by the doubly-labelled water technique (Westerterp and Bryant, 1984).

In both incubating females and nestling rearers of both sexes, the contribution to total potential energy from protein catabolism is small compared with the contribution from lipid catabolism. Only 7.8% of total potential energy could be liberated through protein catabolism in incubating females, 12% in rearing females, 12.1% in rearing males. Hence the value of protein reserves in flight muscles as an energy reserve is small relative to the value of lipid reserves, contributing a maximum of 5.25% of daily energy expenditure (in incubating females). Most of the energy stored in the body is available on lipid reserves, and in incubating females such reserves contribute 61.7% of the energy necessary for daily existence. A small amount of energy may also be available from any food stored in the gut.

Total lipid and protein reserves contribute a maximum of 66.9% of DEE in incubating females, and only 36.1-38.4% of DEE in nestling rearing adults. The measured reserves are for birds captured at dusk, so in no case considered would a bird be likely to survive throughout the following day without self-feeding. House martins have larger lipid indices than sand martins and have lower flight costs since they flap half as much in flight as do sand martins (Westerterp and Bryant, 1984). Hence house martins can probably survive for one or two days on their body reserves without feeding (Bryant and Gardiner, 1979).

Reserve protein in the pectoralis muscle has been shown to have limited value as an energy reserve. However, flight muscle protein does seem to provide nutrients during egg production in some species (Jones and Ward, 1976; Ankney and MacInnes, 1978; Fogden and Fogden, 1979; Drobney, 1980; Krapu, 1981), and there is evidence for the use of flight muscle protein during moult (Ward, 1969b). The decline in the protein reserve of the gray-backed camaroptera, Camaroptera brachyura, is small in relation to the total protein required for egg formation, and may represent a store of specialised protein for egg production. However, in white-bellied swiftlets, Callocalia esculenta, lipid reserves fall over laying, while flight muscle LDM varies according to feeding conditions rather than changing systematically over the laying period (Hails and Turner, in prep.). Nevertheless, the smallest pectoralis muscles in swiftlets are found in laying birds, so flight muscle protein may be drawn upon for laying in exceptional circumstances. The white-bellied swiftlet lays a clutch of only two eggs, so total protein demands during laying would be relatively small compared with sand martins laying 4-6 eggs.

House sparrows, Passer domesticus, show a significant decline in flight muscle LDM overnight (Jones, 1980). Hence although flight muscles may serve as protein reserves during periods of high protein demand such as laying and moult, they may also be catabolised relatively quickly over a short time period when the demands for specialised protein are not obvious. Such a reserve may replace body protein denatured during the day (Jones, 1980).

Lipid reserves and pectoralis LDM were both positively correlated with fresh body mass (Table 5.3, Figures 5.5, 5.10). Moreover, extractable lipid and pectoralis LDM were positively correlated (Table

5.3) and the relationship between the variables was linear. It is generally assumed that birds do not utilise flight muscle tissue until lipid reserves are completely exhausted (Pope and Ward, 1972; Houston, 1977; Hirons et al., 1984). In sand martins lipid reserves and pectoralis LDM are intercorrelated and are both correlated with body mass, so some utilisation of flight muscle tissue appears to occur before lipid reserves are exhausted.

Pectoralis muscles provide the power necessary for flight, and as body mass increases, the power required to fly increases allometrically (Pennycuick, 1975). Pectoralis mass is positively correlated with body mass in Cooper's hawks (Marsh and Storer, 1981), and in grey catbirds (Marsh, 1984). Moreover, pectoralis muscle mass often increases prior to migration in several species (Fry, Ferguson-Lees and Dowsett, 1972), including sand martins (Fry, Ash and Ferguson-Lees, 1970).

Marsh (1984) suggested that pectoralis muscle fibre hypertrophy may underlie changes in muscle mass, and that augmentation of muscle mass could make a significant contribution to flight performance. Hence it seems likely that the positive correlation between pectoralis LDM and body mass in sand martins represents a regulation of muscle mass according to power requirements for flight, especially in view of the muscle's limited value as an energy reserve.

Thus changes in the size of the pectoralis muscles can either be viewed as being adaptive in that large muscles provide increased power for flight at high body masses, or alternatively changes in muscle mass may represent energetic or nutritional stress placed on birds with low muscle mass during periods of high energetic or nutritional demand.

Pre-breeding males which had just arrived at the colony had the largest flight muscles of the groups sampled (Figure 5.11), and it seems probable that this represented flight muscle hypertrophy as an adaptation to long distance migration. However, pectoralis LDM fell below expected levels in laying females when protein demands may be high (although the sample size is only two birds), and in nestling rearing adults when energy demands are highest (Turner, 1980; Westerterp and Bryant, 1984). Prelaying and laying females generally had smaller pectoralis muscle LDMs than expected for their increased body mass (Figure 5.10b) prelaying and laying females were 15-20% heavier than non-laying birds, so if pectoralis muscle mass could be increased rapidly, larger muscles would be expected for birds of such heavy body mass if pectoralis hypotrophy is adaptive.

Hence support exists for and against flight muscle hypertrophy as an adaptation to reduce power requirements of flight, and flight muscle atrophy is greatest during two periods of high nutritional or energetic demand. Until more is known of the histology and biochemistry of muscles of different mass, the function of flight muscle mass changes cannot be clearly resolved.

Amongst adult sand martins, pectoralis muscle masses, lipid indices and body masses were generally lowest in nestling rearing birds. Body masses of breeding birds were positively correlated with aerial insect abundance (Chapter 2), so birds deposited reserves in good feeding conditions. Winter fattening of birds is an adaptation to the thermoregulatory demands of low ambient temperatures (King and Farner, 1966; Evans, 1969). Since breeding sand martins were lightest when food abundance was lowest at cold temperatures, the short-term consequences of low temperature for body mass in sand martins

contrasts with long-term adaptations to low temperatures shown by winter fattening in other passerines. However, pre-breeding males, having recently arrived at the colony, tended to have high body masses and lipid indices (Figure 5.9, Chapter 6), and this probably represents an insurance lipid reserve to buffer against the high probability of encountering bad weather early in the year (Turner, 1982), when sand martin mortality in Britain is greatest (Mead, 1979).

The costs and benefits of mass loss and reserve use during nestling rearing are discussed in Chapter 8.

5.4.2 Implications for the brood

Energy reserves of nestling sand martins were calculated using the results of carcass analysis, and compared with daily energy expenditures from published information. Comparisons were made with adult values presented in Table 5.12.

Although Marsh (1979) provides data on the metabolic rates of bank swallow nestlings, his data are from the laboratory, and take no account of differences between daytime and nighttime metabolism, and do not consider the effects of brood size on metabolic rate. Brood size has a considerable influence on nestling metabolism (Bryant and Gardiner, 1979). Therefore, in calculating the potential survival times of unfed chicks, the field respirometry data of Bryant and Gardiner (1979) for house martin broods were used. Differences in metabolic intensities of sand martin and house martin broods were corrected for by the equation of Aschoff and Pohl (1970):

$$M = 0.0317 W^{0.726}$$

where M is energy expenditure during standard metabolism, $\text{kcal h}^{-1} \text{bird}^{-1}$, and W is body mass in grams.

Two extreme cases were considered: firstly a brood of two 14 day chicks taken at the end of the breeding season (3.9.82) when most adults had left the colony, and the chicks were undernourished with little chance of surviving until fledging. The chicks had a mean lipid index of 12.46 ± 3.53 , and a mean body mass of 11.90 ± 1.13 g. The nestlings carried a mean of 0.3656 ± 0.1812 g of lipid, of which 10% was considered as structural, yielding a mean of 12.40 kJ/chick. The average daily metabolic rate (ADMR) of a brood of two house martin chicks is $0.98 \text{ kJ g}^{-1} \text{ day}^{-1}$ (Bryant and Gardiner, 1979). Since the brood of two sand martins would have a metabolic intensity per gram of $1.22 \times$ that of an average brood of house martins at the same brood size and stage (Aschoff and Pohl, 1970, using house martin brood masses of Bryant and Gardiner, 1979), the ADMR of the sand martin brood can be calculated as $1.20 \text{ kJ g}^{-1} \text{ day}^{-1}$, or $28.56 \text{ kJ day}^{-1}$ for the complete brood. Hence the sand martin nestlings would be expected to survive for 27.64h on the energy released from their lipid reserves (24.8 kJ) in the absence of feeding. One well nourished brood of five, 15 day chicks, had a mean lipid index of 70.83 ± 12.03 , and a mean body mass of 18.6 ± 0.46 g. The nestlings carried a mean of 2.6618 ± 0.5547 g of lipid, the metabolisable component of which would yield a mean of 98.82 kJ/chick. The ADMR of a brood of five house martin nestlings was $0.96 \text{ kJ g}^{-1} \text{ day}^{-1}$ (Bryant and Gardiner, 1979), and this brood of five sand martins would have a predicted metabolic intensity $1.11 \times$ that of an average brood of five house martins of the same age. The ADMR of the sand martin brood can hence be calculated as $1.07 \text{ kJ g}^{-1} \text{ day}^{-1}$, or $99.10 \text{ kJ day}^{-1}$ for the complete brood. The brood has 494.1 kJ of lipid reserves, and would hence be expected to survive for 4.99 days without feeding.

Most sand martin chicks of 14-15 days normally have lipid indices between these extremes (Turner and Bryant, 1979), but in each case examined above, the potential survival time of starved chicks living off body reserves is longer than that of nestling-feeding adults, who can obtain 36-38% of their daily energy expenditure from both lipid and protein reserves (Table 5.12). This results from nestlings being able to store larger quantities of lipid than their parents (Figures 5.7, 5.19) and because adults have higher average daily metabolic rates than nestlings, spending considerable time in energetically costly flight (Bryant and Westerterp, 1980; Westerterp and Bryant, 1984). Moreover, chicks may be able to reduce their metabolic rates during fasting - swift nestlings enter a daily reversible torpor after several days of starvation (Koskimies, 1950).

Nestling house martins close to fledging can survive for about seven days without food, whilst starved adults may only live for about two days (Bryant and Gardiner, 1979). The fasting ability of adult swifts is also much smaller than that of nestlings (Koskimies, 1950).

When sand martin chicks are small (days 0-7), they have a high surface area to volume ratio, a low capacity for heat production, little feather coverage, and small lipid reserves (Turner and Bryant, 1979, Figure 5.19). They are therefore liable to lose heat rapidly and carry insufficient lipid to buffer against long periods of parental inattentiveness between feeding and brooding visits.

As the chicks grow, their lipid indices reach generally higher but variable levels. Their increased body mass reduces their surface area to volume ratio, they become covered in feathers, and bank swallow nestlings attain homeothermy at about 14g (Marsh, 1979). The

nestlings' ability to survive parental inattentiveness hence increases, putting less pressure on the adults to return to the nest frequently in bad weather, leaving more time for the adults to self feed in conditions of low food availability.

Hence during the late nestling period sand martin nestlings have the capacity to store considerably more lipid than their parents, whose reserves will have declined since the early stages of nestling rearing (Figure 5.7). The transfer of lipid from adult to brood over the nestling period is probably adaptive (Bryant and Gardiner, 1979). Late in the nestling period, nestling demands are greatest, and adults spend no time brooding, but much time flying to collect food (Turner, 1980). Adult flight costs will be reduced by the metabolism of lipid reserves making the birds lighter (Freed, 1981; Norberg, 1981), thus reducing energy expenditure during the period of highest energy demand during the breeding cycle (Bryant and Westerterp, 1980). Energy for adult self-maintenance will allow parents to reduce self-feeding rates as lipid is catabolised (Norberg, 1981). Older nestlings can carry larger lipid reserves than their parents because they do not fly, and will pay a negligible increase in locomotory costs compared with their parents. These reserves will buffer against food shortages, during a period of high nestling demand, and enable parents to spend considerable time self-feeding when their own reserves are at low levels.

Whether the reduction in adult lipid reserves over the nestling period is enforced or voluntary will be discussed in Chapter 8 for swallows. Parent birds rearing altricial young will be selected to look after their own interests before those of their broods, since successful fledging of the young will depend on provisioning from the parents, and because parental fitness may also be dependent on future

breeding attempts. Because of the low body reserves and high energetic costs of adults compared with their maturing nestlings, the selective premium on adult self-maintenance behaviour in poor conditions is likely to be very high.

CHAPTER 6

6. MATE-GUARDING AND SEXUAL CHASES IN SAND MARTINS

6.1 INTRODUCTION

In monogamous animal species, males can increase their fitness by adopting a mixed reproductive strategy, helping a mate to rear young, while also taking advantage of opportunities to fertilise other females (Trivers, 1972). Several bird species, including bank swallows (Beecher and Beecher, 1979), have been observed to guard their mates from insemination by other promiscuous males (Horn, 1968; Wolf and Wolf, 1976; Mineau and Cooke, 1979; Birkhead, 1979, 1982; Buitron, 1983; Power et al., 1981; Ankney and Scott, 1982; Morris and Bidochka, 1982; Røskaft, 1983), and mates may also seek promiscuous copulations themselves when chances arise (Beecher and Beecher, 1979; Davies, 1983; Fitch and Shugart, 1984).

In many bird species males seem unable to forcefully fertilise females, and a male mixed reproductive strategy would therefore require a complementary female mixed strategy (Fitch and Shugart, 1984). Females may benefit from fertilisation with males other than their mates through increasing offspring variability by mating with genetically dissimilar males (Williams, 1975; Gladstone, 1979), and non-mate sperm may be genetically superior to that of a female's mate (Mineau and Cook, 1979). However, costs are also imposed on females accepting multiple paternity, such as increased intrabrood competition (Hamilton, 1964; Trivers, 1972), or loss of current investment if the mate deserts (Trivers, 1972). Avoidance of these costs may explain why paired females do not attempt to copulate with non-mates despite ample opportunity (Fitch and Shugart, 1984).

In this study the body condition of sand martins during the breeding cycle was investigated to determine the condition of birds rearing nestlings relative to other stages of breeding (Chapter 5). Nestling rearers were found to be in relatively poor condition compared with laying and pre-laying females who carried considerable lipid reserves and reproductive material. Since hirundines are most likely to be fertile during the period of laying and immediately pre-laying (Leffelaar and Robertson, 1984), female sand martins may present flight cues to males seeking promiscuous copulations through their increased body mass affecting their flight behaviour. The aim of this chapter is to investigate whether male sand martins can increase their investment in offspring through multiple matings by detecting such cues.

6.2 MATERIALS AND METHODS

6.2.1 Field observations and experiments

The terminology used in this part of the study follows that of Beecher and Beecher's (1979) work on conspecific bank swallows in North America. Males follow a mixed reproductive strategy (Trivers, 1972), forming monogamous pair bonds with females, but also periodically seeking promiscuous copulations with other females before and after pair bonding. Females are guarded during their fertile period by their mate with which they share parental duties, but the pair are also chased by other males seeking promiscuous copulations. This situation is depicted in Plate 6.1.

All mate-guarding field studies were performed in 1982 and 1983, when the density of breeding pairs at Barbush was high and interactions between birds were more frequent, than when numbers were low during the 1984 breeding season.



Plate 6.1

Sexual chase in sand martins. Bird A is probably a fertile female, B her mate, and C a chasing male seeking promiscuous copulations.

To determine whether the chances of a pair being chased by one or more birds changed over the course of a day, observations were made from 05.00h to 21.30h on 20th May, 1982, when much chasing behaviour was occurring at the colony. One hundred random birds or groups of birds were noted, and the sighting was categorised as to whether a bird was alone, a pair was observed, or a chasing party present.

When seasonal variation in the intensity of mate-guarding behaviour was recorded, data were collected within an hour of mid-day to avoid any biases due to diurnal variation in guarding activity. One hundred burrow exits from different burrows in the same subcolony were observed each week, and records were made as to whether a bird left the burrow alone, or if members of a pair left within 5s of each other. If the latter occurred, mate-guarding was inferred.

This method has a bias in that it fails to consider that birds performing different activities leave their burrows at different rates. For example, incubating birds remain in burrows for a longer period than birds delivering food to their brood. If two counts of burrow exits are made, one when most birds are on eggs, one when the bulk of the colony are feeding nestlings, and on both occasions an equal number of mate-guarding pairs is present in the colony, the former count will record more of the mate-guarding pairs since it will take longer for 100 burrow exits to occur. Nevertheless, if seasonal trends are strong, the method should pick them up.

To examine which birds were chased and which were chasers, observations were made on 153 colour marked birds of known sex, body mass and age class (adult or fledgling) released after mist netting. All released birds were observed for at least one minute. If the bird was chased or chasing, observations continued for another two

minutes whenever possible. The number of chasers following chased birds was documented, and stopwatches were used to record time chased, and time taken for chase initiation.

One of four events was ascribed to the released bird:

- (a) No interaction; the bird was apparently ignored by other individuals at the colony.
- (b) The released bird was 'investigated'. An investigation was defined as a pursuit lasting less than 30 seconds. All investigations recorded ($n = 28$) involved only one pursuing bird.
- (c) The released bird was 'chased'. Chases lasted 30 seconds or longer and may have involved more than one pursuing bird.
- (d) The bird joined a sexual chase as a 'chaser', actively pursuing other birds.

The above observations should elucidate whether birds were chased preferentially according to sex, age class, or body mass. If a released bird was pursued, the chase was generally initiated within 14 seconds of release (see results), so chasing birds must identify birds to chase by cues given soon after release. To attempt to identify cues available through flight performance, two techniques were used.

Birds may be chased on the basis of their body mass affecting their appearance rather than because body mass influences flight performance. Hence a sample of six birds had their primary feathers tied loosely to influence flight performance over the short period the tie remained in place, but body mass was not changed. The primaries were tied with surgical thread in a single knot so that the thread would soon work itself loose, or could easily be removed by the birds.

6.2.2 Flight performance

To investigate how body mass affected some aspects of flight performance, 34 birds captured at dawn were brought to Stirling University and their flight behaviour on release from the hand was video recorded. Two aspects of flight performance were measured.

- (a) Time taken to reach ascending flight.
- (b) Wing beat frequency during the first two seconds of ascending flight.

Recordings were played at 50 frames second⁻¹ for analysis. Birds were chosen at random for video-recording, so that the body mass of birds was not known at the time of release.

A sample of seven birds was artificially weighted to the body mass of prelaying/laying female martins. This was achieved by intraperitoneal injection of 0.85% saline sterile solution. Two grams of water was injected into each bird, 1g at a time. No ill effects were noted on the injected birds, and some of the sample were recaptured later in the season, one experimental bird being controlled during the subsequent breeding season.

6.3 RESULTS

6.3.1 Diurnal and seasonal variation in mate-guarding behaviours

Diurnal variation in chasing behaviour on 20th May 1982 is shown in Figure 6.1. A hundred birds or groups of birds were observed at random over the day, and records were made as to whether the birds were alone, in pairs, or in chasing parties. The percentage of observations consisting of pairs pursued by one or more chasing bird peaked at dawn, when 85% of observations were of chasing parties, rather than single birds or pairs which were not chased. Chasing

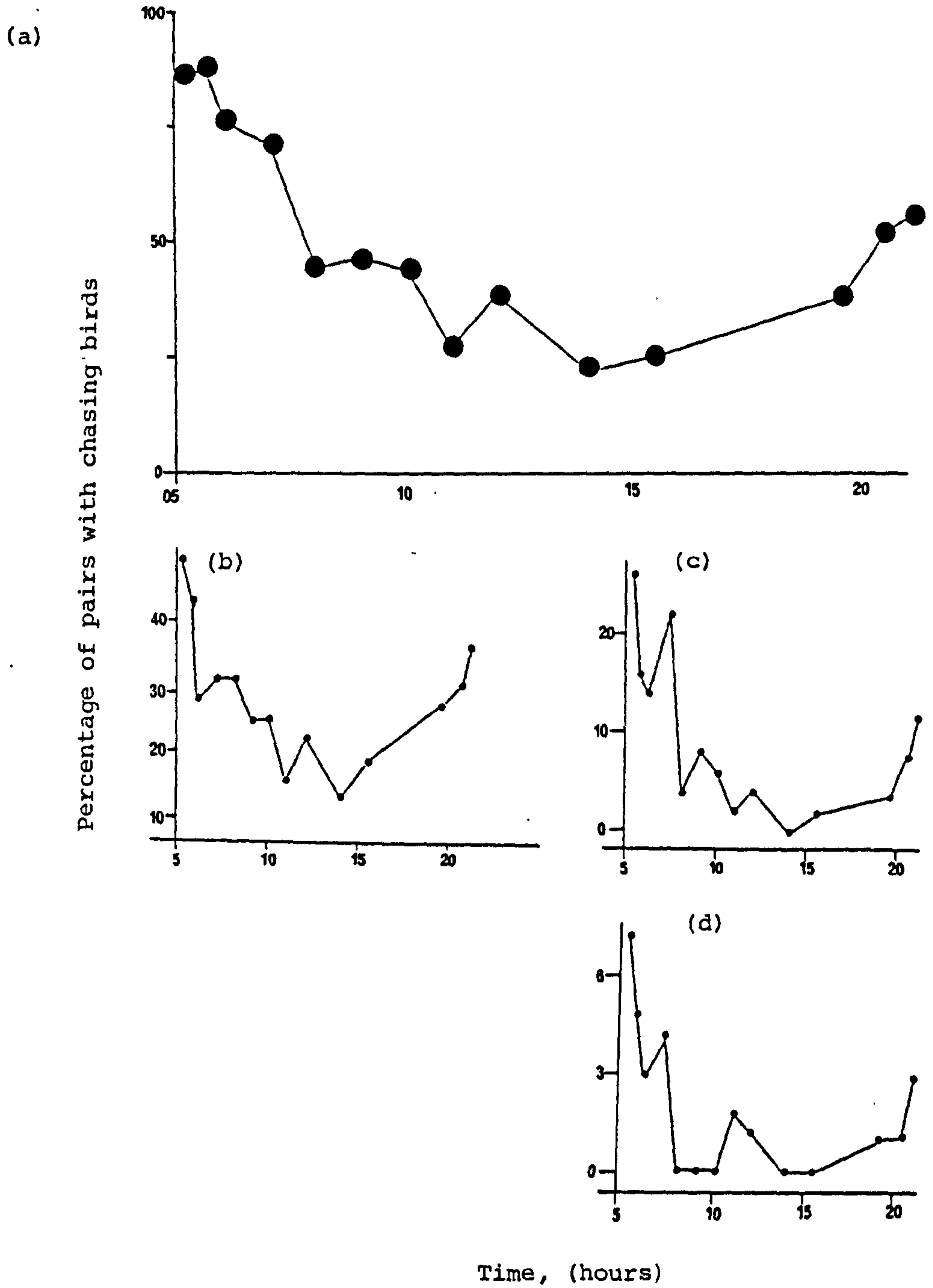


Figure 6.1

Diurnal variation in sand martin chasing behaviour.

- (a) Percentage of pairs with one or more chasing bird.
- (b) Percentage of pairs with one chasing bird.
- (c) Percentage of pairs with two chasing birds.
- (d) Percentage of pairs with three chasing birds.

parties were fewer during the middle part of the day, and a second but lower peak in observations of chasing parties occurred towards dusk, when 55% of observations were of chasing parties. Most pairs had only one chaser, but the same trends occurred for parties with one chasing bird, two chasers, or three chasers (Figure 6.1 (b-d)).

Chasing males presumably invest most time in pursuing pairs at dawn and dusk because food availability is low and feeding is relatively unprofitable. Most Diptera have flight periods over the middle part of the day (Lewis and Taylor, 1965), and feeding at times of low food availability would involve considerable energy expenditure with little energetic return from feeding. At such times it would pay males who are not guarding mates, incubating, or brooding to partake in behaviours other than feeding, such as chasing. Great tits show a peak in the amount of time spent singing at dawn, when foraging is assumed to be unprofitable (Kacelnik and Krebs, 1983).

It is probable that diurnal variation in food abundance influences mate-guarding behaviour as well as chasing. To overcome any such diurnal change in the intensity of mate-guarding, seasonal variation in guarding behaviour was investigated within one hour of mid-day.

The percentage of departures from burrows ($n = 100$) involving two birds leaving their burrow within 5s of one another (and assumed to be mate-guarding) is termed the 'mate-guarding index' and is depicted alongside the first egg dates for subcolony 2 in 1982 in Figure 6.2.

Female birds are most likely to be fertile during early laying and for several days before the first egg is laid (see below). If mate guarding is restricted to the female fertile period, the mate-guarding index should closely track the first egg date distribution. Although such tracking is not exact, the mate-guarding index does roughly

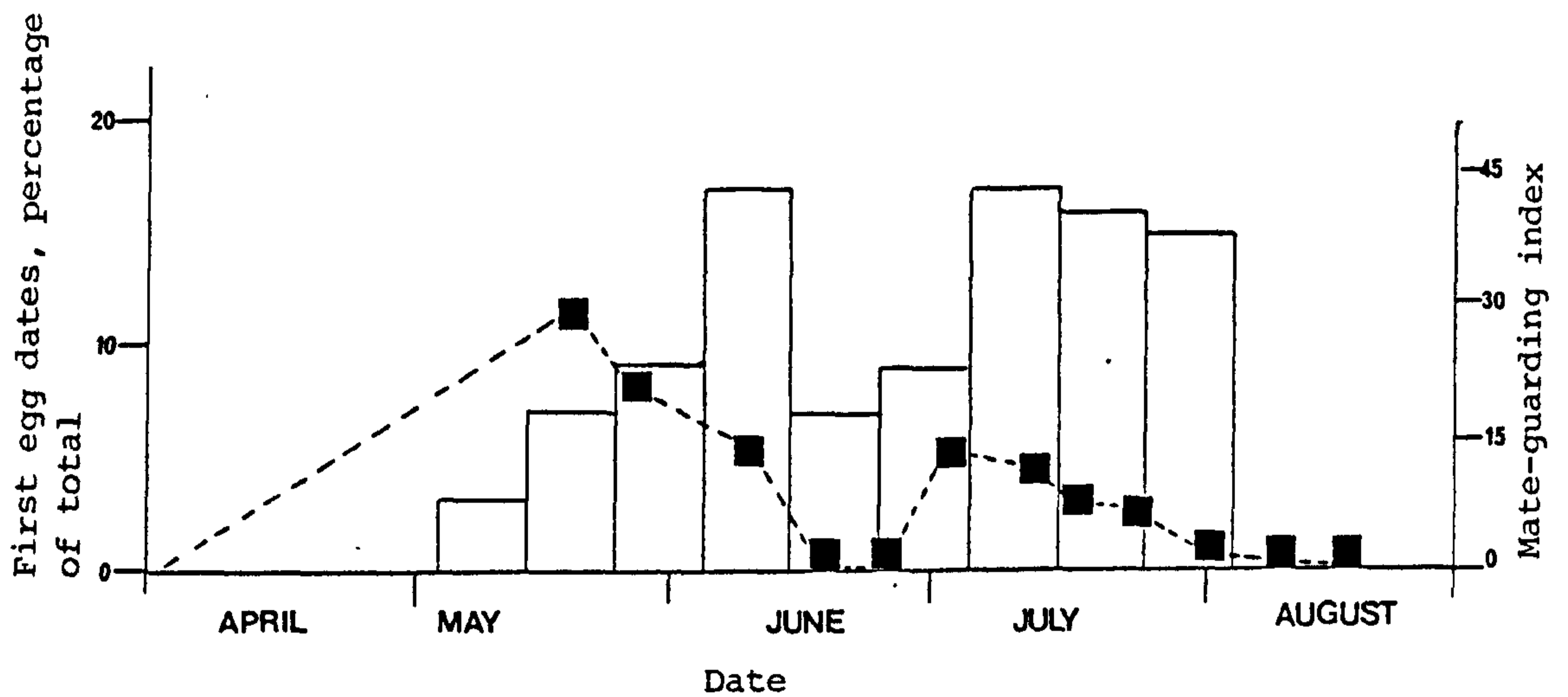


Figure 6.2

Seasonal variation in the mate-guarding index in sand martins, and the first egg date distribution for subcolony 2, Barbush 1982.

The frequency distribution is for first egg dates, while the mate-guarding index is represented by solid squares and the pecked line. $n = 58$ broods.

parallel the first egg date distribution: both distributions are bimodal and peaks occur within two weeks of one another. One explanation for the discrepancy between the two distributions could be because the first egg date distribution was determined by back-calculating from broods of known age, and so represents nests successful up to about two weeks of nestling feeding, when the young were aged. Guarding behaviour would be expected to be linked to actual first egg dates within the subcolony, not to only successful nests. The first peak in the mate-guarding index was higher than the second peak, and this could be because males focus their attention on early arriving females, which may be of high quality. The bimodal seasonal trend in the guarding behaviour of sand martins is likely to differ from that shown by the conspecific bank swallow in North America, which is single brooded (Petersen, 1955).

6.3.2 Which birds are chased by male sand martins?

Having shown a diurnal variation in chasing behaviour and a seasonal variation in mate-guarding behaviour, an investigation was made into which birds within the colony were chased. Observations on 10 chasing parties involving colour marked males showed that only males joined parties as chasers. Data were collected on 153 birds released after mist-netting, the sample consisting of 90 females, 44 males, and 19 fledged young in 1982.

'Investigated' birds were followed after $23.52 \pm 14.42s$ ($n = 7$), and all investigations involved only one following bird. 'Chased' birds were followed after $13.77 \pm 9.22s$ ($n = 10$), and involved 2.8 ± 1.03 chasing birds observed within three minutes.

ANALYSIS 1 : Which sex/age classes are chased?

Of the 153 birds released, only one joined a chasing party as a chaser, and this bird was a male. Twenty-five birds were chased, of which 23 were females and two were males. The observed numbers of birds chased in each sex/age class (male, female, fledgling) were compared with the expected number in each class if chasing were directed randomly (χ^2 analysis). The results are presented in Figure 6.3a, b. In analysis 1(a) males and females are compared, while fledglings are included in analysis 1(b).

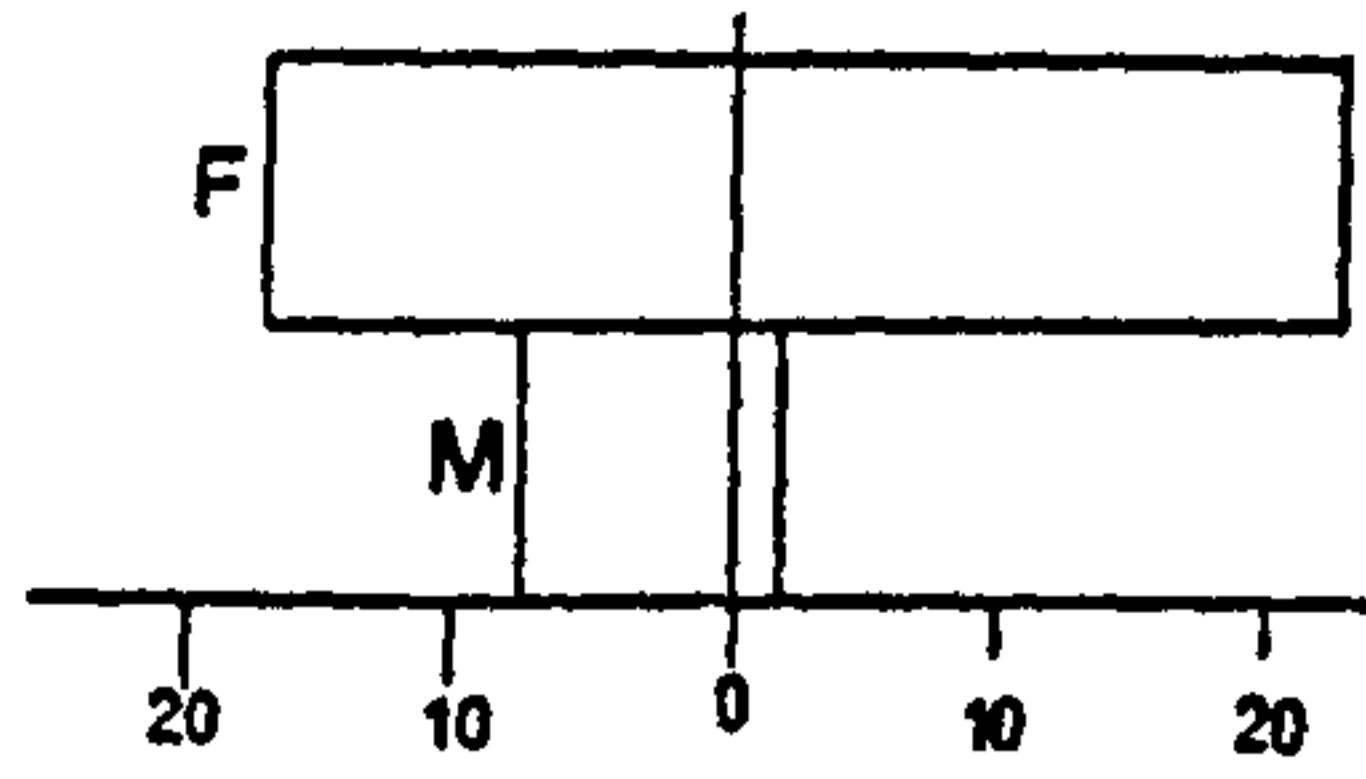
For each analysis, the observed distribution of chases differs significantly from that expected if each sex/age class were chased at random (males/females comparison; $\chi^2 = 6.99$, $P < 0.001$: males/females/fledglings comparison $\chi^2 = 12.96$, $P < 0.001$). The significant difference between observed and expected distributions in each case was because a disproportionately high number of females were chased.

Hence the observations support those of Beecher and Beecher (1979) in that sexual chases are directed at females. Some intermale interaction may be involved in chases however, because two of the 25 chasers recorded were directed at males, although such cases may have been the consequence of poor sex identification by the chasing males.

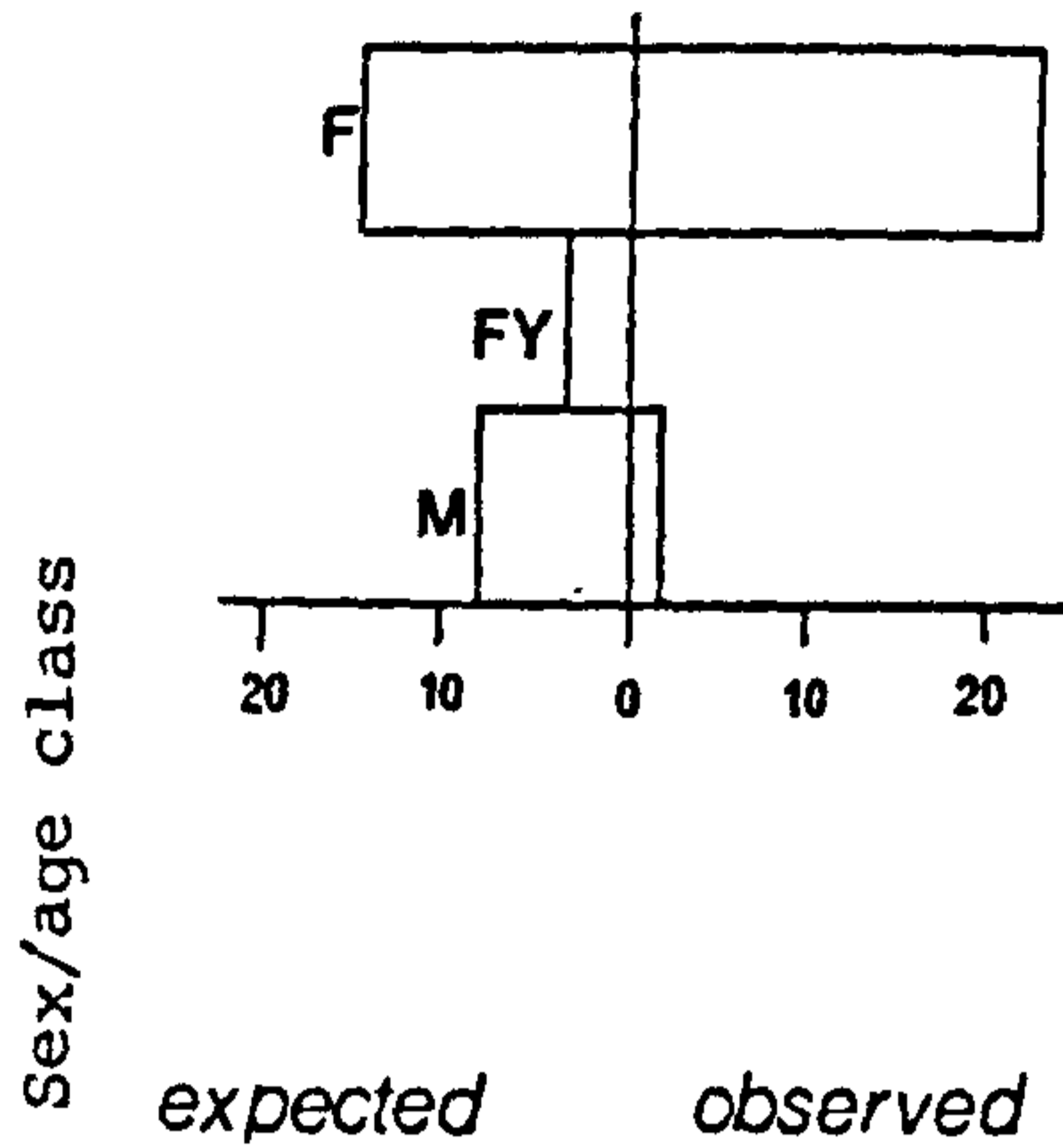
ANALYSIS 2 : Which sex/age classes are investigated?

A further 28 observations on the 153 released birds resulted in 'investigations'. A comparison of the observed distribution of investigations compared with that expected if investigations occurred at random according to the number of birds in each sex/age class released is presented in Figure 6.3(c). The observed distribution almost mirrors that expected ($\chi^2 = 0.6$, ns), and so no sex/age class in a males/females/fledglings comparison was singled out for investigation.

a



b



c

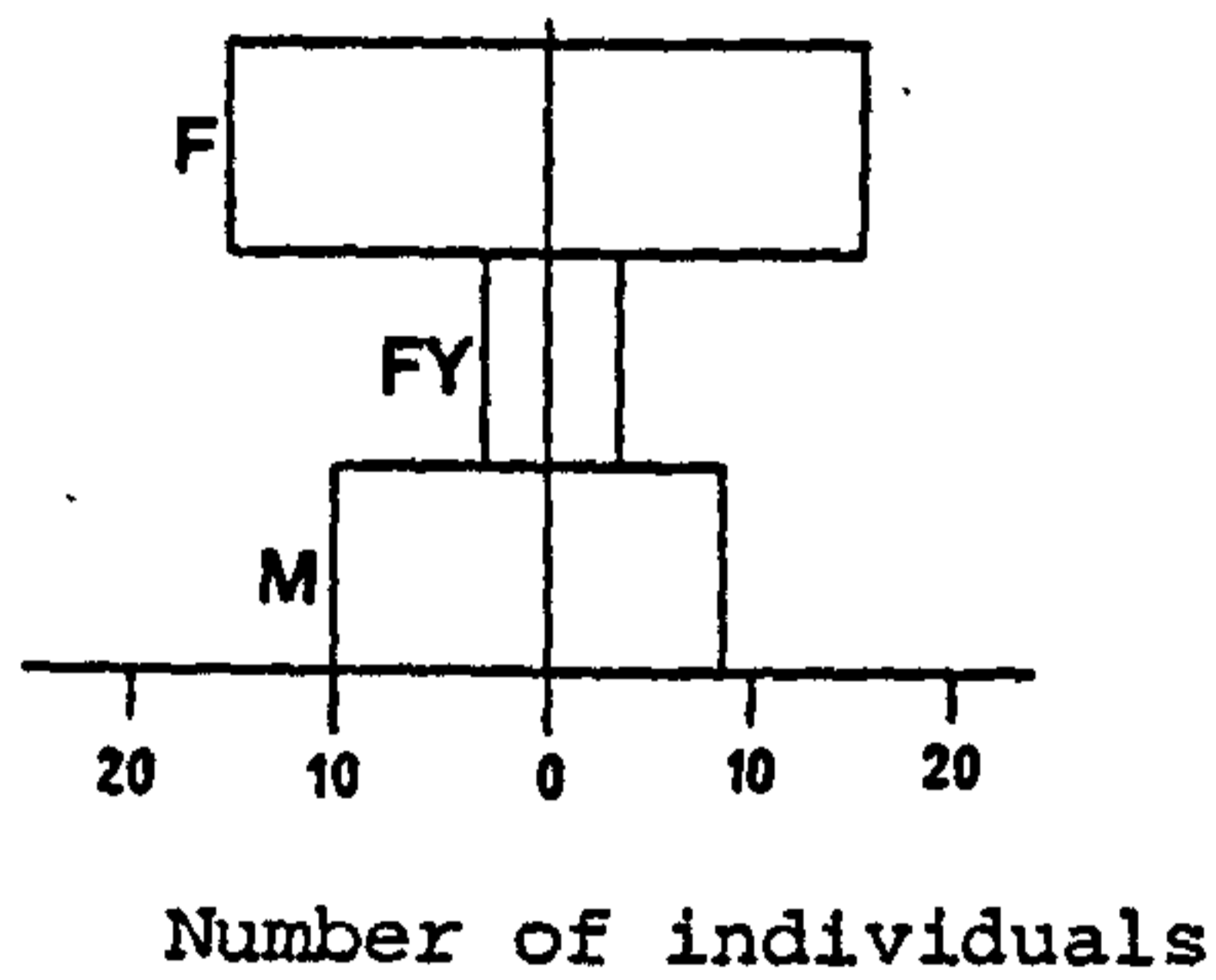


Figure 6.3

Expected and observed numbers of chased and investigated sand martins classified according to sex and age.

F : females; M : males; FY ; fledged young.

- (a) Analysis 1(a) for chasing
- (b) Analysis 1(b) for chasing
- (c) Analysis 2 for investigations.

See text for explanation.

Having determined that no sex/age class was singled out for investigation, but that chases were directed predominantly at females, the next stage in the analysis was to determine which females were singled out for chasing.

ANALYSIS 3 : Which females are chased?

To determine whether females of different body mass were selectively chased on release, the body masses of the 90 observed females were grouped into 0.5g classes and plotted on a frequency distribution in the upper portion of Figure 6.4a. A similar classification was performed for the 44 males which were observed in the study, and is plotted in Figure 6.4b. All observations were made in the evening, so body masses were standardised for time of weighing.

Figure 6.4b shows the distribution of male body masses to be unimodal, skewed towards lighter masses, and having a mean body mass of $13.21 \pm 0.76g$. The distribution of female body mass (Figure 6.4a, upper portion) was bimodal, with a mean body mass of $14.23 \pm 1.35g$. The distribution was probably bimodal because it included two subdivisions, a lighter subdivision including incubating and nestling-feeding birds, and a heavier subdivision consisting of females carrying eggs or bearing well developed reproductive structures. The lighter subdivision tended to follow the distribution of male body masses.

A chasing selection index was derived as the percentage of females in each 0.5g body mass class which were chased on release. This is plotted in the lower portion of Figure 6.4a. The selection index was heavily skewed towards the heavier body masses, with all of the eight birds between 16g and 17.5g in mass being chased on release. The peak of the chasing selection index occurred above the higher peak in the body mass distribution. A comparison of the observed frequencies

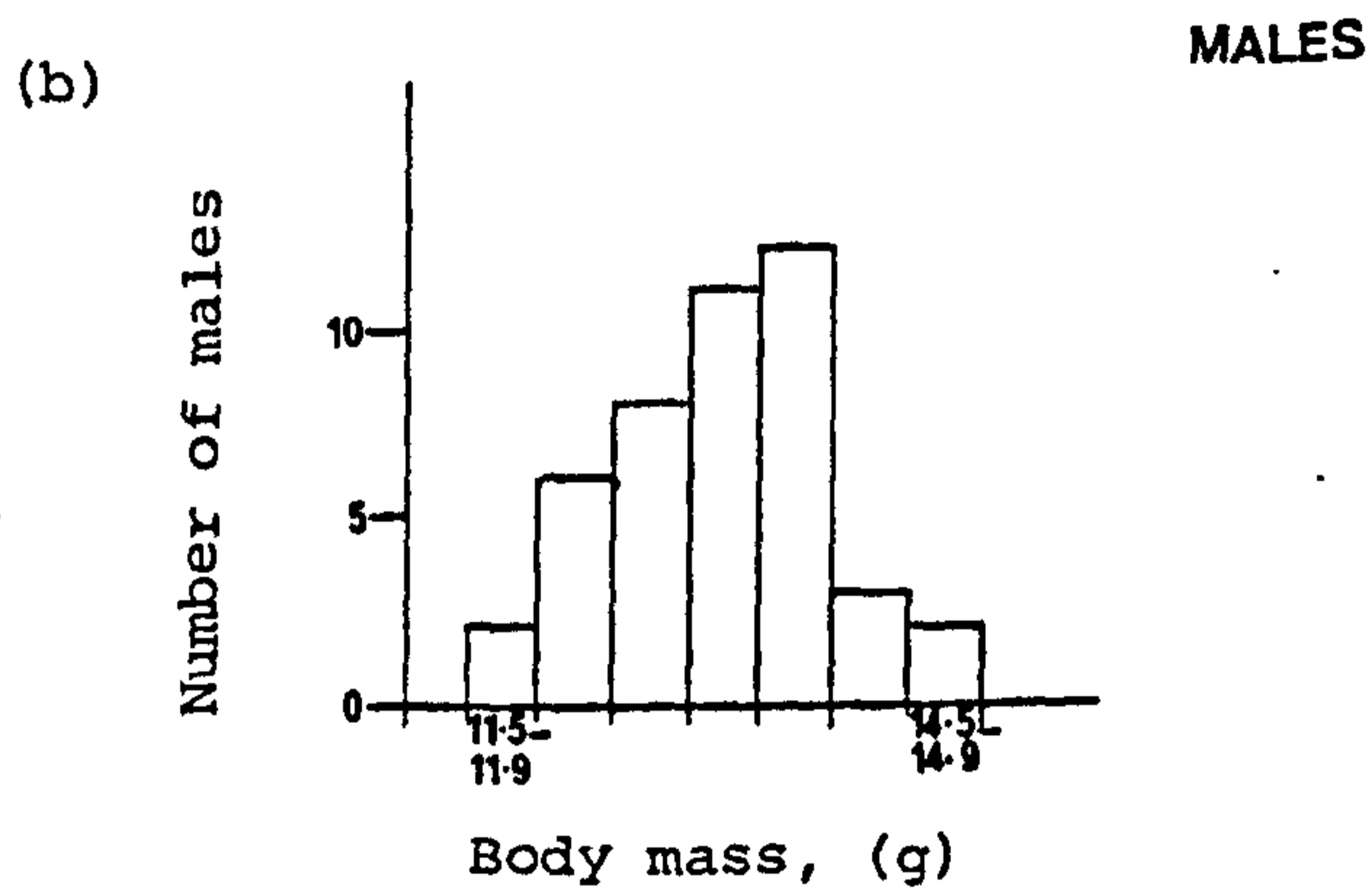
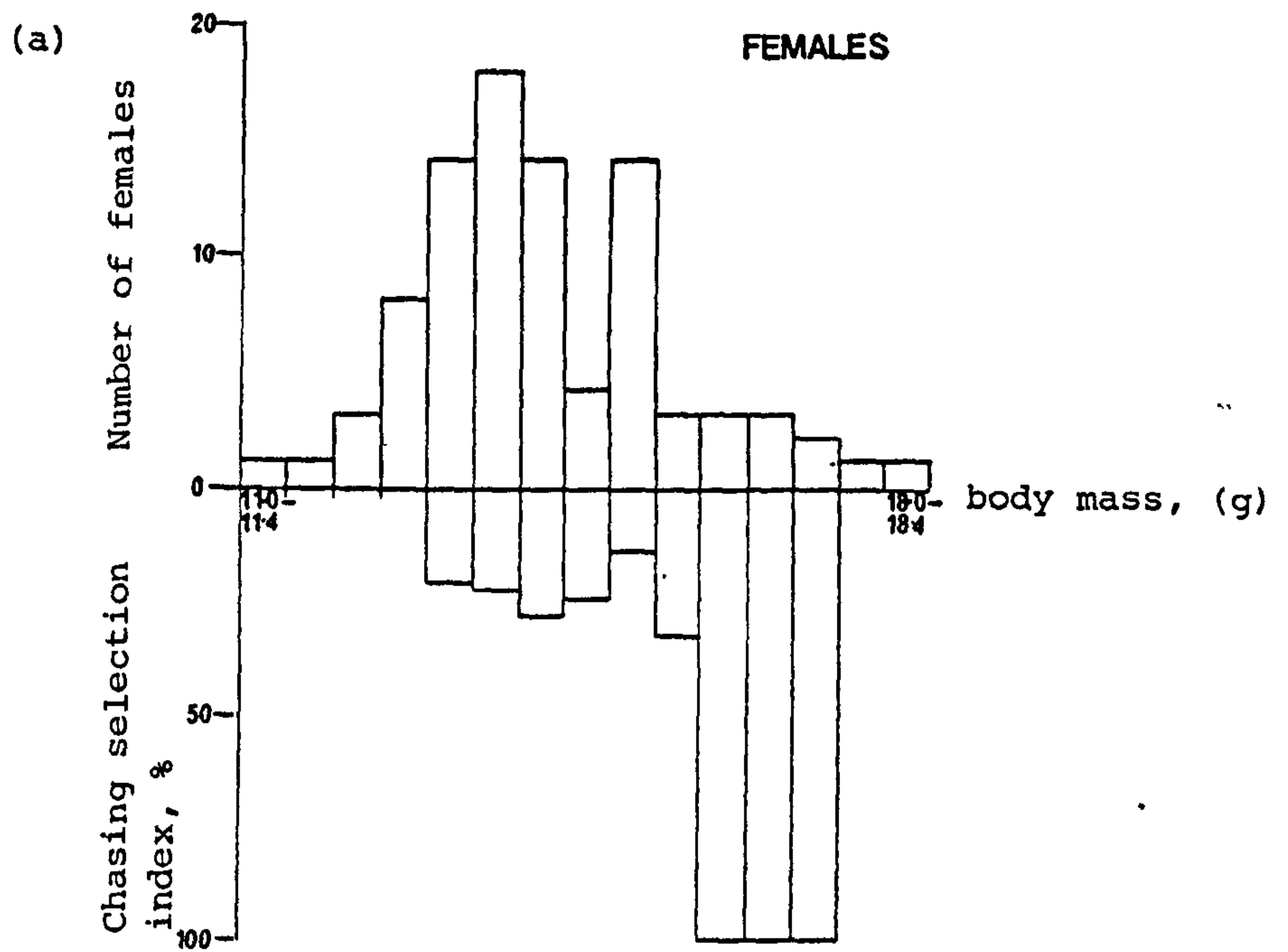


Figure 6.4

Body mass frequency distributions for birds observed in the sand martin mate-guarding study.

(a) Females: the lower portion of the graph shows the 'chasing selection index', i.e. the percentage of females in each body mass class which were chased.

(b) Males.

of birds chased in each body mass class with the frequencies expected if chasing were directed randomly with respect to body mass gives a value of χ^2 of 22.4 ($n = 15$, $P < 0.05$). Hence the chasing of females was not random with respect to their body mass.

To determine whether chased females were significantly heavier than females which were not chased, an analysis of variance was performed on the body mass and behavioural data. The analysis is presented in Table 6.1. Data were categorised into six classes where more than 10 values for body mass occurred in each class. The classes were:

1. Fledglings which were neither chased nor investigated ($F_{n/c}$).
2. Males which were neither chased nor investigated ($M_{n/c}$).
3. Males which were investigated (M_i).
4. Females which were neither chased nor investigated ($F_{n/c}$).
5. Females which were investigated (F_i).
6. Females which were chased (F_c).

The null hypothesis of the analysis is:

$$H_0 : \mu_{F_{n/c}} = \mu_{M_{n/c}} = \mu_{M_i} = \mu_{F_{n/c}} = \mu_{F_i} = \mu_{F_c}$$

where μ = mean body mass.

The analysis of variance gives an F value of 11.9 ($n = 145$, $P < 0.001$). Hence at least one pair of means was significantly different. To determine which means were significantly different, a multiple range test was performed on the data (Table 6.1b). At $P = 0.05$, chased females were significantly heavier than females which were neither chased nor investigated and all other classes. Females which were not chased were significantly heavier than the two lightest classes - fledglings and males which were neither chased nor investigated.

Table 6.1

(a) Analysis of variance of body mass and behavioural data for sexual chases of sand martins

$$H_0 : \mu_{FY_{n/c}^1} = \mu_{M_{n/c}^2} = \mu_{M_i^3} = \mu_{F_{n/c}^4} = \mu_{F_i^5} = \mu_{F_c^6}$$

Source	df	SS	MS
Treatments	5	69.00	13.80
Error	139	160.76	1.16
Total	144	229.76	

$F = 11.9, n = 145, P < 0.001$

(b) Multiple range test of body mass and behavioural data for sexual chases of sand martins. Tabulated values are for $q (= \mu_1 - \mu_2)$

Mean body mass \pm sd (n)	F_c	$F_{n/c}$	M_i	F_i	$FY_{n/c}$	$M_{n/c}$
F_c 15.03 \pm 1.37 (23)		*	*	*	*	*
$F_{n/c}$ 14.10 \pm 1.32 (49)			ns	ns	*	*
M_i 13.82 \pm 0.51 (10)				ns	ns	ns
F_i 13.43 \pm 0.81 (15)					ns	ns
$FY_{n/c}$ 13.12 \pm 0.73 (16)						ns
$M_{n/c}$ 13.00 \pm 0.73 (32)						

1. $FY_{n/c}$: fledglings which were neither chased nor investigated.
2. $M_{n/c}$: males which were neither chased nor investigated.
3. M_i : males which were investigated.
4. $F_{n/c}$: females which were neither chased nor investigated.
5. F_i : females which were investigated.
6. F_c : females which were chased

ns : not significant

* : $P < 0.05$

6.3.3 Female body mass during breeding and sexual chasing

The first stage in determining whether females were heaviest when they were fertile was to plot female body mass as a function of stage in the breeding cycle. In Figure 6.5a female evening body mass is plotted over the nesting period for individuals, while in Figure 6.5b mean body masses \pm sd are plotted with incubation divided into three phases of equal duration, and nestling feeding split into days 0-6 (brooding phase), days 7-17 (nestling demand highest), and days 18-22, when nestling demand falls (Turner, 1980).

Female body mass was highest during the immediate pre-laying and laying period, mainly because considerable lipid reserves were carried at this time, and because reproductive structures and developing eggs contributed considerably to overall body mass (Chapter 5). Body mass fell rapidly after laying and remained relatively stable during incubation. Lowest masses were attained when nestling demands were highest, and body mass rose slightly when brood demands were reduced at the end of the rearing period. The patterns of mass change were similar to those of bank swallows recorded by Petersen (1955).

In Figure 6.5a the mean mass of chased females is plotted, \pm sd. Twelve masses (28% of total) fell within 1 sd of the mean, of which 75% were prelaying or laying females.

Male evening body mass over the breeding cycle is plotted in Figure 6.6. The heaviest males were pre-breeders, these being birds captured early in the season before laying had started at the colony and before mate-guarding observations commenced. The small sample size forbids generalisations, but the two lightest birds again occurred during the period of high nestling demand. Only four male masses

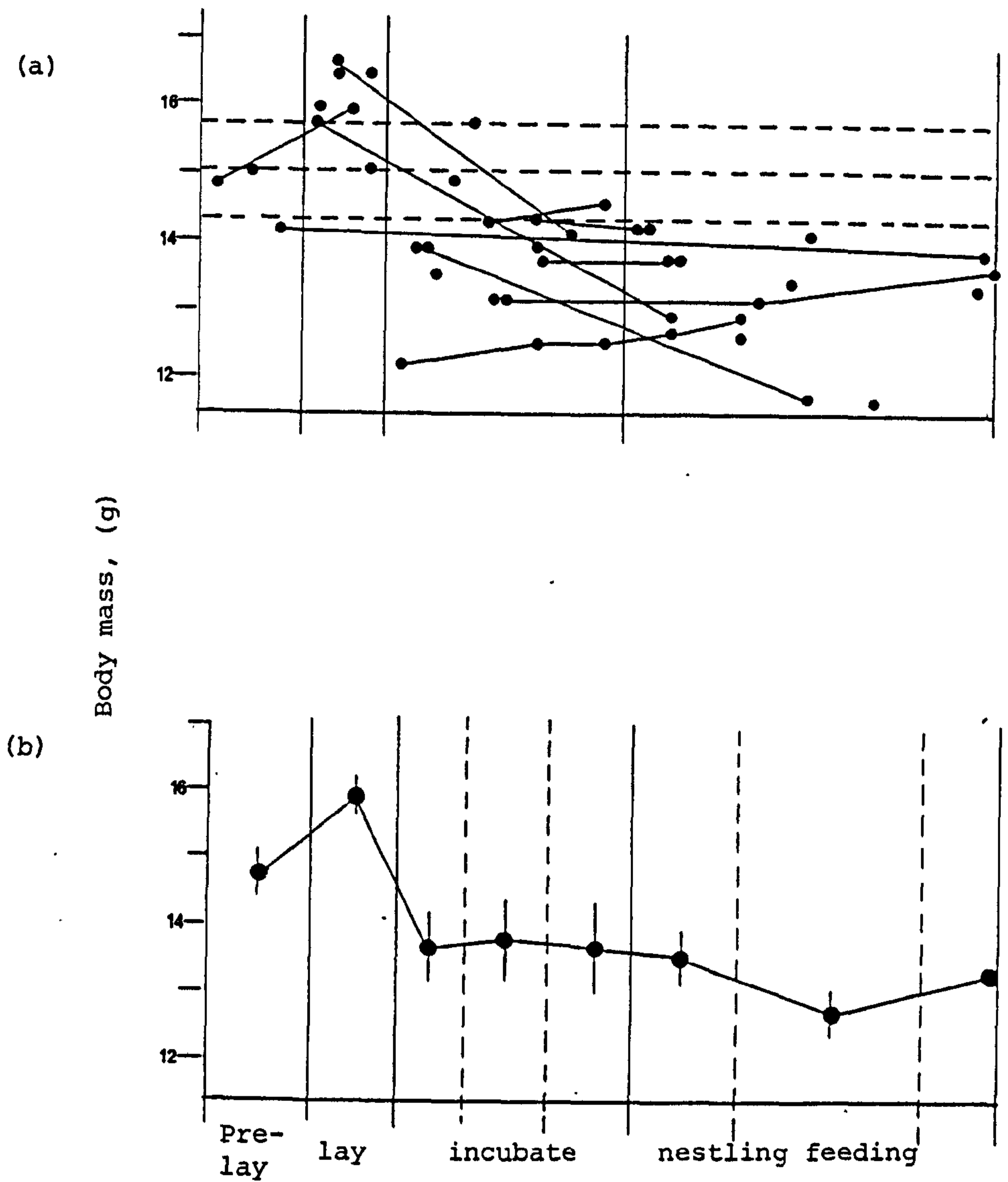


Figure 6.5

Sand martin female evening body masses as a function of stage of the nesting cycle.

(a) Individual females. Solid lines join recaptures of the same female. Pecked lines represent the mean mass \pm sd of chased females (see text for explanation).

(b) Mean values \pm sd.

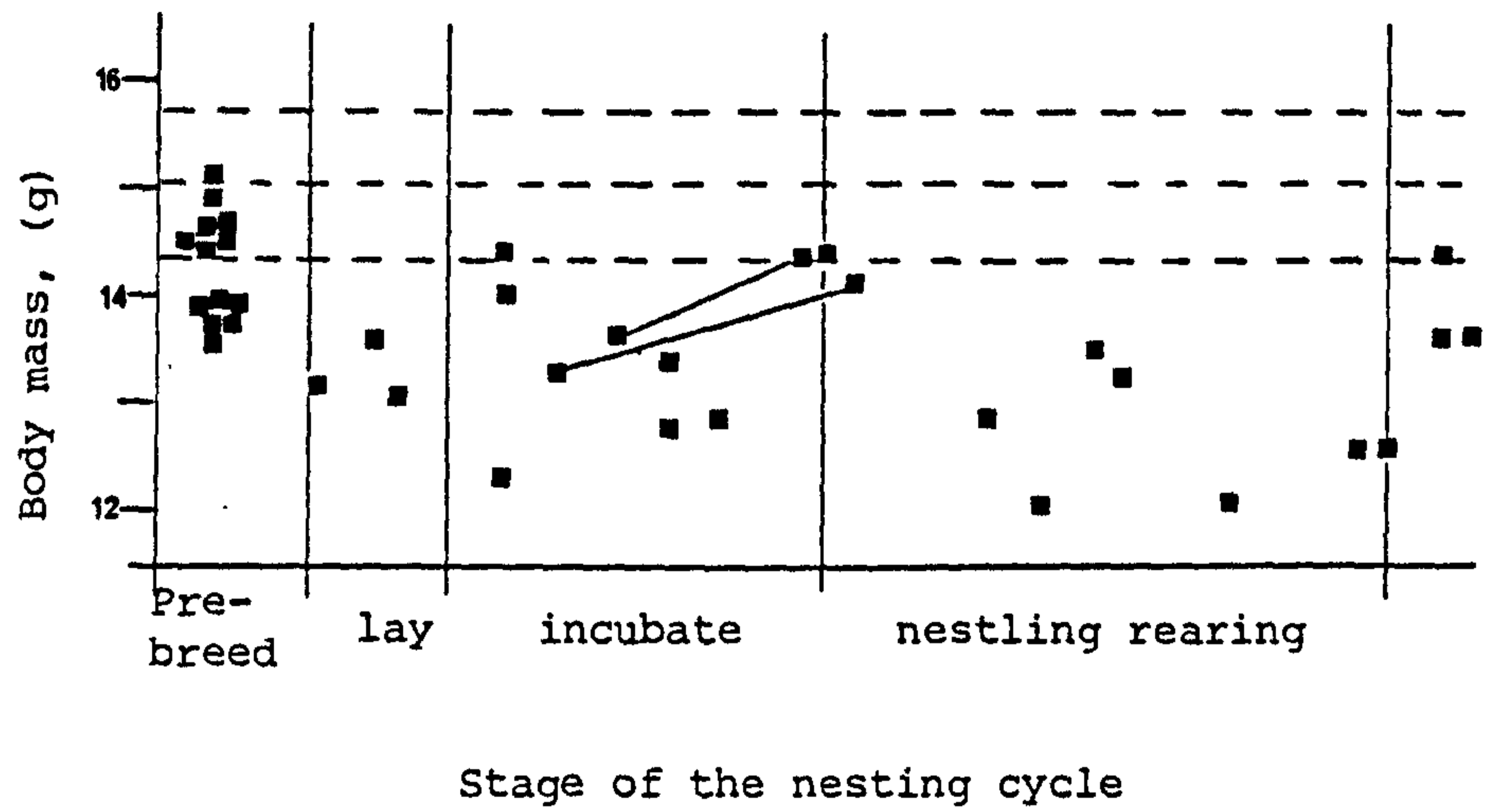


Figure 6.6

Sand martin male evening body masses as a function of stage of the nesting cycle.

Solid lines join recaptures of the same male. Pecked lines represent the mean mass \pm sd of chased females. See text for explanation.

after laying fell within 1 sd of the mean mass of chased females (17% of total). No male masses exceeded the mean body mass of chased females if the early arrivals are excluded. The adaptive value of hirundine body mass changes during breeding are discussed in Chapters 7 and 8.

So, chasing by male sand martins was directed at heavy females, and females were heaviest during the prelaying and laying stages of the breeding cycle. Is this the time when females are most likely to be fertile?

In chickens males have the greatest probability of successful fertilisation if insemination occurs at least 48h before the first ovulation (Lodge, Fechheimer and Jaap, 1981) though sperm may remain viable inside the female's infundibulum for over 10 days (Howarth, 1974). Since both sperm viability and the ability of sperm to compete with fresh sperm declines with time (Howarth, 1974; Lake, 1975) there should be a premium on males fertilising females early during their laying period. The fertile period for ova is less than 0.5 hours after ovulation in chickens (Howarth, 1974). Hence female sand martins are likely to be fertile for at least two days prelaying, and throughout laying when ova are being ovulated. Eight-four percent of copulations in tree swallows occurred during the calculated fertile period of 5 days before laying until the third day after the first egg (Leffelaar and Robertson, 1984).

6.3.4 Female flight performance and reproductive condition

Natural selection should favour males which can detect fertile females, since male fitness is likely to be highest in birds which fertilize most females. Since female sand martins are heaviest during their fertile period, males which are able to detect fertile, heavy females will be selected for.

Flight performance and behaviour varies with body mass in birds. For example, stroke period increases allometrically with increasing body mass in passerines (Rayner, 1979), and flight velocity and flight power also vary allometrically according to body mass (Pennycuik, 1969; Greenewalt, 1975).

The heaviest female sand martin captured during the study weighed 19.7g and had difficulty rising from the ground after release, suggesting that heavy individuals may encounter problems during take off. Moreover, one nestling close to fledging with poor flight capacities was chased to the ground by about 10 birds. If the chasing birds were males seeking promiscuous copulations, this anecdotal observation suggested that birds with laboured flight may present cues to chasing males. The above observation also suggests that 20g may be about the upper limit for body mass in sand martins, birds above this mass probably being unable to take off from level ground.

To investigate whether birds were chased through cues given in flight, a sample of six birds (four females, two males) which were not pre-laying or laying females had their primaries tied loosely with surgical thread. Hence body mass was kept constant, though flight performance was altered. All birds encountered problems during take-off and ascending flight. Observations on these six experimental birds are presented in Table 6.2.

Three of the four females whose primaries were tied were chased soon after release, and the other bird was investigated. One of the experimental males was chased, the other investigated. The results suggest that flight cues are important in providing cues for chasing males. However, the chases were usually of a relatively brief duration, suggesting that either the thread loops fell off soon after

Table 6.2

Observations on sand martins whose primary features had been loosely tied with surgical thread

<u>Sex</u>	<u>Body mass (g)</u>	<u>Interaction with other birds</u>
Female	14.3	Chased for .1 min +, 1 chaser
Female	14.0	Investigated for 12s, 1 chaser
Female	13.4	Chased for 49s, 1 chaser
Female	13.3	Chased for 60s, 2 chasers
Male	13.0	Chased for 30s, 2 chasers
Male	12.9	Investigated for 20s, 2 chasers

the birds were released, or that secondary cues indicating a female's fertility may be used by chasing males.

If sand martins are chased, they are first followed on average 13.8s after release (see above). In one bird whose flight was video recorded for 50s after release, level flight was attained only after 7s (Figure 6.7). Flap rate decreased rapidly over ascending flight, and was generally lower in level flight than in ascending flight, especially when gliding was occurring. Because of the speed in which chased birds are first followed, any flight cues available to chasing males are likely to occur soon after release, when birds descend from the hand and then enter ascending flight. Hence time to reach ascending flight and wing beat frequency during the first 2s of ascending flight were quantified in a video analysis of take-off patterns in 32 adult birds.

For video recording six laying or prelaying female sand martins were captured and ascribed to this period in the breeding cycle on the basis of having a heavy body mass, substantial lipid reserves, and abdominal swellings indicating the presence of fully developed eggs. A further seven females had their body mass increased by 2g (c15%) by interperitoneal injection with saline water. These 13 females were ascribed to the 'weighted birds' category for analysis. Their flight behaviours were compared with 19 adults which were not pre-laying or laying females. The take-off patterns of two fledglings was also video-recorded.

Flight behaviours of the two groups are compared in Table 6.3. The 'weighted birds' group had a significantly higher mean body mass than other birds analysed. There were no significant differences in

Table 6.3 Measured flight behaviour parameters from video analyses of sand martin take-off patterns

<u>Group</u>	<u>Body Mass (g)</u>	<u>Time to ascending flight (\bar{s})</u>	<u>Wing beat frequency in ascending flight (flaps s^{-1})</u>
Weighted birds ^a	14.62 \pm 0.73 (13)	0.79 \pm 0.20 (13)	12.61 \pm 0.59 (10)
Others	12.56 \pm 0.80 (19)	0.61 \pm 0.18 (19)	12.62 \pm 0.96 (17)
t, P	7.4, P < 0.001***	2.7 P < 0.05*	0.03 ns

a: No significant differences occurred between mean body mass of experimentally weighted birds and naturally heavy prelaying or laying females in this category ('t' mass = 0.82, n = 13, ns, 't' time to ascending flight = 0.18, n = 13, ns, 't' wing beat frequency = 0.32, n = 10, ns).

means \pm sd, (n) are described.

ns : not statistically significant, P > 0.05.

mean body mass, time to reach ascending flight, or flap rate between experimentally weighted and naturally heavy birds in the 'weighted birds' category (see Table 6.3 for statistics). The mean time taken for weighted birds to reach ascending flight was significantly longer than that taken by other birds, whilst there was no significant difference in mean wing beat frequency in ascending flight between the two groups.

The mean body mass of two fledglings whose take-off patterns were recorded was $11.65 \pm 0.35\text{g}$. The mean time taken to reach ascending flight was $0.60 \pm 0.06\text{s}$, and the mean wing beat frequency in ascending flight was $13.73 \pm 0.80 \text{ beats s}^{-1}$.

6.4 DISCUSSION

6.4.1 Mate-guarding behaviour and coloniality in birds

Mate-guarding behaviour in sand martins closely resembles that of conspecific bank swallows (Beecher and Beecher, 1979), in that chasing is performed by males and directed towards fertile females. Mate-guarding behaviour is widely distributed amongst bird species, and a list of published studies is given in the introduction to this chapter. Amongst hirundines other than sand martins, mate-guarding is found in rough-winged swallows, Stelgidopteryx ruficollis, (Lunk, 1962), swallows, (Samuel, 1971; Woods, 1982; A Møller, pers. comm.), purple martins, Progne subis, (Brown, 1978), and house martins (D.M. Bryant, pers. comm.).

Generally, mate-guarding and extra-pair copulations are more frequently recorded in colonial bird species (Gladstone, 1979), where males have potential access to many females because of the high density of breeding pairs nearby. Moreover, breeding colonies of birds often

show synchrony in breeding behaviour (e.g. Emlen and Demong, 1975; Feare, 1976, review in Wittenberger, 1981), so fertile females may be relatively abundant, temporally as well as spatially. Hence there will be strong selective pressure for males to guard fertile mates with a high density of male competitors, and probably also selection for males to seek promiscuous copulations amongst a high density of females when their mates are not fertile. When food resources are economically defensible, territory holding males will exclude other males from their defended area, and the necessity for close mate-guarding will be reduced.

Colonial breeding is probably often linked to the predictability and distribution of food resources. An unpredictably distributed food supply which is superabundant when located is usually not economically defensible, and may be better exploited by group foraging (Lack, 1968; Brown, 1969; Davies and Houston, 1984). Hence the benefits of locating food through foraging in groups during the breeding season may be one factor influencing the evolution of colonial breeding. Although other suggestions exist as explanations for the evolution of colonial breeding (for example the reduction in predation pressure at colonies, Hoogland and Sherman, 1976), it seems probable that feeding ecology affects breeding dispersion in birds, and breeding dispersion in turn influences mating strategies (Horn, 1968, review in Wittenberger, 1981). Since aerial insects are an unpredictable food resource (Bryant, 1975b), probably not economically defensible, aerial feeding may have contributed to the evolution of colonial nesting in sand martins, which increased selective pressures for promiscuous behaviour in males. Swallows in Britain tend to nest solitarily or in small, loose colonies, and feed on low-flying insects which are more predictable

in distribution than higher-flying forms (Waugh, 1978). Although mate-guarding occurs in swallows (Samuel, 1971; Woods, 1982; A. Møller, pers. comm.), chasing parties are not seen on the same scale as in sand martins (pers. obs.). Territorial defence by both sexes probably partly explains why tree swallows do not show mate-guarding behaviour (Leffelaar and Robertson, 1984).

There is substantial evidence from several bird species that copulations with individuals other than the mate may result in fertile eggs being produced. Bray, Kenelly and Guarino (1975) vasectomised male red-winged blackbirds, Agelaius phoeniceus, and their mates laid fertile eggs. Hybrid cave x barn swallow young (Petrochelidon fulva x Hirundo rustica) in barn swallow nests suggests successful extra-pair copulations (Martin, 1980). Extra-pair copulations in sand martins were not seen in this study, though inter-pair copulations were only observed on three occasions. Copulation was once seen in a burrow observed from a viewing chamber, and was noted on two occasions in early morning when many pairs were seen mating on the ground. Pairs were often harassed by other individuals during these ground copulations. Beecher and Beecher (1979) noted promiscuous copulations resulting from sexual chases in bank swallows, and Hoogland and Sherman (1976) observed promiscuous copulations with stuffed birds by males, and found semen on the dead bird.

Male sand martins arrive at the colony in spring with well developed testes, which atrophy over the course of a nesting attempt (Chapter 5). The opportunities for males to seek promiscuous copulations will probably be reduced when much time is spent incubating, and at its lowest during nestling-feeding. Sperm storage capacity of the testes is likely to be reduced during these periods of testes atrophy.

6.4.2 How body mass changes may affect flight performance in fertile female sand martins: cues for males to increase their fitness

The results of the field observations, experiments and video analyses suggested that natural selection has favoured male sand martins to increase their fitness by detecting fertile females through flight cues resulting from female body condition during the pre-laying and laying period, and chasing such females to attempt promiscuous copulations.

One cue which may be available to chasing males is the increased time that heavy females, likely to be fertile, take to reach ascending flight (Table 6.3). Such a cue may be available when birds leave burrows, and chasing males may be vigilant for birds which dip substantially on exit, or which have problems gaining height.

The failure to detect differences in wing beat frequency during the first 2s of ascending flight is not surprising in view of the rapid change in flap rate over this period (Figure 6.7). Since aerodynamic theory predicts considerable variation in other aspects of flight performance as a function of body mass (Pennycuick, 1969, 1975; Greenewalt, 1975; Rayner, 1979), it is unlikely that the time taken to reach ascending flight is the only potential flight cue given by fertile females.

The extra mass carried by laying and pre-laying female sand martins will increase wing loading, reduce the power:mass ratio, cause a shift in the centre of gravity, and alter the aerodynamic profile of the female. Indeed, the increased mass carried by laying female birds of prey has been used to explain why female raptors evolved to a larger size than their mates: the larger wing area of females relative to males reduces their wing loading during laying, facilitating

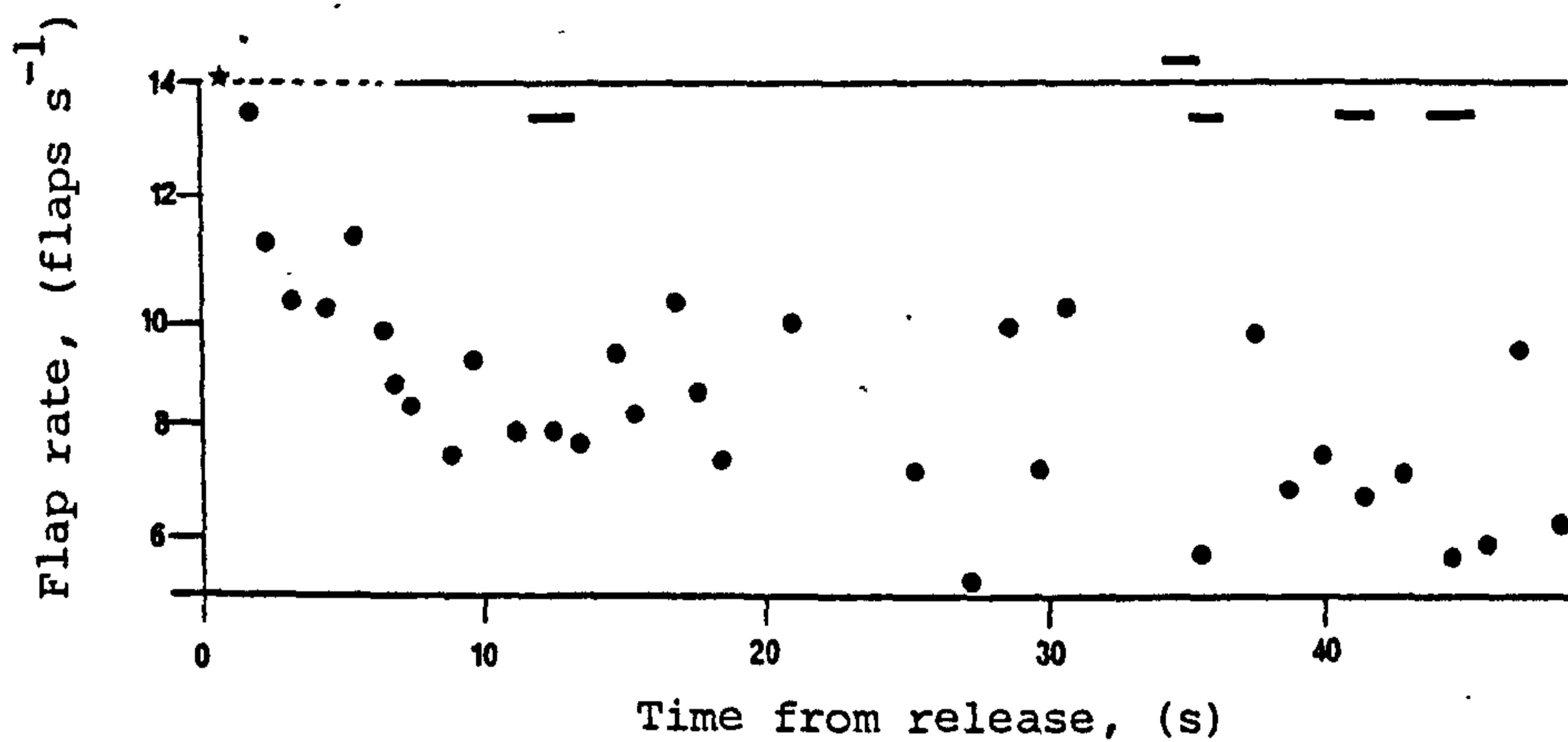


Figure 6.7

Flap rate as a function of time after release from the hand for one sand martin whose flight was video-recorded for 50 seconds.

The data is described by

$$y = 12.2 - 1.37 \ln x$$

$$r = -0.68, n = 34, P < 0.001.$$

The asterisk denotes time of descending flight, the pecked line ascending flight, the thin solid line level flight, during which gliding is illustrated by the thick solid line.

foraging by flight in a period of high energy and nutrient demand (Wheeler and Greenwood, 1983).

In Figure 6.8 wing area is plotted against wing-length (maximum chord) for 29 adult sand martins. Between 101 mm and 112 mm wing area was significantly positively correlated with wing-length, ($r = 0.76$, $n = 28$, $P < 0.001$). The 98.5 mm wing-length point was omitted from the correlation because it is isolated from the remaining data, and may be outside of a linear relationship between wing-length and wing area. The inclusion of this point into the correlation still maintains a high level of significance between the variables ($r = 0.70$, $n = 29$, $P < 0.001$).

Hence sand martins with longer wings are likely to have lower wing loadings for a given body mass than are shorter winged birds. Male house martins become heavier as they get older (Bryant, 1979), and if sand martins also increased in body mass with age, the increase in wing-length with age (Chapter 2) could be viewed as an adaptation to counteract an increased wing loading had wing area remained constant.

The mean wing loadings of birds at different stages of the breeding cycle are presented in Table 6.4. The mean wing loading of prelaying and laying females was significantly greater than that of incubating birds ($t = 2.36$, $n = 13$, $P < 0.05$), and nestling rearers ($t = 5.36$, $n = 19$, $P < 0.001$).

Hence it is likely that female sand martins are flying with suboptimal wing loadings during laying and prelaying. Their wings probably evolved for flight carrying a mass some 15-20% less than that during the fertile period, since laying and prelaying contribute at most about 5% of the annual cycle. Such a sudden change in wing

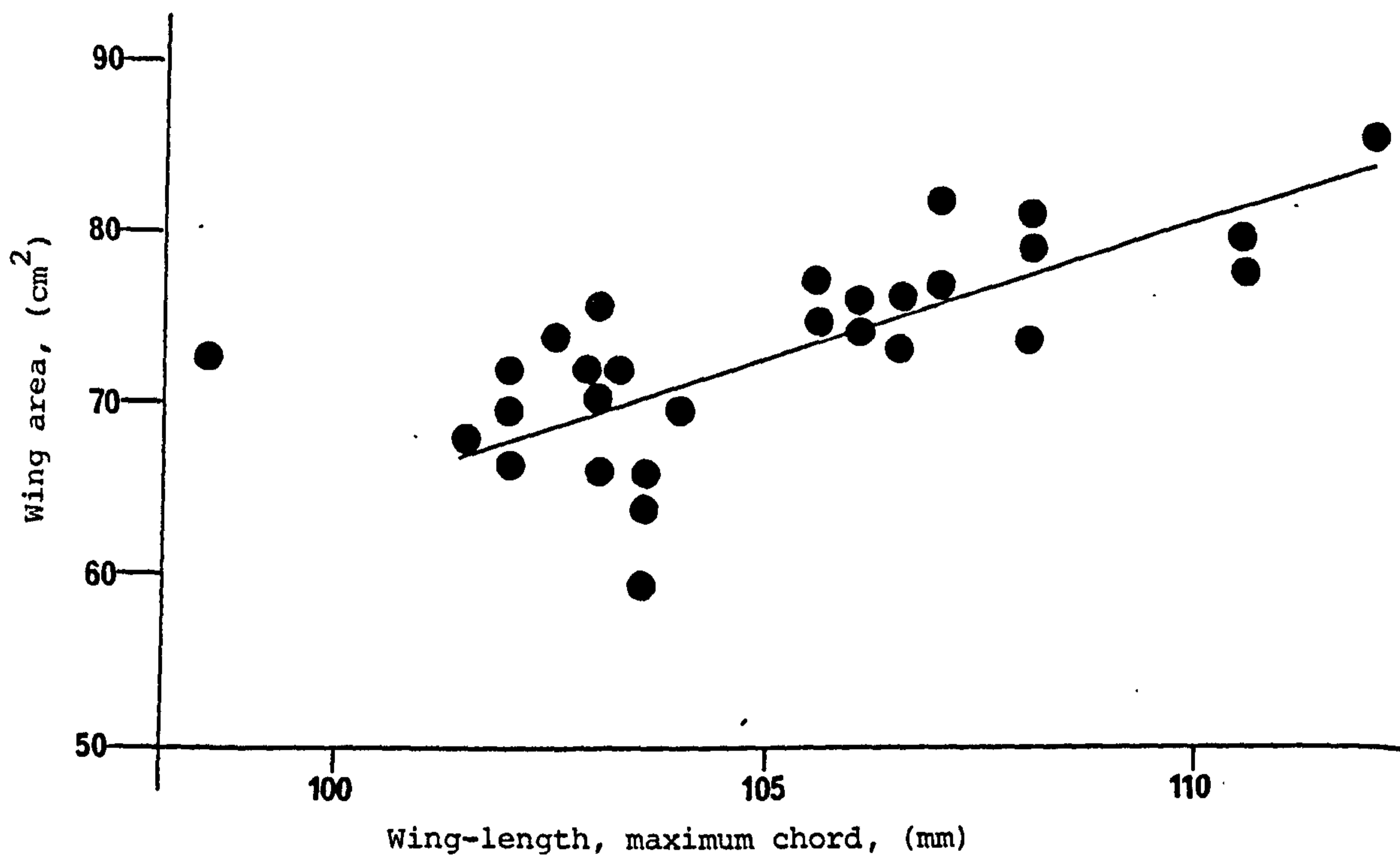


Figure 6.8

The relationship of wing area to wing-length in adult sand martins.

Between 101 and 112 mm wing-length, wing area is described by

$$y = -93.12 + 1.58x$$

$$r = 0.76, n = 28, P < 0.001.$$

Table 6.4

Wing loadings of sand martins during the breeding season.

<u>Breeding Stage</u>	<u>Wing Loading</u> g cm^{-2}	<u>mean, $\bar{x} \pm \text{sd}$ (n)</u>
Pre-laying/laying females ^a	0.211 \pm 0.015	(6)
Incubating birds ^b	0.185 \pm 0.023	(7)
Nestling rearers ^b	0.175 \pm 0.013	(13)
Fledglings	0.186 \pm 0.015	(5)

a: Prelaying and laying female data were combined because females are likely to be fertile during both periods.

There was no significant difference between the mean wing loading of laying females ($0.203 \pm 0.005 \text{g cm}^{-2}$, $n = 2$) and prelaying females ($0.216 \pm 0.017 \text{g cm}^{-2}$, $n = 4$), $t = 1.0$, n.s.

b: Incubators and nestling rearers of both sexes were combined, there being no significant difference between mean wing loadings of males and females in these groups (incubators $t = 0.76$, n.s., nestling rearers $t = 0.20$, n.s.).

loading during the fertile period is likely to be responsible for influencing female flight behaviour during this time.

The findings of this Chapter have two implications for the study of parent:offspring resource allocation in swallows. Firstly, although mate-guarding is likely to involve substantial time and energy in male sand martins, male swallows (not being colonial breeders in this study) may expend little mating effort in guarding and chasing over the breeding cycle. Secondly, the flight difficulties experienced by exceptionally heavy sand martins during take-off suggests that an upper economical limit exists for body mass in hirundines, and such a limit may impose a ceiling on the quantity of reserves that a parent bird is prepared to deposit.

CHAPTER 7

7. RESOURCE ALLOCATION DURING INCUBATION IN SWALLOWS

7.1 INTRODUCTION

During incubation female swallows must make decisions about when to warm their eggs and when to self-feed so as to maximise their chances of survival and reproductive success (McFarland, 1977; McCleery, 1978). In this chapter, the body mass dynamics of incubating swallows are described, and incubation decisions are viewed in the context of parent:offspring resource allocation.

Eggs represent a reproductive investment in offspring by parent swallows, especially by the female, and the clutch needs to be frequently warmed if successful hatching is to occur. Simultaneous foraging and incubating are obviously incompatible activities for female swallows, and it is assumed that fitness is greatest in individuals which maximise their energy gains while foraging between incubation bouts.

A previous attempt to understand the optimal time for parent birds to leave eggs unattended between incubation stints only considered the constraint of clutch cooling rate on adult behaviour (Webb and King, 1983). The time which a bird spends feeding between incubation bouts is also likely to depend on its foraging success during the inattentive period.

A model is developed to predict the optimal time for the inattentive period in female swallows. Clutch cooling rates were investigated using thermistor probes inserted in swallow eggs under laboratory conditions, while constraints on adult foraging behaviour

were derived from instantaneous body mass changes measured by the automated nest-balance system.

7.2 MATERIALS AND METHODS

7.2.1 The use of precision automated nest-balances

The use of Mettler PK2000 electronic balances to monitor instantaneous and long term body mass changes in breeding swallows has been described in Chapter 4, together with observational methods and morphometric measurement techniques.

7.2.2 Field experiments

Observations on control birds incubating their natural clutches were supplemented by an experiment whereby clutch size was manipulated. In 1984 two female swallows of similar body mass each completed a clutch of five eggs on the same day. Eggs were interchanged between their nests for one 2-day and one 3-day period so that one female incubated eight eggs, the other two eggs. Hence each female was observed incubating experimental clutch sizes of two and eight, and her natural clutch size of five eggs. The experimental clutch sizes were outside the range of clutch sizes encountered in natural situations in the study (Chapter 2). The experimental females were nesting within 30m of each other, and fed in similar areas. All eggs used in the experiment hatched successfully.

7.2.3 Egg cooling rates

Egg cooling rates were determined in an incubator in the laboratory. Eggs were pierced, filled with distilled water, and a thermistor probe was inserted. The egg was then sealed with evostick adhesive and candlewax.

Ambient temperatures of 5°C, 15°C, and 25°C were used in the experiment. Clutch size was varied from one to 10 eggs, and at clutch size five, egg cooling rates were recorded with and without the feather insulation in the nest. After the thermistor egg had been heated to 35.7°C, the mean maximum temperature attained by swallow eggs during natural incubation bouts (Turner, 1980), cooling rates were recorded for one hour. The heat source was a 100W light bulb.

Cooling rates obtained by the thermistor egg were compared with those from two other thermistor eggs in a single trial, and no significant differences between the mean cooling rates obtained from the three eggs were found.

The situation of swallow nests in barns resembles laboratory conditions in that radiative heat input to the clutch through sunlight and convective heat losses in draughts are likely to be small in both cases. However, although the incubator was darkened, its metal surface may have reflected more heat than the wooden beams surrounding natural swallow nests.

7.3 THEORY AND RESULTS

7.3.1 Body mass dynamics of incubating female swallows

During incubation, the body masses of female swallows show considerable variation between individuals, and within any individual female. For example, in Figure 7.1 the afternoon body masses of five incubating female swallows are illustrated. One bird weighed only 19g on its lightest day, while the heaviest incubation mass recorded was almost 27g. In this subsection, the reasons for this variation are investigated, and the adaptive significance of the body mass dynamics of incubating female swallows are explored.

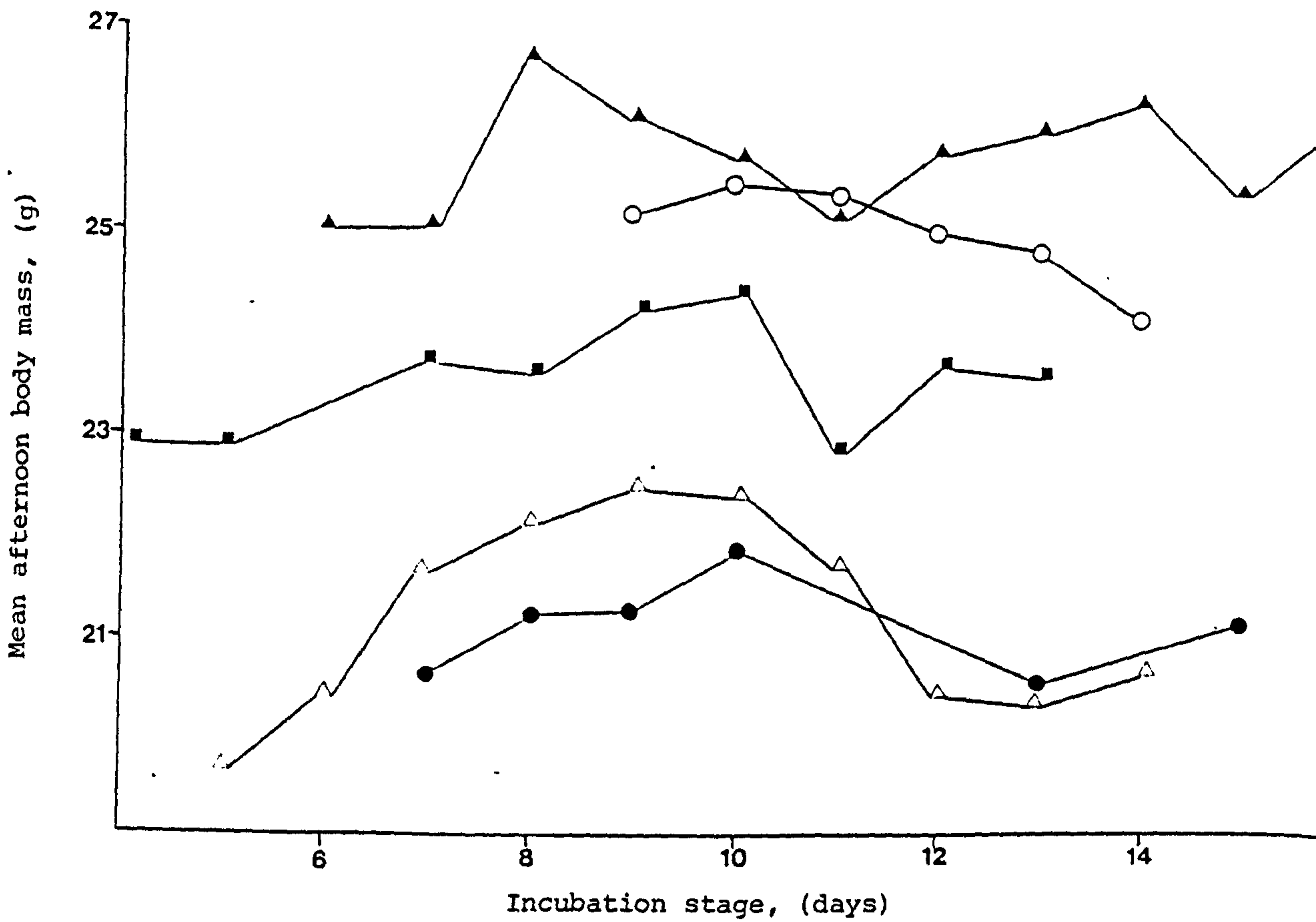


Figure 7.1

Body mass changes of the five incubating female swallows.

Lines terminate on day of hatching.

(a) Intersexual variation in body mass during the incubation period

The mean afternoon body mass of 17 female swallows over 78 days of incubation was $22.48 \pm 1.41\text{g}$. The mean afternoon body mass of 11 male swallows over 17 days when their mates were incubating was $20.46 \pm 0.82\text{g}$. Hence, although female swallows tended to be smaller than males (Chapter 2), they were significantly heavier during the incubation period ($t = 5.7, P < 0.001$).

Since female swallows incubate alone, the fact that they were on average 2g heavier than males at the same time suggests that females maintained a reserve during incubation. There was no consistent trend to lose mass during incubation, which would be expected if reproductive organs were undergoing atrophy. Moreover, the results from sand martin carcass analysis (Chapter 5), suggested that reproductive structures atrophied immediately (i.e. in less than three days) after laying. Since body mass was significantly positively correlated with fat score and lipid content in swallows (Chapter 5), it is concluded that female swallows are indeed maintaining a large lipid reserve over the incubation period.

(b) Inter-individual variation in body mass

Insufficient data were available to examine the relationship between body mass and keel length in male swallows during incubation. Female swallow incubation body mass was strongly positively correlated with keel-length (Figure 7.2), so large females tended to be heavier than smaller birds.

One explanation for this relationship is that long-keeled females are probably structurally bigger than individuals with shorter keels, having larger muscles and body organs, and hence being heavier. Moreover, large birds are likely to experience a higher energy

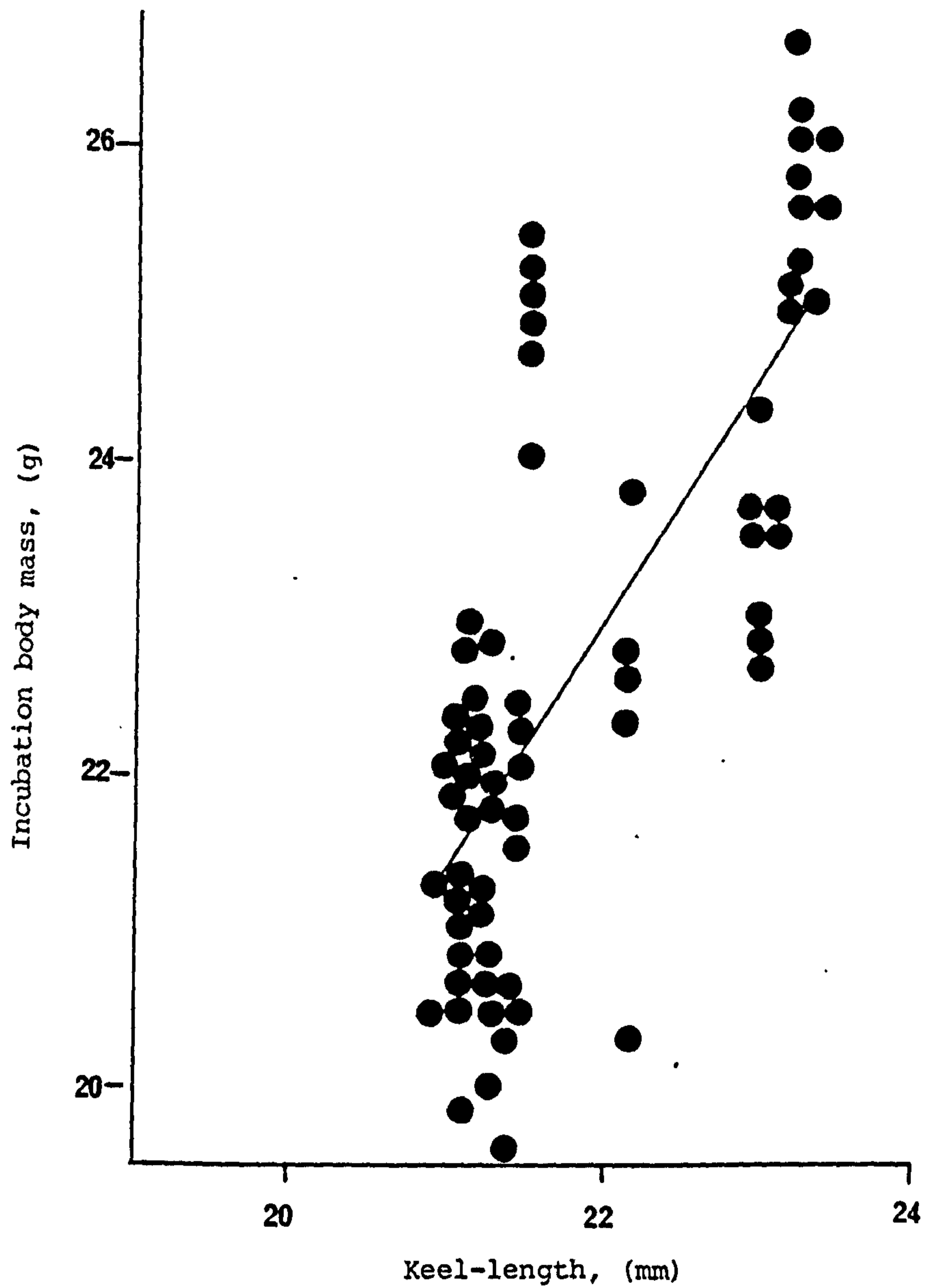


Figure 7.2

Incubation body mass as a function of keel-length in female swallows.

All values are mean value for afternoon sampling periods, data from 13 nests, 10 females, 69 nest days.

The regression equation is

$$y = -12.3 + 1.60x, F = 77, P < 0.001.$$

expenditure than smaller individuals, and may need to accumulate more lipid to meet this greater energetic demand. However, large house martins have a lower average daily metabolic rate and a lower daily energy expenditure than smaller birds (Bryant and Westerterp, 1982), so large female swallows may be more efficient at accumulating reserves than are smaller individuals.

(c) Intra-individual variation in body mass

Variation in body mass within individual incubating females was analysed in relation to daily temperature and food abundance.

Body mass changes of one typical incubating female in relation to maximal daily temperature and food abundance on the same day are illustrated in Figure 7.3. Insect abundance, as measured by the 12.2m suction trap, closely tracks maximal daily temperature, and the female's body mass follows each of these lines reasonably closely. Although insect abundance increases at higher maximal daily temperatures (Chapter 3), temperature and insect abundance may also influence incubation body mass independently: the former for example by modifying cooling rates of eggs, the latter by affecting foraging success.

(i) Temperature effects

Lipid reserves may be mobilised more quickly in colder weather, when metabolic rates are higher as a result of being below the lower critical temperature. Moreover, at cold temperatures birds must spend considerable time on the nest reheating eggs and maintaining egg temperature, leaving little time for self-feeding.

(ii) Food abundance effects

Foraging efficiency is likely to be higher when insects are more abundant, since preferred, large items are commoner at higher tempera-

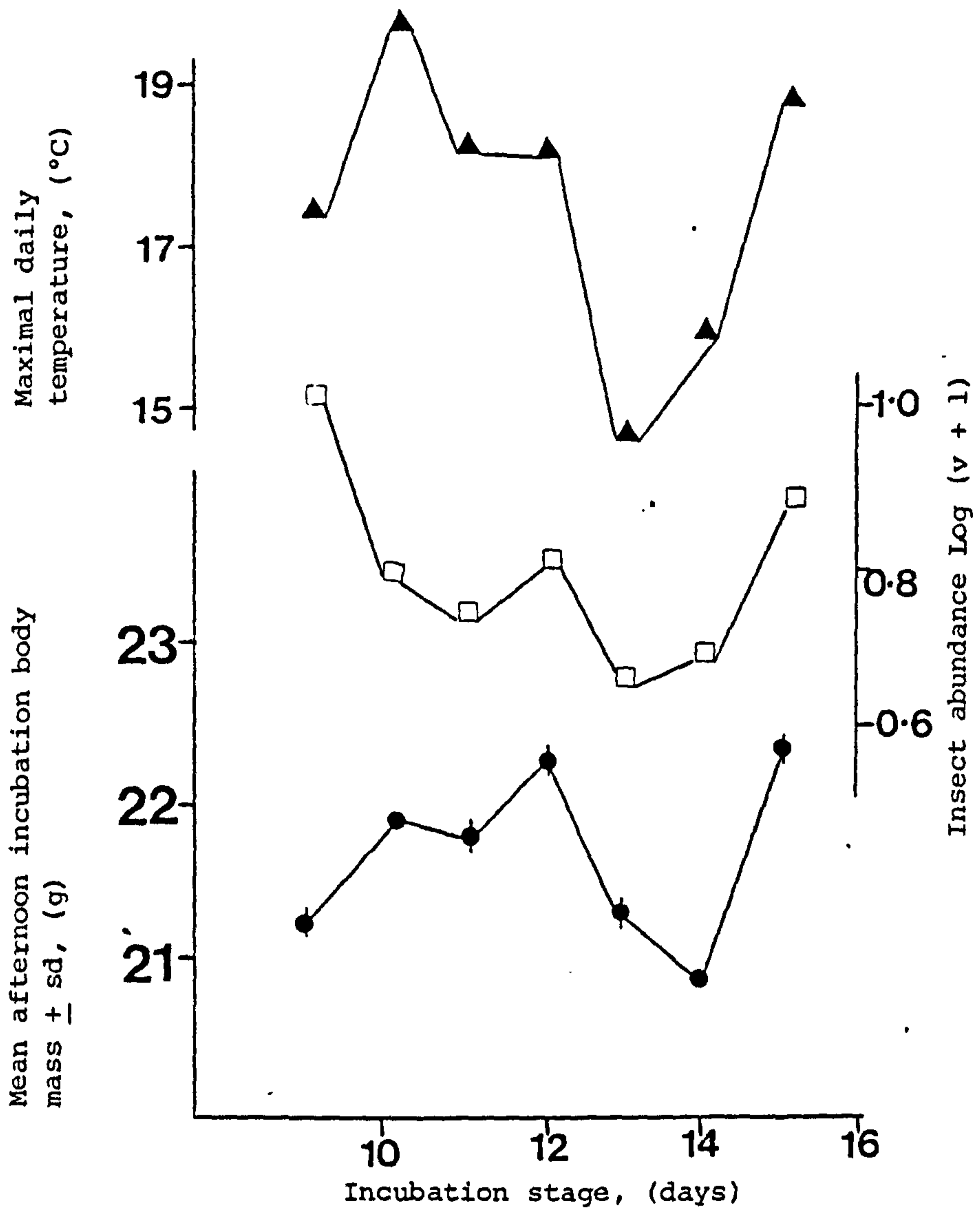


Figure 7.3

Body mass changes of an incubating female swallow (solid circles) in relation to food abundance (open squares) and maximal daily temperature (solid triangles).

tures (Turner, 1980, Chapter 3), and since less time may be spent searching for prey when it is more frequently encountered. Increased foraging efficiency at high levels of food abundance could lead to lipid accumulation, especially if more time is available for self-feeding at higher temperatures.

Correlations for female incubation body mass in relation to incubation stage, food abundance, and body size are presented in Table 7.1.

Body mass was significantly positively correlated with food abundance on the day of weighing, food abundance on the days preceding and following weighing, maximal daily temperature, and keel-length. A stepdown multiple regression analysis of incubation body mass was performed including the suction trap measures of food abundance rather than the hand-net measures, since suction trap data gave a higher value of r^2 than when hand-net data were entered as independent variables. In the abbreviated analysis, only keel-length and maximal daily temperature entered as significant variables (Table 7.2). The correlations of body mass with insect abundance on the days preceding and following weighing probably existed because insect abundance on the day of weighing was itself correlated with suction trap volume on both previous ($r = 0.58$, $n = 60$, $P < 0.001$) and subsequent ($r = 0.55$, $n = 60$, $P < 0.001$) days.

There was no correlation between incubation stage and body mass. Some bird species lose mass over the incubation period by reducing food intake or by fasting, as seen in barnacle geese (Lessells et al., 1979), red jungle fowl Gallus gallus (Mrosovsky and Sherry, 1980), black-browed and grey-headed albatrosses, Diomedea melanophris, and D. chrysostoma, (Prince, Ricketts and Thomas, 1981), and Canada

Table 7.1

Correlations for female incubation body mass in swallows

Variable	r	significance
² Mean available individual prey dry mass, g	0.05	ns
Incubation stage, days	0.08	ns
² Number of insects	0.25	ns
² Insect biomass, g dry mass	0.29	*
¹ $\log(v + 1)_{d-1}$	0.37	**
¹ $\log(v + 1)_{d+1}$	0.38	**
¹ $\log(v + 1)_{d_0}$	0.40	**
maximal daily temperature, °C	0.38	**
² number of large insects (≥ 1.5 mg dry mass)	0.51	***
keel-length, mm	0.60	***

1. $\log(v + 1)$ is insect abundance as measured by the 12.2m suction trap. Measurements included in the analysis were made on the day of weighing (d_0), the preceding day ($d-1$), and on the subsequent day ($d+1$).

2. Hand-net sample measures of food abundance.

n = 49 days, 13 females for all data

ns : not statistically significant

* : P < 0.05

** : P < 0.01

***: P < 0.001

Table 7.2 Stepdown multiple regression analysis of factors influencing the incubation body mass of female swallows

Independent variable	Full analysis			Abbreviated analysis				
	Multiple $r^2 \times 100$	Degrees of Freedom	Regression Equation	t	P	Regression Equation	t	P
$\log (v + 1)_{d0}$	19.30	1,58	$y = 0.354x_1 +$	0.45	ns			
keel-length, mm	35.33	2,57	$0.934x_2 +$	3.72	***	$1.09x_2 +$	4.40	***
$\log (v + 1)_{d-1}$	40.76	3,56	$0.333x_3 +$	0.53	ns			
maximal daily temperature, °C	42.55	4,55	$0.055x_4 +$	1.31	ns	$0.09x_3$	2.84	**
$\log (v + 1)_{d+1}$	44.05	5,54	$0.818x_5 +$	0.82	ns			
incubation stage, days	44.30	6,53	$0.059x_6$	1.06	ns			
				-1.01			-3.11	
				F = 7.08			F = 18.79	
				P < 0.001***			P < 0.001***	

1. $\log (v + 1)$ is insect abundance as measured by the 12.2m suction trap. Measurements included in the analysis were made on the day of weighing (d0), the preceding day, (d-1), and on the subsequent day (d+1).

ns : not statistically significant

* : P < 0.05

** : P < 0.01

***: P < 0.001

geese Branta canadensis moffitti (Aldrich and Raveling, 1983). Conversely, female pied flycatchers tend to increase in mass as incubation proceeds (Askenmo, 1982).

Individual female swallows neither increased nor decreased in body mass consistently as hatching approached. Females appear to aim to become as heavy as possible, fattening up on days of high temperature. However, an economically determined upper limit to female body mass must exist, since exceptionally heavy birds are likely to experience problems in taking off for flight (Chapter 6), or increased flight costs associated with increased mass (Chapter 8).

7.3.2 The cost of incubation

Daily energy expenditure during incubation is substantially lower than during nestling rearing in hirundines where both sexes share incubation duties (Bryant and Westerterp, 1980; Westerterp and Bryant, 1984). Some recent estimates of the energy cost of incubation are presented in Table 7.3. Below 28°C, the rate of oxygen consumption of incubating zebra finches, Poephila guttata, was 20% higher than that of non-incubating finches sitting in a nest at the same temperature (Vleck, 1981). Resting energy expenditure of white-crowned sparrows Zonotrichia leucophrys oriantha, was estimated to be 15% lower in incubating females than in birds perching outside of the nest but exposed to the same microclimate (Walsberg and King, 1978b).

Most of the published work on assessing the energetic cost of incubation has been performed on species where both sexes incubate. The eggs are therefore rarely left unattended, and relatively little energy is expended in reheating them.

For single sex incubators, the eggs are always left unattended

Table 7.3

Some recent estimates of the energetic cost of incubation

Values are expressed as multiples of basal metabolic rate (BMR)

Species	Method	× B.M.R.	Reference
House Martin	D ₂ O ¹⁸ / time budget	2.72 Female 2.93 Male	Bryant and Westerterp (1980)
¹ Swallow	time budget/ D ₂ O ¹⁸	2.1	Turner (1982)
	time budget/ D ₂ O ¹⁸	4.1	Westerterp and Bryant (1984) ²
Wandering albatross <u>Diomedea exulans</u>	mass loss	1.2	Croxall and Ricketts (1983)
Herring gull	mass changes	1.5-2.4	Sibly and McCleery (1983)

¹ Only the female swallow incubates. Both sexes share incubation in the other species listed.

² Based on data from one bird only.

when the incubating parent is foraging, and incubation costs may be higher than in species which share incubation duties. The energetic cost of incubation in a female zebra finch forced to rewarm cold eggs increased by 8% compared with control birds, and none of her eggs hatched (Vleck, 1981). The metabolic rate of starlings increased threefold when cold eggs were rewarmed (Biebach, 1979). Using the D_2O^{18} technique, Westerterp and Bryant (1984) suggested that incubation in female swallows may be more expensive than in sand martins or house martins where the sexes share incubation.

To further investigate body condition costs during incubation in poor weather conditions, time budgets of incubating birds were analysed in relation to instantaneous body mass changes occurring during the attentive and inattentive periods.

The percentage of afternoon time spent incubating increased with decreasing temperature above a maximal daily temperature of about 10°C (Figure 7.4), allowing more time available for foraging at high temperatures.

Insect abundance also decreased as temperature dropped (Chapter 3), so it may be expected that birds have a reduced foraging intake during inattentive periods when food is scarce compared with intake rates during periods of high food abundance. Intake rates during the inattentive period can be estimated by measuring the rate of mass change while foraging. Mass losses while foraging were first excluded from the analysis to minimise the chances of including foraging periods which had defaecations (see Chapter 4).

In Figure 7.5 the mean rate of mass gain while foraging is plotted for four levels of food abundance which represent quartiles of the distribution of suction trap catch volumes.

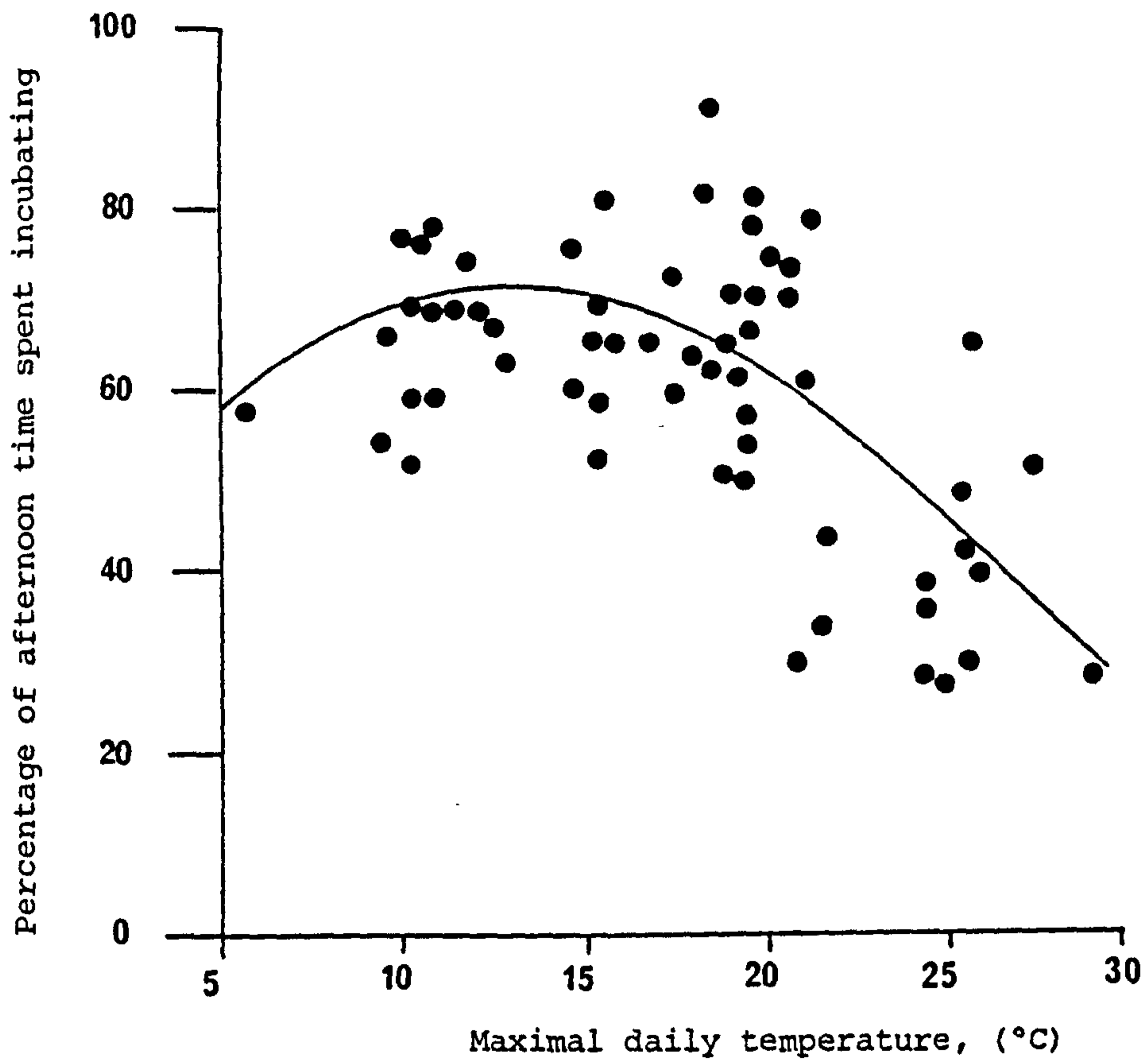


Figure 7.4

The percentage of afternoon time spent incubating by female swallows as a function of maximal daily temperature.

The fitted curve is a maxima function equation;
 $y = 17.64x e^{-0.0918x}$, r for transformed data = 0.90,
 $n = 60$, $P < 0.001$.

Data for one female assumed to be close to desertion are omitted.

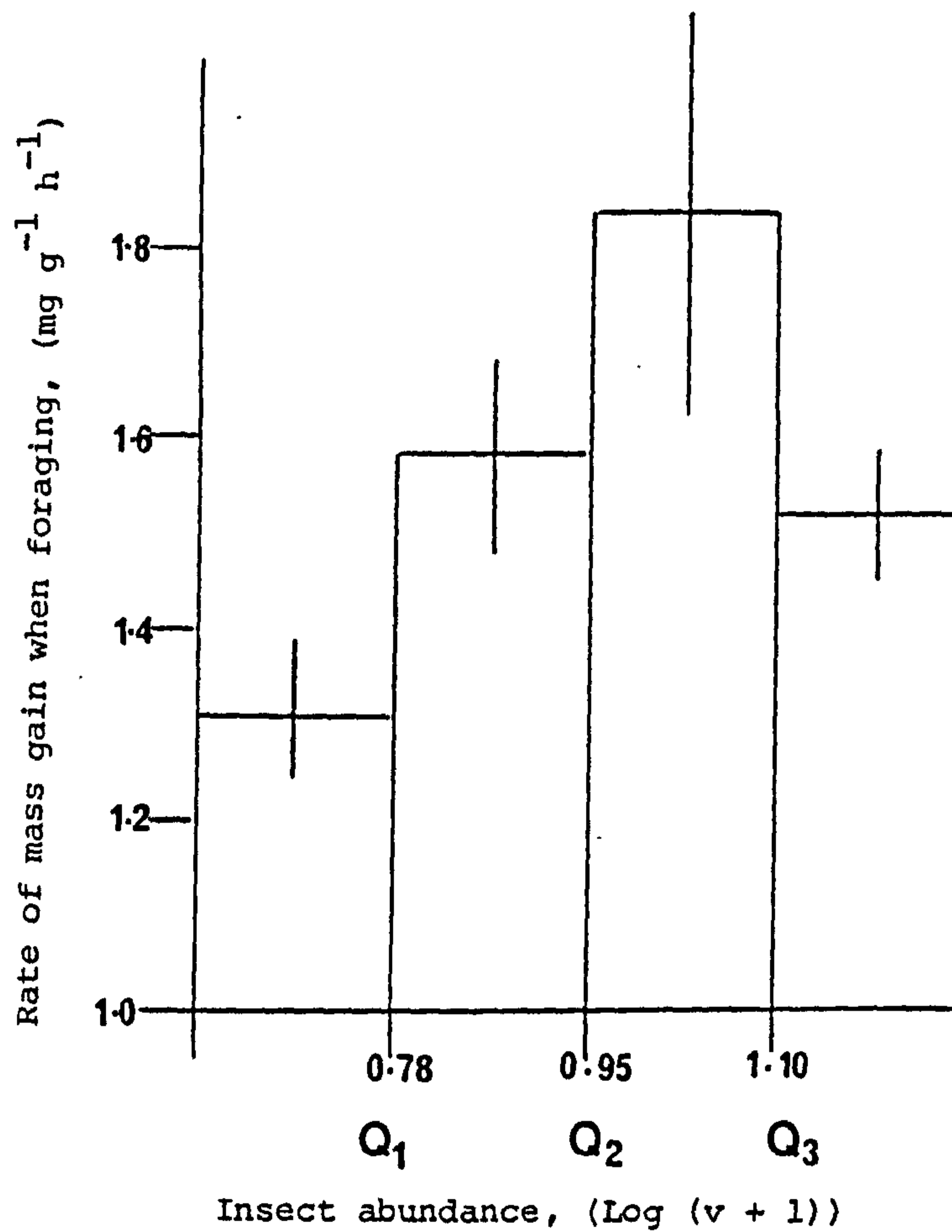


Figure 7.5

Mean female swallow rate of mass gain when foraging in relation to insect abundance as measured by the 12.2m suction trap during the incubation period.

Means ± standard errors are presented.

Q₁ - Q₃ are quartiles of the insect abundance distribution.

Although the mean rate of mass gain while foraging does increase up to the third highest class of insect abundance, none of the differences between means was statistically significant. Rate of mass gain while foraging was not correlated with insect abundance ($r = 0.11$, $n = 161$, ns). This lack of significance may be because when food is more abundant at higher temperatures, prey may become more mobile (Waugh, 1978; Kacelnik, 1979) and therefore more difficult for swallows to capture. This increase in prey mobility may counteract any expected increase in intake rate through prey becoming more abundant. However, when foraging trips resulting in mass losses were included in the analysis (assuming defaecation rate to be independent of food abundance), rate of mass change was positively correlated with insect abundance ($r = 0.16$, $n = 293$, $P < 0.01$). Thus the intake rate of swallows may be reduced in bad weather conditions.

Because of the limitations of reduced foraging time and probably a reduced intake rate at low temperatures it is likely that poor weather conditions encountered during incubation will result in a deterioration in female body condition, maybe leading to desertion in extremely poor conditions.

The spring and early summer of 1983 were unseasonably cold, and aerial insects were often scarce (Chapter 3). In Figure 7.6 the diurnal body mass changes of one incubating female during a changeable day in June are illustrated.

The female gained mass rapidly in relatively favourable feeding conditions up to 15.00h (32 flying insects captured in 300 sweeps of the hand-net at 14.00h). After 15.00h weather conditions deteriorated rapidly as rain fell continuously and ambient temperature dropped, with no insects captured in 300 sweeps at 20.00h.

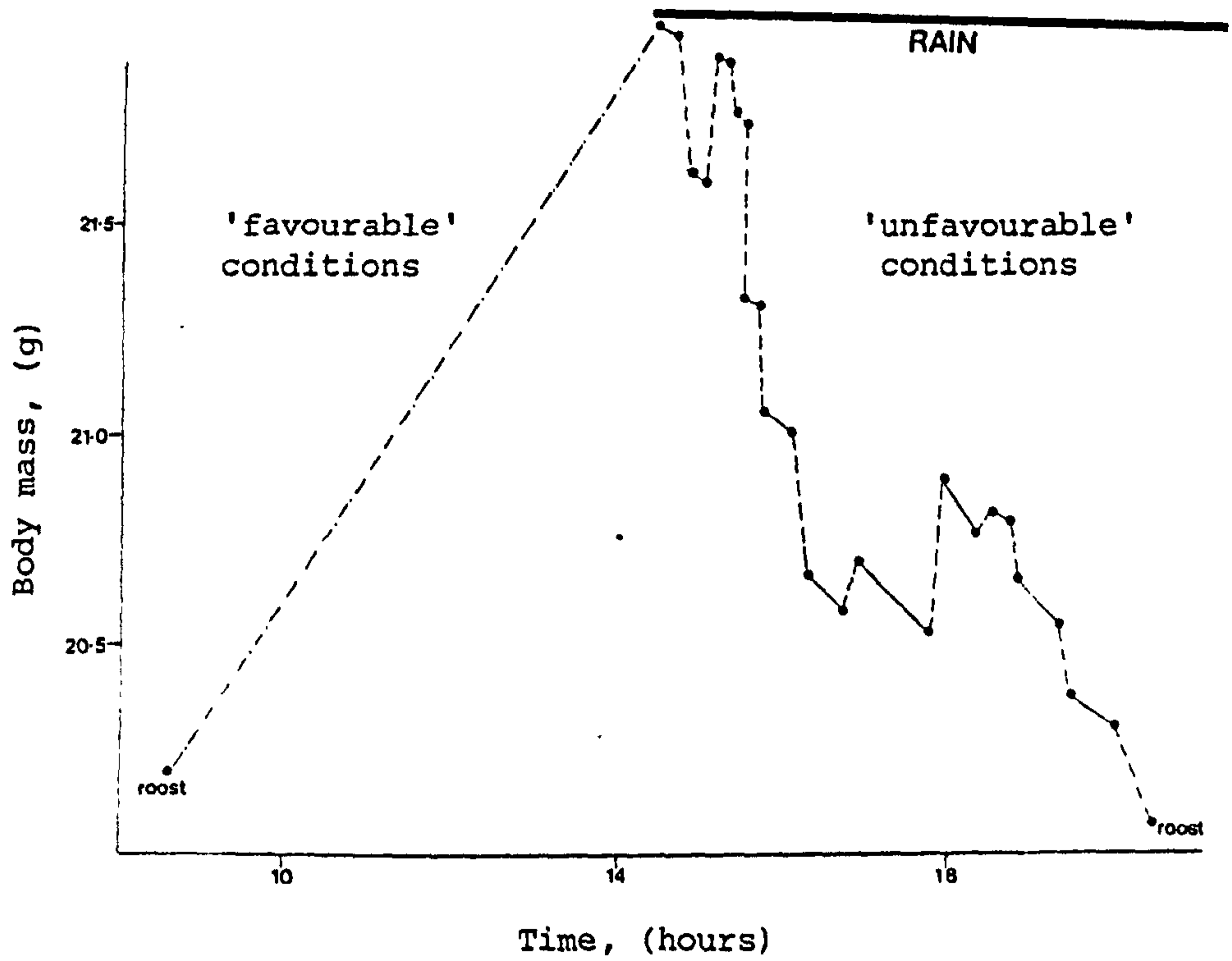


Figure 7.6

Body mass changes of an incubating female swallow on a changeable day.

- : incubation mass loss
- : foraging mass change
- .-.-.- : period when no data recorded.

'favourable' conditions until 15.00h, 32 flying insects caught in 300 sweeps of the hand-net at 14.00h.

'unfavourable' conditions after 15.00h, no flying insects caught in 300 sweeps at 20.00h.

In the six hours after 14.00h the female lost 9% of her initial body mass. During this period of atrocious weather, most of the pre-laying birds at the study site left the farm, presumably to forage at distant but more profitable feeding sites. The incubating female was restricted to feeding close to the nest site because the large time investment in incubation at low temperatures left little time for exploiting distant food patches.

Hence incubating female swallows can lose mass very rapidly in poor weather conditions, as implied by the positive correlation between body mass and food abundance for daily records (Table 7.1), and as shown at the individual level in this example. Figure 7.7 shows the effect of several successive days of bad weather on the body mass of the same female.

Between days 8 and 12 of incubation, maximal daily temperature progressively decreased from 14.5°C to 10°C. Over the same period, female body mass decreased from 22.7g on day 7 to 19.8g on day 12. At point X in Figure 7.7, when her body mass was lowest, the female changed her incubation strategy, from incubating for a mean of $63.06 \pm 9.57\%$ of five 1-hour periods on the preceding day, to incubating for $8.69 \pm 11.69\%$ in seven 1-hour periods on day 12. At this stage the bird left her eggs for two inattentive periods greater than two hours, compared with a mean of 6.37 ± 3.26 minutes ($n = 15$) on the 11th day. The bird was probably near to desertion at point X, when her body mass reached was close to a presumed lower critical level.

Weather conditions improved considerably on day 13, and the female increased in body mass by 14.8% of her day 12 value by the afternoon of day 13. Hence, although female swallows may lose mass rapidly in

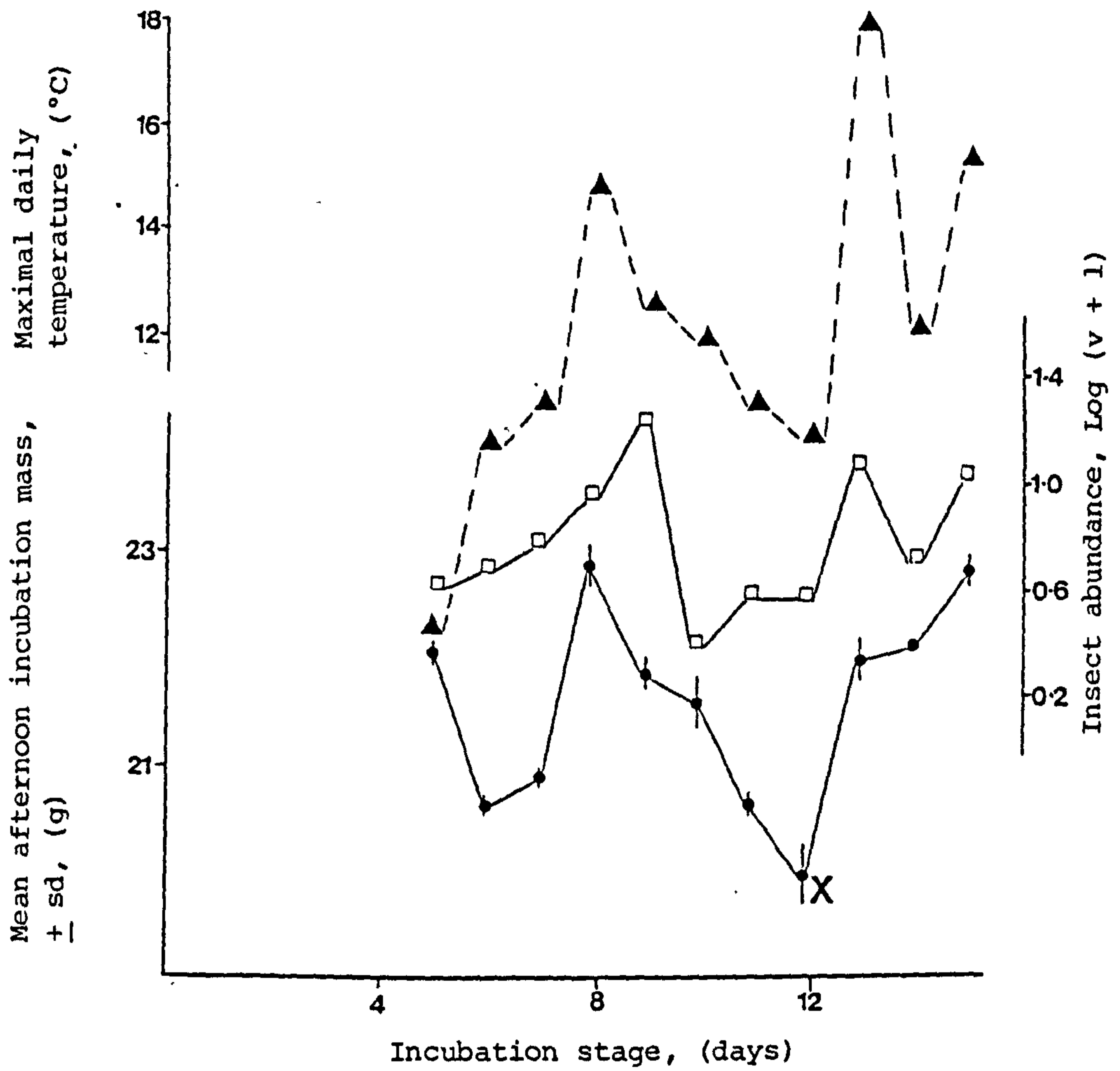


Figure 7.7

The effect of several successive days of unfavourable weather on the body mass of an incubating female swallow.

The bird was assumed to be close to desertion at X, see text for explanation.

poor weather conditions, they may replace lost mass rapidly if conditions improve.

7.3.3 Incubation strategies of swallows: a model of optimal behaviour

A theory of an optimal inattentive period during incubation was developed for bird species where only one sex incubates. The model assumes that individuals maximise fitness by maximising their net energy gain during the inattentive period. The stages in the development of the theory are outlined in Figure 7.8.

The parent bird will experience direct costs and gains associated with foraging during the inattentive period as illustrated in Figure 7.8a. When foraging, the bird will gain energy through food intake, and the gross energy gain curve is likely to decelerate with increasing foraging time as the bird's gut storage capacity is filled and a digestive bottleneck is attained (Kenward and Sibly, 1977). Whilst foraging, however, the bird will expend energy while flying, and since the mass gain through foraging is slight (less than 1% of body mass) and unlikely to influence the energy requirements for flight, flight costs are likely to cumulate linearly over the inattentive period.

The difference between the cumulative metabolizable energy gain and flight cost curves will produce a net energy gain curve (Figure 7.8b), the shape of which depends on the form of its two component curves. For example, flight costs may increase rapidly in some species while the cumulative gain curve quickly attains a relatively low plateau. Then the cost of flying will soon outweigh the foraging benefits, and the foraging time which maximises net energy gains through feeding will be relatively short (Figure 7.8c). If cumulative gain increases steadily with time, however, and flight costs are small,

DIRECT COSTS AND GAINS WHILE FORAGING

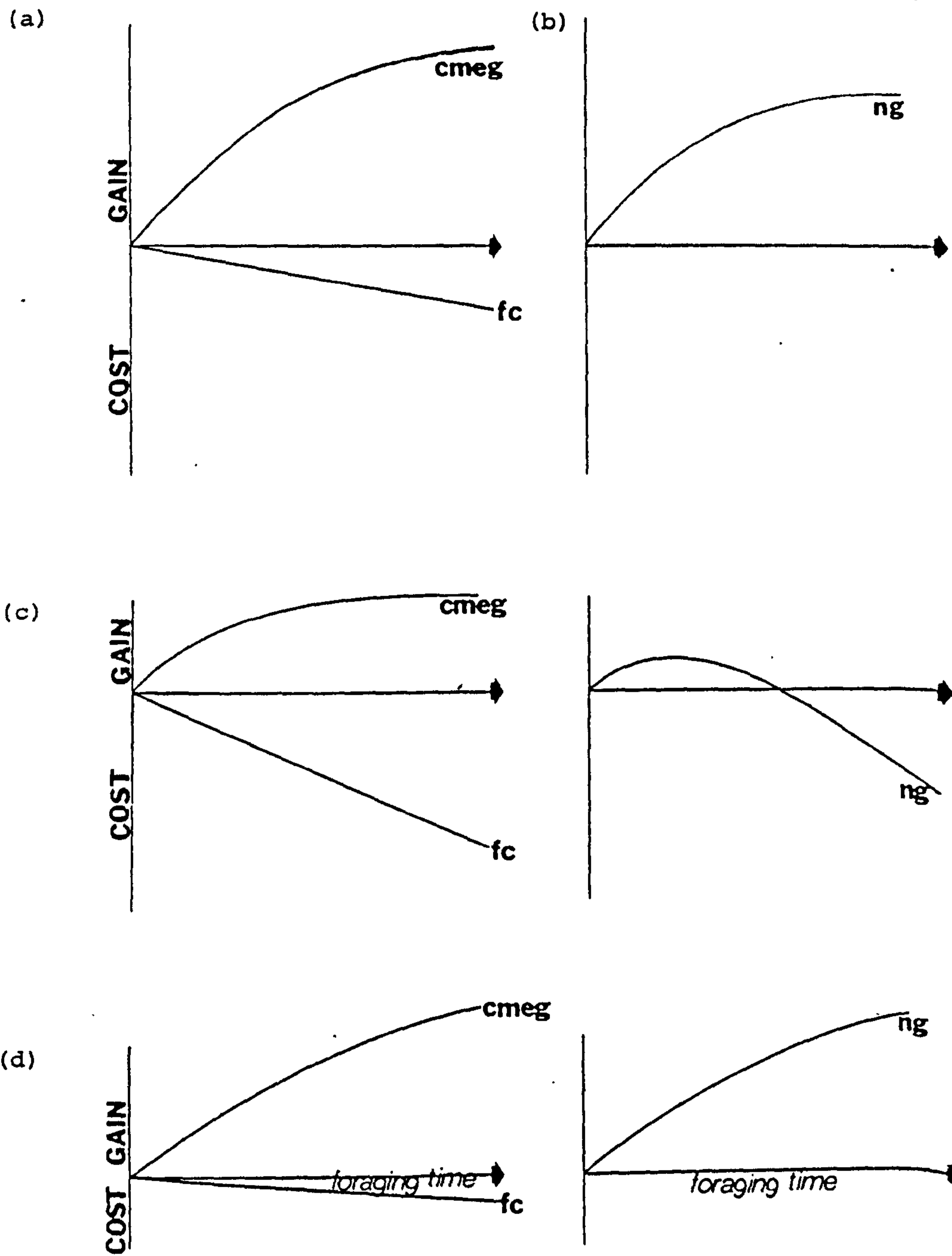


Figure 7.8

Theory of an optimal inattentive period for a single-sex incubating bird species.

cmeg : cumulative metabolizable energy gain

ng : net gain

fc : flight costs

See text for explanation.

INDIRECT COSTS WHILE FORAGING: THE COST OF REHEATING UNATTENDED EGGS

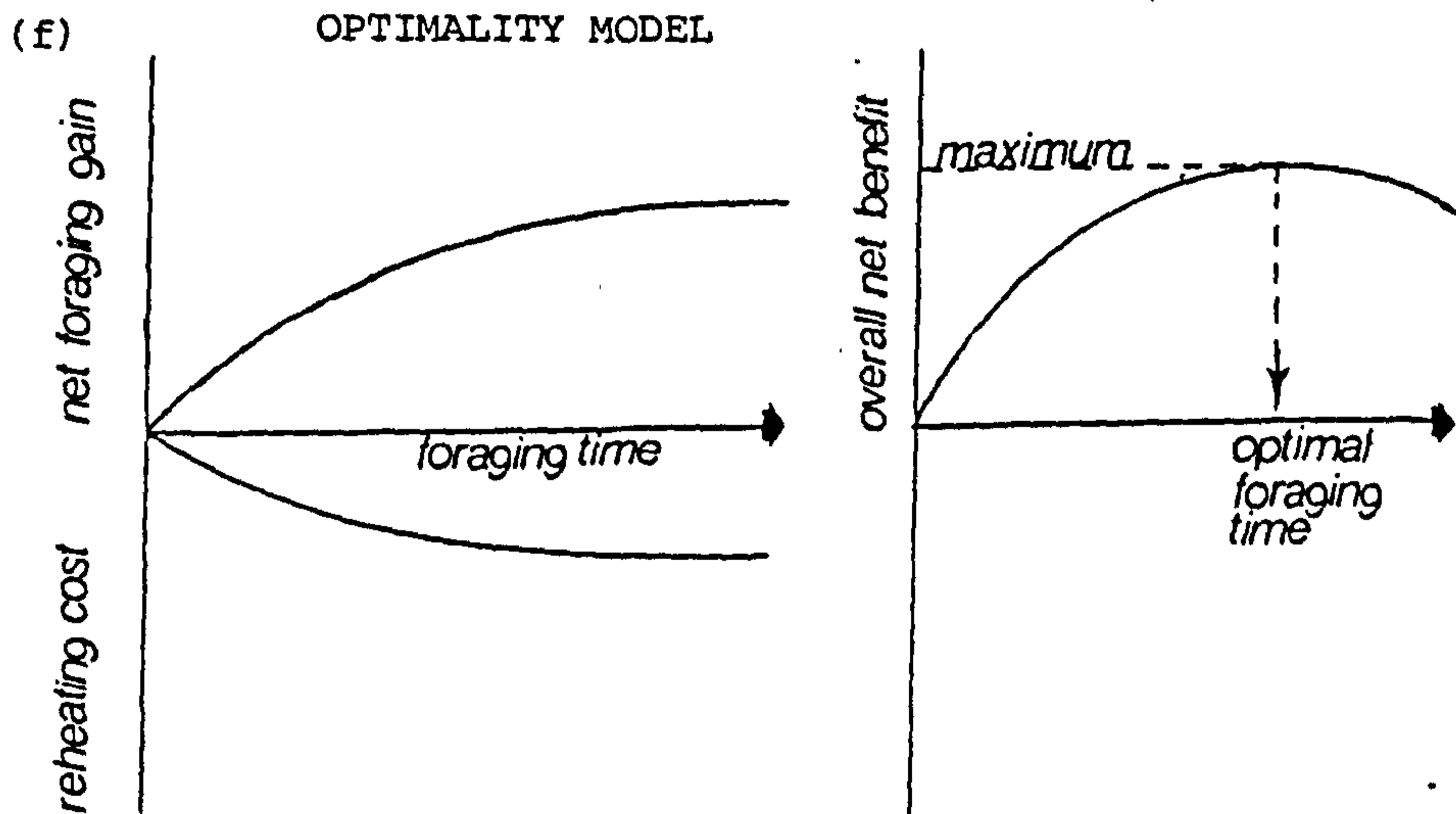
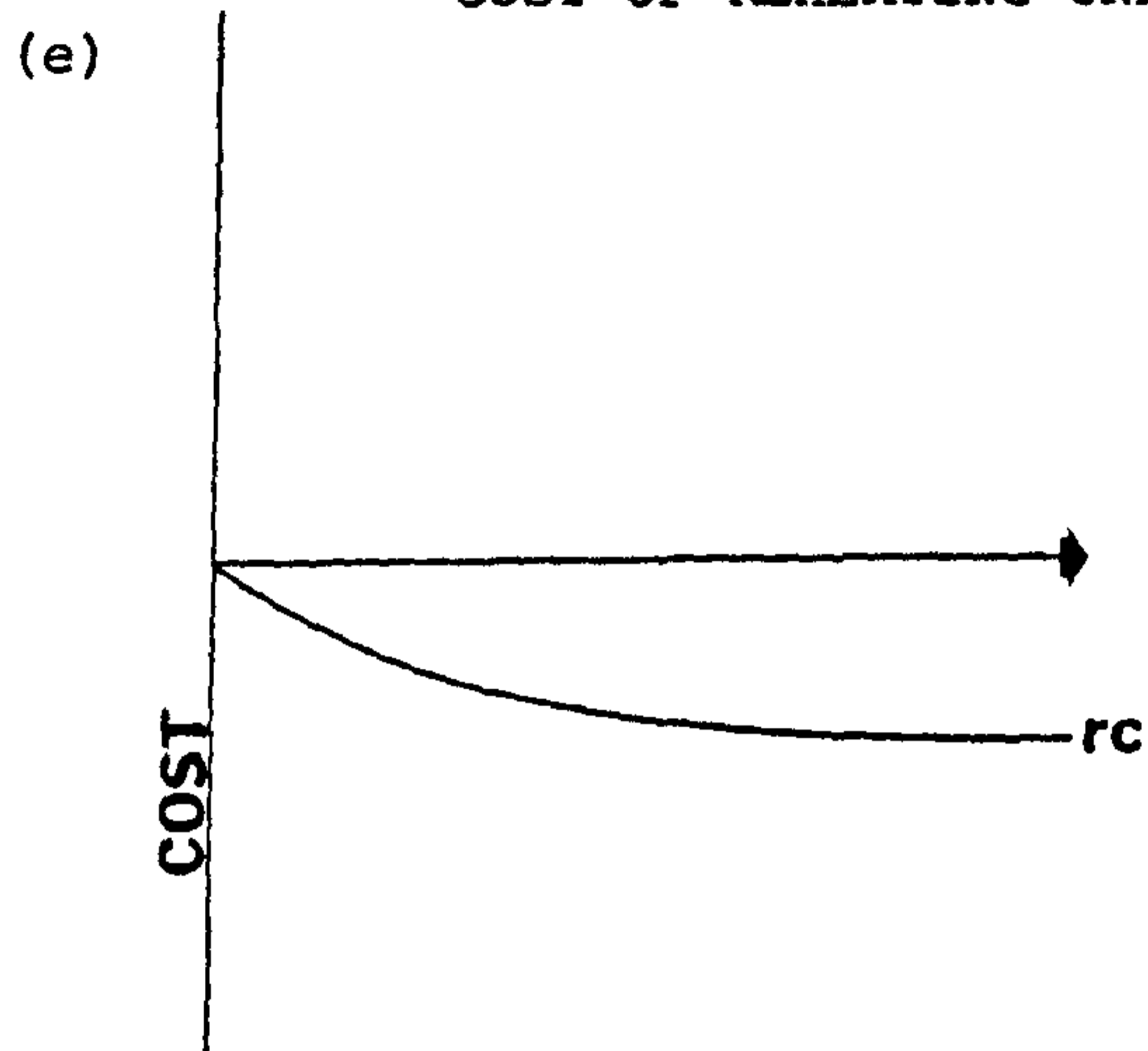


Figure 7.8 (continued)

Theory of an optimal inattentive period for a single-sex incubating bird species.

rc : reheating costs.

See text for explanation.

the net gain curve will be largely unaffected by the influence of flight costs, and the foraging time which maximises net gain will be relatively long (Figure 7.8d).

Whilst foraging between incubation stints, the incubating bird will pay another cost - an indirect cost paid on return to the nest and involving an energy expenditure in reheating eggs which cooled during the bird's absence. Because bodies cool fastest when the temperature gradient is greatest, and since eggs are heated to temperatures generally greater than ambient levels, clutch cooling rates will decelerate over time, and so reheating costs will be greatest for relatively short inattentive periods (Figure 7.8e).

To maximise fitness, it is assumed that birds should maximise the overall net energy benefit attained during the inattentive period, that is to maximise (net gain while foraging - clutch reheating costs). This is illustrated in Figure 7.8f.

7.3.4 The effects of changing costs and benefits on the optimality model - theory

In Figure 7.9 two conditions of reheating costs are incorporated into the model of an optimal inattentive period. High and low cost reheating functions for the clutch are illustrated (C_H and C_L respectively), and optimal foraging times (i.e. when overall net energy benefit is maximised) for the two combinations of costs and benefits calculated. Net foraging gain is depicted by the NFG curve.

Because the C_L curve never crosses the NFG curve over the foraging times considered, feeding trips of any length result in an overall net energetic benefit to the bird when reheating costs are low. The NFG curve intersects the high cost (C_H) curve at point X, so foraging trips

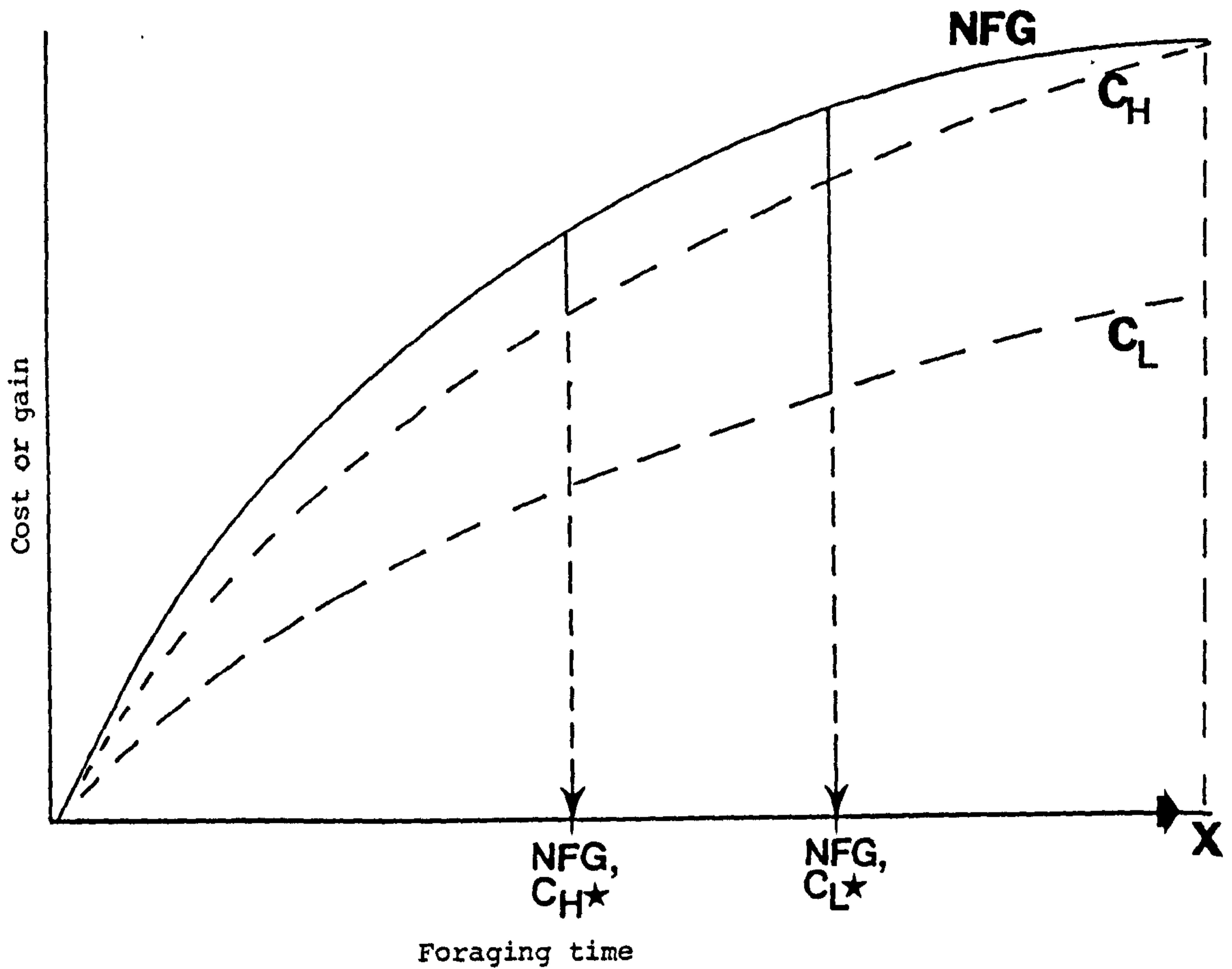


Figure 7.9

The effect of changing reheating costs on a model of an optimal inattentive period.

NFG is the nest foraging gain curve.

C_H a high cost reheating curve

C_L a low cost reheating curve

NFG, C_H^* the optimal inattentive period when reheating costs are high.

NFG, C_L^* the optimal inattentive period when reheating costs are low.

See text for explanation.

longer than X result in a net energetic loss to the bird when reheating costs are high.

The optimal foraging time in each situation occurs where the difference between costs and benefits is greatest. In Figure 7.9, NFG, C_L^* is the optimal foraging time described by the NFG, C_L curves, NFG, C_H^* is described by NFG and C_H .

Because NFG, $C_L^* > \text{NFG}, C_H^*$, the optimal foraging period is predicted to be longer when reheating costs are lower. Reheating costs are likely to be greater if clutch size is increased or if ambient temperatures are lower, so the reheating cost curves are open to manipulation and in this way the model can be tested experimentally. The NFG curve may also vary with temperature, with foraging gain rates probably being lower when food is scarce at low temperatures (Chapter 2, section 7.3.2). Hence predictions from the model involving the effect of temperature on the length of the optimal inattentive period should consider the manner in which both NFG and C curves vary according to temperature.

7.3.5 Quantification of the parameters included in the model

(a) Flight costs: Flight costs were taken from the D_2O^{18} data of Turner (1982a) as $0.3063 \text{ kJ g}^{-1} \text{ h}^{-1}$. The average afternoon body mass of an incubating female swallow was $22.48 \pm 1.41 \text{ g}$. Hence on average a female swallow expends $114.76 \text{ J min}^{-1}$ of flight during incubation.

(b) Foraging energy gain rates: When swallows returned to their nests after foraging, their body mass changes were recorded. To minimise the chances of including defaecations in mass changes, it was considered that foraging trips involving defaecations could not have resulted in mass gains by the birds, and so only mass gains while

foraging were included in the model (Chapter 4). No drinking was assumed to occur on foraging trips (Chapter 4). Water loss during flight was predicted as described in Chapter 4, and mass gains through food consumption were converted to energy units by assuming that insect prey contained 72.94% water, and insects liberated 22.84 kJ g^{-1} dry mass (Turner, 1980). Seventy percent of ingested energy was assumed to be assimilated (Waugh, 1978; Turner, 1980; Bryant and Westerterp, 1980), 30% of ingested energy was assumed lost via the faeces.

The cumulative metabolizable energy gain curve could thus be constructed as net energy gain (from mass gains) plus energy expended in flight for a known time period (using the D_2O^{18} flight cost results of Turner (1982a)).

(c) Reheating costs: Clutch reheating costs were calculated from the laboratory thermistor probe study. The cooling rate of a clutch of five eggs at 15°C ambient temperature in an insulated swallow nest was calculated. The mean mass of 34 swallow eggs weighed to the nearest 0.01g was $1.85 \pm 0.15\text{g}$, and $3.3\text{J g}^{-1}\text{C}^{-1}$ was assumed to be expended by the female in reheating eggs (Ricklefs, 1974). Eggs were to be heated to 35.7°C during incubation (Turner, 1980).

7.3.6 Egg cooling rates

In the cooling rate experiment, eggs cooled at a decreasing rate with time (Figure 7.10). In all experimental treatments, egg temperature was monitored for one hour, with readings taken every minute for the first 20 minutes. To compare cooling rates between treatments, slopes of egg temperature as a function of time were obtained for the first 20 minutes of cooling. All cooling rate regression equations were significant at $P < 0.001$, although signifi-

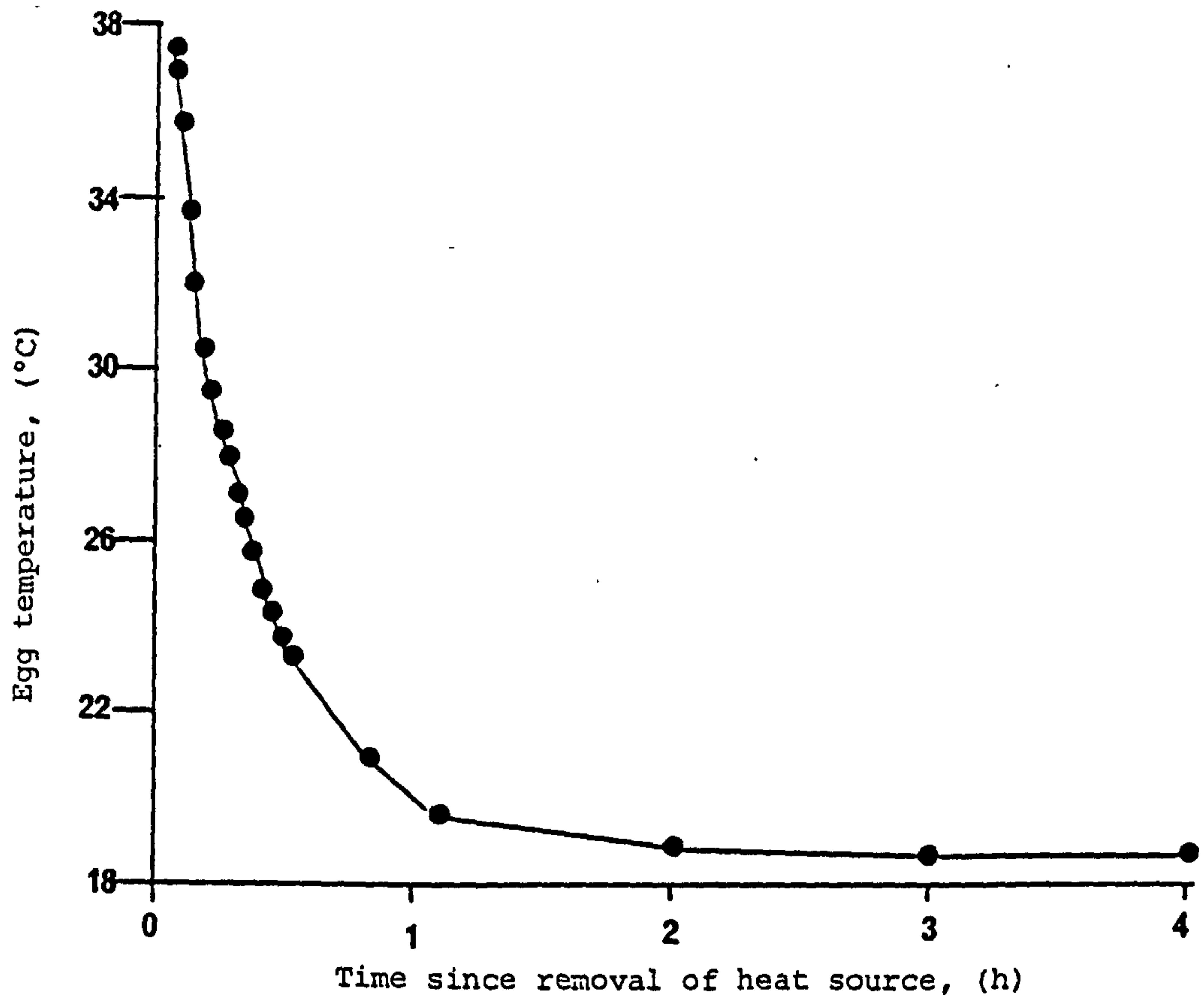


Figure 7.10

Cooling rate curve for a swallow egg in a clutch size of three eggs at ambient temperature 15°C in an insulated nest in the laboratory.

cance may have been boosted even further by plotting the logarithm of egg temperature as a function of time.

Cooling rates for 14 experimental treatments whereby ambient temperature, clutch size, and nest insulation were varied are presented in Table 7.4. An analysis of covariance of the cooling rate slopes between experimental treatments is summarised in Table 7.5.

All treatments resulted in significantly different cooling rates except for clutch size three in an insulated nest at 15°C when compared with clutch sizes seven and 10 in a non-insulated nest at the same temperature. No significant difference existed between the cooling rates of eggs in clutch sizes of seven and 10 in non-insulated nests at 15°C. The results are summarised below.

(i) The effects of ambient temperature on egg cooling rate

Cooling rates for eggs in a clutch of five are plotted in Figure 7.11 for both insulated and non-insulated nests. In both cases eggs cool more rapidly at lower ambient temperatures, when the temperature gradient between egg and environment was greatest. Ambient temperatures of about 15°C are typical of afternoon barn temperatures around swallow nests (mean afternoon barn temperature in 1982 was $16.6 \pm 4.0^\circ\text{C}$, $n = 46$), though ambient temperature may fall to 5°C in the early morning, and may reach 25°C or above on very hot days. At higher temperatures cooling rates tended to stabilise more rapidly than at lower temperatures.

(ii) The effects of clutch size

Cooling rates for eggs at 15°C with clutch sizes ranging from one to 10 eggs, in insulated and non-insulated nests, are plotted in Figure 7.12. Cooling rates were more rapid in small clutches where

Table 7.4

Cooling rates of swallow eggs in fourteen experimental treatments

Treatment				^A Egg Cooling Rate
Treatment Number	Ambient temperature °C	Clutch size	Nest Insulation	°C min ⁻¹ b + s.d.
1	5	5	-	0.930 + 0.038
2			+	0.767 + 0.025
3	15	1	-	0.726 + 0.047
4			+	0.542 + 0.044
5		3	-	0.598 + 0.041
6			+	0.481 + 0.026
7		5	-	0.506 + 0.019
8			+	0.397 + 0.012
9		7	-	0.481 + 0.018
10			+	0.379 + 0.010
11		10	-	0.473 + 0.012
12			+	0.322 + 0.006
13	25	5	-	0.234 + 0.009
14			+	0.183 + 0.015

^A Cooling rates were recorded for 20 mins in each treatment. For each treatment the cooling rate slope was highly significant $P < 0.001$.

Table 7.5 Analysis of covariance for cooling rates of swallow eggs presented in Table 7.4

Tabulated values are for 't'.

ns : not statistically significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

Treatment	1	2	3	4	5	6	7	8	9	10	11	12	13	14
°C ambient temp.	5	5	15	15	15	15	15	15	15	15	15	15	25	25
clutch size	5	5	1	1	3	3	5	5	7	7	10	10	5	5
nest insulation	-	+	-	+	-	+	-	+	-	+	-	+	-	+
1	14.6***	30.9***	29.0***	25.6***	43.9 ***	45.0 ***	61.1 ***	48.2 ***	65.4 ***	52.5 ***	74.8 ***	84.6***	86.1***	
2		3.30**	19.3***	15.2***	35.8 ***	37.6 ***	61.0 ***	42.2 ***	67.8 ***	48.8 ***	82.7 ***	96.0***	94.3***	
3			12.1***	8.6***	20.0***	19.1***	30.2 ***	21.4 ***	32.8 ***	23.3 ***	39.3 ***	47.5***	50.6***	
4				4.02***	5.38***	3.39**	14.5 ***	5.79**	16.8 ***	6.92***	23.4 ***	32.5***	36.4***	
5					10.78***	9.12***	21.3 ***	11.72***	24.0 ***	13.29***	16.70***	40.8***	44.5***	
6						3.65***	13.93***	0 ns	17.9 ***	1.33 ns	29.6 ***	44.7***	48.7***	
7							22.95***	4.52***	29.02***	7.06***	46.0 ***	64.6***	65.2***	
8								18.5 ***	5.67***	21.3 ***	27.7 ***	54.3***	54.3***	
9									24.1 ***	1.78 ns	42.1 ***	61.8***	62.5***	
10										30.2 ***	26.3 ***	57.7***	55.2***	
11											57.2 ***	81.3***	74.4***	
12												44.6***	44.1***	
13													15.1***	
14														

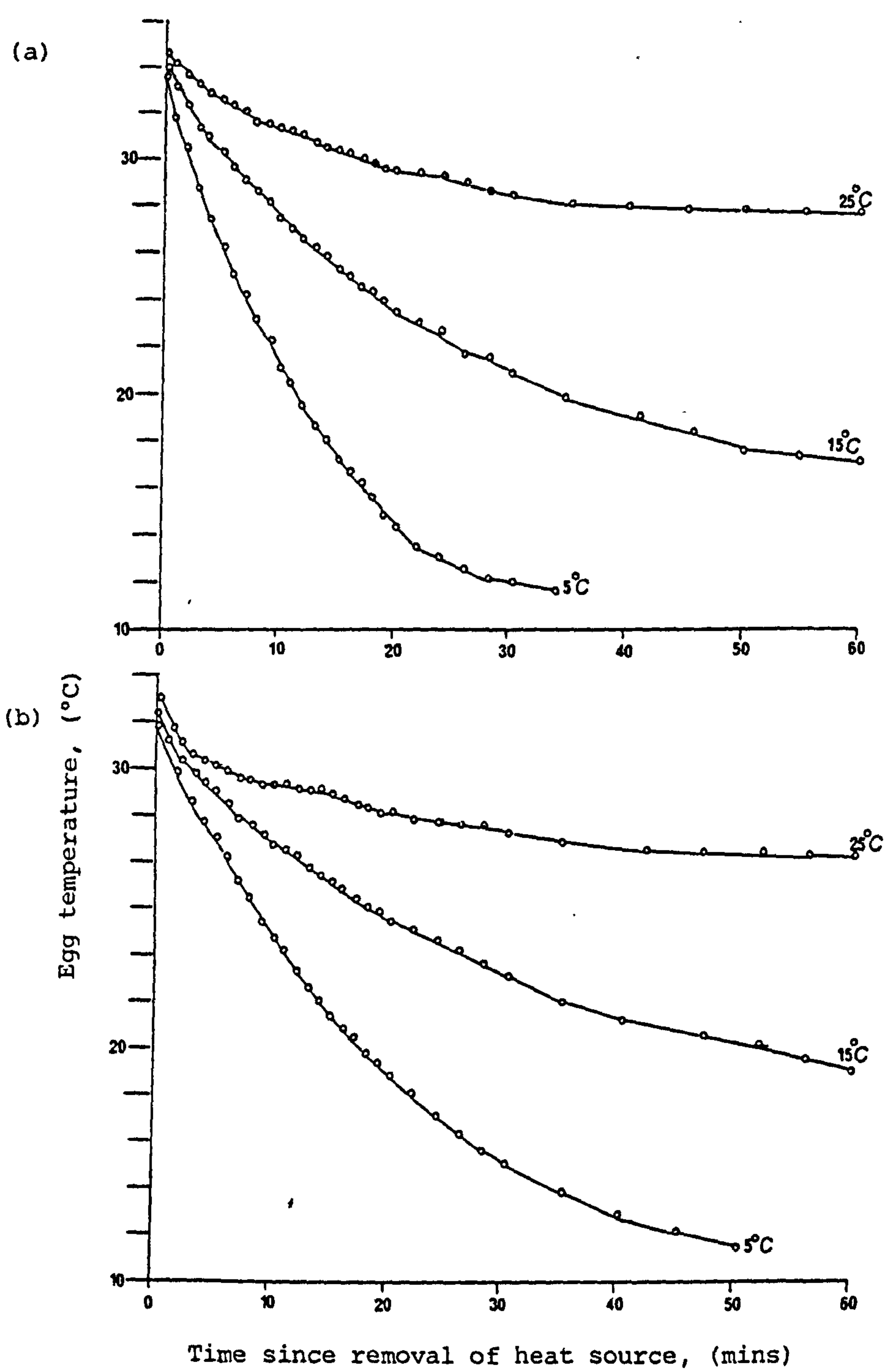


Figure 7.11

The effect of varying ambient temperature on swallow egg cooling rates in the laboratory.

- (a) non-insulated nest
- (b) insulated nest

Clutch size = five eggs.

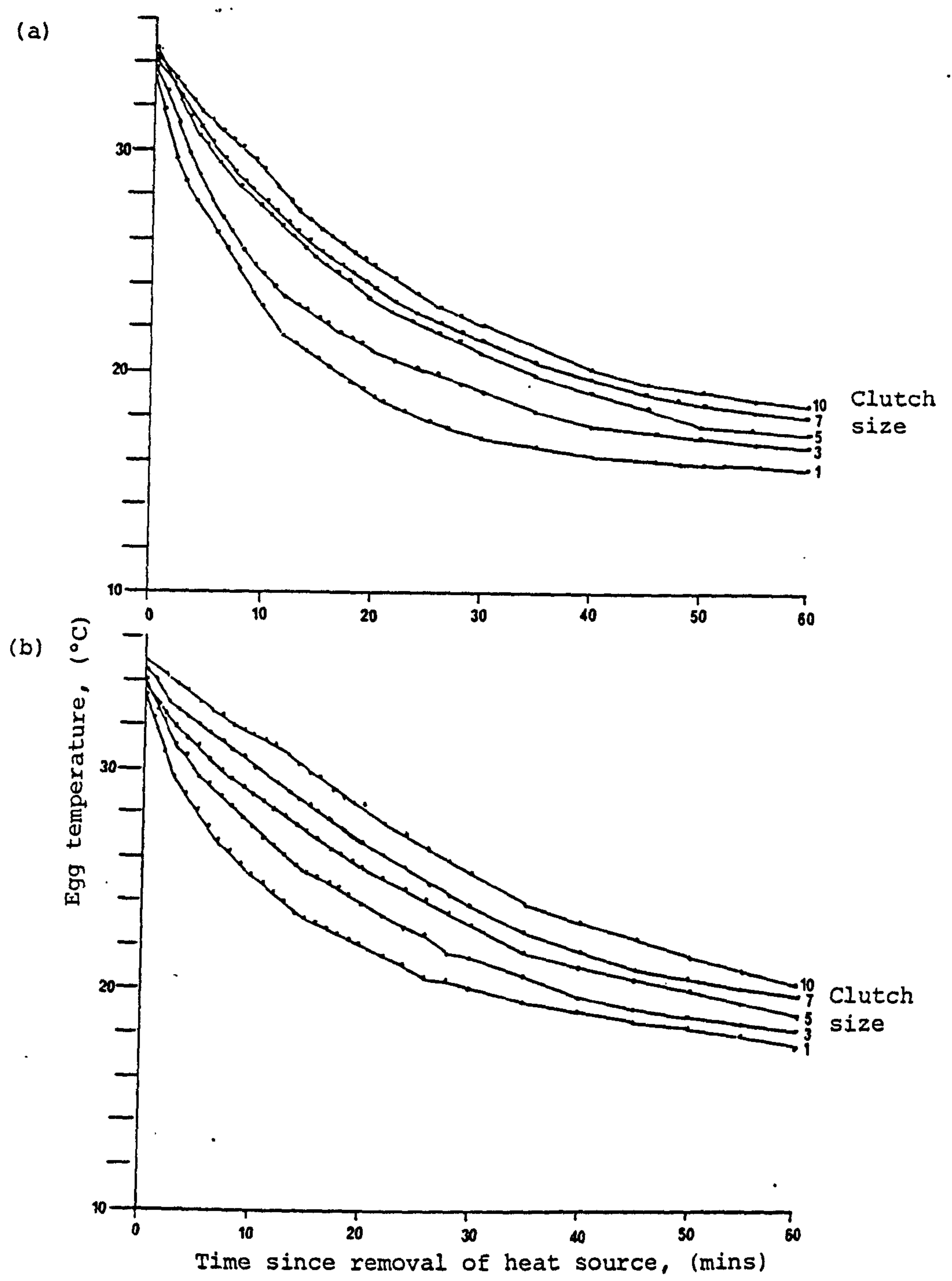


Figure 7.12

The effect of varying clutch size on swallow egg cooling rates in the laboratory.

(a) non-insulated nest

(b) insulated nest.

Clutch size was varied between one and ten eggs, ambient temperature was 15°C.

there were fewer surrounding eggs to buffer against heat loss, leaving a greater egg surface area exposed.

Although individual eggs cool more rapidly in smaller clutches, a large clutch will take more energy to reheat than a small clutch simply because a larger volume of eggs is present. However, it is predicted that individual eggs in large clutches will take relatively shorter to reheat than eggs in small clutches because eggs in small clutches lose heat more rapidly (Mertens, 1977). Because not all eggs in large clutches may be covered by the brood patch, incubation costs may increase linearly with increasing clutch size (Biebach, 1984). The cost of nighttime incubation in starlings increased by about 4% (only below the lower critical temperature) for every egg added, even without reheating costs being considered. Bigger clutches also shift the incubating parent's lower critical temperature towards higher temperatures (Biebach, 1981, 1984).

(iii) The effects of egg position

If eggs in small clutches lose heat more rapidly than those in large clutches because eggs in small clutches have a greater exposed surface area, it should follow that egg position will influence egg cooling rate. Eggs on the edge of clutches will have a greater exposed surface area and should lose heat more rapidly than those in the centre of a clutch.

In a clutch size of seven eggs in an insulated nest at 15°C, a central egg cooled at $0.397^{\circ}\text{C min}^{-1}$, an egg at the edge of a clutch at $0.500^{\circ}\text{C min}^{-1}$, the difference in cooling rates being highly significant ($t = 21.1$, $P < 0.001$). One function of 'egg turning' in incubation may be to shuffle egg positions so that the same eggs are not consistently at the edge of the clutch where they cool more rapidly and develop more slowly.

(iv) The effects of nest insulation

Swallows line their nests with feathers and feather insulation may serve to reduce the rate of heat loss from the clutch or from small chicks (White and Kinney, 1974; Møller, 1984a). For each treatment studied, eggs cooled more rapidly in a nest where the feather insulation had been removed compared with eggs in the same nest lined with feathers (Tables 7.4, 7.5).

The relationship of egg cooling rate with ambient temperature, clutch size, and nest insulation is summarised in Figure 7.13. As clutch size increased, cooling rate per egg decreased but tended to level off in clutches with more than five eggs. The difference in cooling rate was greater between 25°C and 15°C than between 15°C and 5°C. The importance of insulation appears to be greater at 5°C and 15°C than at 25°C.

(v) Other factors influencing egg cooling rates not considered in the experiment

(a) Egg age: Swallow eggs show an allometrical increase in oxygen consumption during development (Birchard and Kilgore, 1980). Since the capacity for embryos to produce metabolic heat increases over the incubation period (Drent, 1970; Walsberg and King, 1978a; Gessaman and Findell, 1979), older eggs may cool more slowly than younger ones. Ricklefs (1974) suggested that embryonic heat production was only significant at the end of incubation. Female swallows spent less time incubating as egg age increased ($r = -0.32$, $n = 61$, $P < 0.01$), and the decrease in incubation time may be associated with increased heat production by older embryos.

(b) Egg mass and egg composition: Large eggs will have relatively smaller surface area:volume ratios than smaller eggs, and although

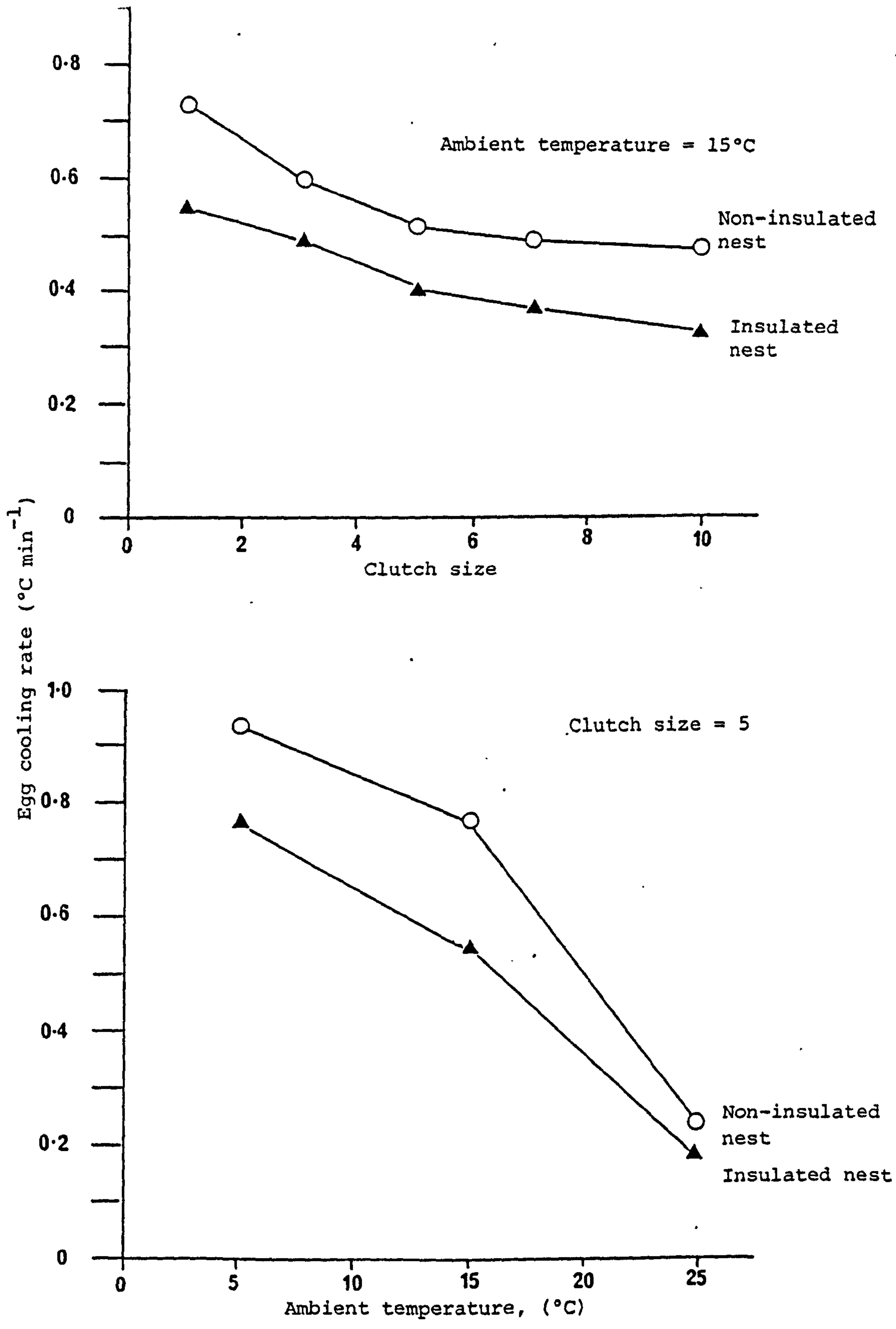


Figure 7.13

Swallow egg cooling rates in the laboratory in relation to ambient temperature, clutch size and the presence of nest insulation.

large eggs will take longer to reheat, they may cool relatively more slowly than smaller eggs. Egg composition may also influence clutch cooling rates. Four swallow eggs weighed every day lost a mean of $15.44 \pm 4.09\%$ of their mass over the incubation period, as water was lost through the eggshell (Rahn and Ar, 1974). Any change in egg composition would alter the egg's specific heat capacity and may hence influence egg cooling rate.

(c) Attributes of the nest and nest microhabitat: Smaller nests may retain heat more efficiently than larger nests, and the positioning of the nest in relation to surrounding shelter will influence egg cooling rates.

(d) Parental attributes: Variability in parental attributes such as brood patch vascularity may influence a parent's efficiency at reheating eggs. Adult body condition may also influence incubation behaviour - heavier female Canada gees, Branta canadensis moffiti, were more attentive to their nests than were lighter females (Aldrich and Raveling, 1983), and female body condition appears to influence incubation behaviour in swallows (Section 7.4).

7.3.7 A test of the model of optimal inattentive period

(a) Energy gains while foraging

Two hundred and seventyfour mass gains during foraging bouts of known duration were recorded, and converted to net energy gains (Figure 7.14a). Mass gains were converted to net energy gains by

- (i) Subtracting predicted mass losses through flying (Chapter 4).
- (ii) Multiplying this corrected mass by 0.27 to calculate the dry mass of insects ingested (see section 7.3.5), and then calculating energy gains by assuming that insects liberated 22.84 kJ g^{-1} dry mass (Turner, 1980).

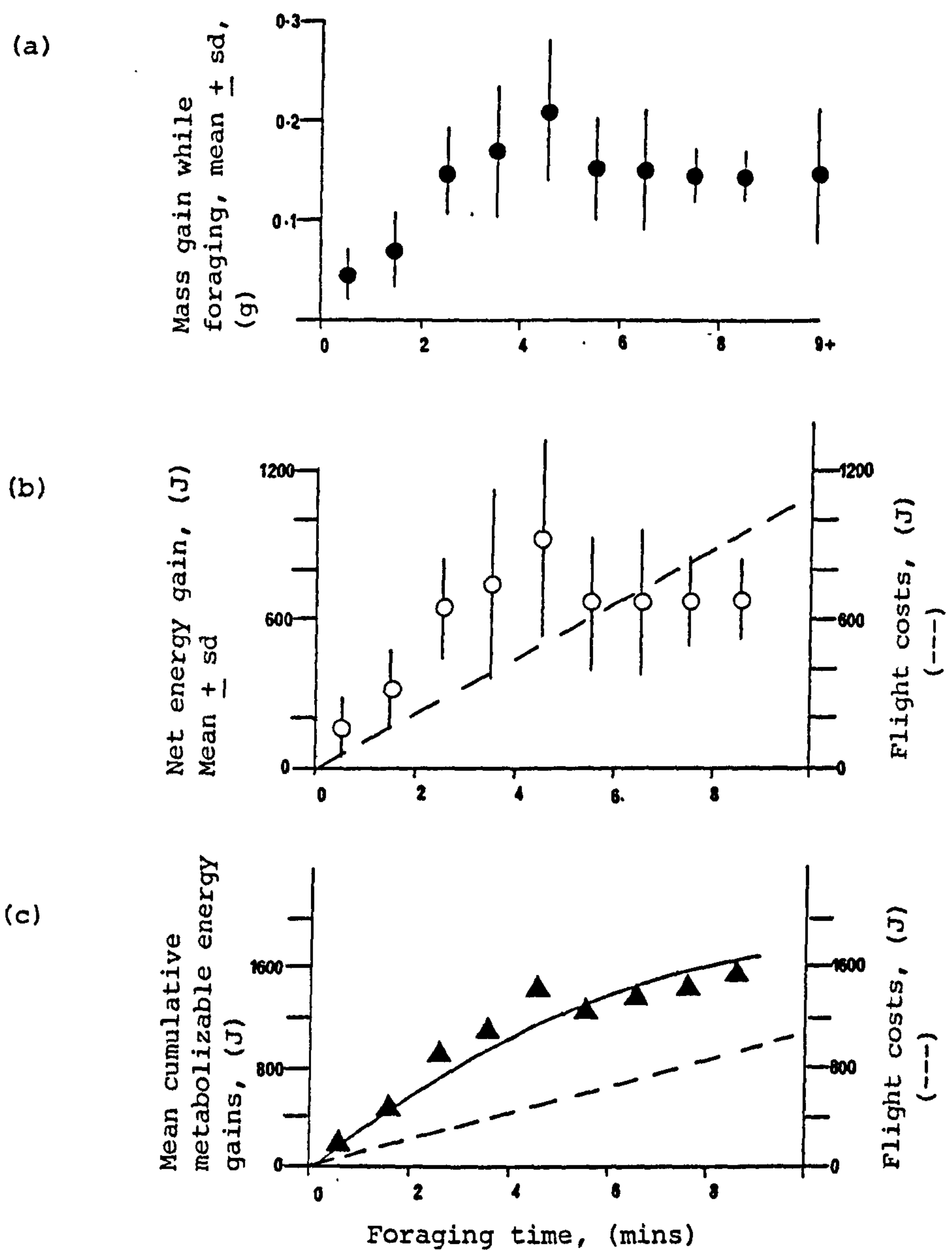


Figure 7.14

Energy gains and costs during swallow inattentive periods.

- (a) Mass gains for foraging periods of different durations.
- (b) Net energy gains (open circles) and flight costs (pecked line).
- (c) Cumulative metabolizable energy gains (solid triangles) and flight costs (pecked line). Curve fitted by eye.

Net energy gain data are described by
 $\ln y = 5.65 + 0.35 \ln x$, $r = 0.22$, $n = 257$, $P < 0.001$.

(iii) Multiplying the energy gain by 0.7 to calculate the assimilable net energy gains (section 7.3.5).

A curve is described for the net energy gain rate in the legend to Figure 7.14. Predicted flight costs for the foraging periods are also illustrated, and the cumulative metabolizable energy gain curve is constructed as (net energy gain + flight costs) in Figure 7.14(b). The cost of flying exceeds the average net energy gain from foraging after about 5.5 minutes of feeding.

Net energy gain levels off after about four minutes foraging time, suggesting that a digestive bottleneck may be reducing intake, rate at longer foraging periods. The maximum mass gain of $0.21 \pm 0.15\text{g}$ occurs at foraging periods of 4-5 minutes. Since about 0.03g would also be lost as water while flying for this period (Chapter 4), an average maximum mass gain of 0.24g of insects during the inattentive period seems to occur in incubating female swallows. This corresponds to twice the maximum load mass delivered to nestlings by females (Chapter 8).

Net energy gain did not level off with increasing foraging time partly because longer foraging periods were recorded in poor weather when mass gains were low. The mean mass gain for foraging trips longer than four minutes (mass gains remain relatively constant after four minutes) in conditions where greater than the average biomass of insects was sampled in the hand-net was $0.151 \pm 0.148\text{g}$ ($n = 47$). When the insect catch was of lower than average biomass, foraging trips longer than four minutes resulted in a mean mass gain of $0.139 \pm 0.090\text{g}$ ($n = 39$). This difference between means was, however, not significant ($t = 0.4$, ns).

Incubating female swallows lost mass rapidly when first settled on eggs, but the rate of mass loss declined as the incubation period increased in duration (Figure 7.15). The initial rapid rate of mass loss probably occurred because of a relatively high metabolic rate during the beginning of an incubation bout. Great tit breathing rate, for example, is also most rapid when birds first settle on eggs, and reaches a second peak just before the clutch is left (Haftorn and Reinertsen, 1982). Similarly, tachycardia is highest soon after resettling on eggs in incubating ptarmigan, L. lagopus, (Gabrielsen and Steen, 1979). Such a high initial metabolic rate may be the result of birds having just returned from high cost locomotory activity, or may represent an early burst of heat delivered to the eggs by the incubating bird.

Clutch reheating costs were calculated from the thermistor experimental data for a clutch of five eggs (average mass 9.25g) in an insulated nest at ambient temperature 15°C (corresponding to afternoon barn temperature) for incorporation into the optimality model. The cost to the female swallow in reheating eggs was estimated by assuming $3.3\text{J g}^{-1} \text{ }^{\circ}\text{C}^{-1}$ was expended in warming a cooled clutch (Ricklefs, 1974, section 7.3.5). Three costs curves are plotted in Figure 7.16, for clutch size five at ambient temperatures 5°C, 15°C, and 25°C. Reheating costs increased as ambient temperature decreased.

In order to test the optimality model, reheating costs must be subtracted from the net energy gains for foraging trips of differing duration. This is performed in Figure 7.17a.

For each one minute time class overall net energy benefits were calculated as (net benefit while foraging - cost of reheating eggs)

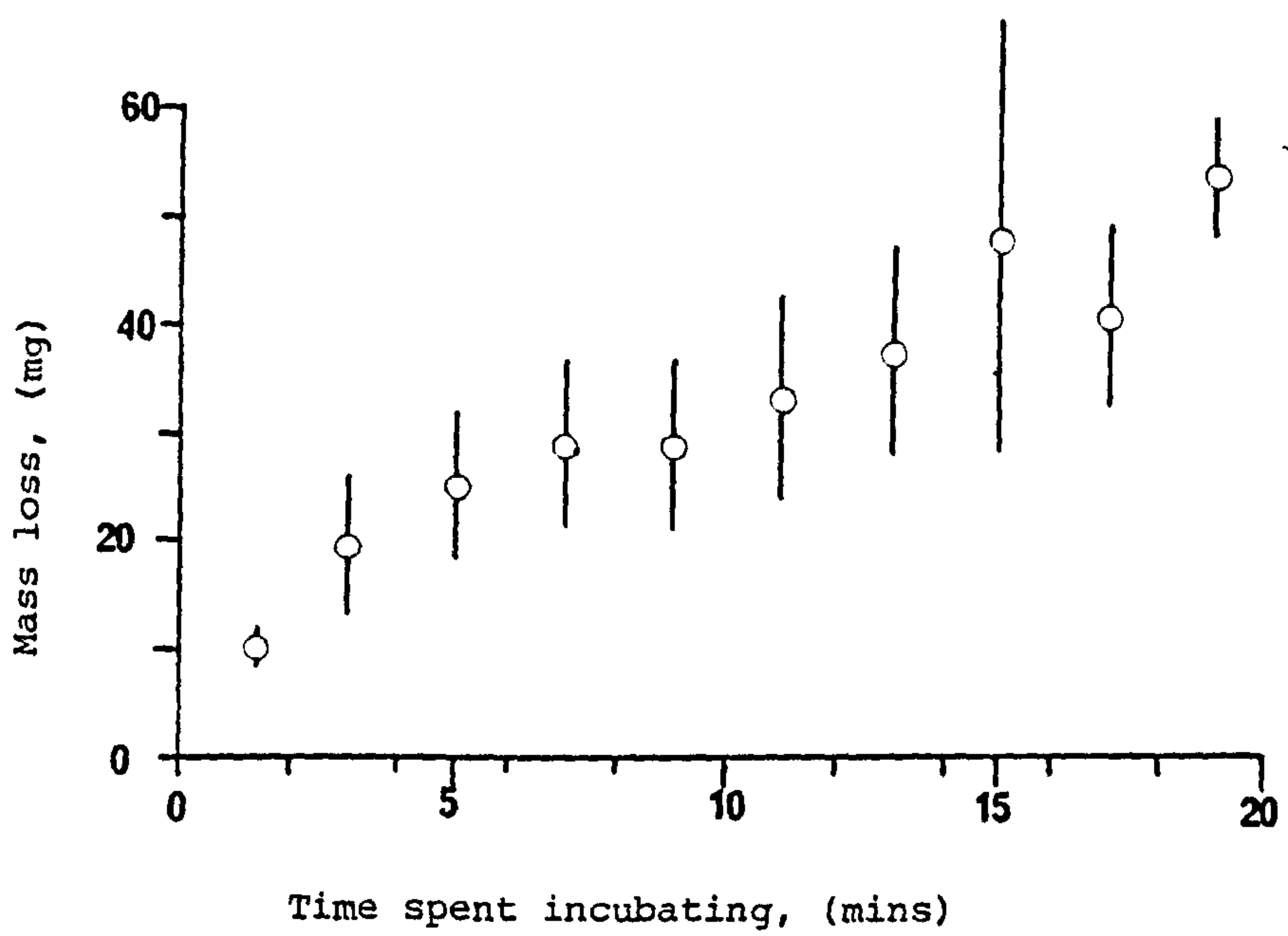


Figure 7.15

Mass loss in female swallows as a function of time spent incubating.

Between 1.5 and 19.5 mins the data is described by $\ln y = -4.23 + 0.061x$, $n = 236$, $r = 0.37$, $P < 0.001$.

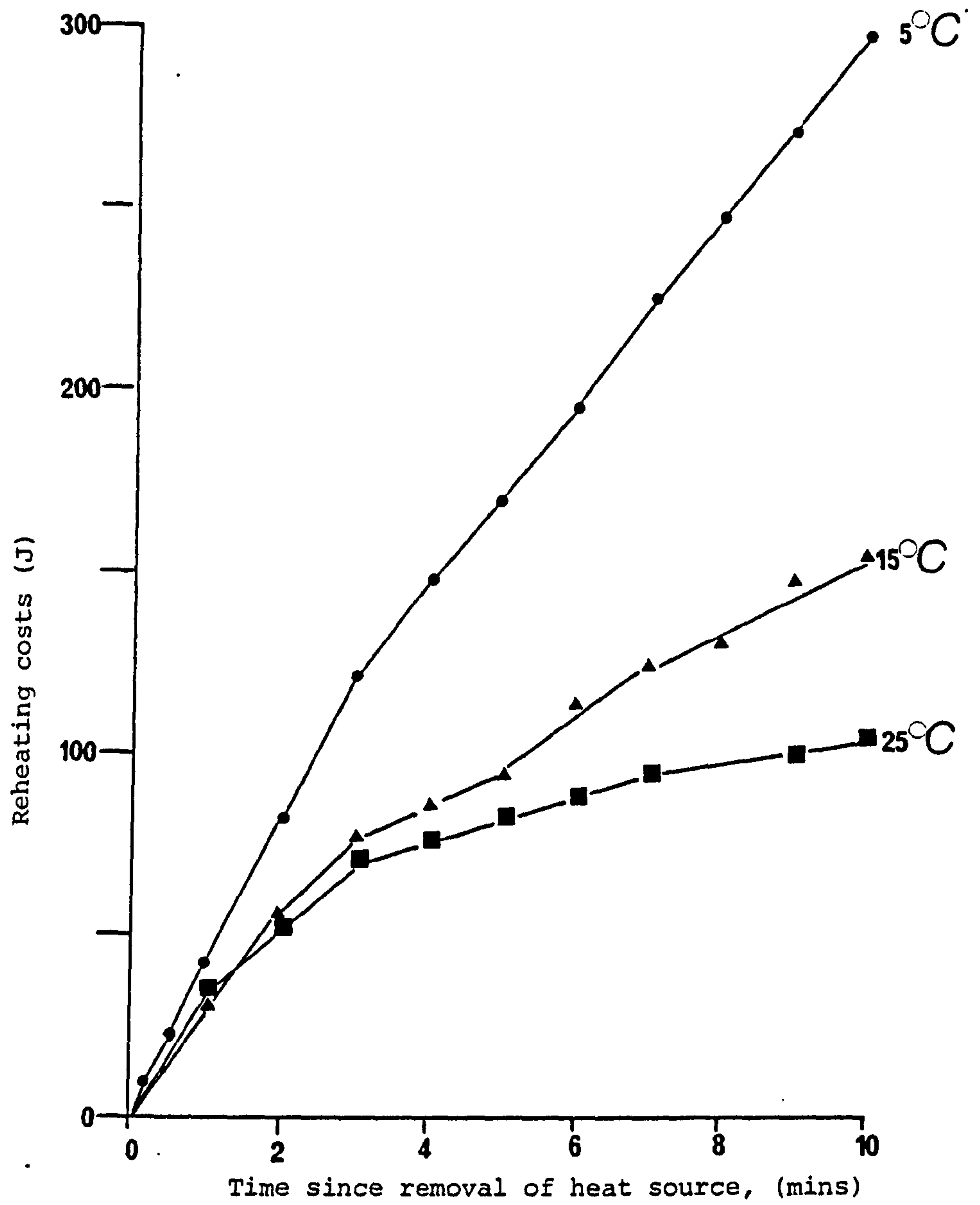


Figure 7.16

Calculated reheating costs for female swallows incubating clutches of five eggs at 5°C, 10°C, and 15°C ambient temperatures.

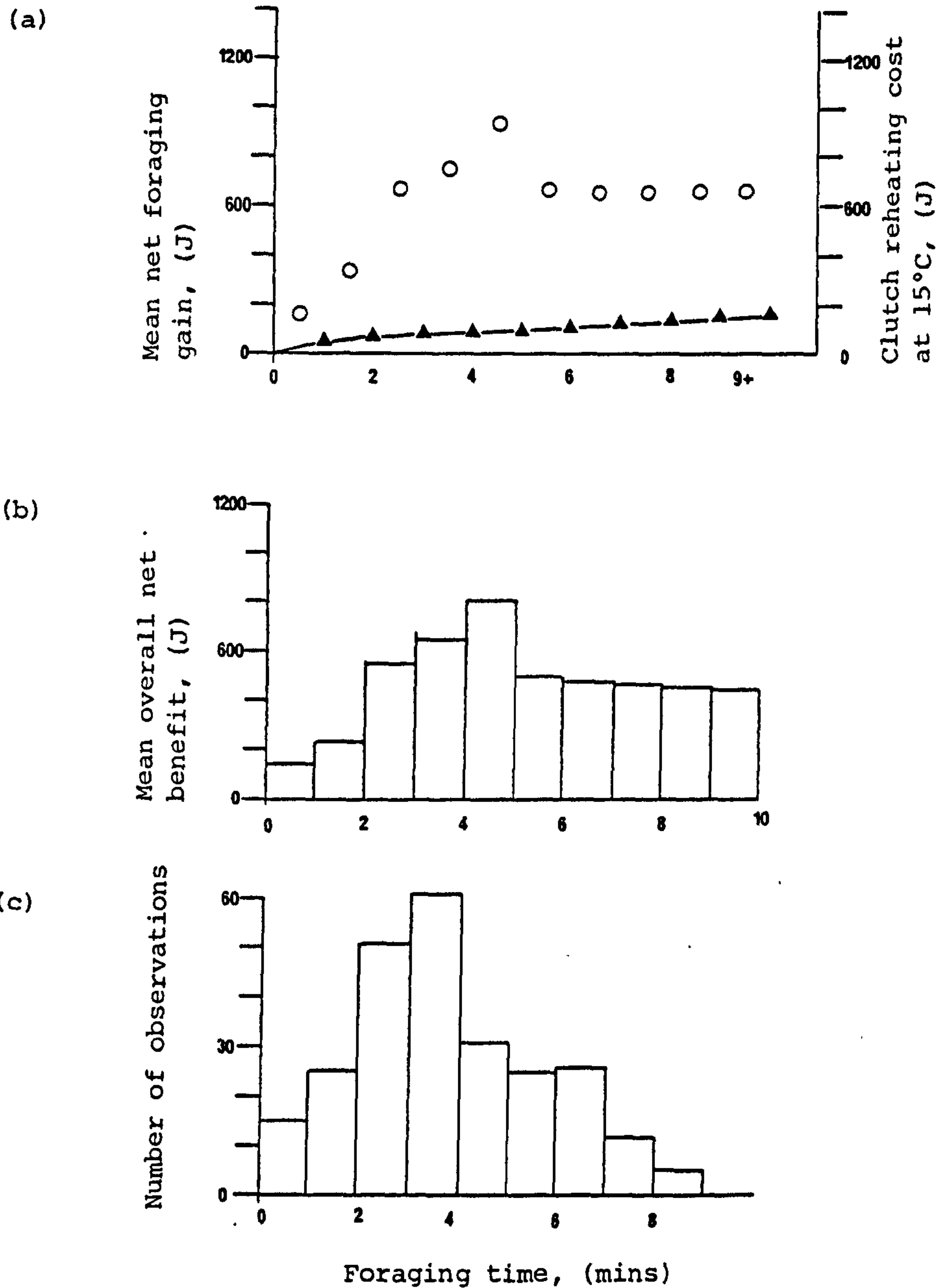


Figure 7.17

A test of the model of an optimal inattentive period in swallows.

- (a) Mean net foraging gains (open circles) and clutch reheating costs (triangles) for foraging periods of different lengths.
- (b) Overall net benefit (net foraging gain - reheating costs) distribution.
- (c) Frequency distribution of foraging periods.

in Figure 7.17b. The frequency distribution of foraging periods observed in the study is plotted in Figure 7.17c.

Overall net energy gains increase up to a maximum for the 4-5 minute time class. The mean foraging time of incubating swallows was 4.107 ± 2.624 mins ($n = 293$) - a close approximation to the optimal foraging time predicted by the model. However, because the frequency distribution of foraging periods is skewed towards shorter inattentive periods, the modal foraging bout class (3-4 mins) does not precisely coincide with that predicted to be the most energetically profitable.

Expected foraging bout duration classes were generated assuming that birds chose bout durations according to their profitability. The observed bout distribution closely tracked that expected up to and including the 3-4 minute bout class ($\chi^2 = 0.273$, $n = 4$ classes, $P > 0.95$ ns). Once the 4-5 minute bout class was included in the analysis however, the observed distribution became significantly different from that expected if birds were choosing bout lengths according to their profitability ($\chi^2 = 22.76$, $n = 5$, $P < 0.001$). Although the 4-5 minute bout class was calculated as that which maximised overall net benefit while foraging, only 12.7% of bouts recorded were of that duration. Moreover, foraging periods longer than 4-5 minutes were calculated as being relatively profitable, but were avoided by the swallows.

Why were longer foraging bouts avoided even though they were energetically profitable? There are likely to be costs associated with leaving the eggs unattended for long periods which are not considered in the model. Periodic chilling of eggs comparable with long parental inattentive periods may substantially reduce the metabolic rate of the embryos, increasing the length of the incubation

period, as seen in fork-tailed storm petrels, Oceanodroma furcata, (Vleck and Kenagy, 1980). Abnormal development of embryos is likely to occur at temperatures above and below the predicted optimum, as found in the Adélie penguin, Pygoscelis adeliae, by Weinrich and Baker (1978). If eggs experience prolonged spells between the optimal temperature and the point of zero development (usually 25-27°C), disproportionate development of body organs may occur (Lundy, 1969). Although one female swallow in this study successfully hatched eggs neglected for two 2h periods on one day, frequent long inattentive periods may delay the hatching of the chicks, or result in abnormal development of the embryos.

7.3.8 The effects of changing costs and benefits on the optimality model - results

The model developed in Figure 7.9 predicts that inattentive periods should become shorter when clutch reheating costs are increased. Low temperatures will increase reheating costs, although also probably depressing foraging gain rate, while manipulation of clutch size will only influence the form of the reheating cost curve. Both low temperatures and increased clutch size were therefore expected to decrease the length of the optimal inattentive period. The observed effects of temperature and clutch size on foraging times will be described below.

(a) Temperature effects

The influence of temperature on incubation behaviours varies considerably among bird species. Some species vary the lengths of both attentive spells and recesses with temperature, while others vary only recesses or attentive spells (von Haartman, 1956). Both great tits (Kluijver, 1950) and white-crowned sparrows, Zonotrichia leucophrys, (Webb and King, 1983) decrease the length of inattentive

periods at low temperatures, as predicted by the model. Experimental heating of pied flycatcher nests to 33°C causes female to shorten their attentive periods compared with controls at 16°C, though inattentive periods were similar for both control and experimental treatments (von Haartman, 1956).

In Figure 7.18 mean afternoon inattentive periods are plotted ($n = 532$) as a function of maximal daily temperature. The longest inattentive periods occurred at the lowest temperatures, not at the highest temperatures as predicted by the model. The shortest recesses occurred at intermediate temperatures, and inattentive periods became longer at higher temperatures. Hence, although the model's predictions may hold between 17°C and 29°C, they ran against expectations below 17°C.

If incubation is viewed in terms of parent:offspring resource allocation, this trend may be explained. Above 17°C, incubating swallows behave as predicted by the optimality model. During a 16-hour day, incubating female swallows cannot meet their daily energy requirements if temperatures fall below 8°C or two degrees higher if it is wet (Turner, 1982a). Day length is normally less than 16h in Central Scotland over the entire breeding season (Bryant and Westerterp, 1983b), and so the increase in the duration of swallow inattentive periods at 12°-15°C could be because females cannot, on average, meet their daily energy requirements through foraging for relatively short periods at these temperature. Hence at low temperatures, females may have problems maintaining a positive energy budget and may extend their foraging periods beyond that predicted by the optimality model to compensate for low feeding success, at the cost of prolonging egg development time.

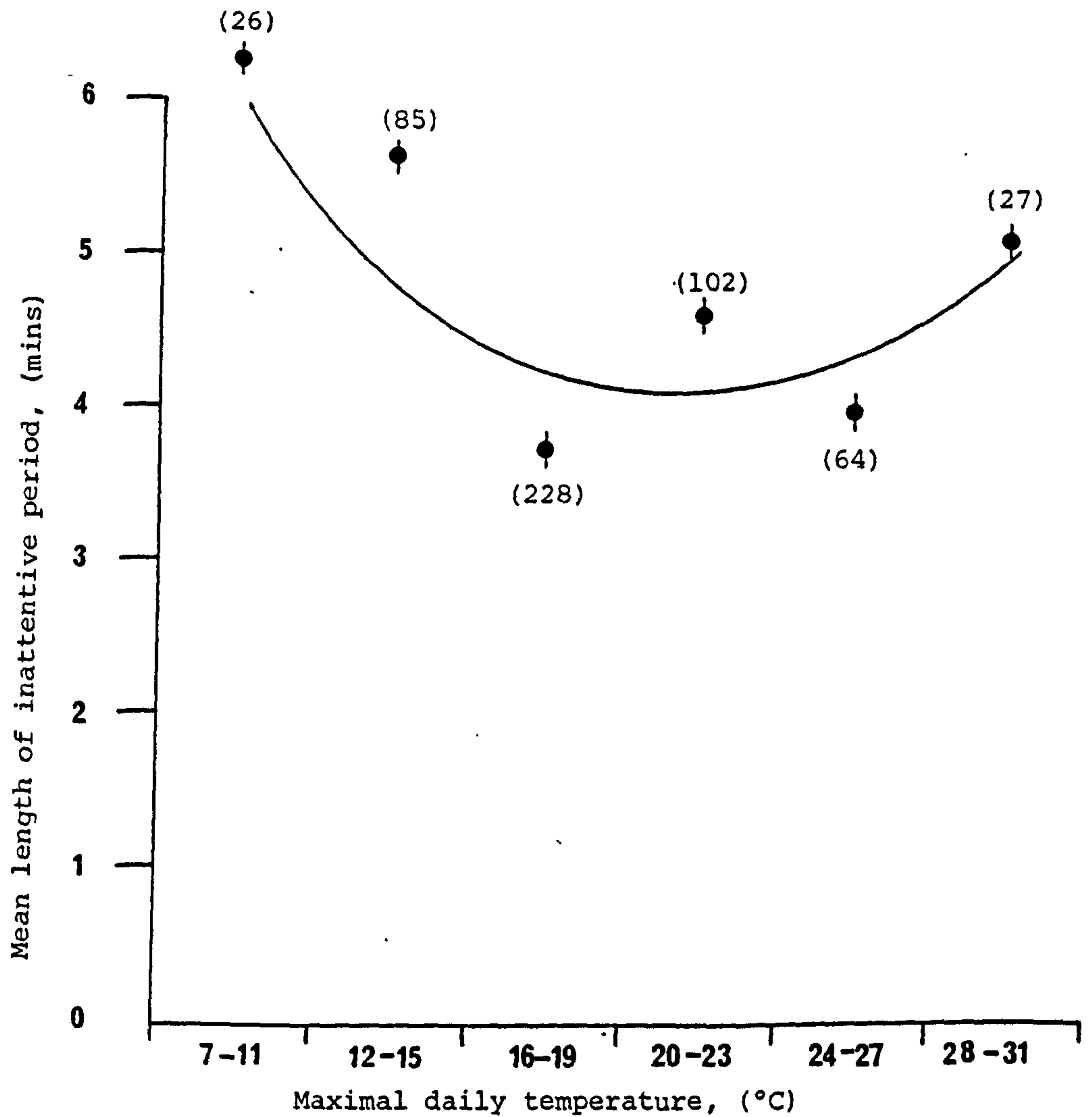


Figure 7.18

Mean inattentive period in relation to maximal daily temperature for incubating female swallows.

Means \pm standard errors illustrated, sample size in brackets.

Curve fitted by eye.

(b) Experimental manipulation of clutch size

The effects of changing the reheating costs but not changing energy gain rates on the predictions of the optimality model were investigated by experimentally changing the clutch sizes of two female swallows nesting within 30 metres of each other. Each female was similar in body size, body mass, clutch size, timing of laying and nesting situation.

One bird was given eight eggs while the other incubated two eggs for two days in mid-incubation. The bird given eight eggs in the first experimental period was given two eggs for a three day spell in late incubation, when the other bird incubated eight eggs. For four days of incubation each female incubated a natural clutch size of five eggs (the control period). During the experimental and control periods incubation behaviours were time budgeted and body mass changes documented.

The experiment is of value on two accounts:

- (i) It tests a prediction of the optimality model developed above with changes occurring only in the reheating costs between treatments.
- (ii) It may provide insight into whether clutch size in swallows is limited by constraints on female body condition in incubation.

A clutch of eight eggs is greater than that found naturally (Chapter 2), and if females incubating eight eggs are committed to long periods of incubation with little remaining time for foraging, their body condition may deteriorate to a point where desertion is possible.

The results for the percentage of afternoon time spent incubating, mean attentive periods, and mean inattentive periods for the control and two experimental treatments is illustrated in Figure 7.19.

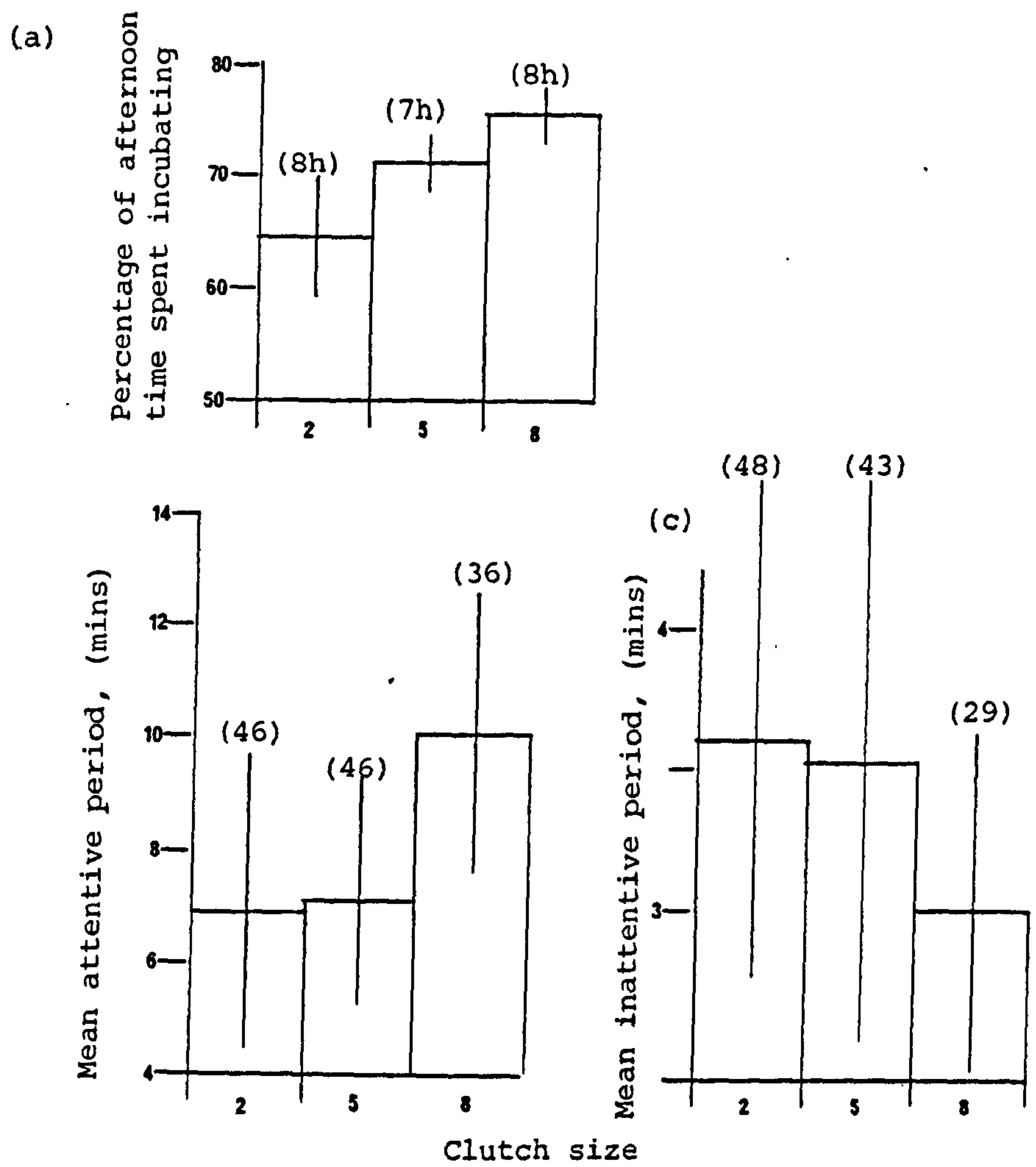


Figure 7.19

Time budgets of female swallows incubating clutches of two, five, and eight eggs.

(a) Percentage of afternoon time spent incubating.

(b) Mean attentive period.

(c) Mean inattentive period.

Means + sd illustrated, sample size in brackets. Note difference in scales between (b) and (c).

Percentage of afternoon time spent incubating increased with increasing clutch size, so that females spent significantly longer (11% more of their afternoon time) incubating clutches of eight eggs than they did incubating two eggs ($t = 2.32$, $P < 0.05$).

The mean length of the attentive period increased with increasing clutch size, so that females on average had longer bouts sitting on eggs at clutch size eight than at either clutch size five or two ($t(8,5) = 2.93$, $P < 0.01$, $t(8,2) = 3.5$, $P < 0.001$).

The mean length of the inattentive period was considerably shorter than that of the mean attentive period for each treatment (t tests, $P < 0.05$ all comparisons) since egg cooling rate exceeds the reheating rate by the female for any given time (Drent, 1973). No significant differences existed between mean inattentive periods for the treatments, though the trend was for inattentive periods to decrease with increasing clutch size as predicted by the model.

Since the females spent longer incubating a clutch of eight eggs than they did two eggs, foraging time for self-maintenance may be limited at large clutch sizes and female condition, measured by changes in body mass, may deteriorate.

The body mass changes of the two females over the course of the experiment are illustrated in Figure 7.20. In the first experimental period, the female incubating eight eggs increased in mass by 5.49% over two days, while the female with two eggs put on 3.52% of her body mass. In the second experimental period the female with eight eggs increased in mass by 0.69%, while the female with two eggs put on 2.88% of her body mass over three days. Hence female swallows can successfully incubate clutches of eight eggs for short periods

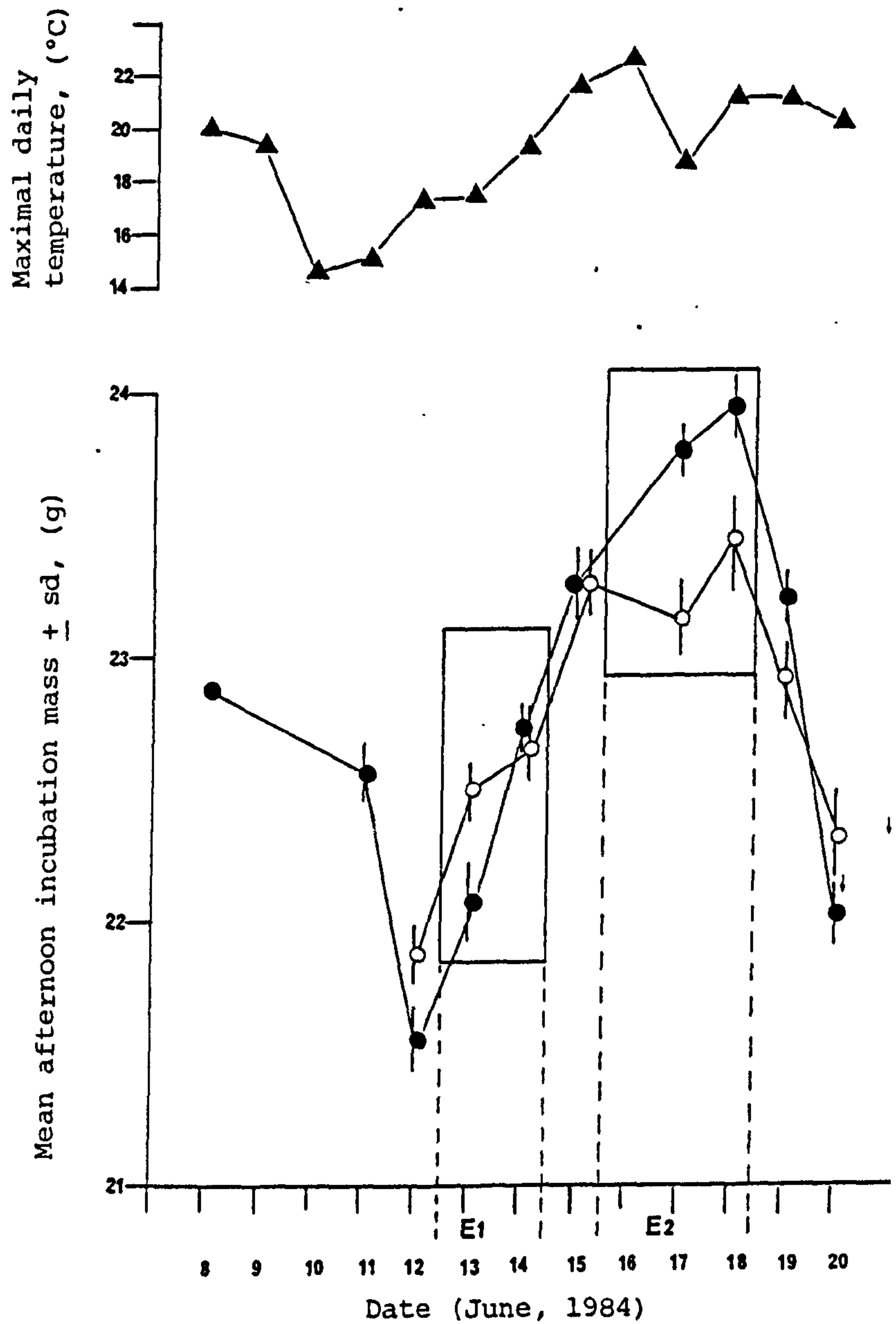


Figure 7.20

Body mass changes of two incubating female swallows during an experiment whereby clutch size was manipulated. Arrows denote day of hatching.

During experimental period 1 (E1), the female illustrated by solid circles incubated eight eggs, the female illustrated by open circles, two eggs.

During experimental period 2 (E2), the female illustrated by solid circles incubated two eggs, the female illustrated by closed circles eight eggs. At all other times both females incubated five eggs.

without any deleterious effects on their body condition, at least in favourable conditions for food availability.

Condition costs may occur for birds incubating large clutches in bad weather, however. On June 17th maximal daily temperature dropped by 4°C from the previous day, and although the female incubating two eggs increased in mass, the female on eight eggs lost mass. This was the only occasion on the eight days of observations when masses of both females were obtained that one bird's direction of mass change differed from that of the other.

Pied flycatchers also spend more time incubating experimentally enlarged clutches: Blagosklanov (1977) manipulated clutch sizes between four and 12 eggs. Females with four eggs incubated for 40% of their time and were not fed by their mates, while females incubating 12 eggs spent 78% of their time on the nest and received 5.3 feeds per hour from their mates.

Thus the predicted effects of changing costs and benefits in the optimality model were not seen in relation to ambient temperature changes or convincingly when clutch size was manipulated. Limitations on total foraging time probably result in females not significantly decreasing their inattentive periods when their incubation commitments are substantially increased, since decreased inattentive periods may jeopardise a female's body condition.

7.3.9 Motivational factors influencing swallow incubation behaviour

Swallow incubation is to some extent a Markovian process since the female's future behaviour is partly dependent on her past behaviour: a bird returning to eggs will not leave again immediately because she may have filled her digestive capacity and her eggs will need warming (Webb and King, 1983).

Internal motivational factors are likely to affect incubation behaviours. Incubating herring gulls eat more if they had less time to feed in their last absence, and also eat more if they will have more time to feed in the next absence. Hunger motivational factors account for 40% of the variance in herring gull ingestion rates (Sibly and McCleery, 1983).

Both time and energy factors may influence the duration of foraging bouts and attentive periods in swallows. For example, if a female leaves her clutch for a relatively long period, she may incubate for a relatively long period on returning to the nest. If a female increases in mass substantially on a foraging trip, she may incubate for a relatively long period to digest her large meal. A shorter incubation period may be expected if the female made only a small mass gain on her preceding foraging trip. This situation is illustrated in Figure 7.21.

In Figure 7.21a foraging energy gains are constant, but the time required to attain the fixed energy gain is variable. Birds foraging for long periods incubate for long spells to meet the increased reheating costs resulting from long absences. Short foraging periods are associated with shorter incubation bouts because of the reduced reheating costs compared with longer foraging bouts.

In Figure 7.21b foraging times and energy gains are both variable. A larger energy gain while foraging is associated with a longer incubation bout because birds will take longer to digest large meals than small meals. After a small energy gain while foraging, the bird may shorten its subsequent incubation bout to provide more time for foraging in the subsequent inattentive period.

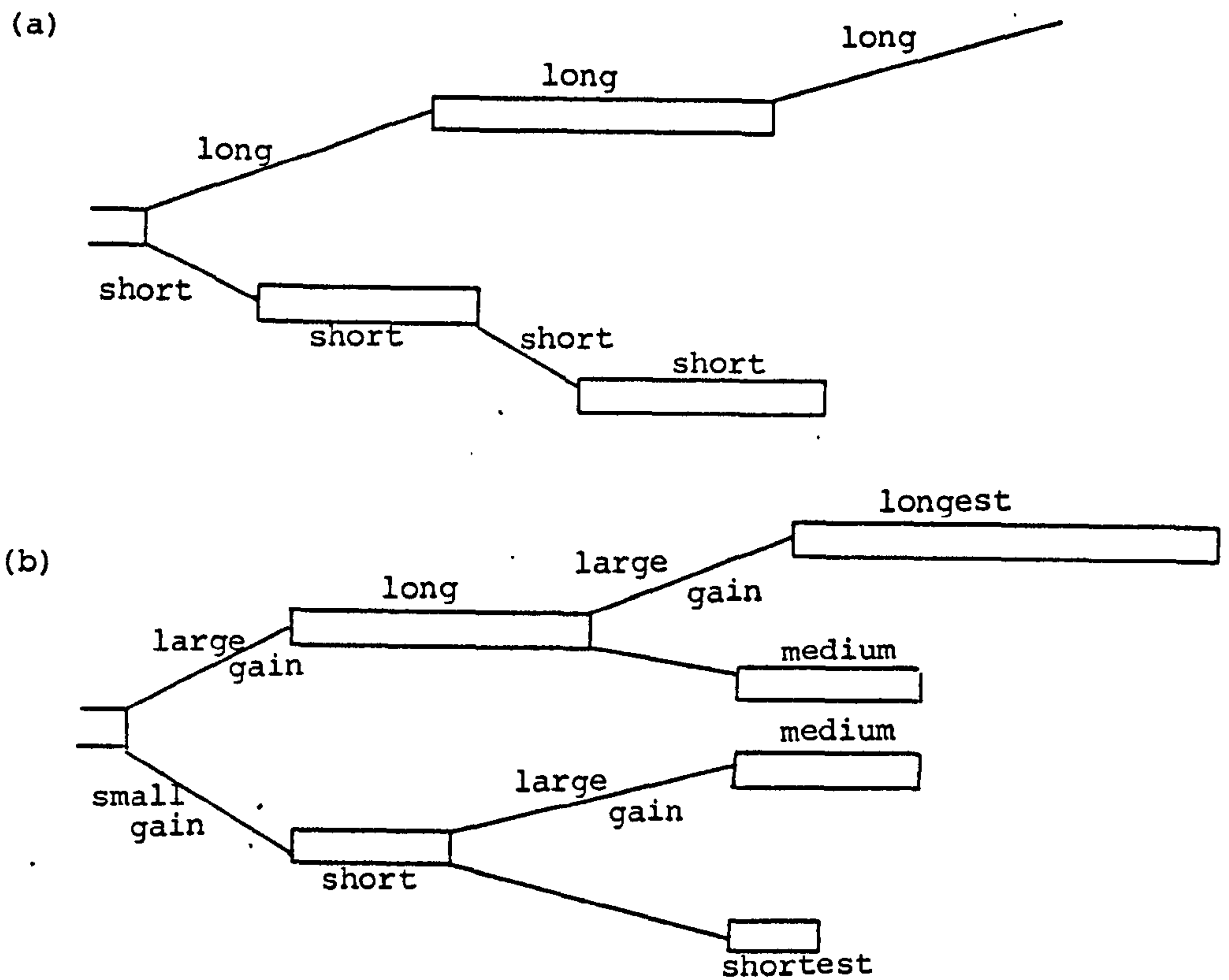


Figure 7.21

Some ways in which time and energy factors may influence incubation behaviours.

Attentive periods are represented by boxes, inattentive periods by solid lines.

In (a) foraging energy gains are constant, but the time required to attain a fixed energy gain varies.

In (b) foraging times and energy gains are both variable.

See text for explanation.

The validity of this interpretation was investigated by detailed analyses of short-term mass changes while foraging and of incubation time budgets. To minimise the chances of including foraging trips where defaecations occurred, only foraging trips resulting in mass gains were included in the analysis (Chapter 4).

The variables entered in stepdown multiple regression analyses and their abbreviations are presented in Table 7.6. A correlation matrix showing interdependence of the variables used in the analysis is presented in Table 7.7.

Abbreviated stepdown multiple regression results are presented with 't' values for the independent variables. One hundred and sixty-one behavioural sequences were considered in the analysis.

(a) Foraging time:

$$FT = 4.13 - 1.85 (\text{LOG}(v + 1)) + 0.015 (\text{INCP}) + 0.090 (\text{INCS})$$

$$t = \quad 2.32, P < 0.05 \quad 4.55, P < 0.001 \quad 2.72, P < 0.01$$

$$(r^2 = 29.3\%, F = 23.4, P < 0.001).$$

Hence foraging periods were longer in conditions of low food abundance. The inattentive period was longer if the preceding incubation spell was relatively long, and if the subsequent incubation spell was relatively long.

(b) Length of the preceding incubation spell

$$\text{INCP} = 13.9 + 0.804 (\text{FT}) - 0.053 (\text{BM}) + 0.289 (\text{INCS})$$

$$t = \quad 4.88, P < 0.001 \quad 2.83, P < 0.001 \quad 3.97, P < 0.001$$

$$(r^2 = 36\%, F = 26, P < 0.001).$$

Incubation bouts preceding the foraging bouts considered were longer if the ensuing foraging time was long, and longer if the

Table 7.6

List of variables entered in a stepdown multiple regression analysis of female swallow incubation behaviours, with their abbreviations .

(a) dependent variables:

Foraging time (mins) : FT

Length of the preceding incubation spell (mins) : INCP

Length of the subsequent incubation spell (mins) : INCS

(b) independent variables:

Mass gain during foraging (g) : $M\Delta F$

Rate of mass gain while foraging (g min^{-1}) : $M\Delta F/FT$

Body mass (g) : BM

Maximal daily temperature ($^{\circ}\text{C}$) : TMAX

Suction trap catch volume : $\text{LOG}(v + 1)$

Foraging time, and lengths of preceding and subsequent incubation spells were also entered as independent variables when not entered on dependent variables.

Table 7.7 Correlation matrix of variables used in a stepdown multiple regression analysis of female swallow foraging times and incubation bout durations

	FT	INCP	INCS	MAF	MAF/FT	BM	TMAX	LOG(v + 1)
Foraging time (mins) FT	-	0.488***	0.426***	0.102 ns	-0.435***	-0.117 ns	-0.208**	-0.303***
Previous incubation bout (mins) INCP		-	0.487***	0.133 ns	-0.119 ns	-0.308***	-0.127 ns	-0.232**
Subsequent incubation bout (mins) INCS			-	0.053 ns	-0.118 ns	-0.277***	-0.199*	-0.285***
Mass gain while foraging, g MAF				-	0.738***	-0.005 ns	-0.078 ns	-0.050 ns
Mass gain rate while foraging, g min ⁻¹ MAF/FT					-	-0.039 ns	0.050 ns	0.111 ns
Body mass, g BM						-	-0.073 ns	-0.083 ns
Maximal daily temperature, °C, T MAX							-	0.539***
Aerial insect abundance LOG(v + 1)								-

Tabulated values are r: n = 161 all cases

ns : not statistically significant; * : P < 0.05; ** : P < 0.01; *** : P < 0.001

ensuing incubation bout was long. Incubation bouts were longer for birds of low body mass, although in this case body mass was not corrected for body size.

(c) Length of the subsequent incubation spell.

$$\text{INCS} = 18.9 + 0.500 (\text{FT}) - 0.498 (\text{BM}) - 4.51 (\text{LOG}(v + 1)) + 0.288 (\text{INCP})$$

$$t = 2.77, P < 0.01 \quad 2.54, P < 0.05 \quad 2.40, P < 0.05 \quad 3.64, P < 0.001$$

$$(r^2 = 34\%, F = 39, P < 0.001)$$

Incubation bouts following the foraging bouts considered were longer if the preceding foraging period or incubation period was relatively long. The incubation bouts were shorter when body mass was high and at high levels of food abundance.

The relationship between the duration of an incubation spell and the length of the preceding foraging bout is illustrated in Figure 7.22. Incubation periods exceeded the duration of the preceding foraging bout as shown by the regression equation in the legend to Figure 7.22, at least for most naturally occurring foraging periods.

Hence time factors seemed to be important in determining the duration of foraging bouts and incubation periods in female swallows, but there was no evidence for energy gain factors being important: neither the magnitude of the mass gain during foraging nor the rate of mass gain during foraging influenced how long the female spent sitting on the eggs.

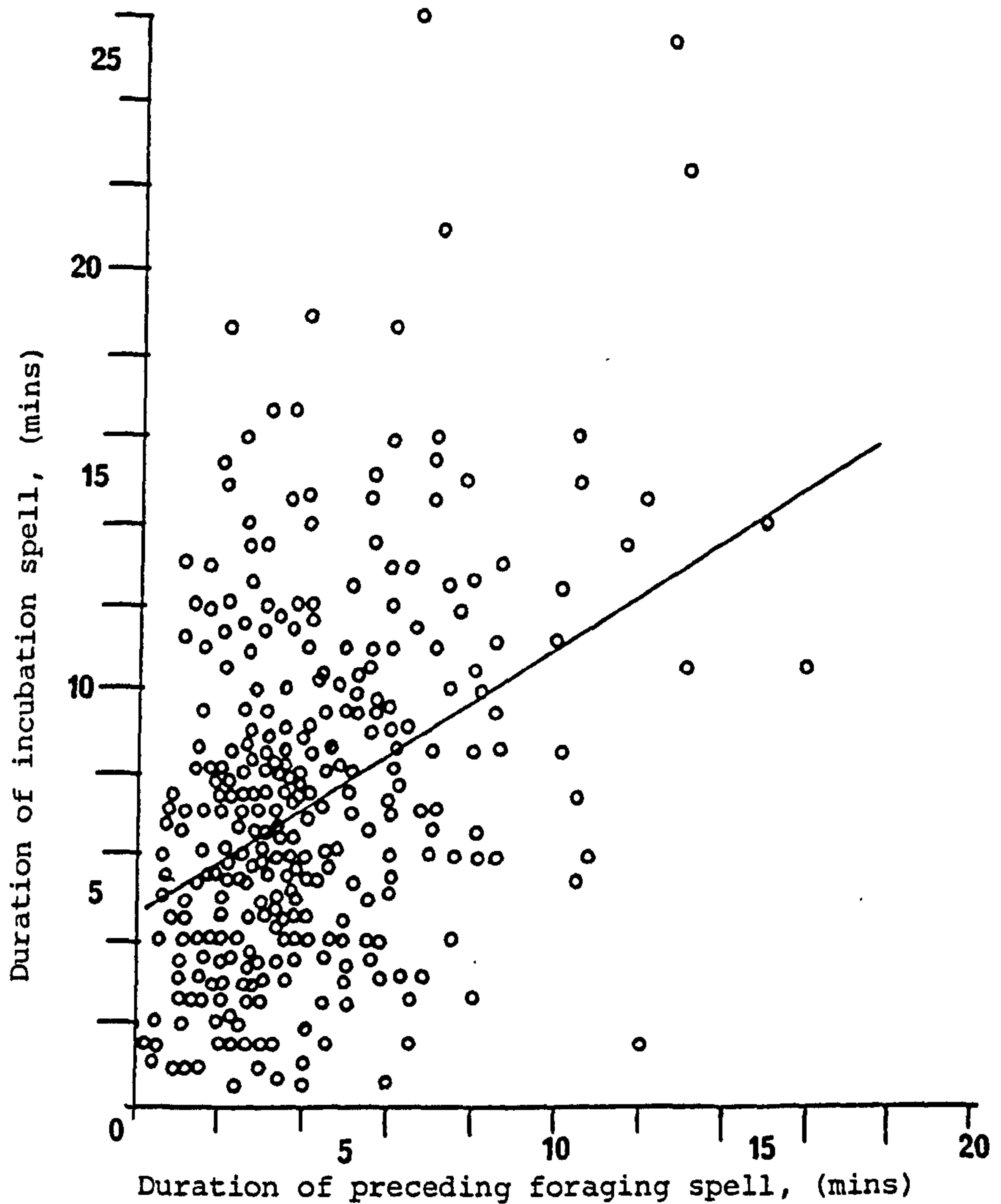


Figure 7.22

The relationship between the length of an incubation spell (INCS) in female swallows, and the duration of the preceding foraging bout (FT).

The regression equation is

$$y = 4.90 + 0.622x$$

$$r = 0.37, n = 293, P < 0.001$$

Naturally occurring foraging periods (generally < 10 mins) are followed by longer incubation bouts.

7.4 DISCUSSION

Incubation from a parent:offspring resource allocation perspective

Female swallows are relatively heavy during incubation, and lose mass rapidly during the early stages of nestling rearing (Chapter 8). The adaptive significance of mass loss during nestling rearing is discussed in Chapter 8, but what are the advantages of being heavy in incubation?

Incubating female swallows are heaviest when ambient temperatures are highest, when the amount of time spent flying to forage during incubation is greatest. During nestling rearing females lose mass to reduce flight costs at a time when brood demands are high and they must spend most of their daylight time flying. The benefits of losing mass for reducing flight costs will be relatively small during incubation, when, even on the warmest days, females spend most time incubating and little time flying.

Three advantages of being heavy during incubation are:

- (a) A large lipid reserve will buffer against condition costs in bad weather when female self-feeding time is reduced.
- (b) Substantial body reserves may supply much of adult energy expenditure during the brooding phase. If weather conditions deteriorate during brooding, females may allocate any harvested food to their offspring rather than keeping it for self-maintenance.
- (c) Incubation is a relatively early stage of the breeding cycle when the future cumulative investment required is still high. If a clutch was chilled or lost to predators, a female's incubation body reserves may allow her to attain suitable body condition for relaying more rapidly than if she were lighter and carried less reserves. Any benefits of being heavy to allow

relaying rapidly decline as chicks hatch and grow and the cumulative future risk of offspring loss through chilling or to predators decreases.

Incubation provides a situation for the study of parent:offspring conflict behaviours (Trivers, 1974), with the eggs representing an early stage of cumulative parental investment, especially for the female. Since incubating eggs (investment in offspring) and foraging (investment in self-maintenance) are incompatible activities for a female swallow, situations may arise whereby excessive investment in offspring causes body condition to deteriorate and maybe reduces the female's chances of survival. The desertion of eggs by females in poor conditions is presumably an adaptation to promote female survival chances when the costs of maternal care are high.

There are several lines of evidence suggesting that incubation can be costly to females when weather conditions are poor, and that females impose a ceiling on the amount of time they invest in incubating their clutches.

Although maintaining egg temperature is considered to be relatively cheap in energetic terms (Mertens, 1977, 1980; Walsberg and King, 1978a, b; Vleck, 1981), any cost to the female is likely to occur from a restriction in her inattentive time reducing her energy gain from foraging. Female body mass during incubation is positively correlated with ambient temperature (Table 7.1) and can be reduced rapidly in bad weather conditions (Figure 7.6), especially if poor weather persists (Figure 7.7). Yom-Tov and Hilborn (1981) suggested that an energetic bottleneck may occur during late incubation, and this could act as a constraint on clutch size.

Female swallows respond to low temperatures by spending relatively long spells foraging (i.e. inattentive periods) (Figure 7.18), although total time for feeding per day is reduced, and by not normally spending more than about 70-80% of their afternoon time sitting on eggs (Figure 7.4). The relationship between the amount of time spend in attentive behaviour and ambient temperature typically follows a rectangular hyperbola, with attentive time levelling off at a maximum level below a critical temperature (White and Kinney, 1974). Swallows in this study actually appeared to decrease their incubation time at the lowest temperatures recorded, the relationship between percentage time incubating and maximal daily temperature fitting a maximum function equation (Figure 7.4).

A female's body condition will probably reflect several preceding days' feeding conditions, and not only immediate conditions. The relationship between female attentive behaviour and body condition is plotted in Figure 7.23, where 'body condition index' is defined as $\text{body mass/keel-length, g mm}^{-1}$ (to standardise for incubation body mass increasing with increasing keel-length, Figure 7.2).

The percentage of afternoon time spent incubating during 67 hours of observation at 13 nests increased as body condition decreased down to a condition index of about 1.01. This is probably because females are normally heavier at higher temperatures when eggs need less reheating and more time is available for foraging. Below a condition index of 1.01, attentive behaviour decreased slowly until a condition index of 0.96, and then dropped precipitously until zero attentiveness was attained at a condition index of 0.92. Canada geese increase the amount of recess time taken during incubation once a lower critical body mass is attained, probably when lipid reserves are depleted (Aldrich and Raveling, 1983).

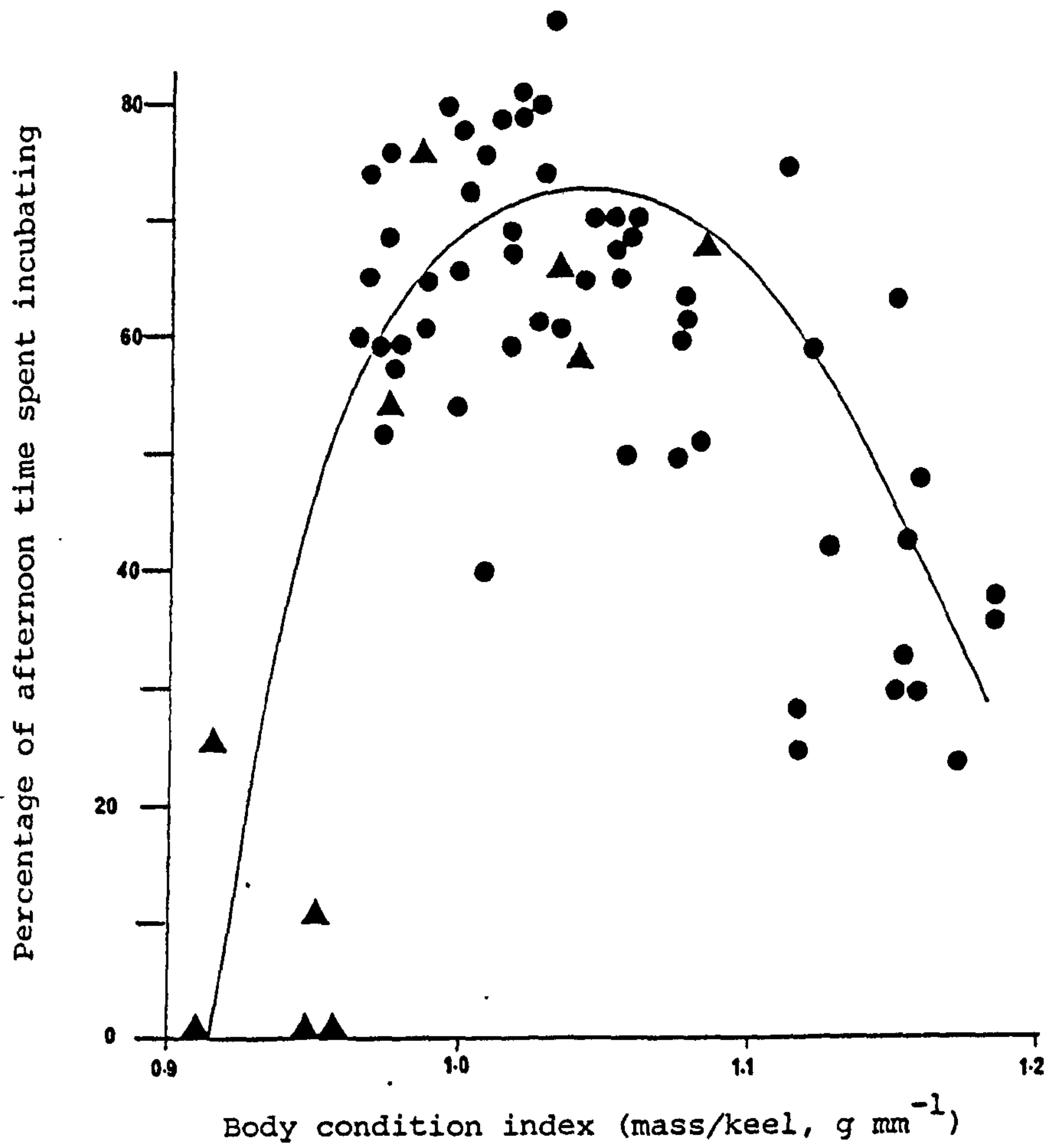


Figure 7.23

The relationship between the percentage of time spent in afternoon incubation and body condition in female swallows. Curve fitted by eye.

n = 67 hours, 13 females. Solid triangles are data for female M/C A83.

Below condition indices of 0.9 desertion may be expected, even though birds in this body condition would be considered relatively heavy if they had been rearing chicks. Although the optimal mass of nestling-feeding birds is probably lower than that of incubating individuals (Chapter 8), it is likely that incubating females would not risk their body condition falling to that of nestling-rearers since excessive mass loss may be costly (Nur, 1984a) and incubating birds still have considerable time available for a repeat breeding attempt compared with nestling-rearers (Dawkins and Carlisle, 1976).

CHAPTER 8

8. RESOURCE ALLOCATION BETWEEN PARENT SWALLOWS AND THEIR NESTLINGS

8.1 INTRODUCTION

Recent theories of life history strategies have assumed that an individual's inclusive fitness is maximised by optimising resource allocation between the opposing demands of rearing offspring and surviving to breed again. Breeding is often believed to reduce the chances of adults surviving to breed again, and the greater the reproductive effort, the greater the assumed reproductive cost to the parent (Williams, 1966b; Charnov and Krebs, 1974; Stearns, 1976; Calow, 1979).

In birds, four studies have provided evidence for increased reproductive effort reducing adult survival rates. Great tits rearing large brood sizes within a season have lower survival rates than individuals rearing fewer young (Kluyver, 1971). Askenmo (1979) found a lower return rate of male pied flycatchers rearing enlarged broods compared with controls. Bryant (1979) showed that the survival rate of single brooded female house martins was greater than that of double brooded females, and Nur (1984a) demonstrated reduced survival of female blue tits rearing enlarged broods.

One way in which the survival rate of birds expending considerable reproductive effort is lowered may be through physiological stress, as shown by mass loss when rearing chicks (Nice, 1937; Hussell, 1972; Ricklefs, 1974). Adult energy expenditure often peaks during the nestling rearing phase (Bryant and Westerterp, 1980; Drent and Daan, 1980), so this period may impose maximal physiological stress on the parents. Increased mass loss in adult birds rearing enlarged broods

compared with controls has been found in snow buntings, Plectophenax nivalis, (Hussell, 1972), pied flycatchers (Askenmo, 1977), and house martins (Bryant, 1979), but not in tree swallows, Iridoprocne bicolor, (De Steven, 1980). Nur (1984a) has shown links between increased reproductive effort, increased mass loss during nestling rearing, and reduced female survival rate in blue tits.

Alternative hypotheses exist to explain mass loss in adult birds feeding nestlings. Norberg (1981) and Freed (1981) suggested that mass loss could be an adaptation to reduce power consumption in flight during trips to feed nestlings. Nur (1984a) hypothesised that mass loss during nestling rearing may be costly mainly as a consequence of brooding behaviour restricting adult self-feeding time.

The aim of this chapter is to examine the adaptive significance of body mass changes in adult swallows feeding nestlings, and to relate adult mass changes to demands imposed on the parents by their offspring.

8.2 MATERIALS AND METHODS

8.2.1 The use of precision automated nest balances

The use of Mettler PK2000 electronic balances to monitor instantaneous and long term body mass changes in breeding swallows, together with observational techniques, has been described in Chapter 4.

Chicks in swallow nests lost mass continuously by evaporative water loss. When an adult arrived at the nest with a food load, the load mass was calculated as the mass of the brood after being fed minus brood mass before food delivery. To minimise errors in estimating load masses caused by the nestlings losing mass during food delivery, bolus mass was only measured for feeding trips lasting

less than five seconds, when loss of water from the brood and nest would be less than 0.01g. Adult masses were then calculated as (mass of parent + load mass) - (load mass). Masses of adults and their loads were not recorded if parents removed faecal sacs from the nest. When nestlings were older than about eight days, they usually defaecated over the edge of the nest, and faecal sac masses could be recorded since nestling defaecations results in instantaneous drops in mass which were relatively large compared with continuous mass losses resulting from evaporative water loss by the brood.

8.2.2 Carcass analysis

Carcass analysis methods have been described in Chapter 4.

8.2.3 Field experiments

Observations of control birds rearing their own chicks were supplemented by a series of experiments whereby either brood size or brood age was manipulated.

(a) Brood size manipulation

A total of five nests had nestlings added in brood enlargement experiments. Of these four nests had brood size enlarged within the first three days of the chicks hatching. Two broods of three had three and four chicks added, one nest which hatched four chicks had three added, and one nest hatching five chicks had another three added on the day of hatching.

One nest underwent experimental brood enlargement when the brood was eight days old, with three nestlings added to three already present. This enlargement occurred after a replacement experiment (see below) which had included seven days of control data, seven days of experimental data. In all 49 days of data were obtained from the five nests which underwent brood size enlargement.

Three nests had nestlings removed from them in brood size reduction experiments. One nest had two of four chicks removed one day after hatching, another had three of five chicks removed on the day of hatching.

In all experiments described above, introduced chicks differed by less than two days from chicks hatched in the nest. In the third brood size reduction experiment brood size was reduced from six to three on day 7, but the introduced chicks were five days older than the nestlings which they replaced.

Single brood size enlargement and brood size reduction experiments were run simultaneously, on two pairs with identical laying dates, clutch sizes and initial brood sizes. The pairs were nesting within 30 metres of one another on the same farm. One nest had three chicks added on hatching to form a brood size of eight, the other nest had three chicks removed from an initial brood size of five.

(b) Brood age manipulation

Brooding behaviour by female swallows generally occupies less than 10% of the female's afternoon time budget when the brood is seven days old or more. In four experiments, it was attempted to re-establish a high level of brooding by the female, and to observe the consequences for body mass of the parents by replacing chicks with younger nestlings at a time when daytime brooding had almost ceased.

Such manipulations were termed 'replacement experiments'. In one nest five 7-day chicks were replaced by four 1-day chicks, in a second nest four 7-day chicks were replaced by four 2-day chicks.

One nest had an enlarged brood of six nestlings replaced by four 2-day chicks on the eight day of rearing, and a final experimental nest had three 17-day chicks replaced by three 9-day nestlings. Seventeen days of data were obtained from the four replacement experiments.

8.3 RESULTS

8.3.1 Adult body mass changes during nestling rearing

In order to understand the normal patterns of adult body mass changes during nestling rearing, comparisons have been made with incubation body masses in Figure 8.1 for birds rearing natural brood sizes.

Mass changes of parents have been compared with brood demands by plotting food delivery rates (FDR's) to the broods in Figure 8.1c. Food delivery rates were calculated as feeding rate multiplied by mean load mass during the afternoon sampling periods for each day of observation. Food delivery rates are a more reliable indicator of brood food requirements than are brood masses - brood food requirement is the sum of energy demands for maintenance, growth, and activity, which peaks in mid-growth when provisioning rates by the parents are highest (Bryant and Gardiner, 1979).

Parents on average deliver roughly equal quantities of food to the brood (Turner, 1980, this chapter). Food delivery rates do not necessarily represent brood demands, since offspring demands may exceed the nourishment that parents are willing to provide for their brood (Trivers, 1974).

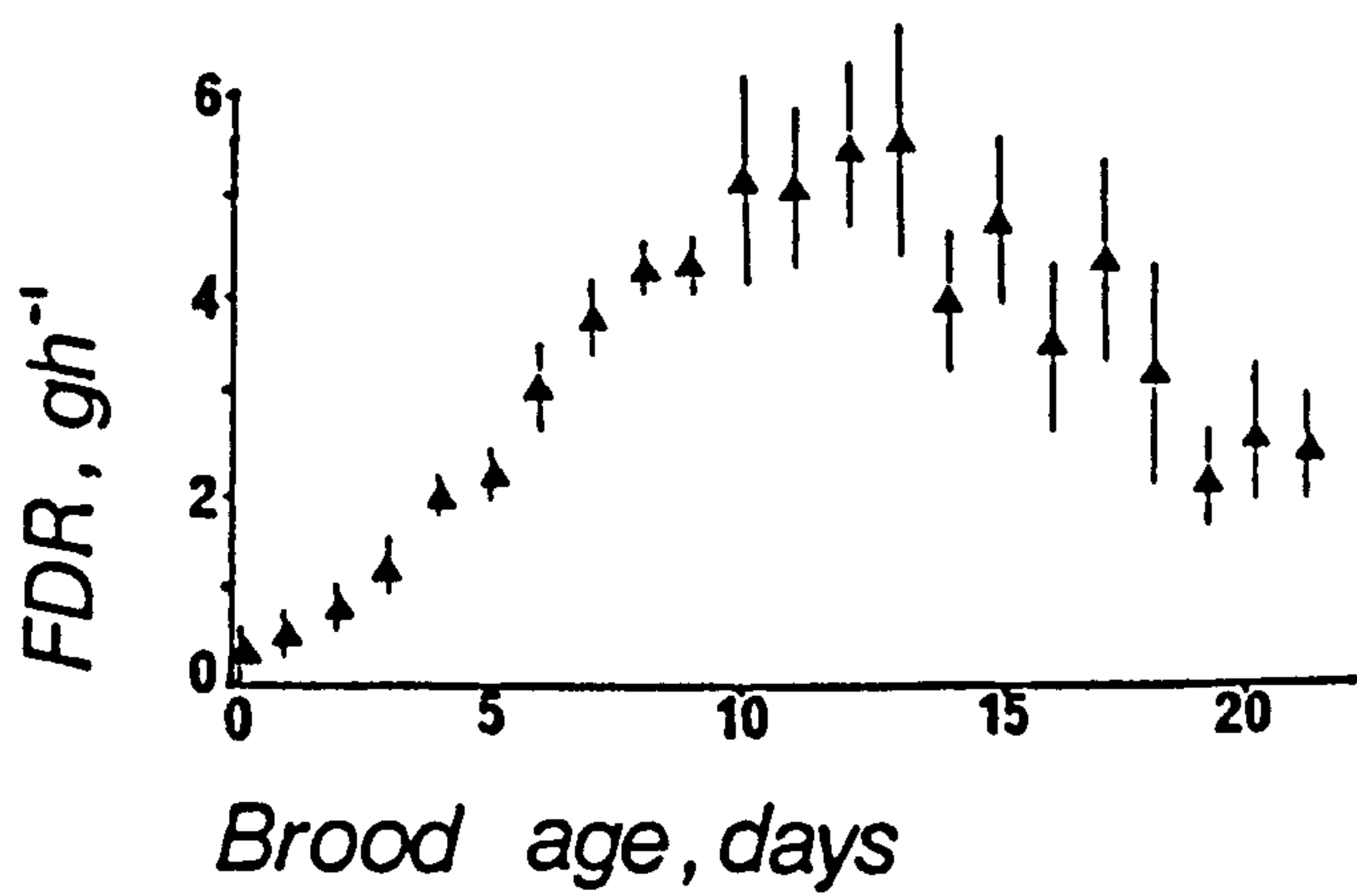
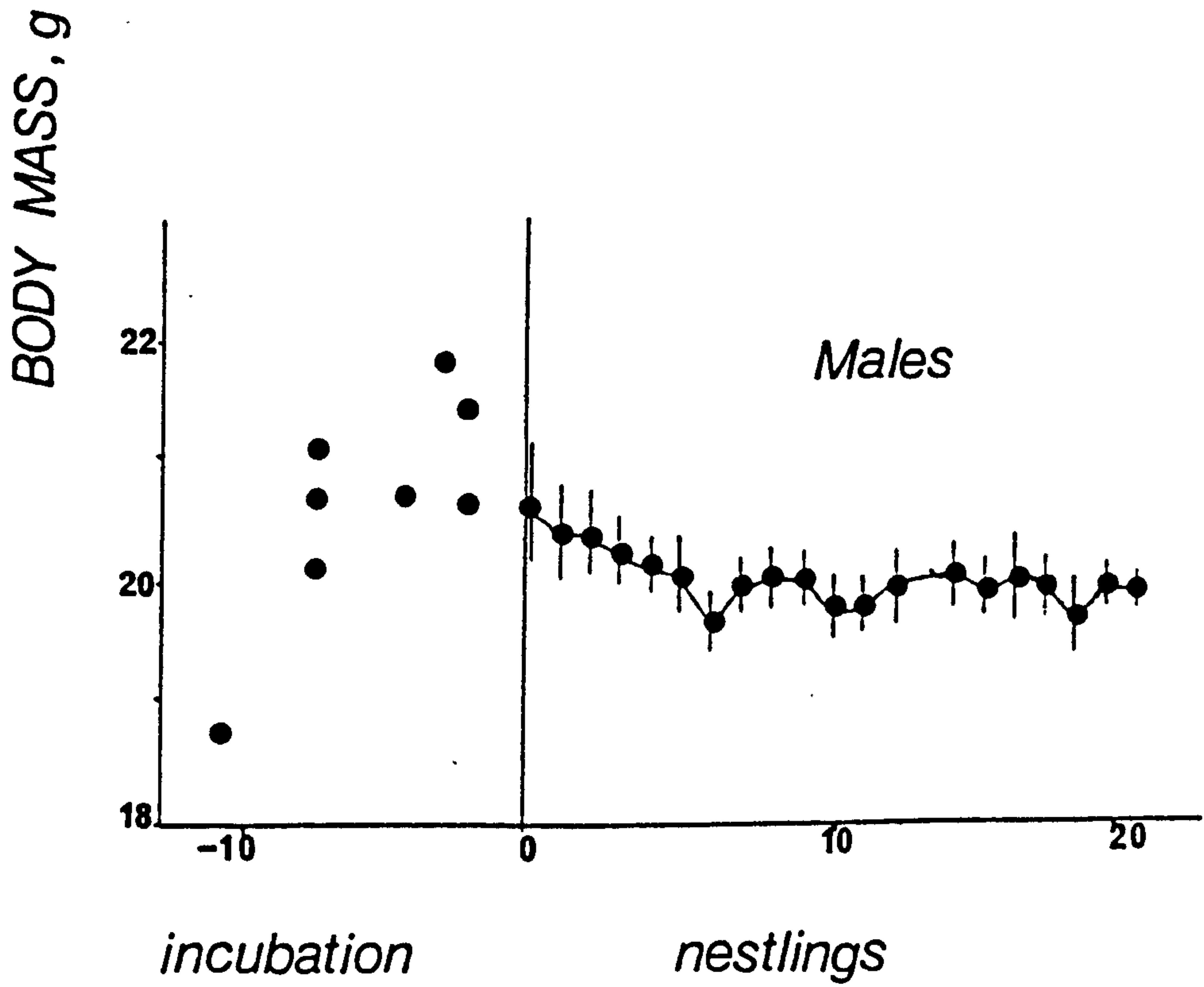
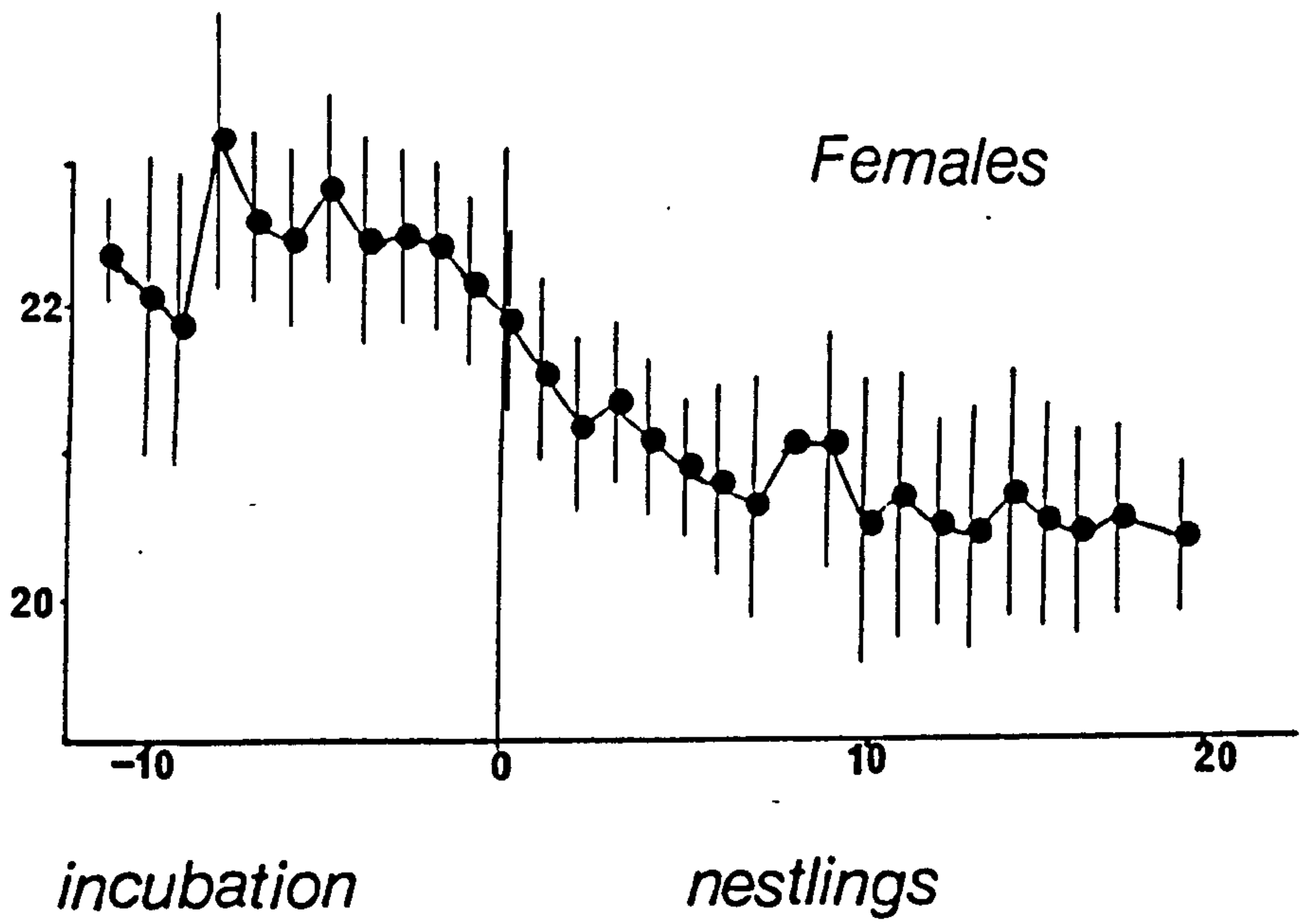
The heaviest body masses recorded were those of incubating females. Females on average lost mass rapidly during the first week

Figure 8.1

Body mass changes of adult swallows during incubation and nestling rearing compared with food delivery rates to their broods.

Data is for control pairs only, and means \pm sds of afternoon body masses are presented.

- (a) Females: n = 190 days, 14 nests, 11 females
- (b) Males: n = 104 days, 14 nests, 10 males
- (c) Food delivery rates: n = 109 days, 13 nests



of nestling rearing, when food delivery rates were low but brooding commitments high (section 8.3.3). Body mass tended to be lowest and relatively stable between days 8 and 21 of nestling rearing, the young leaving the nest on average at 31 days of age (Turner, 1980).

Males entered the nestling rearing phase with a lower average body mass than females, since they were significantly lighter during the incubation period (Chapter 7). A period of mass loss appeared to occur during the first week of rearing, though this was not as dramatic as in females. Body masses attained relatively stable, low values between days 8 and 21 of nestling rearing.

Food delivery rates rose rapidly to reach a maximum value at day 13, thereafter falling off until fledging occurred. Hence for both males and females the rate of mass loss during nestling rearing appeared to be greatest before peak food delivery rates to the brood were attained.

Patterns of body mass change for control pairs together with brood growth patterns are presented in Appendix IV. A great deal of variation in masses was evident amongst both males and females, not all individuals conforming to the average patterns shown in Figure 8.1. For example, the male and female in nest M/C G 1983 tended to increase in mass over the first week of nestling rearing, and males M/C B 1982 and g 1983 tended to remain at a relatively stable mass over the first week of the rearing period.

In the subsequent subsections of this chapter, the factors influencing body mass changes of adults during nestling-rearing are considered. In Figure 8.2 the masses of one pair and their brood are presented as an example in relation to insect abundance measured

Figure 8.2

Concurrent body mass changes of a pair of swallows and their brood during incubation and nestling rearing in relation to food abundance (overlay).

Solid triangles : female parent

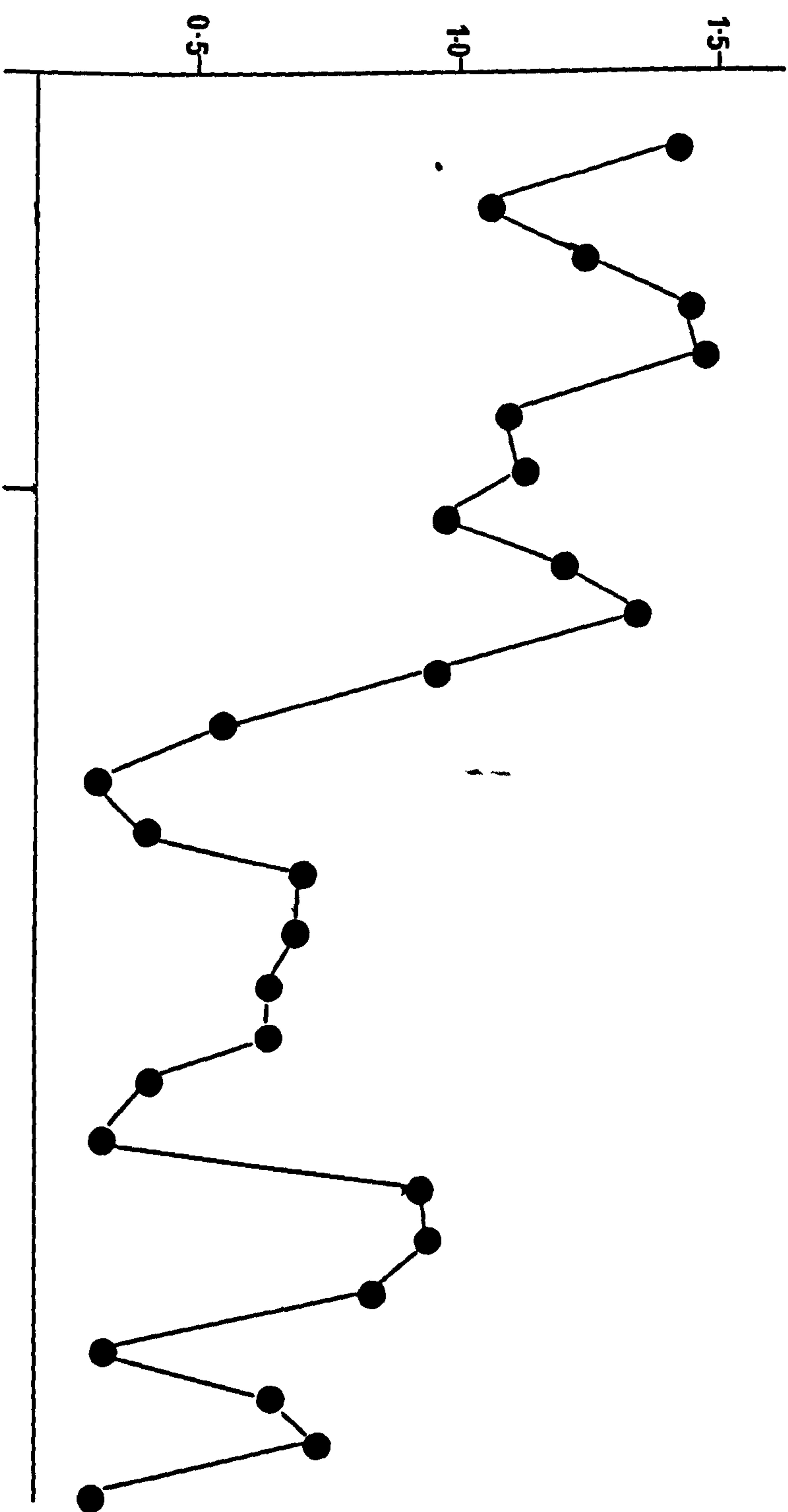
Open triangles : male parent

Open circles : brood (brood size 5).

The overlay shows aerial insect abundance as measured by the 12.2m suction trap.

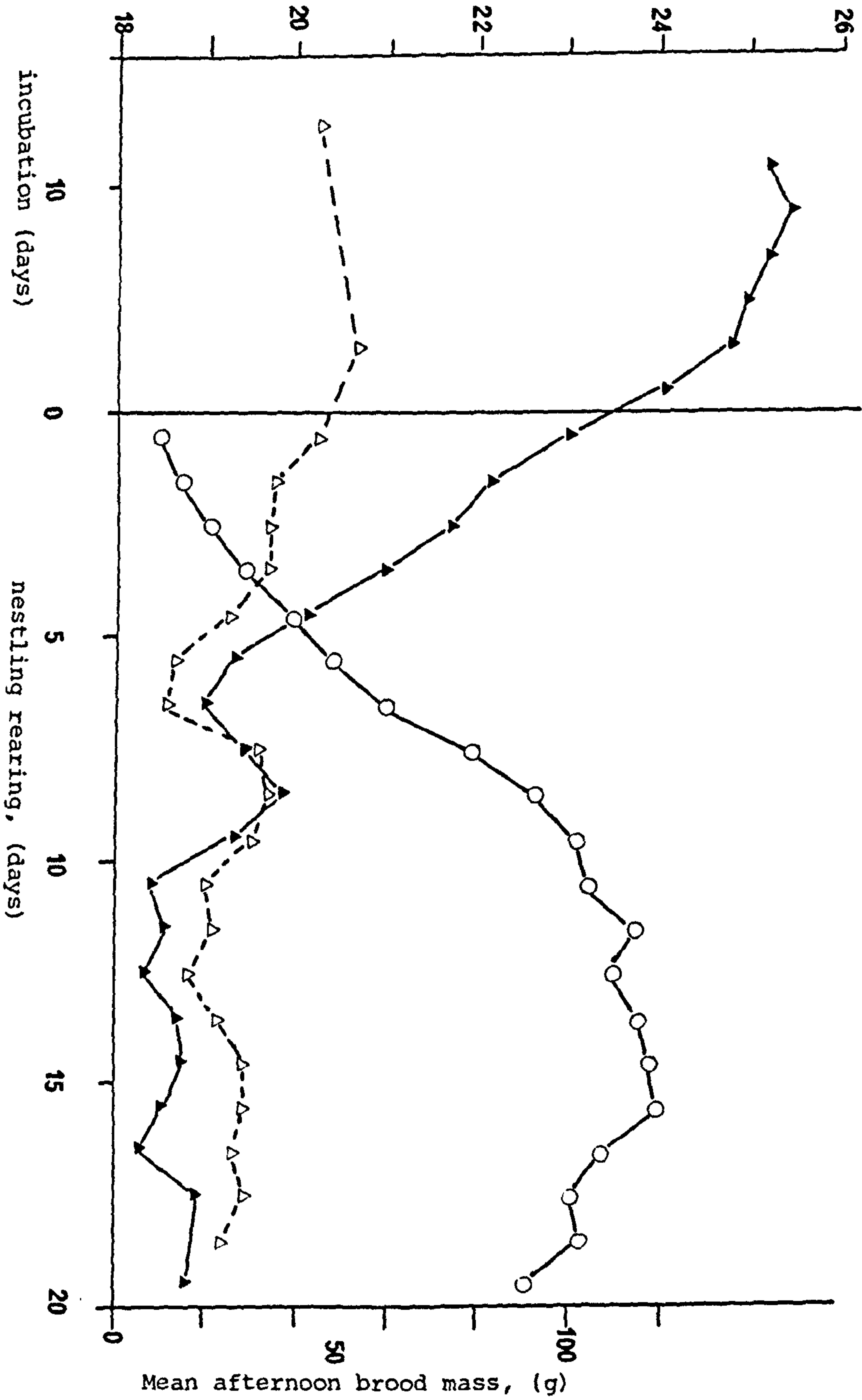
All masses are means of the afternoon sampling period.

Day 0 is day of hatching.



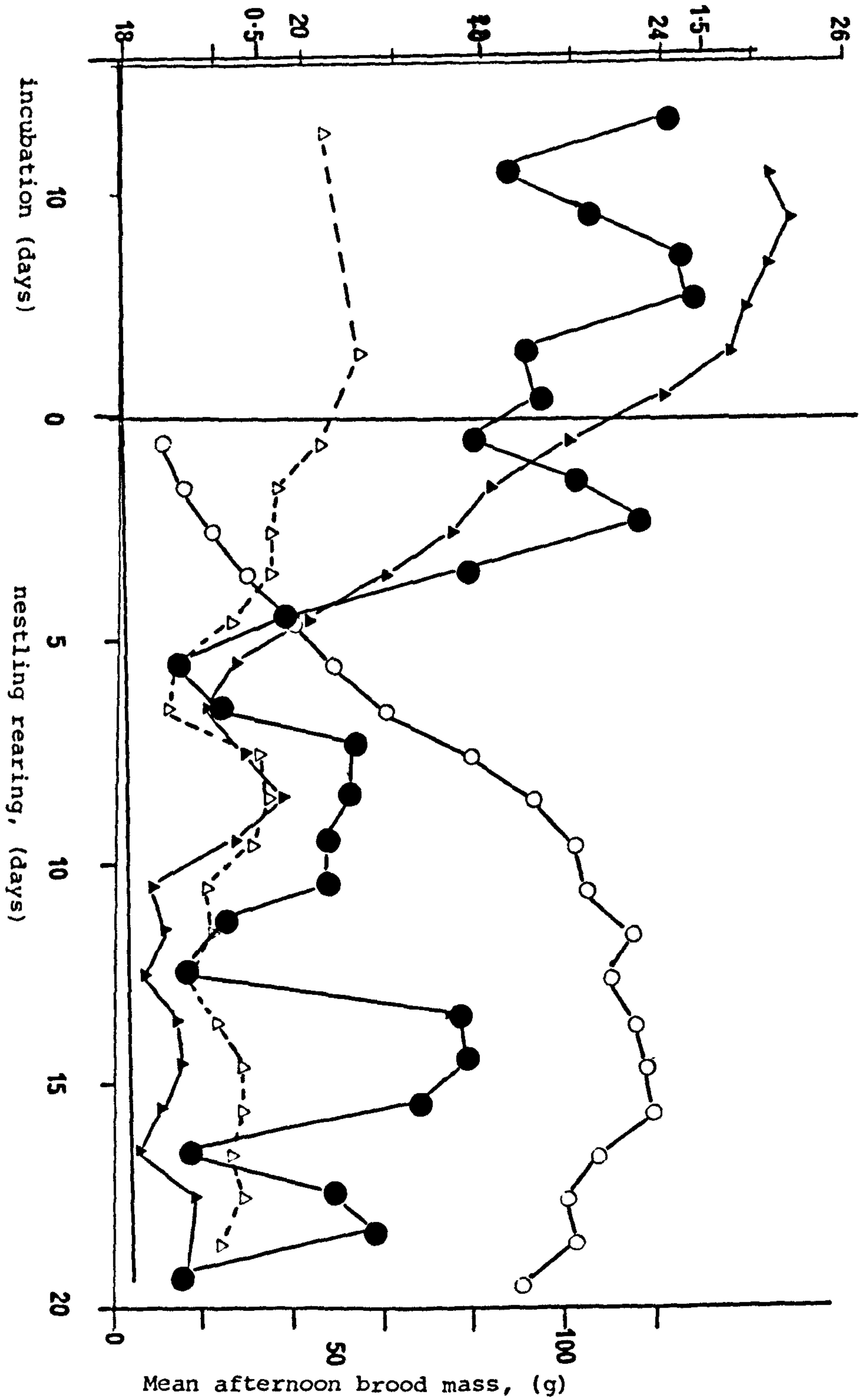
Log (v + 1) : (overlay)

Mean afternoon adult body mass, (g)



Log (v + 1) : (overlay)

Mean afternoon adult body mass, (g)



by the suction trap. Similar factors appeared to influence body masses of the male, female, and the brood: on days of low food abundance, masses of both parents tended to decrease, and after day 11, the mass of the brood also fell when insects were relatively scarce. Hence both adults and nestlings may share the costs associated with food scarcity, and this is explored in more detail in the following analysis.

The nestling rearing phase was considered in two phases:

- (a) The brooding phase: day 0 to day 7 of nestling rearing

The brooding phase is defined as the stage when female afternoon brooding behaviour contributed 10% or more of the female's afternoon time budget. Food delivery rates were relatively low during this period.

- (b) The non-brooding phase: day 8 to day 21 of nestling rearing

Male and female body masses on average reached relatively stable, low values during this period, and female afternoon brooding contributed less than 10% of her afternoon time budget. Afternoon brooding was on average terminated by day 15.

8.3.2 Adult masses during the brooding phase

- (a) Factors influencing adult masses during the brooding phase

An analysis was performed on 34 days of data where male and female body masses, female keel-length, and food abundance information were available for seven pairs rearing natural brood sizes.

Correlation matrices of female mass and male mass in relation to season (days after June 1st), brood age, brood size, sweep net biomass, female keel-length, maximal daily temperature on the day of study and on the preceding and subsequent days and body mass of the mate are presented in Table 8.1.

Table 8.1

Correlation matrices of male and female body mass in swallows during the brooding phase (days 0-7 of nestling-rearing)

<u>Variable</u>	<u>female mass, g</u>	<u>male mass, g</u>
season (days after June 1st)	0.259 ns	-0.234 ns
brood age, days	-0.285 ns	-0.187 ns
brood size	-0.088 ns	0.523**
maximal daily temperature °C on day of weighing	0.681***	0.443**
maximal daily temperature, °C on preceding day	0.706***	0.316 ns
maximal daily temperature, °C on subsequent day	0.639***	0.388*
sweep net biomass, g dry mass	0.577***	0.297 ns
female keel-length, mm	0.724***	-
mate mass, g	0.483***	

Tabulate values are correlation coefficients, r.

ns : not significant;

* : P < 0.05;

** : P < 0.01;

***: P < 0.001

n = 34 days of data

Female body mass during the brooding period was significantly positively correlated with keel-length, sweep net biomass, and the three measures of maximal daily temperature. Male body mass was significantly positively correlated with brood size and with maximal daily temperature on the day of weighing and on the subsequent day.

Within a pair, male and female body masses were positively correlated, suggesting that similar factors may influence the body masses of both sexes, even though only the female broods the young.

Stepdown multiple regression analyses were performed on the data with the variables used in the correlation matrix entered as independent variables. The results are presented in Table 8.2.

Variation in keel-length, brood age, brood size, and maximal daily temperature contributed 87.7% of the variance in female body mass during the brooding phase. Females with longer keels and those rearing larger broods were heavier, and body mass increased at higher maximal daily temperatures. Females tended to lose mass over the brooding period as the brood aged.

Although insufficient data were available for male keel-length to be included in the analysis, 62.7% of the variance in male mass during the brooding phase was attributable to variation in season, brood size, and maximal daily temperature. Males were heavier later in the season, and, as with their mates, when maximal daily temperatures were higher and when rearing larger brood sizes (probably because larger birds reared bigger broods). There was no significant tendency for males to lose mass progressively over the brooding period as determined by the stepdown multiple regression analysis.

Table 8.2

Abbreviated stepdown multiple regression analyses of male and female swallow body masses during the brooding phase

(a) Females

Independent Variable	Multiple $r^2 \times 100$	Degrees of Freedom	Regression Equation	t-value	P
keel-length mm	52.5	1,32	$y = 1.50x_1 -$	9.58	***
brood age, days	62.1	2,31	$0.195x_2 +$	-3.74	***
brood size	78.2	3,30	$0.962x_3 +$	5.56	***
maximal daily temperature °C	87.7	4,29	$0.128x_4$ $- 17.9$	4.75	***
F = 51.7, P < 0.001					

(b) Males:

season (days after June 1st)	5.5	1,32	$y = 0.012x_1 +$	2.36	*
brood size	35.3	2,31	$0.965x_2 +$	5.23	***
maximal daily temperature °C	62.7	3,30	$0.091x_3$ $+ 13.2$	4.69	***
F = 16.8, P < 0.001					

* : P < 0.05

** : P < 0.01

*** : P < 0.001

(b) Daily mass changes during the brooding period and the cost of brooding

Swallows of both sexes may gain or lose mass from day to day over the brooding period, although the average tendency is for females to lose mass over this period (Figure 8.1). In Figure 8.3a the distributions of daily mass changes for both sexes during the brooding phase are illustrated. Females tended to lose mass more frequently relative to gaining mass than did males, and the mean average daily mass change between the sexes was significantly different ($t = 2.7, P < 0.01$), although both sexes tended to lose mass. There was no significant difference between male and female daily mass gains during the brooding phase (Figure 8.3b, $t = 1.0, ns$), although female daily mass losses were significantly greater than those of males ($t = 3.1, P < 0.01$).

Female mass losses during the brooding phase may be adaptive, the bird shedding mass to liberate energy from lipid to reduce self-feeding, and to cause flight costs to be reduced (Freed, 1981; Norberg, 1981). Alternatively mass losses may represent a condition cost to the female because the large amount of time invested in brooding limits her self-feeding time, and she is forced to live off her body reserves (Nur, 1984a). Mass losses during early nestling rearing may also be viewed as a balance between the costs and benefits outlined above (Norberg, 1981; Nur, 1984a).

To investigate these hypotheses in more detail, a series of replacement experiments was performed, whereby pairs were given younger nestlings after the brooding phase had ended. If brooding is necessarily costly to the female, she would be expected to undergo a further decline in body mass once her brooding time is increased,

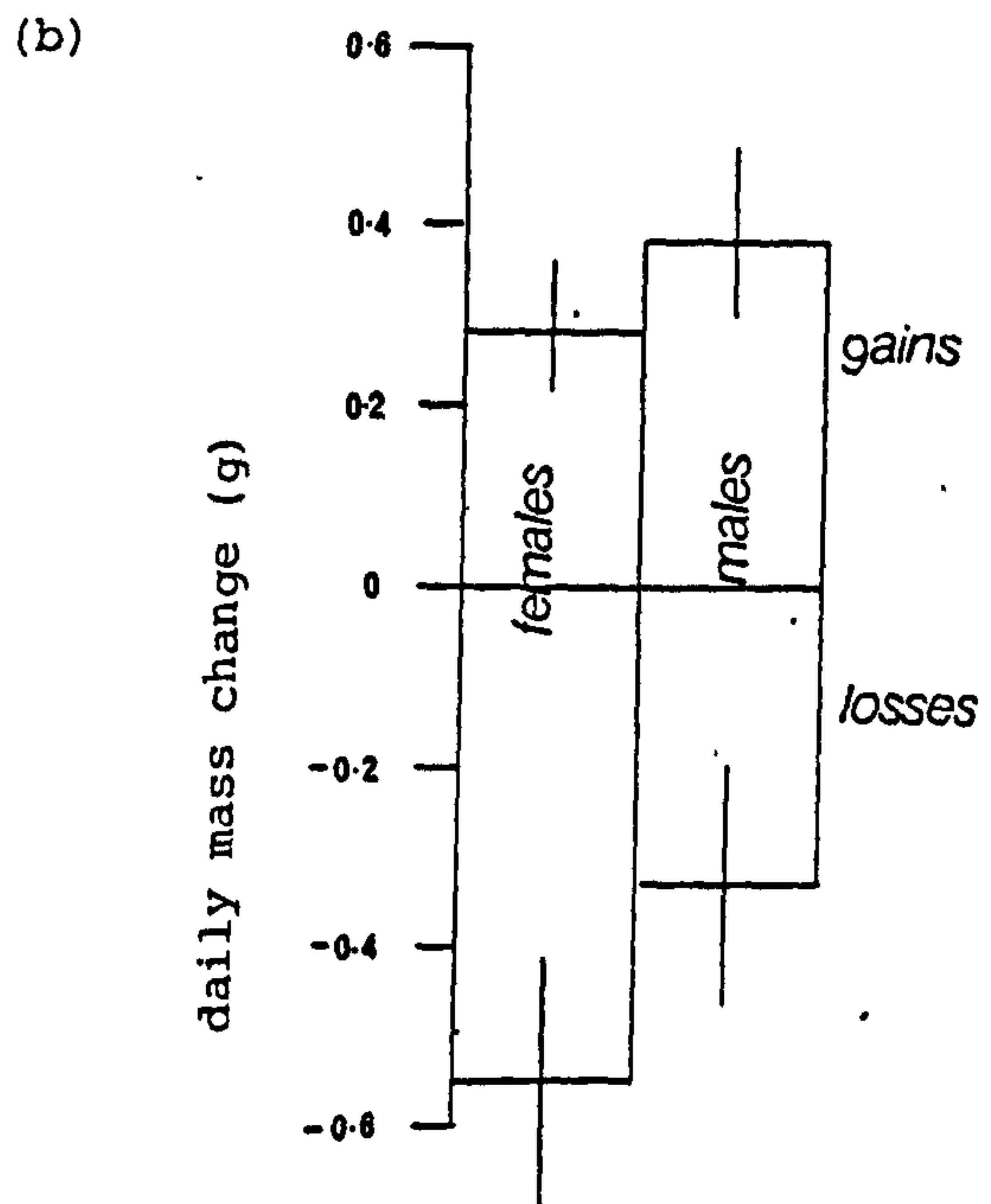
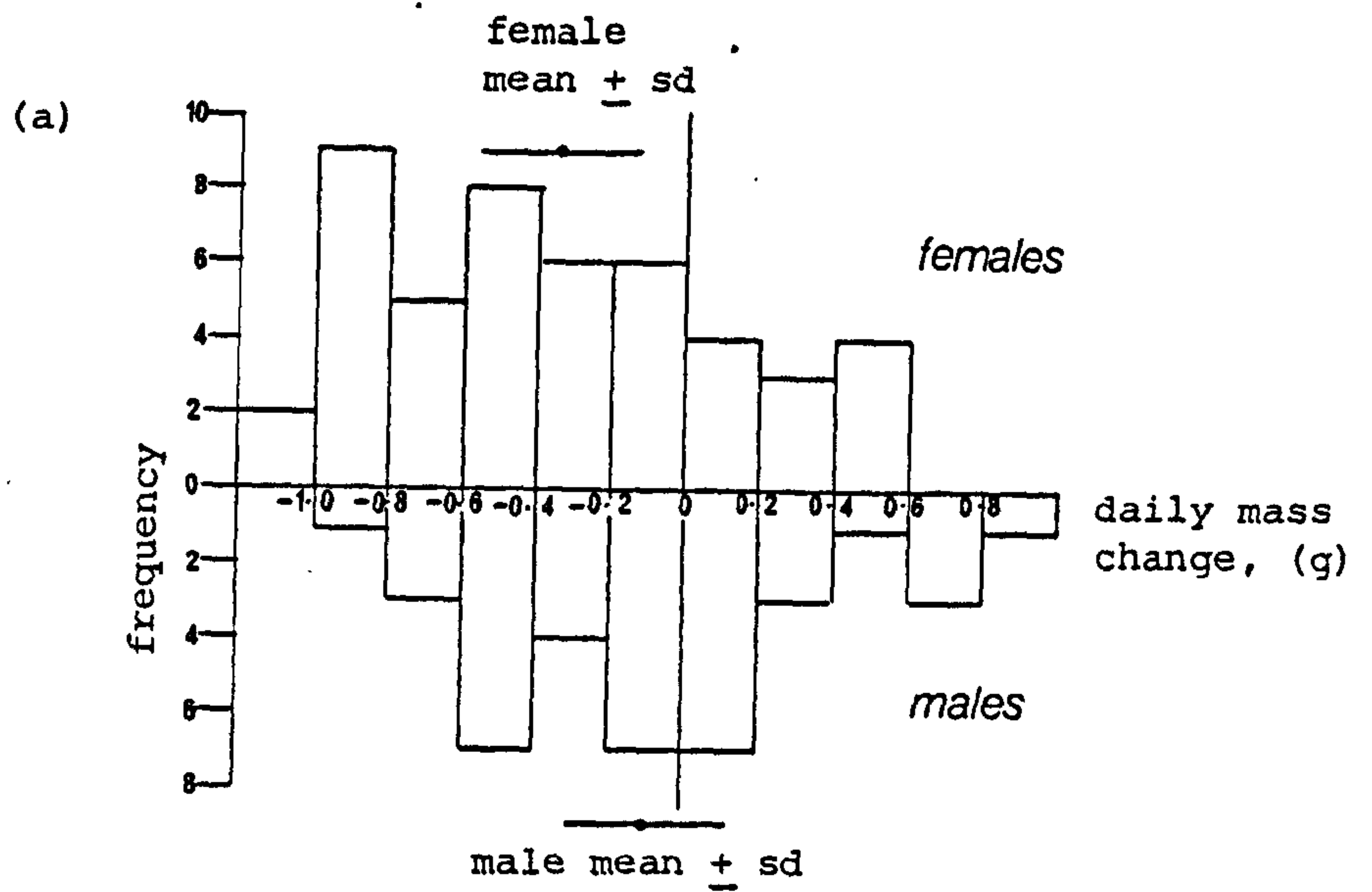


Figure 8.3

Daily mass changes of swallows during the brooding phase.

- (a) Frequency distribution of male and female daily mass changes.
- (b) Mean values (\pm sd) of daily mass gains and losses for each sex.

or alternatively any costs may be directed towards the brood, which may show decreased growth rates if insufficiently fed. The results of the replacement experiments will be presented after an analysis of brooding behaviour by female swallows.

8.3.3 Female brooding behaviour

The decline in the amount of afternoon time spent brooding (% BROOD) as the chicks become older is illustrated in Figure 8.4. % BROOD declined sigmoidally as the brood aged, decreasing to under 10% after day 8. The decline in % BROOD between days 0 and 7 is almost linear, and a stepdown multiple regression analysis was performed for this period with brood age, brood size, and maximal daily temperature entered as the independent variables (Table 8.3).

Females spent less time brooding as the chicks became older and with larger brood sizes. An increase in brood size by one chick reduced % BROOD by 0.7 of a day, due in part to the reduced thermoregulatory demands of larger broods (Royama, 1966a). Maximal daily temperature did not enter the analysis as a significant variable, although female gray catbirds spent more time brooding at low ambient temperatures (Johnson and Best, 1982).

8.3.4 Replacement experiments

(a) The effect on female brooding behaviour

Female swallows markedly increased % BROOD when given younger chicks in replacement experiments (Figure 8.5). For example, female (a) had completed afternoon brooding by day 7, but spent 70% of her afternoon time brooding on the subsequent day after being given one day old chicks.

Although % BROOD was increased to high levels in replacement

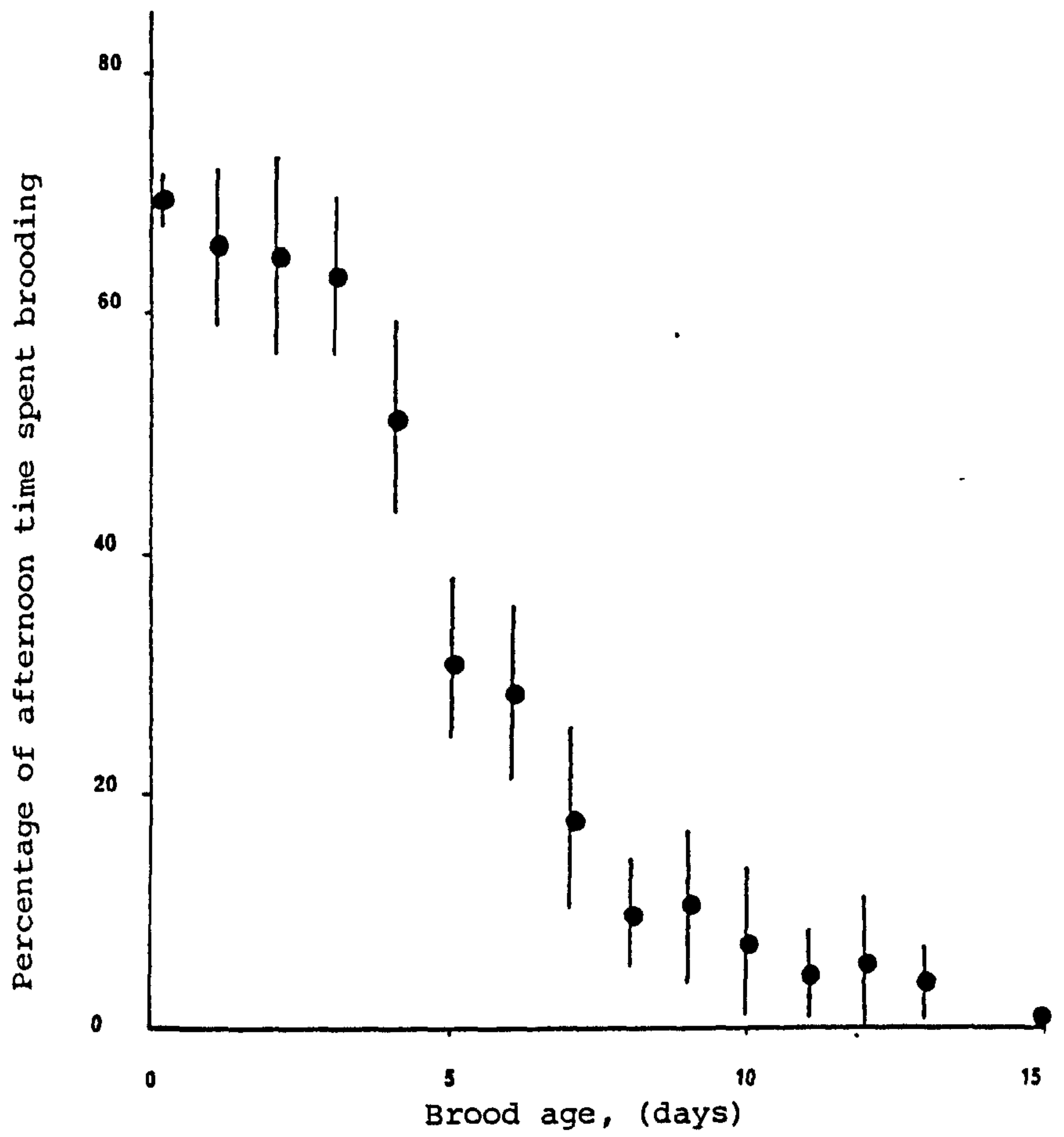


Figure 8.4

The percentage of afternoon time spent brooding by female swallows as a function of brood age. Means \pm sds illustrated.

Table 8.3

Abbreviated stepdown multiple regression analysis of percentage of afternoon time spent brooding during the first eight days of the nestling-rearing phase in female swallows

Independent variable	Multiple $r^2 \times 100$	Degrees of Freedom	Regression Equation	t-value	P
Brood size	7.1	1,76	$y = -4.49x_1$	4.03	***
Brood age, days	65.7	2,75	$-6.49x_2 + 91.5$	9.36	***

$$F = 74.8, P < 0.001$$

*** : $P < 0.001$

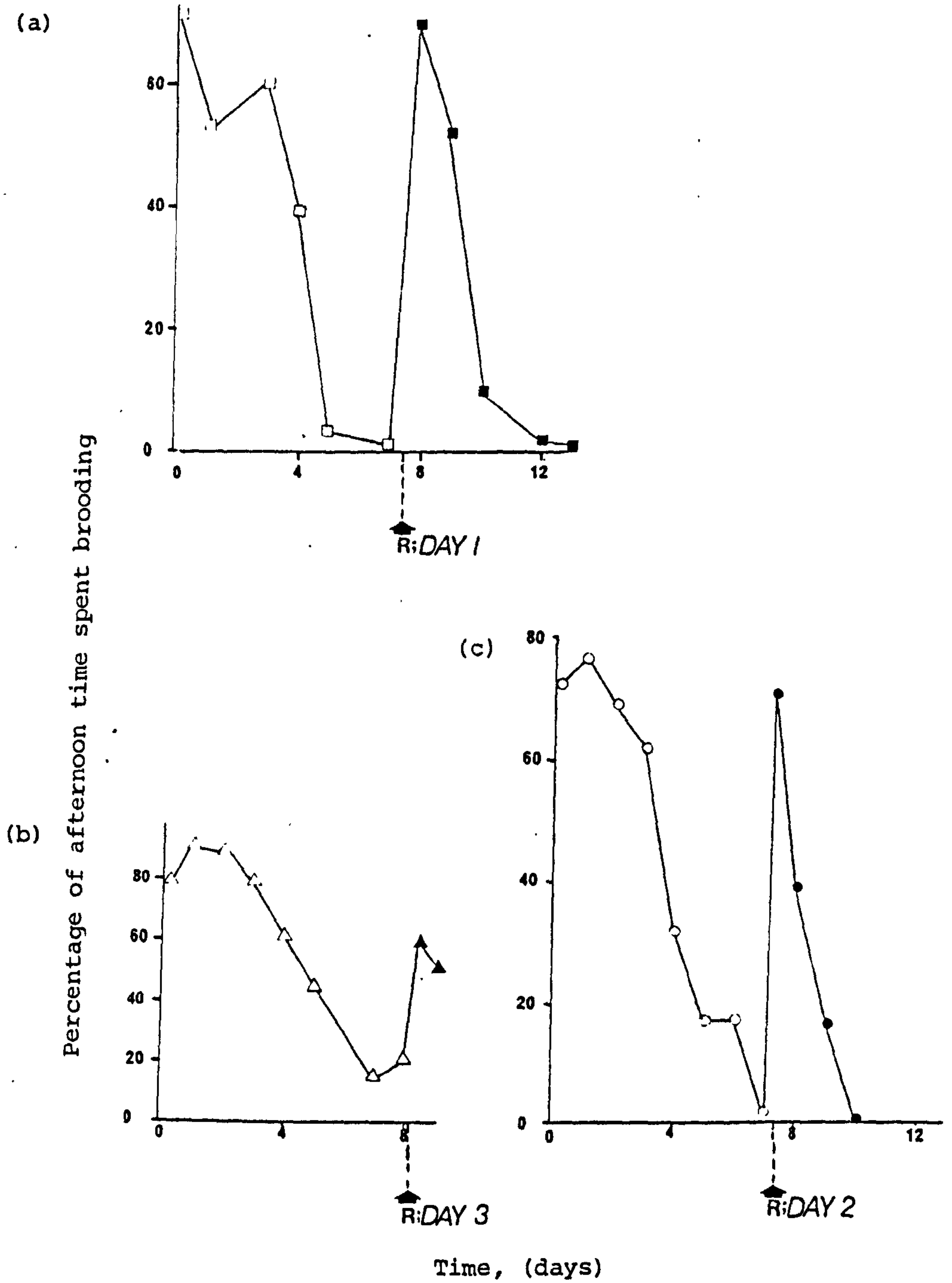


Figure 8.5

The consequences of replacement experiments for the brooding behaviour of three female swallows.

Open symbols - period when natural brood present.

Closed symbols-period when experimentally replaced brood present.

R denotes the timing of the replacement experiment, and arrows point to the age of the newly replaced chicks.

experiments, it rarely attained levels expected for control broods of known age as determined from the regression equation in Table 8.3 (Figure 8.6). Expected % BROOD was greater than that observed in nine of the 12 hours of observation, the difference between observed and expected being highly significant ($\chi^2 = 132.5$, $P < 0.001$).

(b) The effect on brood growth and chick mortality rates

Despite the slight decrease in brooding which replaced chicks encountered, brood masses in replacement experiments were not significantly different from control brood masses of the same brood size and age ($\chi^2 = 2.3$, $n = 13$, ns). However, in only one replacement experiment did all of the chicks survive the brooding phase.

In one experimental nest one chick in a brood of four died, whilst two complete broods of three and four died. In one of these nests, day 9 chicks, still requiring some daytime brooding, were given to parents rearing day 17 chicks, which required no brooding. Although the replaced chicks were fed as frequently as expected (1.76g of food delivered h^{-1} to a brood of three), they were never brooded and appeared to chill. Indeed, all chick mortality in replacement experiments was probably due to chilling rather than undernourishment. No nestlings in control broods died at the same period as replacement experiments were being conducted.

(c) The effects on adult foraging behaviour

The mass of food loads delivered to broods increased rapidly over the brooding phase, as did the provisioning rate by the parents (section 8.3.7). Hence if adults are given younger chicks to rear, they may modify their foraging behaviour to meet the reduced demands of the younger chicks, or may continue provisioning the new chicks

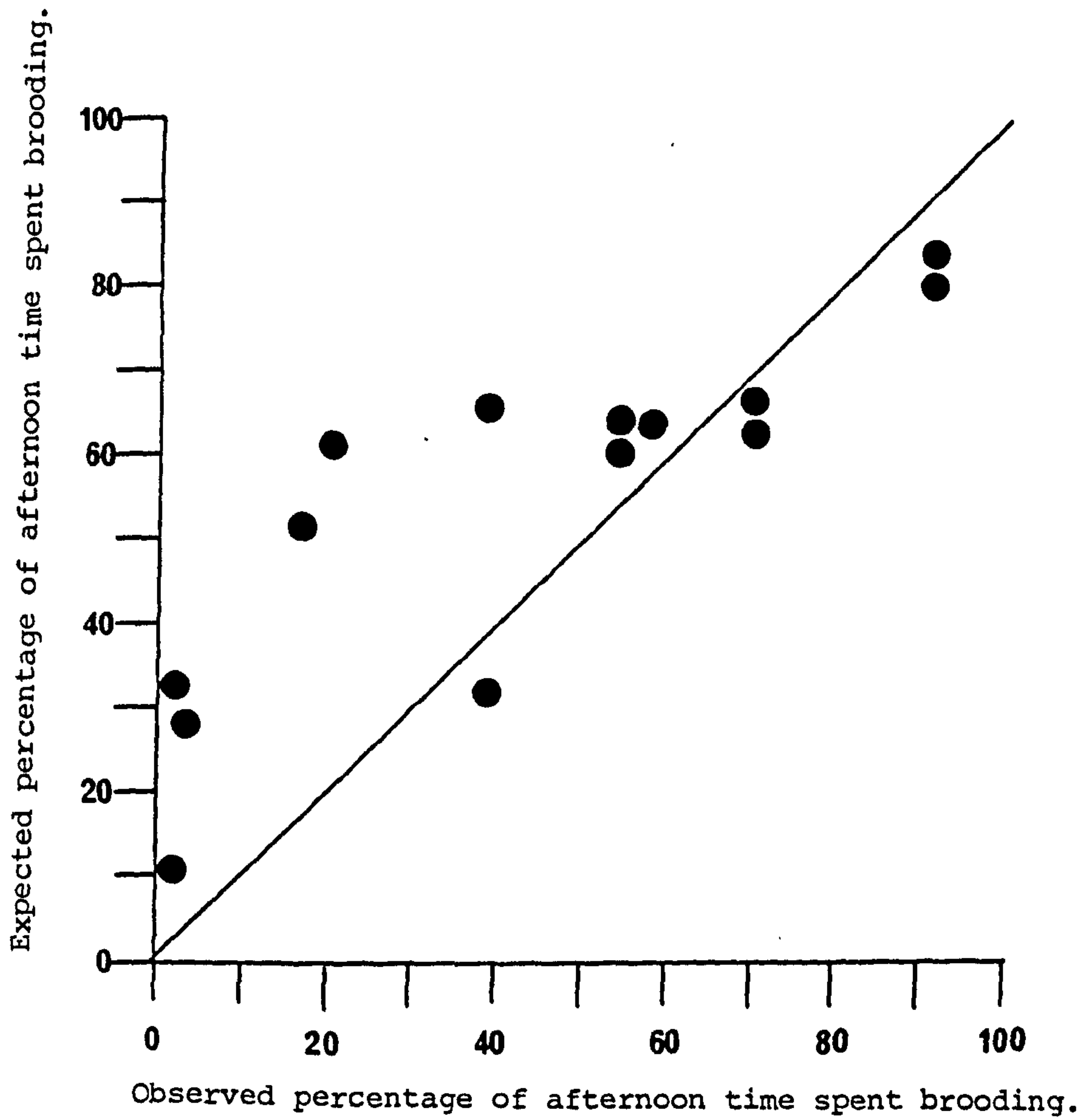


Figure 8.6

Observed and expected percentages of afternoon time spent brooding by female swallows in replacement experiments.

The solid line represents observed = expected.

See text for calculation of expected brooding time.

according to their 'expected' behaviour as if still rearing older chicks. The latter situation occurs in puffins, Fratercula arctica, (Hudson, 1979).

(i) Changes in load mass:

Load mass changes during replacement experiments are shown in Figure 8.7 for three males and two females. In all birds load size increased over the control period of six to seven days, though the shape of the load mass/brood age curve varied considerably amongst individuals.

Both sexes at nest 'gu' brought back smaller loads when given younger chicks, as did the male at nest 'SLB'. Moreover, the load mass reduction response at nest 'gu' was immediate, with smaller loads returned within two hours of the experiment commencing. However, neither parent at nest 'G' showed any obvious tendency to reduce load mass when given younger chicks.

(ii) Changes in feeding rates and food delivery rates:

Changes in feeding rates and FDRs during two replacement experiments are illustrated in Figure 8.8.

In both cases feeding rates and FDRs fell at the start of the replacement experiment, and increased during initiation of brood enlargement experiments, showing that the parents were responding to the demands of the experimental broods rather than to the expected demands of the broods they initially hatched. Behavioural modification was rapid, occurring seemingly to its full extent within one day of the transfers.

During each replacement experiment the feeding rate of the male parent fell below that of the female, although the male feeding

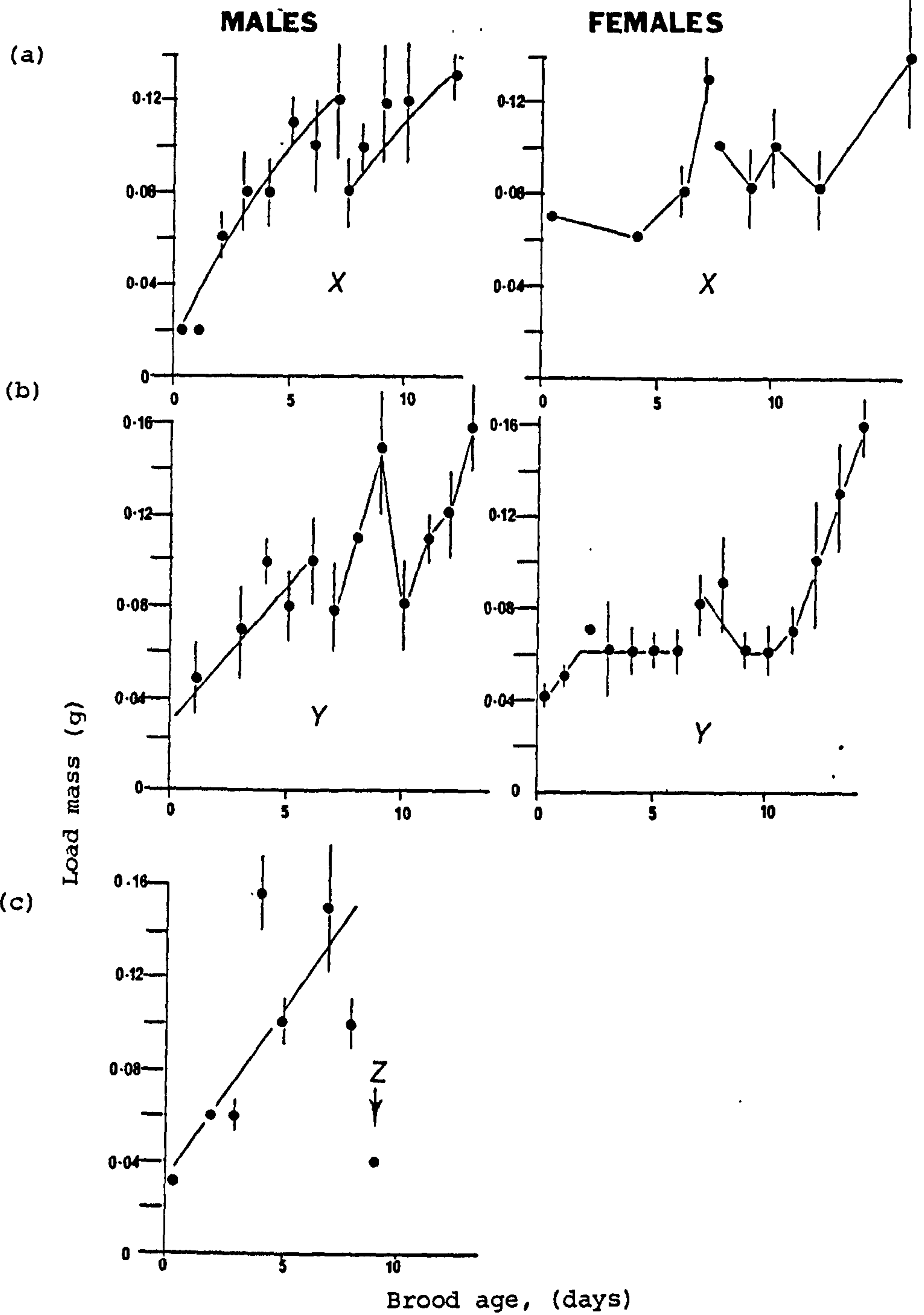


Figure 8.7

Load mass changes of adult swallows during replacement experiments.

(a) Nest 'gu': day 2 chicks replaced day 7 chicks at X.

(b) Nest 'G' : day 2 chicks replaced day 7 chicks at Y.

(c) Nest 'SLB' : day 3 chicks replaced day 8 chicks at Z.

Means \pm sds of load masses are illustrated, curves fitted by eye.

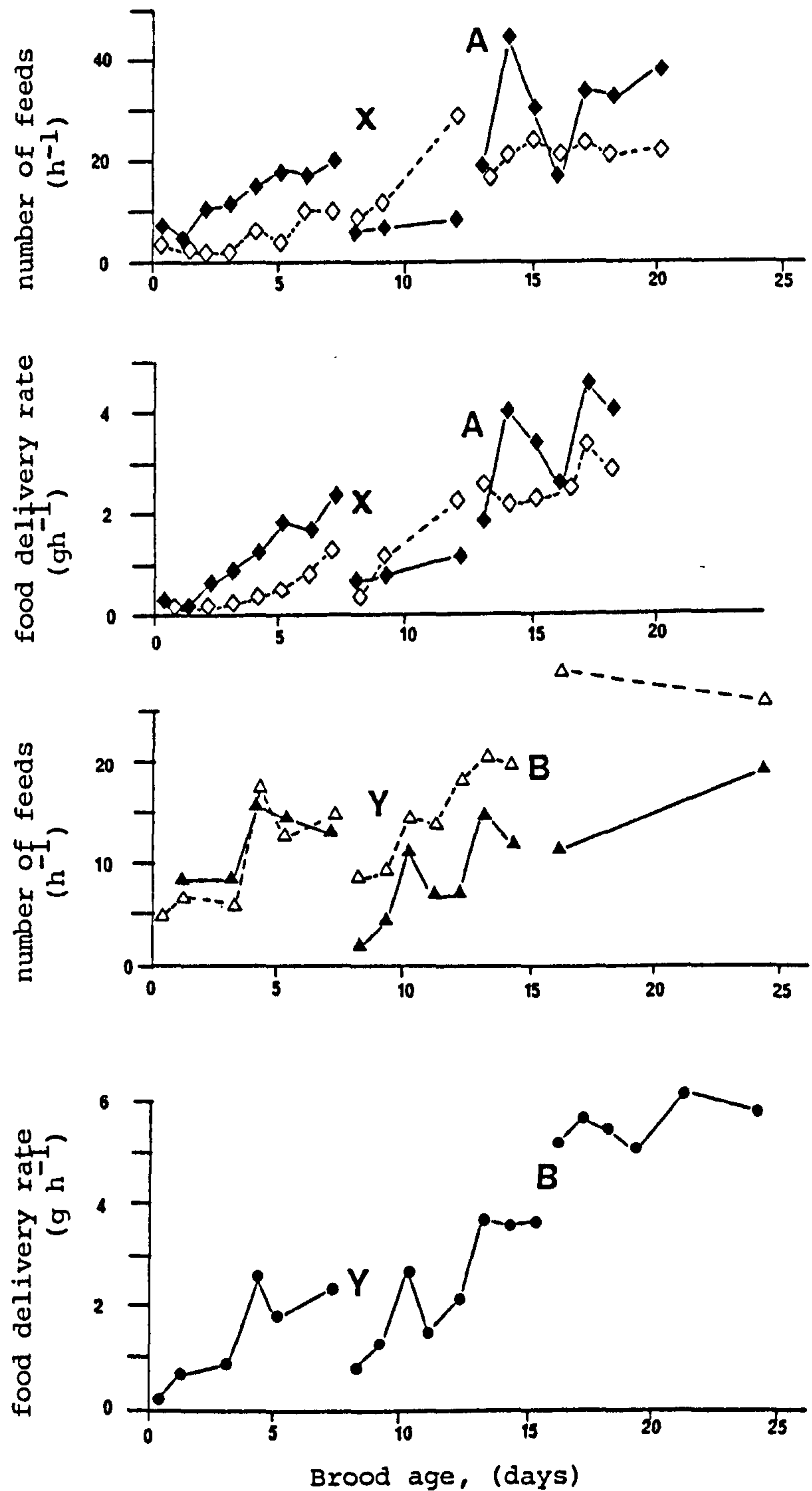


Figure 8.8

The effects of experimental manipulation of brood age and brood size on feeding rate, and food delivery rates of adult swallows at two nests.

- (a) Nest 'gu'. Solid diamonds - male, open diamonds - female. At X day 2 chicks replaced day 7 chicks, at A brood size was enlarged from four to seven chicks.
- (b) Nest 'G'. Solid triangles - male, open triangles - female. Solid circles represent data for both sexes combined. At Y day 2 chicks replaced day 7 chicks, at B brood size was enlarged from three to five young.

rate was similar to or higher than that of the female during the control period. There may therefore be reduced male investment relative to the female during replacement experiments, although it remains possible that males may have been more sensitive to disturbance associated with manipulation than females.

(d) The effects on adult body mass changes:

As outlined above, if brooding is necessarily costly to a female in that it reduces her time available for self-feeding, artificially increasing her brooding time after the brooding phase is completed should induce the female to undergo further rapid mass loss.

Parental body mass changes during three replacement experiments are illustrated in Figure 8.9. Both sexes tended to lose mass over the control period (males, $r = -0.47$, $n = 22$, $P < 0.05$; females $r = -0.55$, $n = 23$, $P < 0.01$), although neither sex lost mass significantly during the replacement experiments (males $r = -0.26$, $n = 10$, $P > 0.2$; females $r = -0.08$, $n = 11$, $P > 0.5$) even though % BROOD was increased from 0-15% to 60-70%. Hence the results from the replacement experiments do not support the view that female mass loss during the brooding phase is costly as a consequence of limited time for self-feeding.

8.3.5 Adult masses during the non-brooding phase

Between days 8 and 21 of nestling-rearing, the body masses of both male and female swallows attained relatively low, stable values (Figure 8.1). To determine the factors influencing adult body mass during this period, a stepdown multiple regression analysis was performed on 30 days of control pair data with the same independent variables entered as for the brooding phase analysis. A correlation

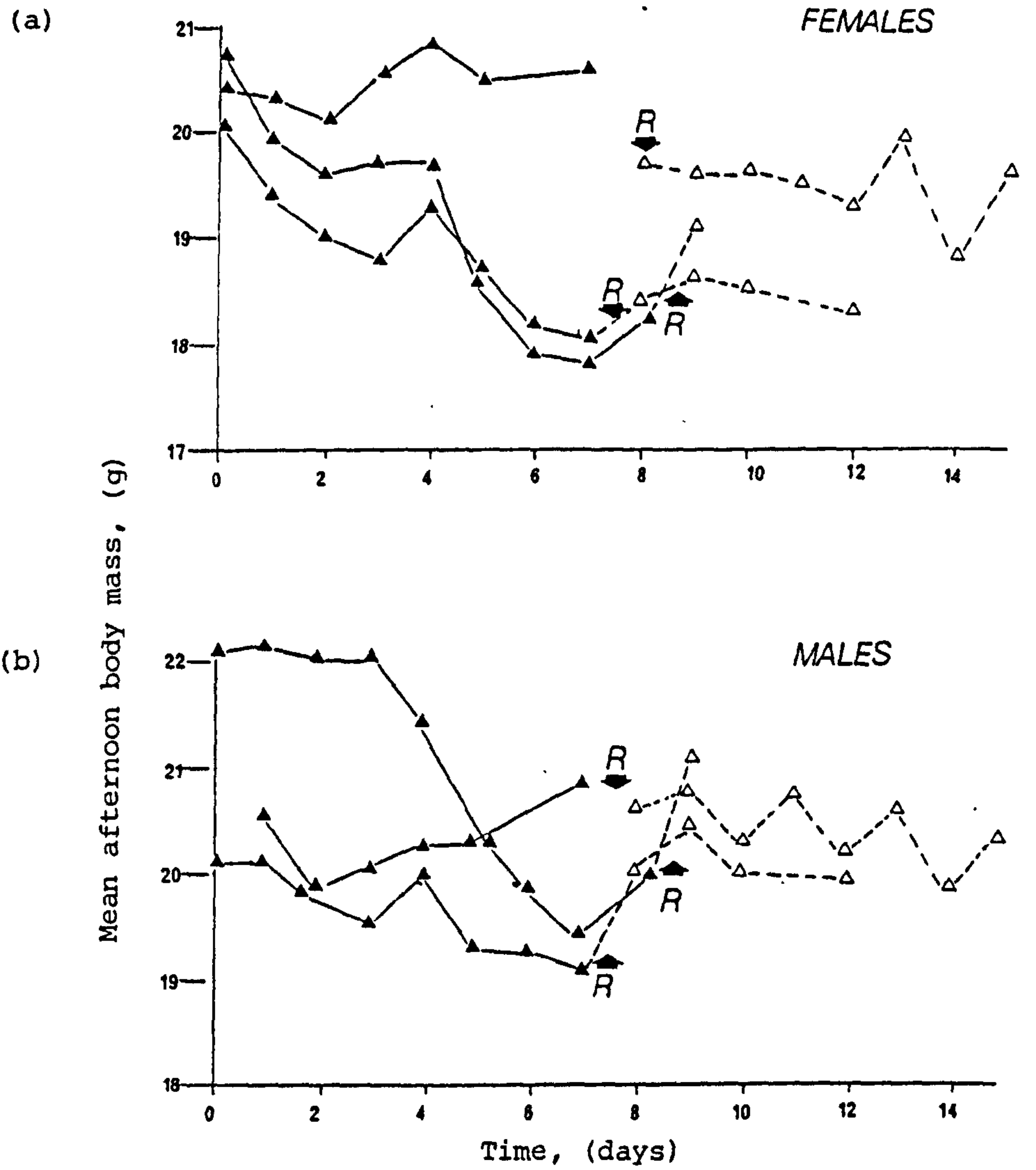


Figure 8.9

The effects of replacement experiments on adult body mass changes in swallows.

Solid triangles and solid lines: control period

Open triangles and pecked lines: replacement experimental period.

R denotes timing of replacement experiment.

- (a) Females
- (b) Males

matrix is presented in Table 8.4, and the abbreviated stepdown multiple regression analysis is summarised in Table 8.5.

Both male and female body masses correlate with similar variables and the correlation between males and female body mass of pairs was positive and highly significant. In both sexes body mass was positively correlated with season, temperature measurements, and sweep net biomass. The results from the stepdown multiple regression analysis show that both male and female body masses were higher if conditions were favourable on the previous day ($t_{\max_{d-1}}$ high), if current levels of food abundance were high, and if the birds were rearing large brood sizes. These variables contributed to 85% of the variance in female mass and 74% of the variance in male mass. There was no significant tendency for birds to lose or gain mass progressively over the non-brooding phase.

Once the relatively stable, low body masses have been attained after the brooding phase, it is more likely that mass losses incurred by the parents represented body condition costs, implying a negative effect on survival. The relationship between adult body mass changes and FDRs could elucidate if high provisioning rates are energetically costly to the parents. For example, in pied kingfishers, Ceryle rudis, parents tended to lose mass when energy expenditure was high at a time when feeding rates to the brood were high (Ryer and Westerterp, in prep.).

Swallows tended to reduce their FDRs when food was scarce (section 8.3.8), and adult body masses also tended to be low when food was less abundant (see above). The percentage mass change from the previous day in adult swallows (including control and experimental

Table 8.4

Correlation matrices of male and female body mass in
 swallows during the non-brooding phase
 (days 8-21 of nestling-rearing)

Variable	female mass, g	male mass, g
season (days after June 1st)	0.736***	0.667***
brood age, days	-0.058 ns	0.044 ns
brood size	-0.105 ns	-0.050 ns
maximal daily temperature, °C on day of weighing	0.740***	0.682***
maximal daily temperature, °C on preceding day	0.649***	0.563**
maximal daily temperature, °C on subsequent days	0.754***	0.669***
sweep net biomass g, dry mass	0.828***	0.776***
mate mass	0.936***	-

Tabulated values are correlation coefficients, r.

ns : not significant;

** : P < 0.01

*** : P < 0.001

n = 30 days of data

Table 8.5

Abbreviated stepdown multiple regression analyses of male and female swallow body masses during the non-brooding phase

(a) Females:

Independent Variable	Multiple $r^2 \times 100$	Degrees of Freedom	Regression equation	t-value	P
brood size	1.1	1,28	$y = 1.16x_1 +$	4.04	***
maximal daily temp. on preceding day °C	55.9	2,27	$0.220x_2 +$	5.20	***
sweep net biomass, mg, dry mass	85	3,26	$0.019x_3 + 9.25$	7.09	***
$F = 49.0, P < 0.001$					

(b) Males:

brood size	0.25	1,28	$y = 0.452x_1 +$	3.10	**
maximal daily temp. on preceding day, °C	45.7	2,27	$0.073x_2 +$	3.40	**
sweep net biomass mg, dry mass	73.8	3,26	$0.007x_3 + 15.8$	5.27	***
$F = 24.2, P < 0.001$					

** : $P < 0.01$ ***: $P < 0.001$

brood sizes) was negatively correlated with the bird's FDR ($r = 0.37$, $n = 68$, $P < 0.01$ all data; $r = -0.42$, $n = 32$, $P < 0.05$ males; $r = -0.35$, $n = 32$, $P < 0.05$ females), so that birds of both sexes tended to lose mass when their delivery rates were sustained at a high level. In a stepdown multiple regression of adult percentage mass changes with FDR and food abundance entered as independent variables, food abundance did not enter as a significant variable (t -value, > 0.05). Logarithmic transformation of FDR and mass changes did not improve the significance of the relationship between delivery rate and mass change in double-log or semi-log plots.

Hence the relationship between FDR and percentage adult mass change from the previous day is apparently linear, suggesting that increases in feeding rate by the adult may be physiologically costly. Nur (1984b) showed a linear relationship between feeding frequency and body mass in blue tits, though no such trend was apparent in males. These linear results contrast with the shape of the response in a female starling, where rate of mass loss increased with increasing time spent flying during nestling-rearing (Drent and Daan, 1980, analysing data of J.M. Tinbergen and co-workers).

The difference between the slopes of male and female mass changes in relation to FDRs was not statistically significant (equations in legend in Figure 8.10: analysis of covariance, $t = 1.93$, $n = 68$, ns).

When experimental brood sizes were removed from the analysis, no correlation existed between mass changes and FDR for the combined data set, or for males and females treated separately (all data; $r = -0.09$, $n = 24$, ns; females, $r = -0.18$, $n = 12$, ns; males, $r = 0.03$, $n = 12$, ns). Individuals delivering food at faster rates to control brood sizes are likely to be of higher quality than birds

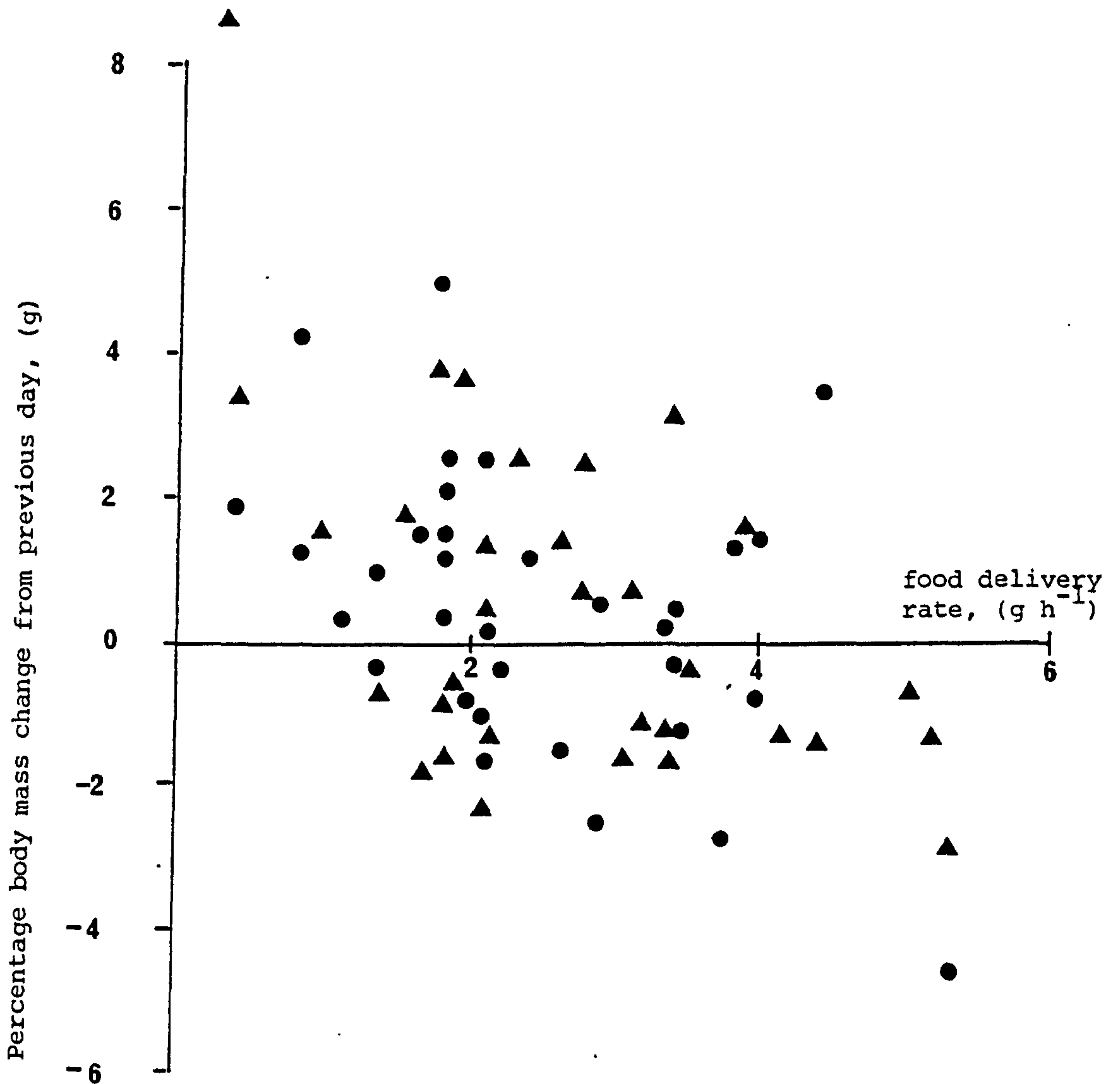


Figure 8.10

The relationship between an adult swallow's percentage body mass change from the previous day and adult food delivery rate to the young.

Data for experimental and control brood sizes is plotted.

Triangles: males; circles: females.

All data: $y = 2.29 - 0.627x$; $r = -0.37$, $n = 64$, $P < 0.001$

Females: $y = 1.99 - 0.47x$; $r = -0.35$, $n = 32$, $P < 0.05$

Males: $y = 2.62 - 0.81x$; $r = -0.42$, $n = 32$, $P < 0.05$

Masses were all recorded during the non-brooding phase.

delivering food at slower rates to their natural broods, and therefore may not suffer any deterioration in body condition despite their rapid delivery rates.

8.3.6 Brood size manipulation experiments

(a) Brood size reduction

One nest (B84) had its brood size reduced from five to two at hatching, while another (GR) had two of its four chicks removed one day after hatching. The consequences for adult body mass changes are illustrated in Figure 8.11. Both males maintained or increased body mass over the rearing period, whilst each female underwent a rapid period of mass loss during the brooding phase as normal, stabilising at a low body mass from day 8 onwards.

(b) Brood size enlargement

Five brood enlargement experiments were conducted, four of which were run throughout the rearing period. Details of the enlargement experiments are presented alongside Figure 8.12, where the effects of brood enlargements on adult body mass change are illustrated.

In only one instance was body mass reduced to a level whereby immediate survival seemed jeopardised: female 'gu' lost 5.4g or 24% of her incubation mass after being subjected to a replacement experiment followed by a brood enlargement.

Two females who reared broods of seven throughout the rearing period (HH, A84) dropped in mass midway through nestling rearing, but completed rearing with masses near to that of control females, despite entering the nestling-rearing phase with body masses substantially lower than the value for controls. Two other females which were given enlarged broods at an early stage of rearing (CN, SLB) lost substantial mass during the brooding phase.

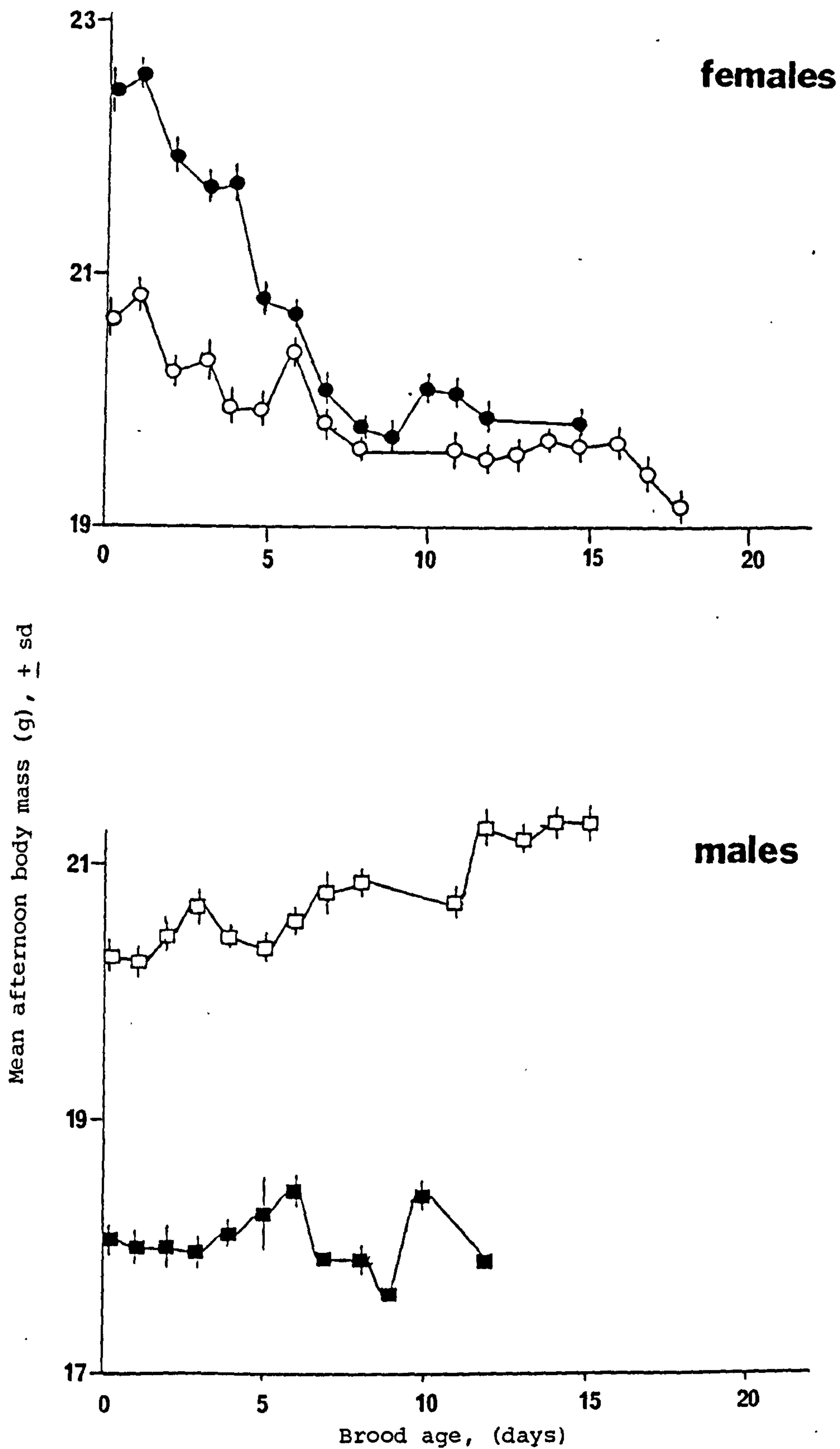


Figure 8.11

The effect of experimentally reducing brood size at hatching on adult body mass changes for two pairs of swallows.

Solid symbols: nest 'GR'; brood size reduced from 4 to 2.
 Open symbols: nest 'B84', brood size reduced from 5 to 2.

Figure 8.12

The effect of brood size enlargement experiments on the body mass changes of adult swallows.

(a) Females

(b) Males

The following brood size enlargement experiments are illustrated:

Number on graph	Nest	Initial brood size	Experimental brood size	Day of transfer
1	'A84'	5	7	0
2	'HH'	4	7	2
3	'CN'	3	7	2
4	'SLB'	3	6	3
5	'gu'*	4	7	8

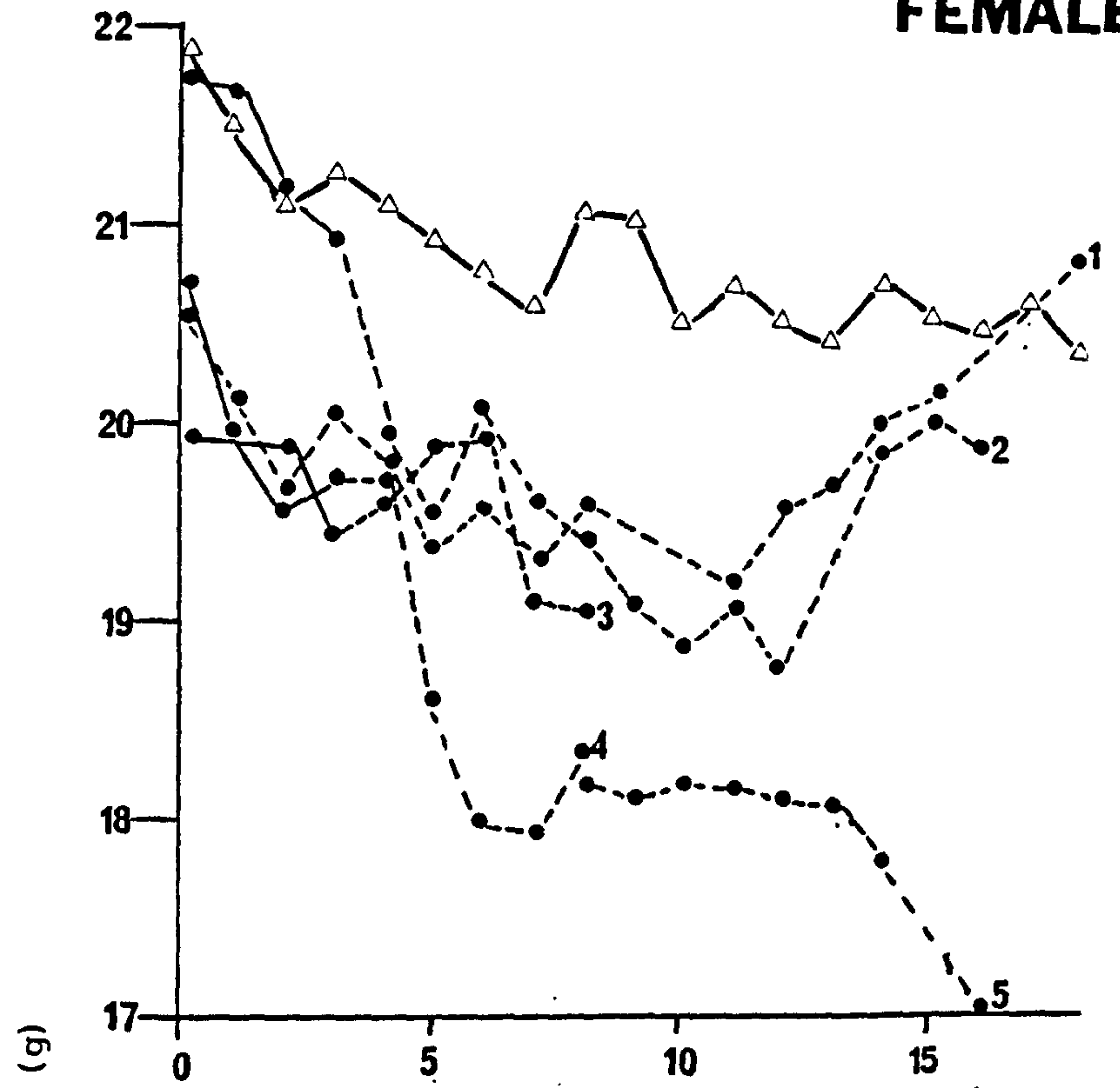
* nest 'gu' underwent a replacement experiment for seven days before the brood enlargement.

Thin solid lines in the figure represent the control period (natural brood sizes), thin pecked lines the experimental period of brood enlargement.

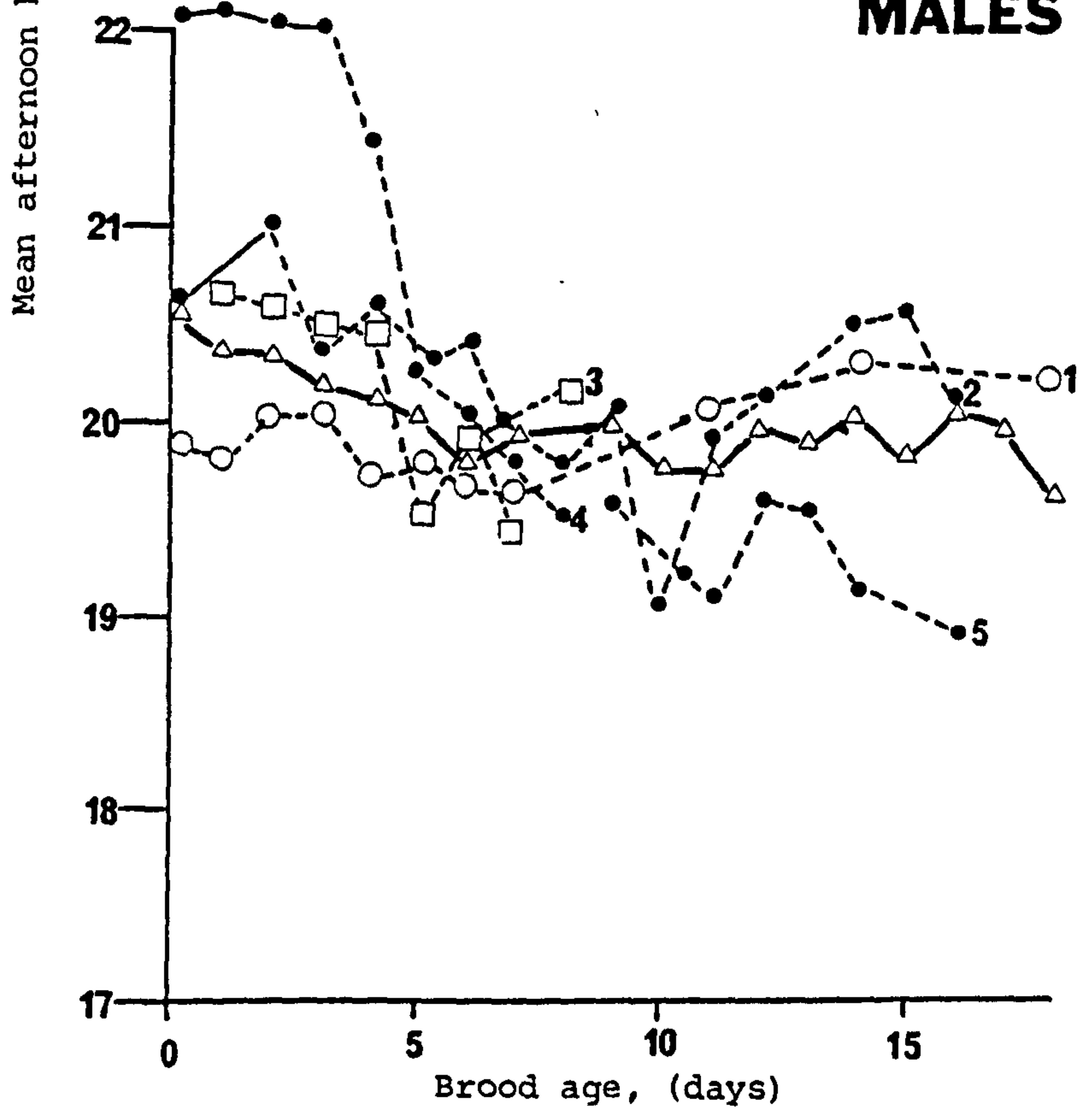
Thick solid lines terminating in 'C' are mean afternoon masses of all birds of one sex raising natural brood sizes.

Different symbols are used to illustrate some individual male masses.

FEMALES



MALES



The only male to deviate substantially from the body mass of control males was 'gu', the bird given a brood size enlargement after a replacement experiment. Males appeared to deviate from the body mass of control birds to a lesser extent than did their mates.

To investigate the significance of brood size enlargement and reduction experiments in greater detail, two pairs nesting within 30 metres of each other, and completing the same clutch size on the same day had their chicks transplanted on the day of hatching. One pair was given eight young (of which one died from falling out of the nest on day 8), the other two young. Hence a simultaneous brood size reduction and enlargement experiment occurred side by side with parent birds subjects to similar environmental circumstances. The consequences of the experiment for adult body mass changes are shown in Figure 8.13.

Males of both pairs increased in mass over the rearing period, the male which was rearing the reduced brood size more so than the male rearing the enlarged brood size. Both females decreased in mass rapidly during the brooding phase, the female rearing brood size two being heavier than the female rearing brood size seven until day 14, after which time the female rearing the larger brood size increased in mass, being 1.6g heavier than the female rearing two chicks by day 18.

The consequences of brood size manipulation for the body mass changes of swallows are not clear cut. Three salient points emerge from the experiments:

(i) There is no strong evidence to suggest that rearing an enlarged brood normally causes deterioration in the body condition of swallows. Mass losses are most likely to be costly during the non-brooding

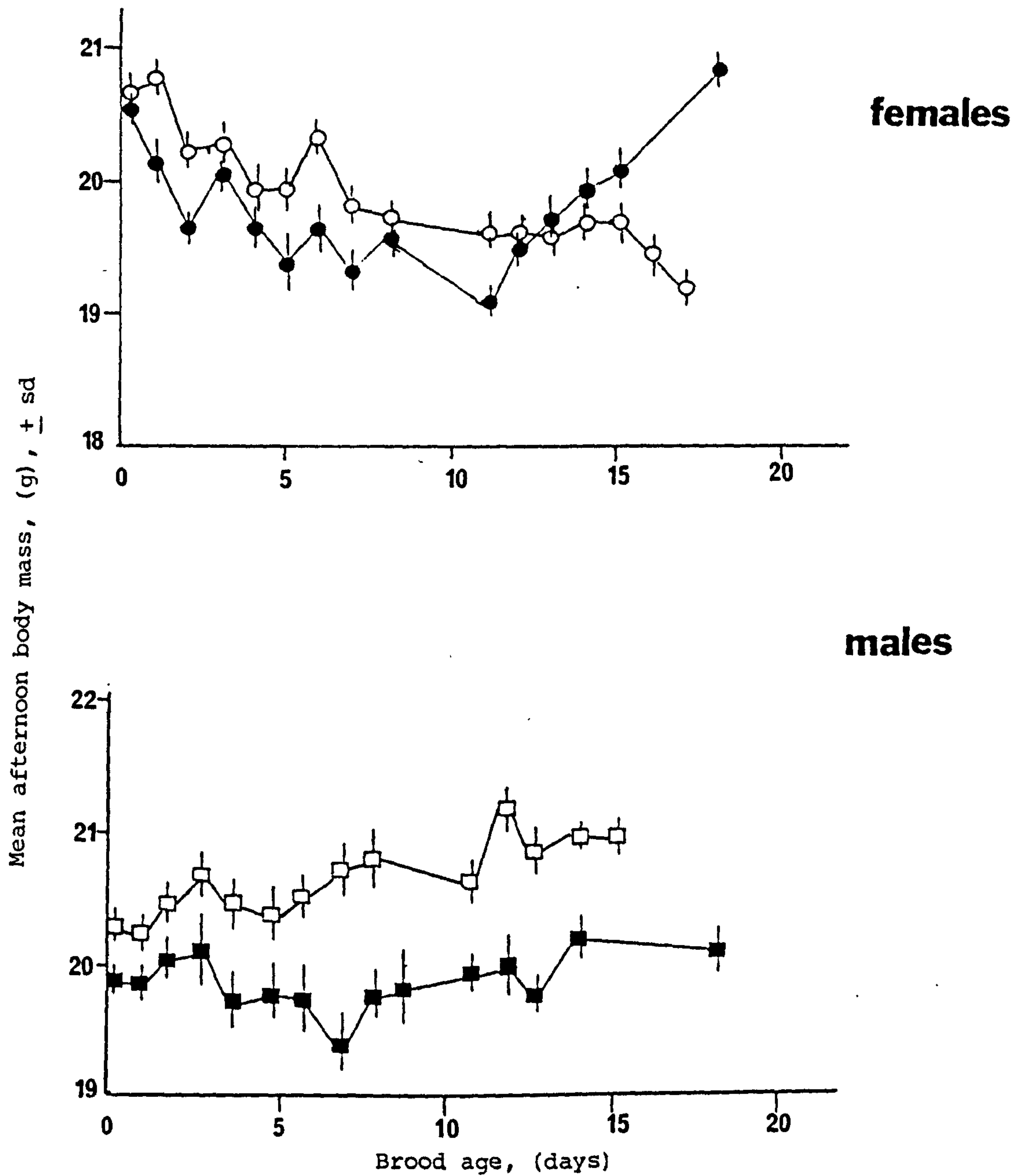


Figure 8.13

The effects of a simultaneous brood size enlargement and brood size reduction experiment on the body mass changes of two pairs of swallows.

Closed symbols: nest 'A84', brood size 8 (7 after day 8)
 Open symbols: nest 'B84', brood size 2

Both nests initially hatched five young and chicks were transferred between nests on the day of hatching.

phase (see above). In Figure 8.14, mean daily mass changes from the previous day, expressed as percentages, are plotted for the non-breeding phase in swallows rearing either reduced, enlarged, or control brood sizes. Males appeared to gain mass when given reduced brood sizes, and to lose mass when rearing control or enlarged brood sizes. Females appeared to lose mass during all treatments. However, none of the differences between means was statistically significant (t-tests, $P > 0.05$), so any effects of changing brood size on adult mass during the non-brooding phase appear to have been slight, although the sample sizes were small using the Mettler balance technique. Female house martins rearing reduced brood sizes gained mass at 0.19g day^{-1} . Those rearing control brood sizes lost -0.07g day^{-1} , while females given enlarged broods lost -0.36g day^{-1} (Bryant, 1979).

(ii) Female swallows shed mass rapidly over the brooding phase when brood size was reduced or enlarged. Incubation body mass, standardised for body size by dividing by keel-length, was positively correlated with clutch size (Figure 8.15) in swallows. There was no evidence to suggest that clutch size was correlated with keel-length ($r = 0.05$, $n = 25$, ns). A heavy body mass in females incubating large clutches may be adaptive in providing considerable lipid reserves to buffer against the increased incubation costs of reheating a large clutch (Chapter 7). A female incubating a clutch of five eggs may 'expect' to hatch five chicks, and may then shed any mass which would have been adaptive during incubation but costly during nestling-rearing regardless of how many chicks actually hatch. Mass loss during rearing will presumably be a function of reproductive commitments during incubation as well as demands during rearing, and incubation and rearing commitments would be different if fewer chicks

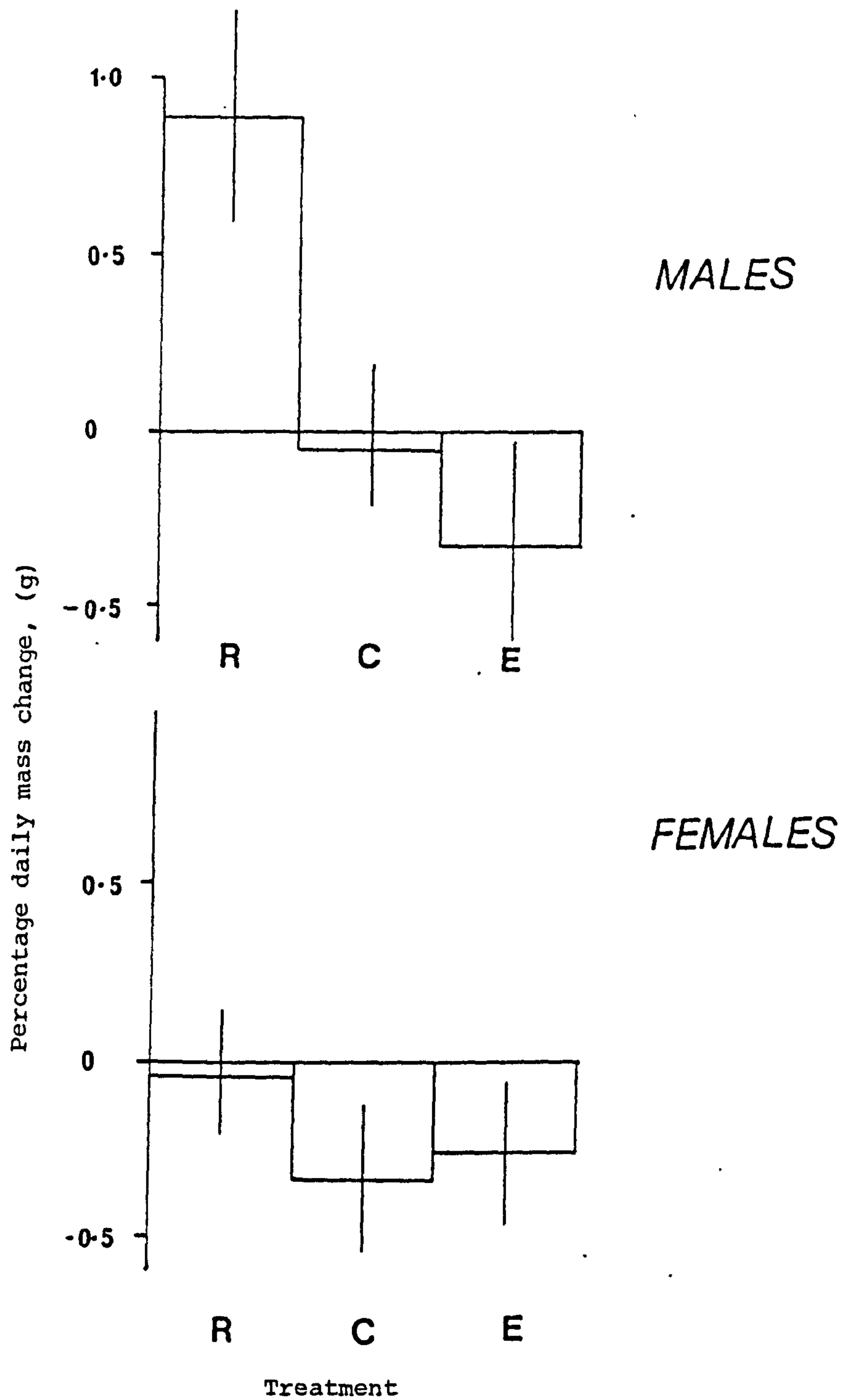


Figure 8.14

Percentage daily mass changes from the previous day during the non-brooding phase for male and female swallows rearing reduced, enlarged, and control brood sizes.

- R - reduced brood sizes of 2
- C - natural brood sizes of 4 and 5
- E - enlarged brood sizes of 7

Means \pm standard errors illustrated.

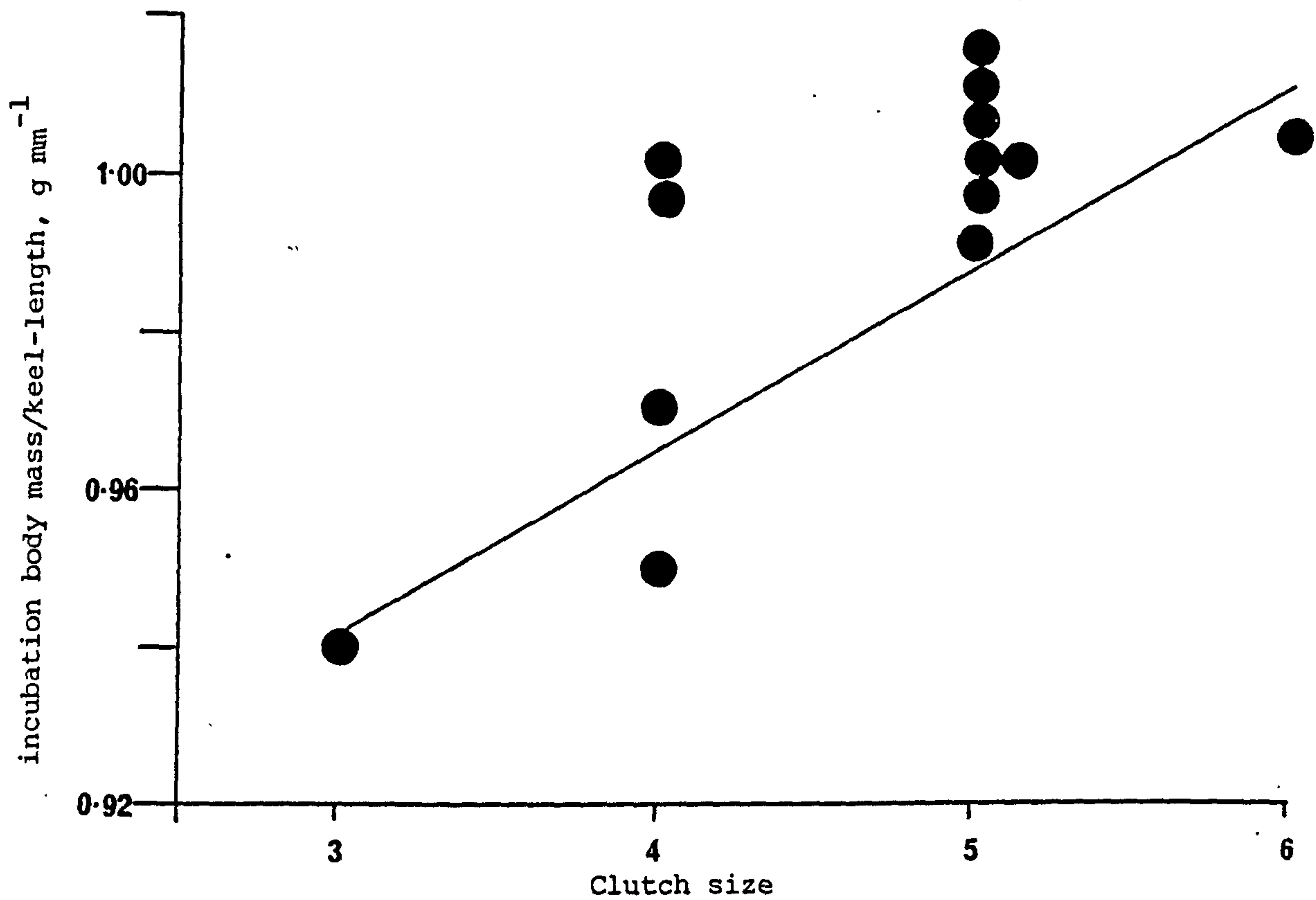


Figure 8.15

The relationship between incubation body mass (means of incubation period) and clutch size in female swallows.

Incubation masses are divided by keel-length to standardise for body size differences.

The regression equation is:

$$y = 0.784 + 0.053x; \quad r = 0.63, \quad n = 14, \quad P < 0.05.$$

were hatched than the number of eggs laid, or if brood size were experimentally manipulated.

(iii) Females appeared to deviate more from the masses of control birds during brood size manipulation experiments than did males.

8.3.7 Parental foraging ecology and feeding behaviour during nestling rearing

The behavioural ecology of swallow foraging has been studied in the context of optimal foraging theory by Waugh (1978) and Turner (1982b), and central place foraging theory (Orians and Pearson, 1979) by Bryant and Turner (1982). Previous tests of theories of avian foraging ecology have drawn on load size data collected by collaring nestlings, which may influence chick begging behaviour and load sizes delivered by the parents (Johnson et al., 1980). Moreover, previous studies of swallow foraging have made assumptions about parental self-feeding rates during bolus collection. The use of precision automated nest balances allows load masses to be monitored without collaring nestlings, and allows adult self-feeding behaviour to be investigated through an analysis of instantaneous body mass changes during foraging.

Parental self-feeding behaviour while collecting food for the brood is central to an understanding of long-term parent:offspring resource allocation in swallows since adult self-feeding rates will be responsible for longer term changes in body mass during nestling rearing. In this sub-section, factors influencing load masses, brood provisioning rates, and adult self-feeding rates will be considered in the context of parent:offspring resource allocation strategies.

(a) Load masses

(i) The effects of brood age

Load masses delivered by both male and female swallows increased as the brood aged, attaining an asymptotic mass from day 8 onwards, although female load mass may perhaps decline towards the end of the rearing period (Figure 8.16). Load size increased with nestling age in starlings (Dunnet, 1955; Tinbergen, 1981), great tits (Royama, 1966a), and wheatears O. oenanthe, (Carlson and Moreno, 1982).

Presumably the optimal load size delivered to the brood will be constrained in part by chick gape size (Fagerström, Moreno and Carlson, 1983). Small chicks may not be able to swallow large loads, and it may be uneconomical for the parents to split one large load amongst the brood. Although load splitting in swallows does occur for a few days after the nestlings hatch, it is an infrequent event. Five per cent of 40 closely observed feeding visits to day 0-2 nestlings resulted in bolus splitting by the parents.

The similarity between the load mass/brood age curves for males and females during the brooding phase suggests that female brooding behaviour does not modify her optimal load size over this time. Once the brooding phase is complete, load masses reached stable, relatively high values for both sexes when adult body masses had attained relatively stable, low values. This asymptotic load mass may be that which maximises parental feeding efficiency (Orians and Pearson, 1979; Bryant and Turner, 1982) at a time when nestling demand is greatest (Figure 8.1).

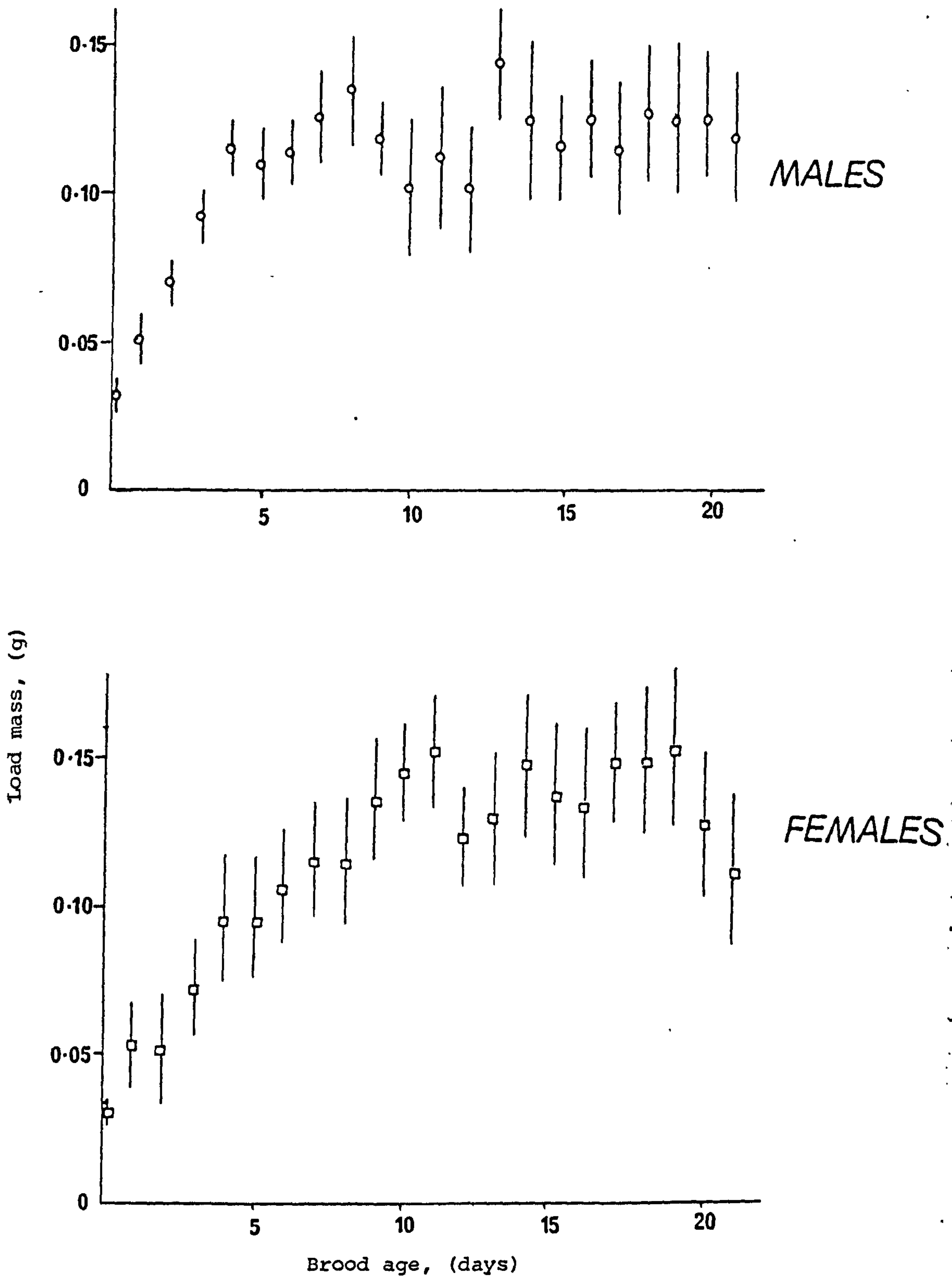


Figure 8.16

Load mass as a function of brood age for male and female swallows.

Means \pm sds are illustrated.

(ii) Sexual differences in load mass

Sexual size dimorphism in birds may result in a different optimal load mass for each parent, as seen in wheatears (Carlson and Moreno, 1983). Male swallows in this study tended to have significantly longer keels than females (Chapter 2), and if differences in bill morphology between the sexes also occur, male and female swallows may deliver different load sizes to their broods.

Male and female load masses were compared in parents rearing natural broods for eight females at 10 nests and three males at six nests for loads delivered between days 8 and 16 for the nestling-rearing period. The males delivered significantly smaller loads than females (0.115 ± 0.005 g males, $n = 281$; 0.137 ± 0.006 g females, $n = 425$; $t = 5.2$, $P < 0.001$), despite the males having significantly longer keels than the females (22.98 ± 0.45 mm keel length of males; 21.82 ± 0.82 mm females; $t = 19.8$, $P < 0.001$).

(iii) The influence of adult age on load mass delivered to the nestlings

Several studies have shown that adult birds forage more efficiently than youngsters, harvesting more energy per unit of time spent feeding (Orians, 1969; Dunn, 1972; Groves, 1978; Burger, 1980). Indeed, age differences in foraging ability may persist for several years in some species (Norton-Griffiths, 1968; Recher and Recher, 1969). If the foraging ability of swallows improved with adult age, older adults may be able to rear more offspring than younger birds because of their age-related foraging efficiency.

Two male swallows had balances placed under their nests for more than one year of the study. Male B47 had load sizes monitored for two broods in 1982 and one brood in 1983. Male B69 was studied for

one brood in 1982, two broods in 1983, and one brood in 1984. Mean load masses for these birds over days 8-16 of the nestling-rearing period are illustrated in Figure 8.17. Although there was a tendency for both these males to increase their mean load mass as they became older, differences in mean load masses between years were small and statistically insignificant ($t > 0.05$ all cases).

Foraging efficiency will also be a function of the feeding rate of adults, but insufficient data were available to examine differences in feeding rate of birds of known age.

(iv) Other factors influencing load mass in swallows

For eight female swallows at 10 nests, load mass between days 8 and 16 of the nestling-rearing period was significantly positively correlated with keel-length ($r = 0.18$, $n = 425$, $P < 0.001$). Insufficient keel-length information was available for a similar comparison to be made amongst males, though when male loads and female loads were combined, the keel-length/load mass correlation was lost because males, although having longer keels, collected lighter loads than females (see above).

When 706 loads from 11 birds (eight females, three males) at 16 nests were analysed, load mass was significantly negatively correlated with season (days after June 1st, $r = -0.09$, $P < 0.05$), but was not significantly correlated with brood size ($r = 0.03$, ns) or with adult body mass ($r = 0.07$, ns). The load size delivered to second brood swallow nestlings was found to be smaller than that delivered to first broods earlier in the season by both Waugh (1978) and Turner (1980).

A stepdown multiple regression analysis of load mass with the

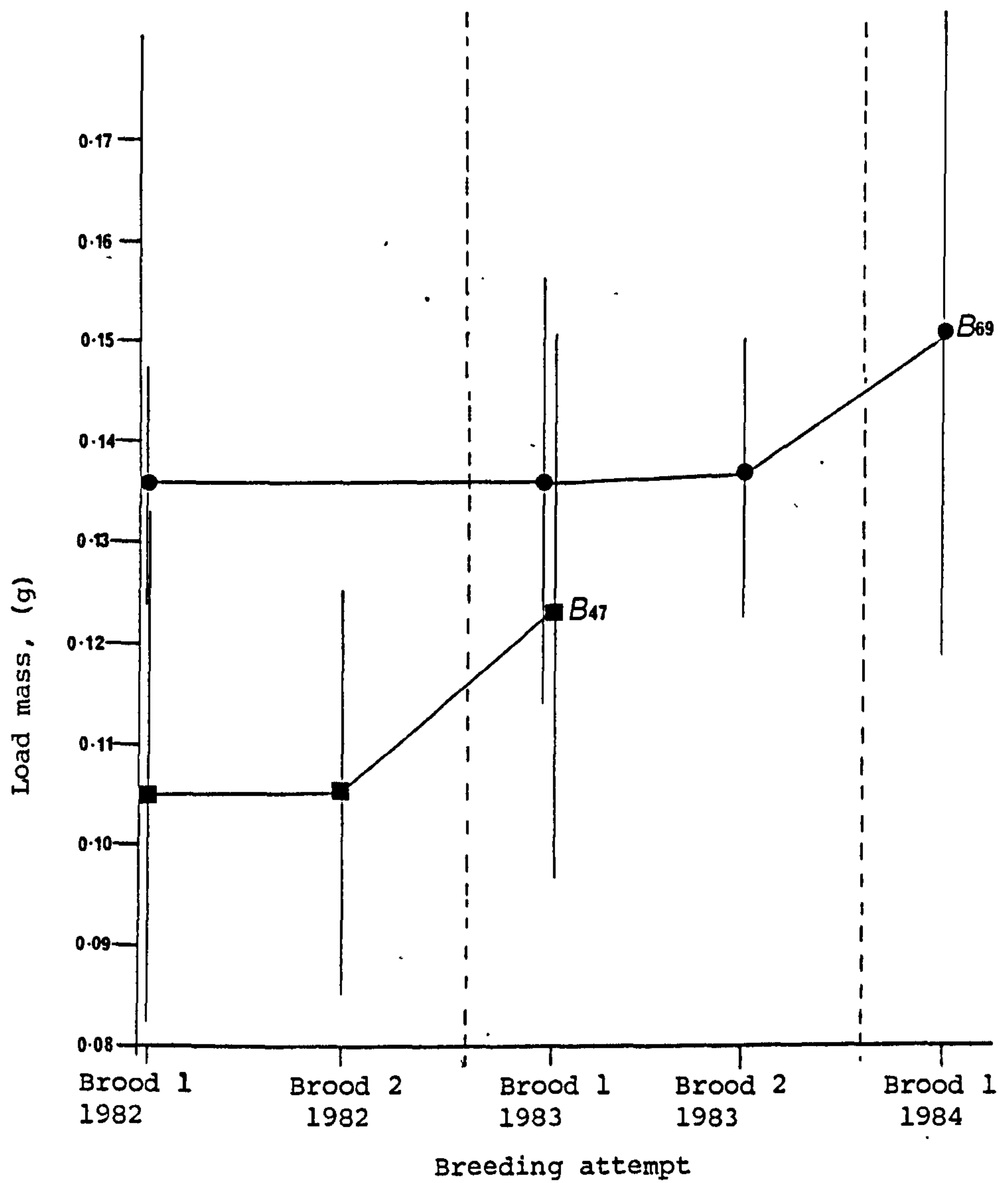


Figure 8.17

The effect of age on load masses delivered by two male swallows (B69 and B47).

Load masses are mean values between days 8 and 16 of nestling rearing.

Means \pm sds illustrated.

above mentioned independent variables entered in the analysis resulted in season ($t = 2.8$, $P < 0.01$), and adult body mass ($t = 2.3$, $P < 0.05$) entering as significant variables. The regression equation was

$$(100 \times \text{load mass, g}) = 5.19 - 0.022 (\text{season}) + 0.442 (\text{adult body mass, g})$$

($r^2 = 1.3\%$, $F = 5.5$, $n = 706$, $P < 0.05$).

The suggestion that load mass was greater in heavier birds may be because the females sampled were significantly heavier than the males ($t = 5.7$, $P < 0.001$), and females delivered significantly heavier loads than males.

Meal mass may act as a constraint on optimal load size in hummingbirds (De Benedictis et al., 1978) because heavier birds would have increased flight costs, and meal mass contributes substantially to overall body mass. Load mass contributes only 0.6 - 0.7% of total body mass in swallows, and is unlikely to significantly increase flight costs. Flight costs for a fully loaded house martin were calculated to increase by only 2.75% (Bryant and Turner, 1982).

(b) Feeding rates and food delivery rates

Given the considerable variation in load mass with brood age and between individuals, quantification of food delivered to the brood by monitoring feeding rates alone may be misleading (Bédard and Meunier, 1983). This point is illustrated by one example in Figure 8.18, where mean load masses of a male and female feeding a brood of five nestlings are depicted. On day 11, the mean load mass delivered by the female was 0.21g, that by the male 0.14g. If the 48 feeds recorded in one hour's observation were split equally between the parents, assuming an overall average load mass of 0.175g for each parent would overestimate male FDR by 14.3% and underestimate female FDR by 17.5%.

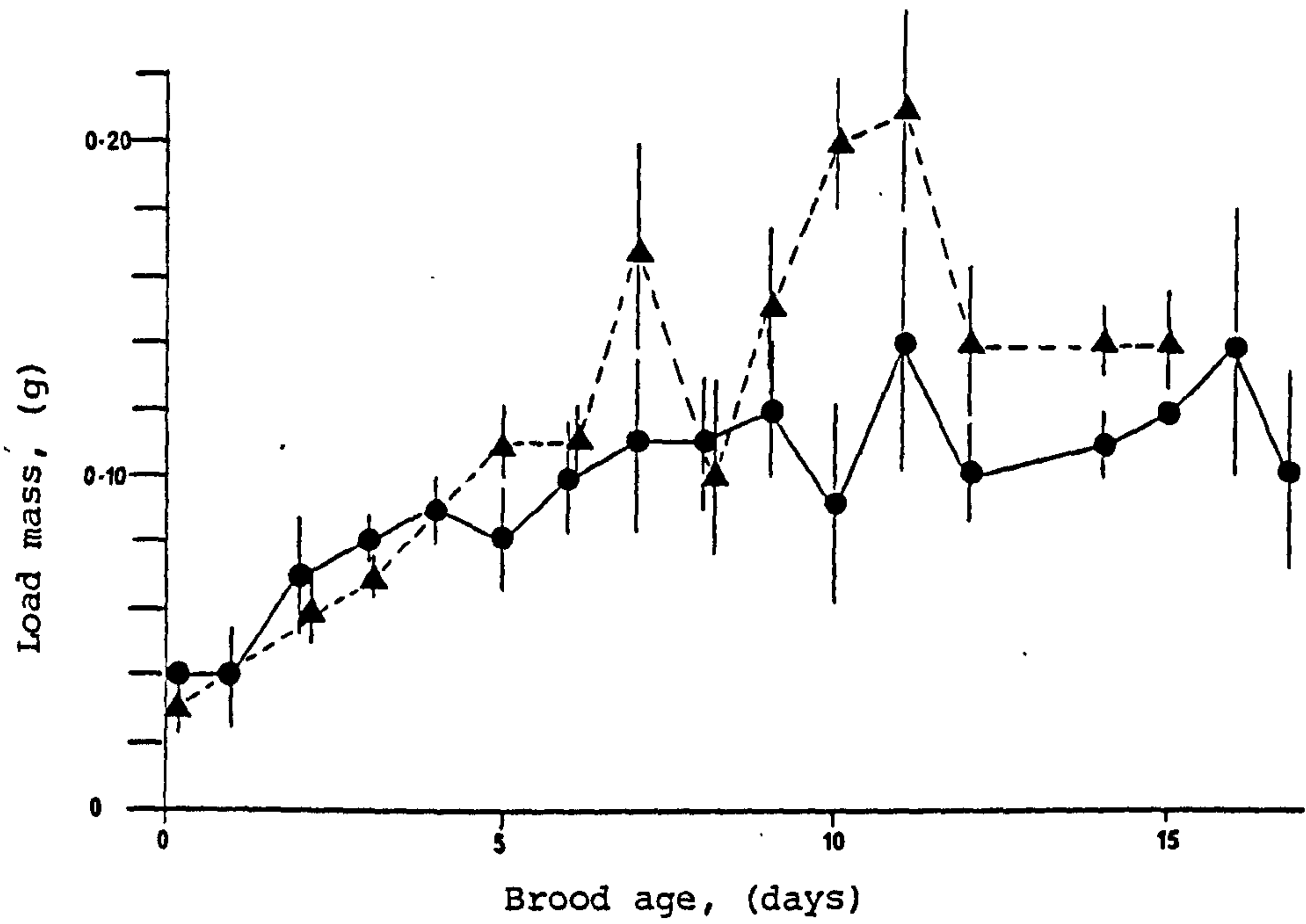


Figure 8.18

Load mass as a function of brood age for a pair of swallows.

Triangles and pecked line: female.

Circles and solid line: male.

Means ± sds illustrated.

Food delivery rates over days 8-16 of nestling-rearing increased linearly with increasing brood size (Figure 8.19). The linear regression was more significant than a log-log or semi-log relationships between FDR and brood size. Moreover, the slope of the linear relationship is 0.97, suggesting that a doubling of brood size resulted in a virtual doubling of food delivery rate, and that chicks in larger broods were not relatively undernourished. Feeding rate increases linearly with increasing brood size in blue tits, although individual chicks in medium sized and large broods did receive less food than nestlings in very small broods (Nur, 1981, 1984b). Amongst the largest swallow broods, however, the pattern was probably different from the apparent trend across all brood sizes. Individual chicks in brood sizes of seven received less food ($0.91 \pm 0.19 \text{g chick}^{-1} \text{h}^{-1}$) than did nestlings in brood sizes of five ($1.11 \pm 0.34 \text{g chick}^{-1} \text{h}^{-1}$), although the difference between means is not statistically significant ($t = 1.72, n = 30, ns$), possibly because of the small sample size. Most studies report a decline in feeding visits per nestling as brood size increases, with feeding rate per chick apparently declining most steeply at brood sizes less than or equal to the modal brood size (review in Nur, 1984b).

As the brood grows, FDRs by parent swallows increased until the middle of the nestling period (Figure 8.1), partly because load size increases over the brooding phase (Figure 8.16) but mainly because feeding rates increased over this period.

In Figure 8.20 feeding rates and FDRs to three control broods are illustrated. Both male and female feeding rates increased over the early nestling period. During the brooding phase $51.77 \pm 20.57\%$ of feeds ($n = 35$ hours of observation) were made by females at control

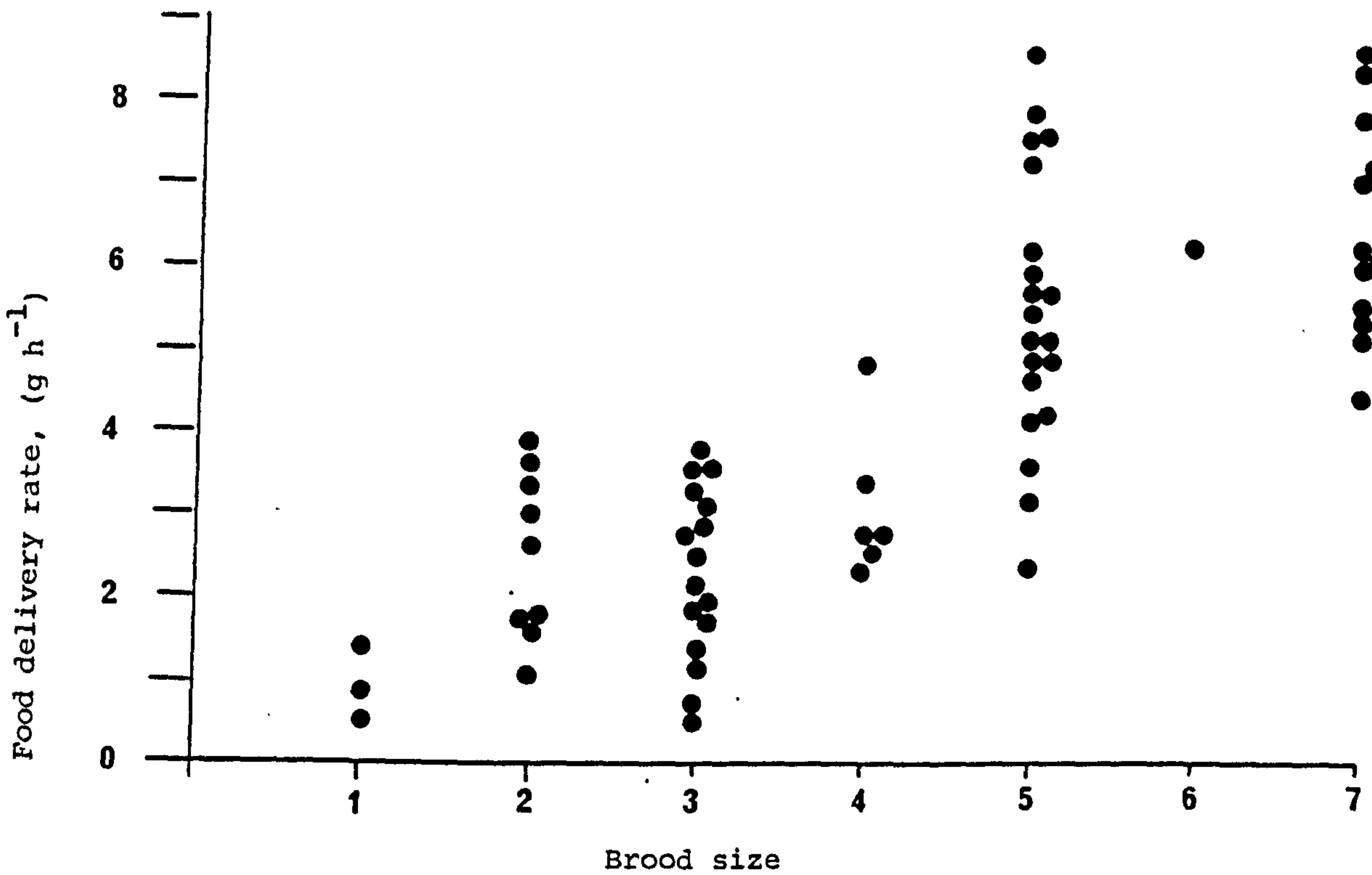


Figure 8.19

Food delivery rate as a function of brood size in swallows.

All data were collected during afternoons, and are described by the regression equation:

$$y = 0.134 + 0.969x; \quad r = 0.81, \quad n = 67, \quad P < 0.001$$

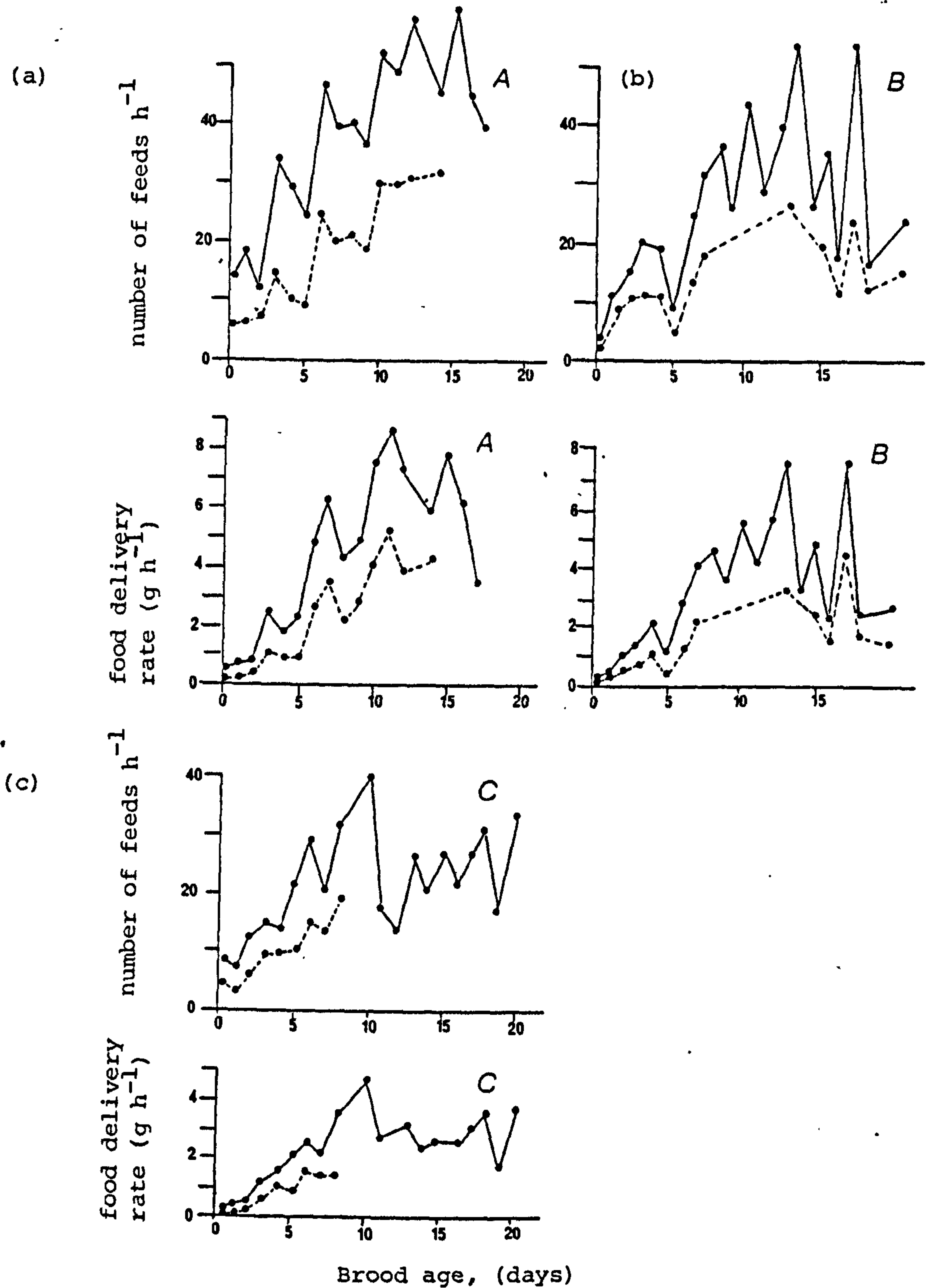


Figure 8.20

Feeding rates and food delivery rates to three natural brood sizes of swallows.

The contribution by both parents (solid circles, solid line), and by the female alone (solid circles, pecked line) is illustrated.

- A : brood size 5
- B : brood size 5
- C ; brood size 4

nests. The large standard deviation occurs because of the great variability in parental feeding contributions between nests. At one nest the female delivered all feeds to the brood over one hour, at another nest the female contributed only 8.3% of the total number of feeds. During the brooding phase females delivered food to the brood on almost every visit, although occasionally birds settled to brood without feeding the chicks (pers. obs.). Much less variability in the feeding rates of males and females occurred during the non-brooding phase (days 8-21). On nine hours of observation, females delivered $54.24 \pm 3.05\%$ of feeds to the brood.

(c) Adult self-feeding on foraging trips

When collecting food for the brood, adult birds must also harvest food for self-maintenance. On reaching a food patch, parents must decide whether to eat prey encountered themselves, or to collect it for the brood. Female yellow-headed blackbirds, X. xanthocephalus, self-fed on 77% of trips when collecting food for their nestlings, whilst males self-fed on 50% of occasions (Orians, 1980).

Optimal prey size may be different for adults and nestlings. Adult swallows select smaller prey for self-maintenance when broods have hatched (Waugh, 1978), as do blue tits (Royama, 1966a), long-billed marsh wrens Telmatodytes palustris (Verner, 1965), and blue-gray gnatcatchers, Polioptila caerulea (Root, 1967). Thus any relatively small prey encountered by swallows when foraging for food for the brood may be consumed for self-maintenance before a bolus is collected. Theoretical aspects of optimal foraging in patches containing several sorts of prey have been explored by Heller (1980).

Brood size may also influence adult self-feeding behaviour: adult

food intake for self-maintenance decreases as food delivery rates to large broods increases in starlings (Kacelnik, 1984).

Body mass changes of five adult swallows during foraging bouts when food was also collected for the brood are illustrated in Figure 8.21. Mass loss resulting from flying is also calculated using assumptions outlined in Chapter 4.

Adults tended to show an increase in mass exceeding the predicted mass loss through flying in 42% of cases, suggesting considerable self-feeding when collecting food for the nestlings. The graph will include some trips when adults defaecate as well as feeding, so self-feeding may occur on more than 42% of foraging trips.

The age of the brood may also influence adult self-feeding behaviour. During the brooding phase female swallows apparently undergo anorexia, and lose mass or gain relatively little mass while foraging. The rate of mass gain increases as the nestlings become older and adult fat reserves decline (see section 8.4).

Mass gains while foraging were significantly positively correlated with foraging time ($r = 0.45$, $n = 39$, $P < 0.01$), the longest foraging bouts resulting in the greatest mass gains for the adults. Load mass also increased as foraging time increased (Figure 8.22), but reached an asymptote after about four minutes. Hence during foraging trips longer than about four minutes food collected for the brood remained roughly constant, and increasing rates of self-feeding presumably occurred. The decelerating form of the loading curve may occur because of increased handling difficulties as load size increases (Bryant and Turner, 1982; Carlson and Moreno, 1982), or as the consequence of birds travelling different distances in different

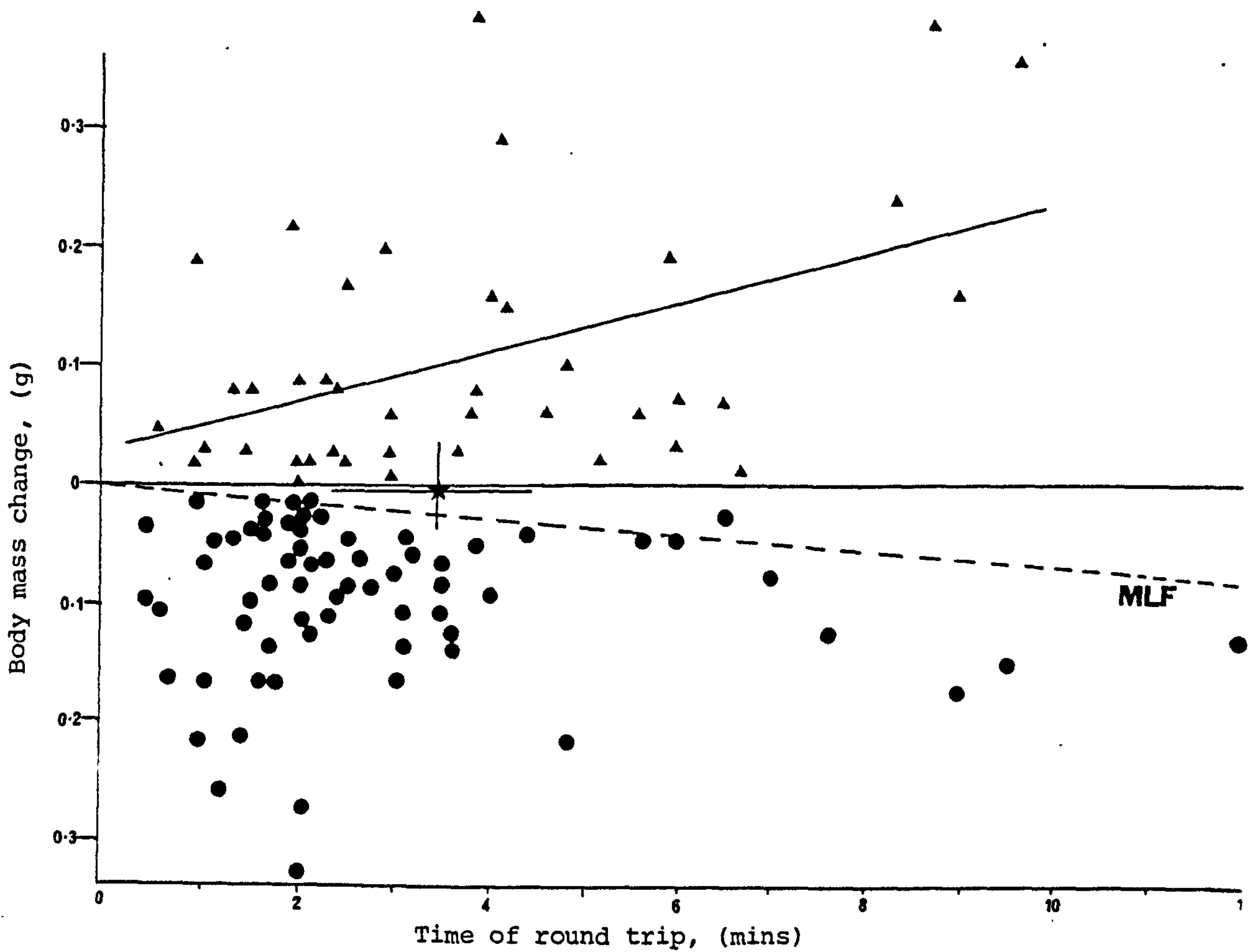


Figure 8.21

Body mass changes of five swallows collecting food loads for their nestlings.

Predicted mass loss through flying (MLF) is also illustrated. The relationship between mass gain and time of round trip is described by the regression equation:

$$y = 0.036 + 0.02x; \quad r = 0.45, \quad n = 39, \quad P < 0.01.$$

The asterisk denotes mean time of round trip (sd also illustrated).

Triangles : mass gains

Circles : mass losses

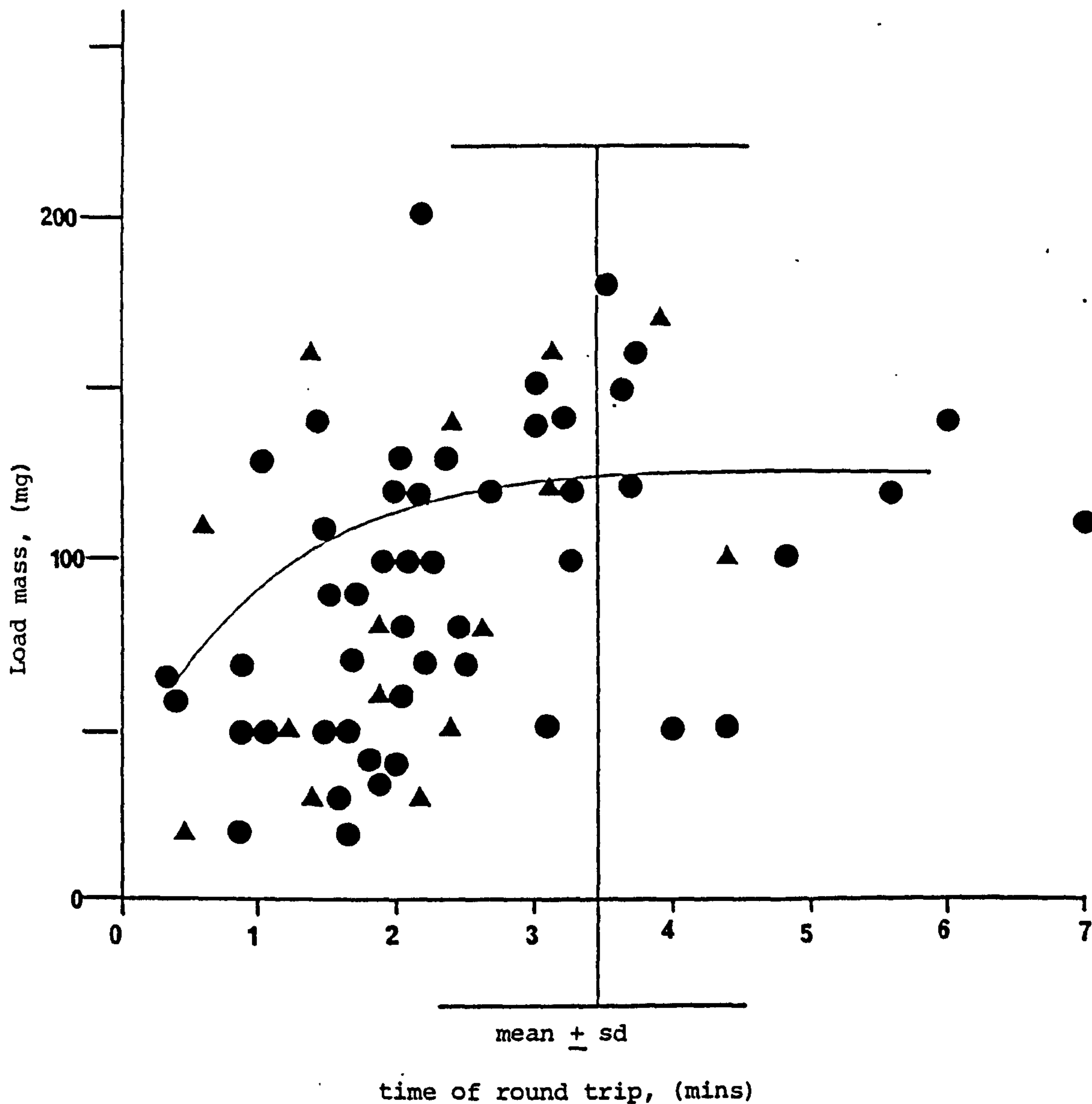


Figure 8.22

Load mass as a function of time of round trip in swallows.

Triangles : male loads

Circles : female loads

Data presented is for when birds lose mass while foraging, to minimise the chances of including foraging trips during which adults fed themselves.

The fitted curve is

$$y = 0.084 + 0.02 \ln x, r = 0.28, n = 52, p < 0.05.$$

conditions of prey availability (Kacelnik and Houston, 1984). Since time of round trip was not divided into travel time and time in patch, this problem cannot be resolved from the data presented here.

Adult white-fronted bee-eaters, Merops bullockoides, eat more of the total food captured themselves relative to that delivered to the brood as foraging distance and foraging time increased (Hegner, 1982), as seems to occur in swallows (Figure 8.21).

8.3.8 Differences in parental investment between male and female swallows during nestling rearing

(a) Body mass changes

When adult swallows attained relatively low, stable body masses at the end of the brooding period, mass changes were negatively correlated with FDRs, and birds delivering food above a critical rate tended to lose mass (section 8.3.5). Hence mass losses during the non-brooding phase may be costly to the parents, reflecting the amount of work done in feeding the brood.

To determine whether females were prepared to lose more mass than males during the non-brooding phase, percentage mass changes of males and females in control pairs from the previous day were plotted against each other in Figure 8.23.

Females and their mates showed the same direction of mass change on 26 of 30 days of data. The relationship between female and male percentage body mass changes was nonlinear, with females losing more mass than their mates when percentage mass losses of both sexes were relatively high. Since body mass was positively correlated with food abundance in both sexes during the non-brooding phase (section 8.3.2), Figure 8.23 suggests that males may not be prepared to lose

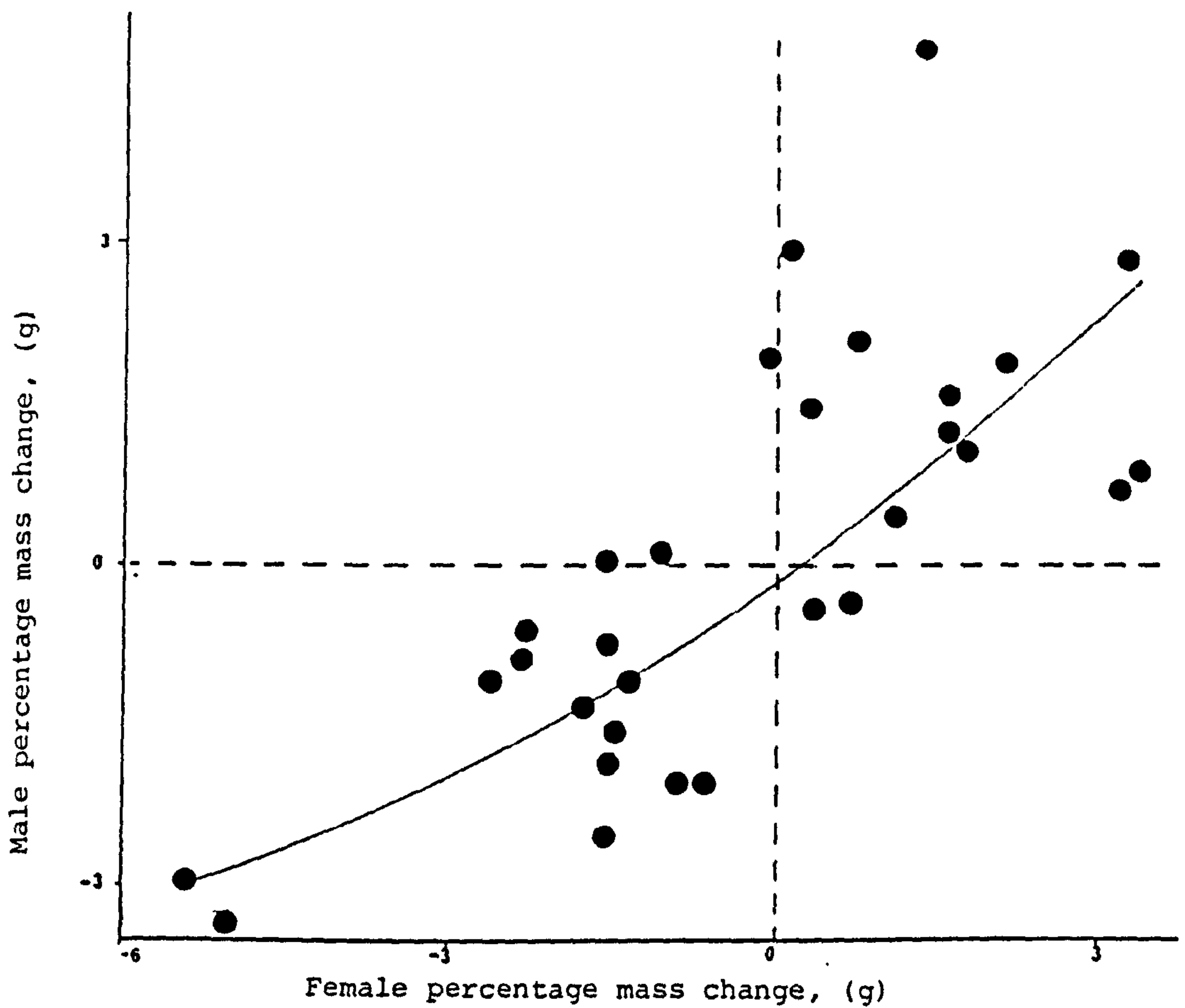


Figure 8.23

Female and male daily percentage mass changes during the non-brooding phase for pairs of swallows rearing natural brood sizes.

The fitted curve is described by the equation:

$$\ln y = 2.3 + 0.067x; \quad r = 0.77, \quad n = 30, \quad P < 0.001,$$

whereby y values were increased by +10 for logarithmic transformation of the data.

more than a critical amount of their body mass in poor feeding conditions or when feeding rates to the brood were high, while their mates may lose more mass by investing relatively more in the offspring relative to self-maintenance (Chapter 9).

In Figure 8.24, the ratio of female body mass to the body mass of their mates is plotted as a function of food abundance as determined by hand-net catch biomass. Body masses were not corrected for body size in this instance, and hand-net catch biomass was chosen as an index of food abundance because it gave the largest r^2 value of any measure of insect abundance considered. Female mass was greater than male mass above 60-70g (dry mass) of insects captured in the hand-net. Below this threshold males tended to be heavier than their mates, again suggesting that in poor feeding conditions female investment in the brood exceeded that of their mates.

Behavioural data from a time-budget study of swallows feeding nestlings supports these conclusions. Turner (1980) found that in poor weather females spent less time feeding themselves than the nestlings, while males fed themselves for as much time as they fed the brood.

(b) Food delivery rate measurements

(i) The effects of brood mass

During the non-brooding phase, both sexes increased their FDRs to heavier brood masses at more or less identical rates (Figure 8.25, analysis of covariance, $t = 0.86$, ns). Logarithmic transformations of the data did not increase the significance of the correlation coefficient. Male house martins increased their feeding rates to larger first brood masses at a faster rate than did females (Hails and Bryant, 1979). Turner (1980) found no significant difference

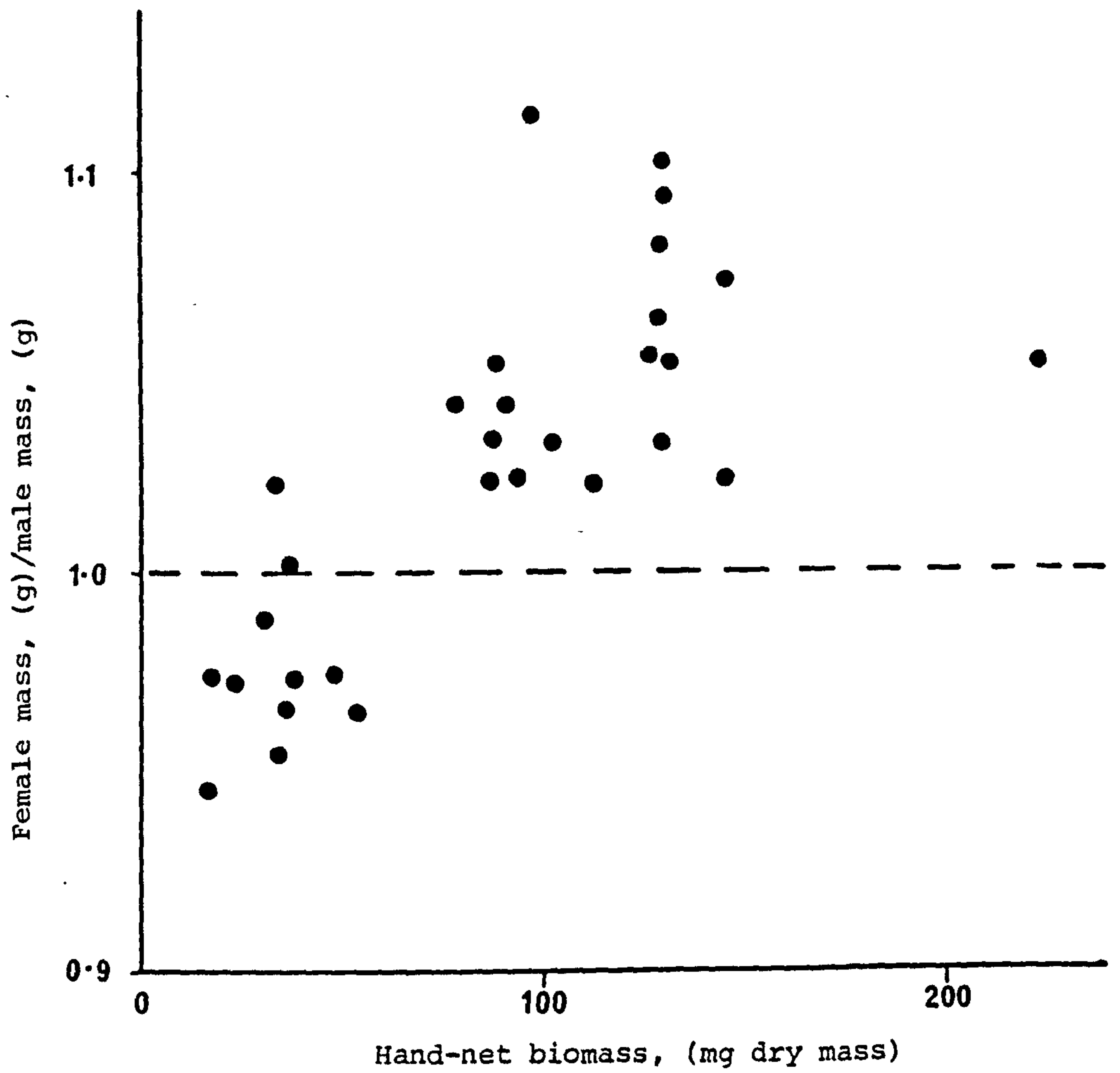


Figure 8.24

Female mass/male mass during the non-brooding phase as a function of food abundance in swallows rearing natural brood sizes.

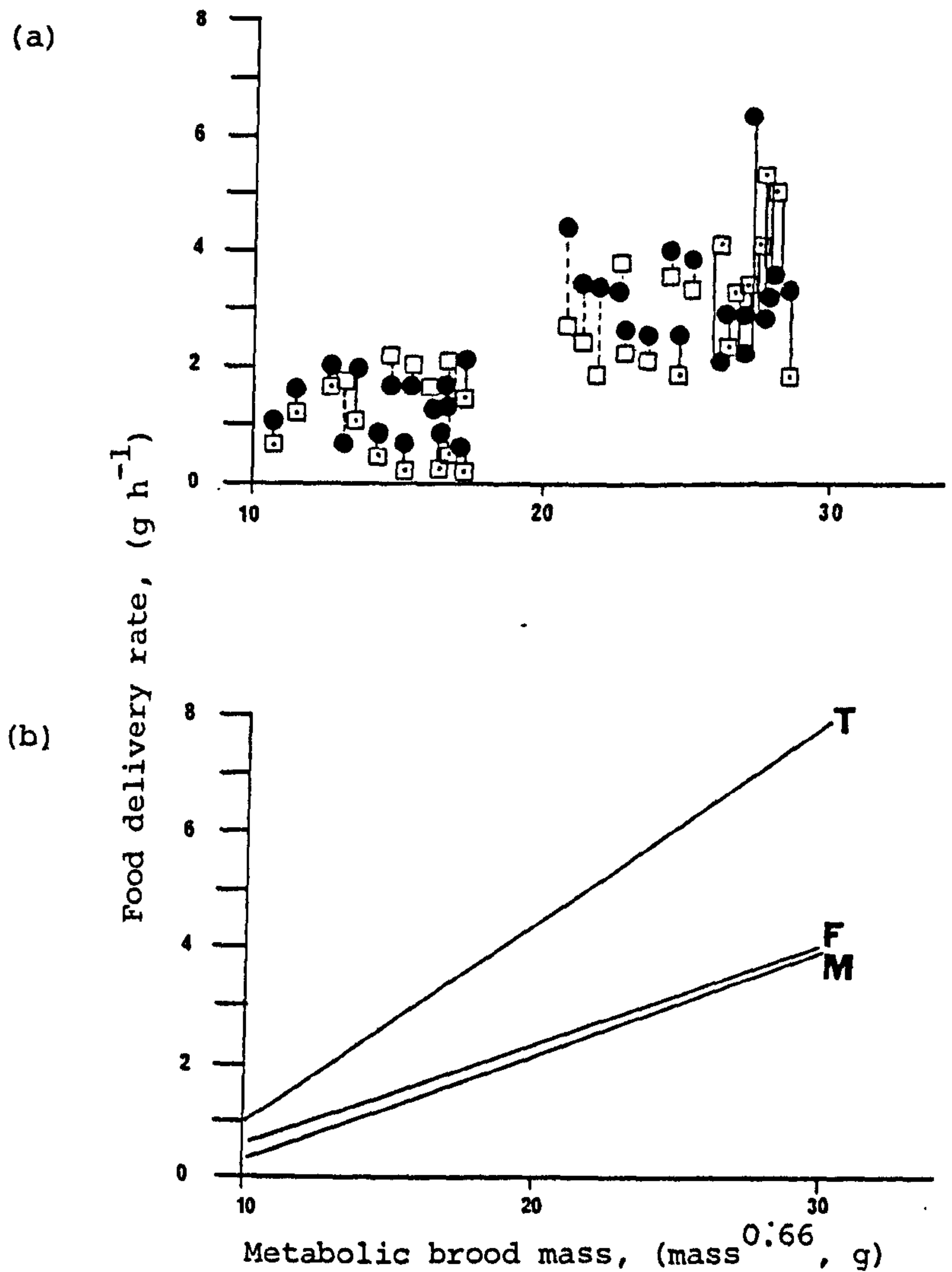


Figure 8.25

Food delivery rates of male and female swallows as a function of metabolic brood mass ($\text{mass}^{0.66}$).

(a) Data for pairs. Solid circles - female food delivery rate; open squares - male food delivery rate. Lines join data from pairs collected on the same day. Squares containing dots are for males rearing experimental brood sizes.

(b) Regression lines of food delivery rates as a function of metabolic brood mass.

$$\text{Total FDR (T)} = -2.34 + 0.34x, F = 66, P < 0.001$$

$$\text{Female FDR (F)} = -1.0 + 0.17x, F = 37.3, P < 0.001$$

$$\text{Male FDR (M)} = -1.34 + 0.17x, F = 36.3, P < 0.001.$$

$n = 33$ in all cases.

between the feeding rates of male and female swallows to large and small broods, though the males made slightly fewer visits to the nest per hour than did the female. In this study, females on average delivered slightly more food to their broods than did their mates between days 8 and 16 of nestling-rearing, although the difference between means was not statistically significant (female FDR = $2.35 \pm 1.29 \text{ g h}^{-1}$, male FDR = $2.18 \pm 1.36 \text{ g h}^{-1}$, $n = 33$ hours for each sex, $t = 0.52$ ns).

(ii) The effect of food abundance

The ratio of female FDR to her mate's FDR increased as food abundance decreased ($r = -0.34$, $n = 33$, $P > 0.05$). The significance of the correlation is raised if female FDR/mate FDR is transformed to (\log_e) and plotted against hand-net biomass ($r = -0.44$, $P < 0.01$).

Both male and female FDRs were significantly positively correlated with food abundance, as shown in Figure 8.26a (males, $r = 0.54$, $n = 33$, $P < 0.001$, females $r = 0.40$, $n = 33$, $P < 0.05$). Significance of the relationships is increased if \log_e FDR is plotted against the \log_e of food abundance (males $r = 0.60$, $P < 0.001$, females, $r = 0.48$, $P < 0.01$), as shown in Figure 8.26b. When the log-log plot is considered, males increased their FDRs at a higher rate than did females with increasing food abundance (analysis of covariance, $t = 8.4$, $P < 0.001$), such that male FDRs were lower than those of females when food was scarce, but exceeded those of females at high levels of food abundance. Hence the reason for males not losing as much mass as their mates when feeding broods in poor weather is probably a consequence of reduced male investment in the brood, relative to the female, when food is scarce.

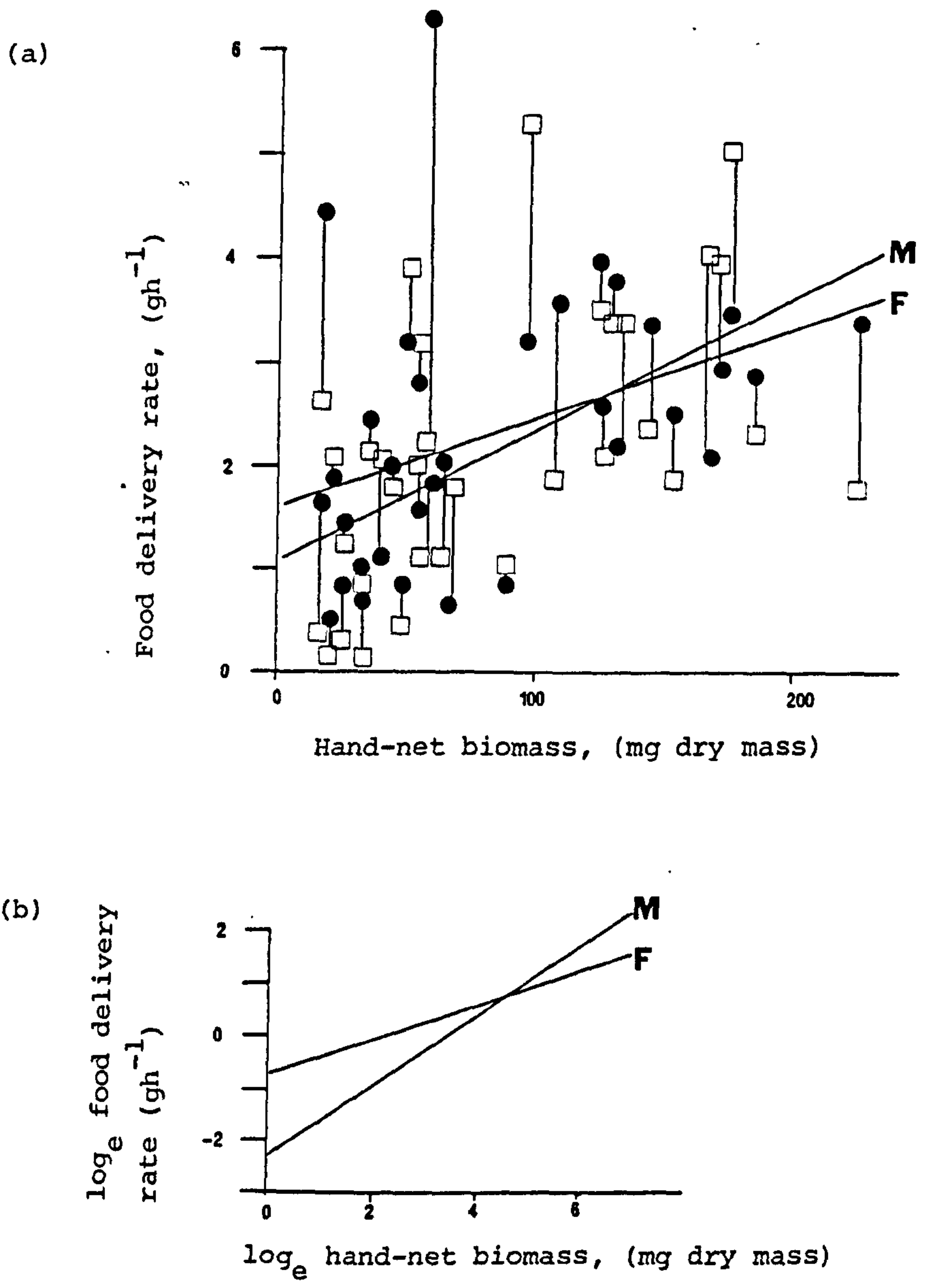


Figure 8.26

Food delivery rates of male and female swallows as a function of food abundance.

(a) Data for pairs: symbols as in Figure 8.25.

(b) Regression lines for log_e male FDR and log_e female FDR as a function of log_e food abundance.

$$\log_e \text{ male FDR} = -2.26 + 0.663 (\log_e \text{ food abundance});$$

$$r = 0.60, P < 0.001$$

$$\log_e \text{ female FDR} = -0.712 + 0.339 (\log_e \text{ food abundance});$$

$$r = 0.48, P < 0.001$$

n = 33 both cases.

M = male FDR; F = female FDR

8.3.9 Factors influencing nestling growth

The pattern of swallow nestling growth for 32 nestlings in eight broods weighed during afternoons in 1982 is illustrated in Figure 8.27. The growth curve is of the characteristic hirundine form (Ricklefs, 1967; McGinn and Clark, 1978), with a peak mass of $24.33 \pm 1.00\text{g}$ occurring on day 15 followed by mass recession. The peak mass was intermediate between values of 23.8g and 25.3g on days 14-14+ documented in southern Scotland by McGinn and Clark (1978), though significantly heavier than the peak mass of $22.8 \pm 1.7\text{g}$ ($t = 3.06$, $n = 34$, $P < 0.01$) on the 14th day obtained by Turner (1980) for swallows in the Stirling area (which may have been weighed earlier in the day).

Between days 0 and 6, swallow nestlings of unknown age could be aged according to body mass where afternoon body mass (g) = $1.09 + 1.68$ (age, days) ($F = 774$, $n = 103$, $P < 0.001$). Thereafter, chicks were aged according to their wing-length (maximum chord) whereby wing-length (mm) = $-2.72 + 4.69$ (age, days) ($F = 1027$, $n = 170$, $P < 0.001$).

To determine whether similar factors influenced chick growth as affected adult masses during nestling rearing, nestling body masses over the first 14 days of the nestling period, the period of rapid mass gain, were related to nestling age, food abundance, and brood size. Afternoon masses of 56 nestlings from 11 broods of brood sizes two to seven were obtained to the nearest 0.01g on 468 nestling days. Individual nestling mass was entered as the dependent variable in a stepdown multiple regression analysis with brood size, sweep net biomass, and nestling age entered as independent variables. The results of the analysis are presented in Table 8.6.

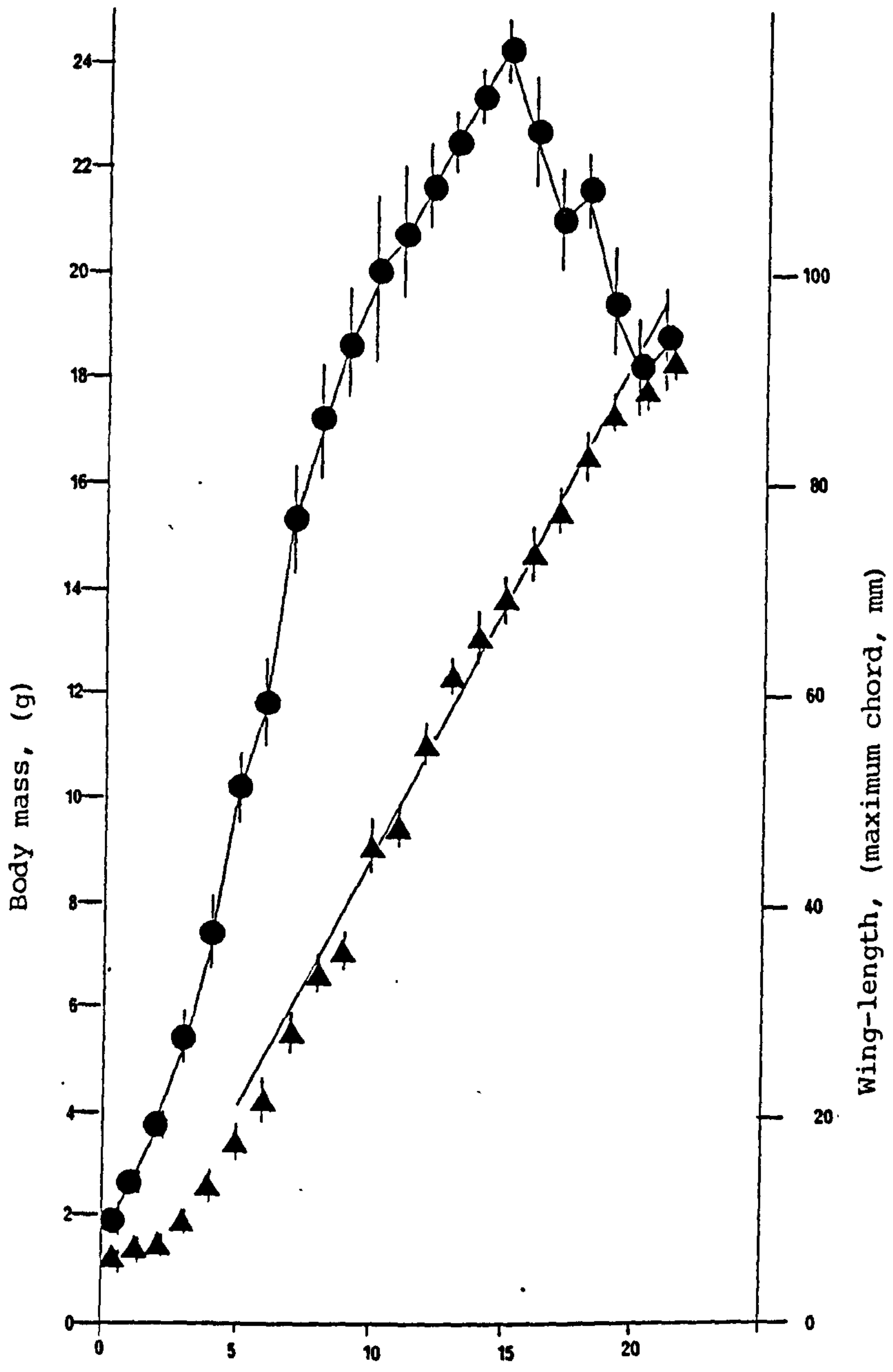


Figure 8.27

Growth curve for thirty-two swallow nestlings weighed to the nearest 0.01g during afternoons.

circles - body mass

triangles - wing-length

Means ± sds illustrated.

Table 8.6

Stepdown multiple regression analysis of nestling growth,
days 0-14

Independent variable	Multiple $r^2 \times 100$	Degrees of Freedom	Regression equation	t-value	P
Brood size	0.06	1,466	$y = -0.188 x_1 +$	2.33	*
Sweep net biomass g dry mass	2.24	2,465	$0.0199x_2 +$	10.50	***
Nestling age days	91.30	3,464	$1.96x_3$ $- 0.033$	69.06	***

$F = 1643, P < 0.001$

* * $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$

The three independent variables contributed towards 91.3% of the variance in nestling mass. Chicks tended to increase in mass with age, be heavier when food was abundant (and adult provisioning rates were high, (section 8.3.8)), and be heavier in smaller brood sizes.

Nestling growth rates were almost linear between days 2 and 11, (Figure 8.27) and were compared in three treatments:

- a. Experimentally reduced brood sizes of two
- b. Control brood sizes of four - six chicks
- c. Enlarged brood sizes of seven.

Each experimental treatment had a brood size differing by at least two chicks from the initial clutch size. The regression equations for nestling growth as a function of age between days 2 and 11, and mean peak masses of nestlings in each treatment are presented in Table 8.7.

Nestling growth rates were significantly different in each treatment (Analysis of covariance: reduced brood sizes vs controls, $t = 3.20$, $P < 0.01$; enlarged brood sizes vs controls $t = 6.03$, $P < 0.001$; enlarged broods sizes vs control brood sizes, $t = 9.2$, $P < 0.001$). The fastest growth rates occurred in reduced brood sizes of two, the slowest in enlarged brood sizes of seven young. On only one day did a brood show negative growth during days 2-11, this being in a brood size of seven chicks.

Chicks in reduced brood sizes on average attained a heavier peak mass than those in natural brood sizes, which in turn attained heavier average peak masses than chicks in enlarged broods. Nestling peak mass was negatively correlated with brood size ($r = -0.49$,

Table 8.7

Nestling growth rates between days 2 and 11, and mean nestling peak masses in control, enlarged and reduced brood sizes

Treatment	Regression Equation (nest days)	Nestling peak mass, g (number of chicks)
Reduced brood sizes (2)	$y = 2.27 + 2.4x, (42)$	$25.28 \pm 0.95, (4)$
Control brood sizes (4, 5)	$y = -0.20 + 2.2x, (241)$	$24.41 \pm 1.36 (20)$
Enlarged brood sizes (7)	$y = 0.18 + 1.18x, (185)$	$23.31 \pm 1.20 (14)$

Regression equation slopes give nestling growth rates, g day^{-1} . All regression equations were significant at $P < 0.001$.

$n = 38$, $P < 0.01$). Fledging success was 100% for all broods included in the analysis.

Hence although manipulation of brood size has no significant effect on adult daily body mass changes during the non-brooding period, brood size significantly influences both nestling growth rate and nestling peak mass. Rearing broods larger than those observed in natural situations may therefore reduce parental inclusive fitness if fledgling survival overwinter was related to chick growth rate or peak mass. Although brood size does not seem to have any marked influence on overwinter survival of fledgling hirundines (Snapp, 1973; Bryant, 1978, 1979; De Steven, 1980), the frequency of exceptionally light young increases in enlarged broods of house martins, and such young may have poor post-fledging viability (Bryant and Westerterp, 1983b).

8.4 DISCUSSION

8.4.1 Optimal body mass of adult birds rearing nestlings

Parent:offspring resource allocation decisions in birds are presumably made by the parent in relation to changes in body condition, which may in turn be related to long term survival probabilities (Drent and Daan, 1980). Hence an understanding of the causes of adult mass changes during nestling-rearing is fundamental to an interpretation of resource allocation decisions made by the parent bird. A decrease in body mass may be beneficial to the parent if it allows the bird to target towards an optimal mass for nestling rearing, but any decrease in mass below the optimum may cause adult body condition to deteriorate to a point whereby the bird's survival probability is progressively decreased.

The rapid rate of mass loss over the brooding phase by female swallows proximately represents utilisation of the bird's lipid reserves. The mean fat score of incubating female swallows was 7.67 ± 0.58 , that during the non-brooding phase 3.78 ± 1.48 . The difference between means is statistically significant ($t = 4.42$, $n = 21$, $P < 0.001$). The mass loss was not attributable to atrophy of the reproductive system since gonadal atrophy in female sand martins occurs soon after the last egg is laid (Chapter 5, Petersen, 1955), and changes in body mass of sand martins during incubation and nestling-rearing are related mainly to changes in the bird's extractable lipid content (Chapter 5). Moreover, male swallows often undergo a mass decline during the early stages of nestling rearing, while their gonads only contribute 0.3% of carcass dry mass (Appendix III). Changes in the birds' protein reserves in the pectoralis muscles may occur in parallel with changes in lipid reserves, but changes in flight muscle mass are likely to be a small component of changes in total body mass (Chapter 5).

Mass loss in adult birds rearing nestlings has been assumed to represent a body condition cost to the parents as a consequence of the considerable reproductive effort expended in collecting food for the nestlings (Nice, 1937; Hussell, 1972; Ricklefs, 1974). This hypothesis does not explain the pattern of mass change in adult swallows which are rearing nestlings because any period of rapid mass loss, especially marked in females, occurs before the time of maximum food delivery rate to the brood. If mass was lost simply as a consequence of an increased feeding rate to the brood, most mass would be lost during the middle of the rearing phase, when FDRs were highest. The tendency for nestling-rearing birds to lose most

mass before the period of highest nestling demand also occurs in marsh warblers, Acrocephalus palustris, (Dowsett-LeMaire and Collette, 1980), house wrens, Troglodytes aedon, (Freed, 1981), starlings (Ricklefs and Hussell, 1984), and sand martins (Chapter 5).

The period of rapid mass loss during the brooding phase could be because this period is the most energetically stressful time for the adult, even though feeding rates to the brood are low. The considerable time investment in brooding by the female may prevent her from self-feeding at a time when she must also collect some food for the brood (Nur, 1984a). However, incubating females may spend more time on the nest than do brooding females, (Chapter 7), and maintain a relatively high body mass for most of the incubation period. The low feeding rates by females to young chicks during the brooding phase seem unlikely to explain the rapid mass loss by females when compared with incubation masses.

Freed (1981) argued that birds may lose mass over the brooding period as an adaptation to reduce flight costs in anticipation of a period of high nestling demand. Moreover, the energy liberated from mass loss would be available for use by the parents, and any harvested food could be diverted to the brood (Norberg, 1981). Excessive mass loss is likely to be costly if it increases the probability of starvation due to a decrease in energy reserves (Norberg, 1981), or if it results in reduced food allocation to the brood, maybe causing slower nestling growth at the expense of parental self-maintenance.

The hypothesis that mass loss during the brooding phase wholly represents the cost of brooding and feeding to the female is attractive at first sight since females lose more mass than males

during this period, and only females brood. However, the hypothesis can be rejected from the results of the replacement experiments, which did not induce females to undergo a further mass decline even though their brooding commitment was substantially increased and their nestlings grew normally.

Although the brooding commitment of the females in replacement experiments was always increased substantially (Figure 8.5), it did not reach the level expected if the female were brooding her own nestlings during a natural brooding period (Figure 8.6).

This observation suggests that female swallows have a programmed and diminishing brooding response, as represented diagrammatically in Figure 8.28.

The brooding response of the female is simplified to a linear declining function of brood age, whereas the actual response may be sigmoidal. At any brood age, a certain amount of flexibility occurs about the brooding response, as illustrated by the vertical bars in Figure 8.28. This flexibility may be adaptive, since if some of the brood dies, for example, the female would have to increase her brooding effort because smaller broods need more brooding than larger broods (Table 8.3).

In Figure 8.28, a female is given four day old chicks in a replacement experiment when she is naturally rearing seven day old nestlings. Four day old chicks require $x\%$ brooding, but the female is only 'programmed' to brood for a maximum $y\%$ of her time at day 7. The nestlings therefore receive a brooding deficiency of $(x - y)\%$.

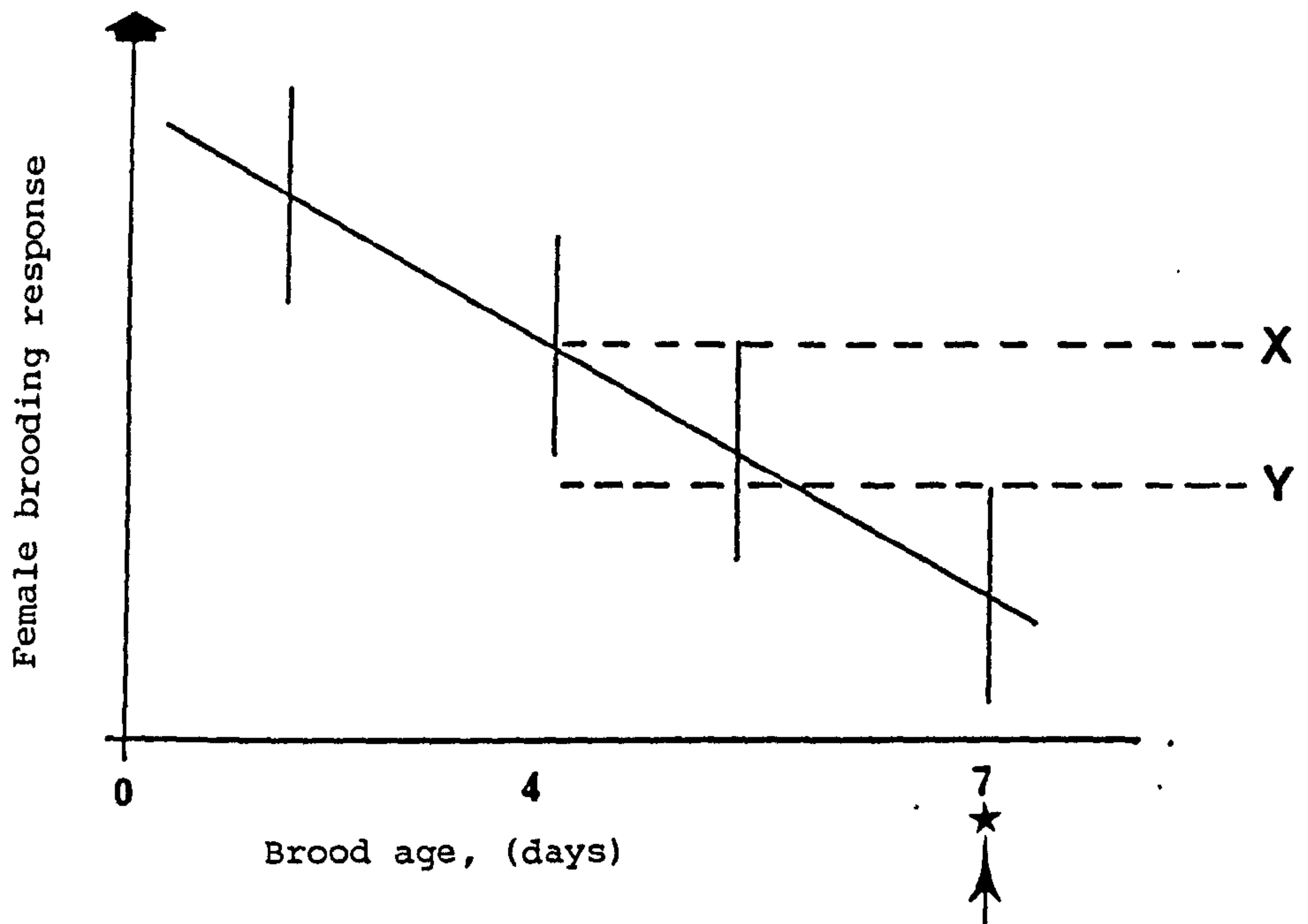


Figure 8.28

Diagrammatic representation of a model of a programmed diminishing brooding response in female swallows.

Vertical solid lines represent the range of a female's brooding response at any time.

X is the expected level of brooding for day 4 chicks.

Y is the maximum attainable level of brooding for a female with day 7 chicks.

A female is given day 4 chicks in a replacement experiment when her own chicks were seven days old (asterisk). The newly transferred chicks experience a brooding deficiency of $(X - Y)\%$. See text for explanation.

The inability to induce a rapid mass loss during the replacement experiments suggests that the females are undergoing an anorexia during the brooding phase, whereby food intake rate is also programmed to be reduced (Mrosovsky and Sherry, 1980). This hypothesis is substantiated in an analysis of the foraging intensities of birds during different stages of the breeding cycle.

Foraging intensity, or food intake rate, can be estimated by calculating the rate of mass change of parent birds on foraging trips when they are collecting food either solely for themselves (incubating females), or collecting food for themselves and for their offspring (nestling-rearing males and females). The rate of mass change between incubation bouts or between times of food delivery to the nestlings will indicate how much food the adult has collected per unit time for self-maintenance. In the analysis, rates of mass loss exceeding four $\text{mg g}^{-1} \text{h}^{-1}$ have been excluded from all classes, since these may represent trips where defaecations occurred (Chapter 4). Mass changes were expressed per gram of bird, although metabolism may normally scale in some allometric way with mass, whereby mass changes would be better expressed per metabolic gram ($\text{g}^{0.66}$). However, units of $\text{mg g}^{-1} \text{h}^{-1}$ were used since no thorough study has been made on intraspecific metabolic costs in relation to body size, except in house martins, where large individuals actually have lower daily energy expenditures than smaller birds (Bryant and Westerterp, 1982, 1983b). Rate of mass change while foraging as a function of stage of the breeding cycle for males and females is illustrated in Figure 8.29. Rate of mass change while foraging will hereafter be described as 'foraging intensity'.

For females, foraging intensity was relatively high during

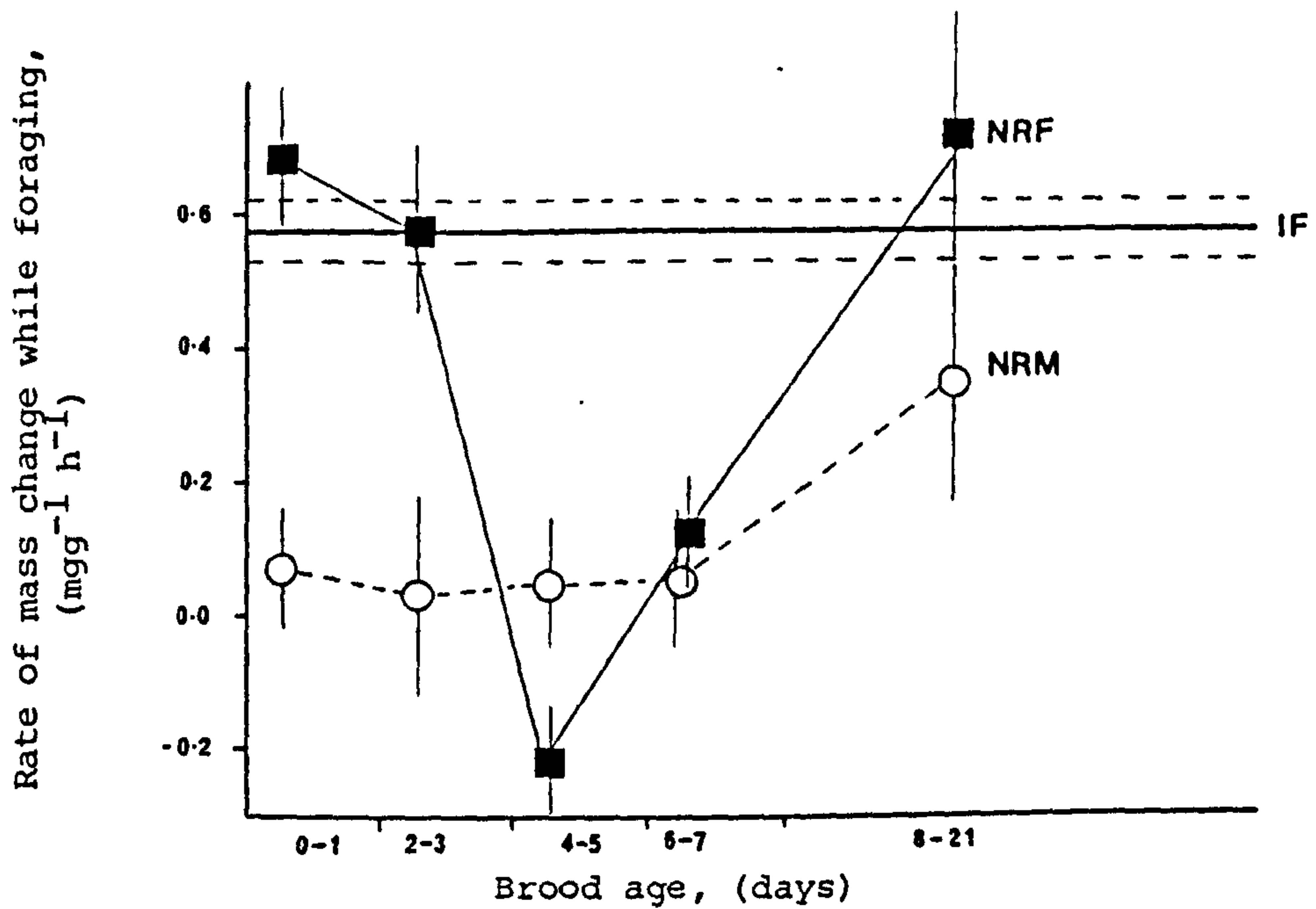


Figure 8.29

Rate of mass change while foraging as a function of stage of the breeding cycle in incubating female and nestling rearing swallows.

Means + standard errors illustrated.

Thick black line, IF; incubating females. Pecked lines represent standard error.

Solid squares, NRF; nestling rearing females

Open circles, NRM; nestling rearing males.

See text for explanation.

incubation, when female body masses were also relatively high (Figure 8.1). Female swallows aim to sustain a heavy mass during incubation (Chapter 7), and achieve this by maintaining a high rate of food intake in the limited time available for foraging. During the first four days of rearing, female foraging intensities remained at high levels, when the birds spent as much time brooding as they did during incubation (Figures 7.4, 8.4). There are no significant differences between mean rates of mass change during incubation and days 0-1 of rearing ($t = 0.4$, $n = 375$, ns) or days 2-3 of rearing ($t = 0.02$, $n = 307$, ns), or between days 0-1 and days 2-3 of rearing ($t = 0.17$, $n = 130$, ns). A rapid mass loss by females over the first four days of brooding may then indeed be due in part to the time constraints of brooding and the energetic cost of collecting some food for the brood, since there was no evidence of a reduced foraging intensity during this period.

However, during days 4-7 of the brooding phase, during which time female mass continues to fall, female foraging intensities were dramatically reduced, with foraging trips on days 4-5 resulting on average in mass losses for the females. Mean rate of mass change on days 4-5 of rearing was significantly lower than during incubation ($t = 2.23$, $n = 307$, $P < 0.05$), and during days 1-2 of rearing ($t = 2.12$, $n = 132$, $P < 0.05$). The female may need to leave the nest during the late brooding phase to exercise her flight muscles, or to collect specific nutrients for self-maintenance. Although adult swallows must collect small prey for young chicks (Waugh, 1978), this is unlikely to act as a constraint on self-feeding time, since foraging intensities of adults were relatively high when the chicks just hatched, and any specialised prey for the brood must have been even scarcer at this time.

Female foraging intensity reached its incubation value again during days 9-20 of the rearing period ($t = 0.38$, $n = 298$, ns). The birds' lipid reserves are low at this period (see above, Chapter 5), and the female will need to forage intensively to maintain her body condition since she can no longer subsidise her energy expenditure from body reserves. Hence female swallows are collecting large loads frequently for the nestlings (section 8.3.7) and foraging intensively for self-maintenance during the non-brooding phase of nestling rearing, when energy expenditure is likely to be at its highest level during the breeding cycle (Bryant and Westerterp, 1980; Drent and Daan, 1980).

Male swallow foraging intensity was less variable than that of females during nestling-rearing. No significant differences between male mean foraging intensities occurred over the rearing period ($t > 0.05$ all comparisons), although male foraging intensity on days 4-5 of rearing was lower than that attained by incubating females ($t = 2.23$, $n = 349$, $P < 0.05$), and females during days 0-1 of rearing ($t = 2.01$, $n = 170$, $P < 0.05$). Mean male foraging intensity on days 8-21 of rearing was not significantly different from that of incubating females or females rearing nestlings aged 8-21 days ($t > 0.05$ both comparisons).

Hence fitness in breeding swallows does not seem to be maximised by always maximising net energy gain while foraging (Caraco, 1980; McNamara and Houston, 1982), because birds forage at different intensities over the breeding cycle. A reduction in net energy gain during brooding in females would have fitness value in that a consequent drop in body mass would reduce flight costs in time for a period of high nestling demand. Rates of prey capture by yellow-

headed blackbirds gathering food for nestlings were higher than those of birds not gathering food for the young, as shown by Orians (1980).

Thus mass losses during the brooding phase are unlikely to be costly in survivorship terms for female swallows. The energetic benefits from mass loss during the brooding phase, which appears to be at least in part the result of a programmed anorexia, can be calculated by considering the energy savings due to a reduction in flight costs, and the energy release from lipid metabolism.

(a) The energy savings through a reduction in flight costs

The energy savings from reducing power required for flight were calculated from the equation of Norberg (1981), based on the theory of Pennycuick (1975).

$$E = \frac{T(\epsilon - \text{BMR})}{24.3600 \text{ BMR}} [1 - (1 - a)^{1.5}] ,$$

where

E = energy saving, as a fraction of the basal metabolic rate (BMR) of one adult during 24h, that would result from a mass loss of proportion a .

T = flight time in s per day

ϵ = metabolic energy cost for flight, s^{-1} .

Both ϵ and BMR are for a bird of 'normal' mass (assumed to be mass on the day of hatching eggs in these calculations).

The following assumptions are included in the equation:

(i) Female swallows spent 67% of a 16h day in flight when chicks were seven days old. This was directly calculated from time budget data, and no female was observed perching away from the nest during daytime in the brooding phase.

(ii) Females lost on average 6.5% of their body mass between the last day of incubation and day 7 of nestling-rearing (from Figure 8.1).

(iii) Flight costs were $5.7 \times$ basal metabolic rate (Turner, 1980).

Solution of the equation implies that females may save 24.4% of basal metabolic rate during 24 hours on day 7 of rearing by losing 6.5% of their body mass over the brooding phase. Assuming a basal metabolic rate of $28.2859 \text{ kJ bird}^{-1} \text{ day}^{-1}$ (Turner, 1980), and a daily energy expenditure (DEE) of 108.52 kJ d^{-1} during nestling-rearing (Westerterp and Bryant, 1984), the energy saving through mass loss is 6.90 kJ day^{-1} or 6.4% of daily energy expenditure during nestling-rearing.

(b) The energy savings through lipid metabolism

Female swallows on average lose 1.44g of their body mass between the end of incubation and the end of the brooding phase. If this mass loss was all lipid, and assuming lipid to liberate 37.7 kJ g^{-1} (Ricklefs, 1974), 48.68 kJ would be released over the entire brooding phase. Assuming energy expenditure during brooding to be equal to that during late rearing, 5.6% of one day's energy expenditure would be subsidised for lipid metabolism on each day of the brooding phase. Since energy expenditure during the brooding phase is likely to be less than that during late rearing, the actual benefits of lipid catabolism could be greater.

Hence during days 8-21 of rearing, females save about 6% of their DEE through having reduced flight costs compared with incubation. During days 0-7 of rearing, at least about 6% of DEE is subsidised from lipid catabolism, and there will also be a progressive energy saving from a reduction in flight costs over the brooding phase.

The two methods of energy saving hence seem to spread the energetic benefits of mass loss evenly over the entire rearing period.

The maximum mass loss over the brooding phase was recorded in a female which lost 4.63g (19.26%) of her body mass between the end of incubation and day 7 of rearing during a spell of cold weather. Such a mass loss was calculated to save 18% of DEE during days 8-21 of rearing through reducing flight costs compared with incubation. Additionally, lipid metabolism would subsidise 20.1% of one day's DEE during days 0-7 of rearing. Hence the potential energy savings from mass loss during the brooding phase in female swallows are substantial, even though most females achieve savings considerably less than the maximum recorded.

Mass loss during nestling-rearing may also enhance flight performance or agility (Andersson and Norberg, 1981), which may improve foraging efficiency in aerial feeders, allowing more food to be collected for the brood.

In Figure 8.30 body mass changes during the brooding phase for six females rearing natural brood sizes are illustrated. Body mass is standardised for body size through dividing mass by keel-length. The solid, thick line represents the regression equation of mass/keel (y) on a function of brood age (x) for all six females, and is described as

$$y = 1.02 - 0.0109x ,$$

$$(r = -0.52, n = 46, P < 0.001).$$

All birds have converged onto the line of average mass by the end of the brooding phase (Table 8.8). Data for one female (A82) has been extended to day 8 because she experienced extremely cold

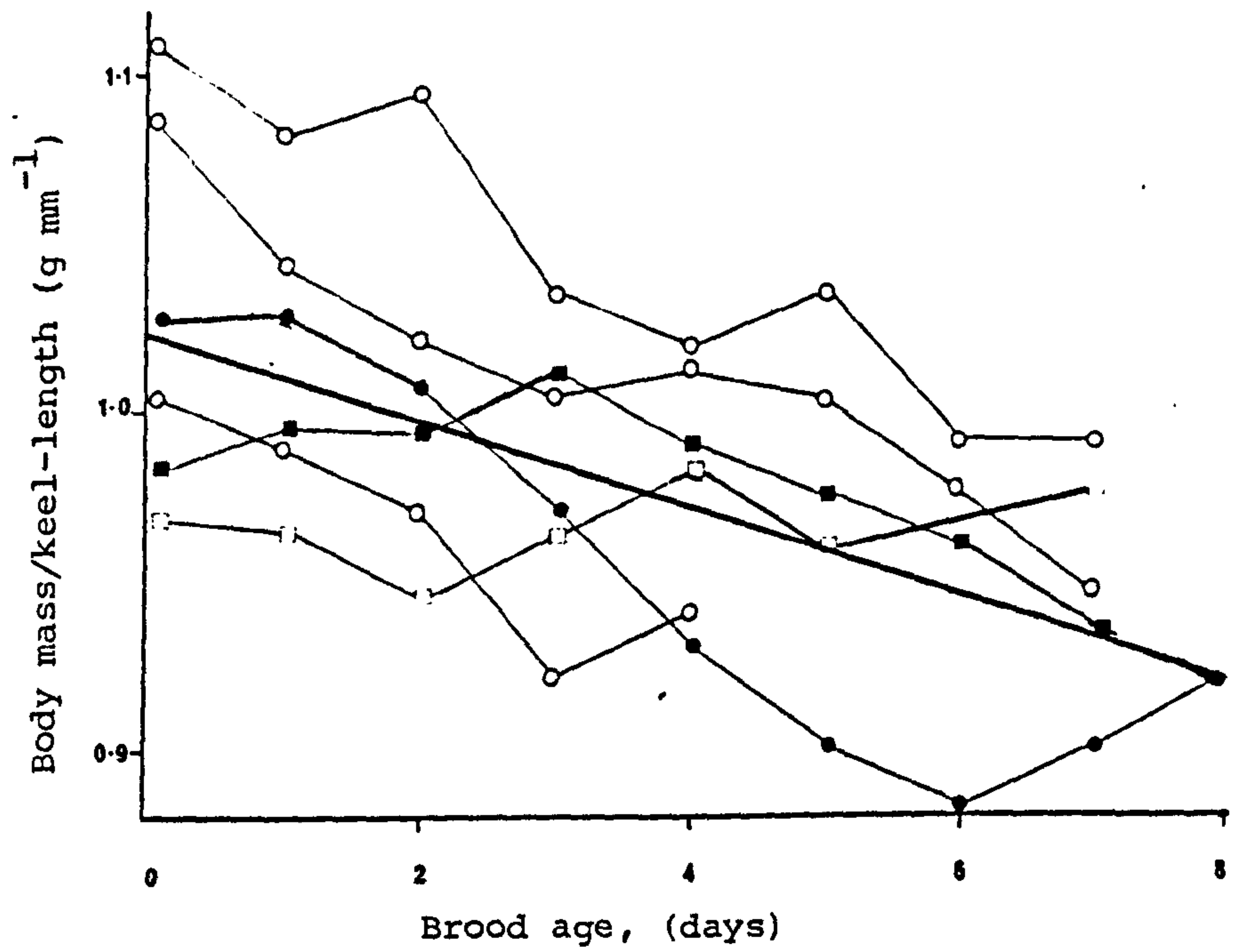


Figure 8.30

Body mass/keel-length changes for six female swallows rearing natural brood sizes over the brooding phase. The thick line represents the regression line for all data (see text for equation).

Table 8.8

Size-corrected body mass deviations (from the average) for six female swallows rearing natural brood sizes during days 0 and 7 of nestling rearing

<u>deviation, day 0, gmm⁻¹</u>	<u>deviation, day 7, gmm⁻¹</u>	<u>trend</u>
+ 0.09	+ 0.05	
+ 0.06	+ 0.02	
+ 0.03	0.00 (day 8)	
- 0.02	+ 0.01	
- 0.04	+ 0.01	
- 0.05	+ 0.04	
		convergence towards average

and wet weather during most of the brooding phase, and thus would have suffered a body condition cost. Overall, females entering the brooding phase below the average mass line tended to increase or maintain mass between days 0 and 7, while females starting brooding at greater than average mass tended to shed mass over this period. Regression equations were computed for the change in size-corrected mass over the brooding phase for each female, and the slopes of rate of mass loss were compared with the average trend. The three females which entered the brooding phase at a greater size-corrected mass than the average lost mass more rapidly than the average trend ($0.015\text{g mm}^{-1}\text{ day}^{-1}$, $0.014\text{g mm}^{-1}\text{ day}^{-1}$, $0.027\text{g mm}^{-1}\text{ day}^{-1}$, compared with $0.011\text{g mm}^{-1}\text{ day}^{-1}$ average, slopes significant at $P < 0.001$ all cases), although only the largest deviation was significantly different from the average rate of mass loss (analysis of covariance, $t = 4.5$, $n = 53$, $P < 0.001$). None of the three females with a lower than average mass on the day of hatching showed a significant tendency to increase or decrease in mass over the brooding phase ('r' values = -0.18 , $n = 5$; -0.07 , $n = 8$; $+0.05$, $n = 7$, $P > 0.05$ all cases).

Figure 8.30 suggests that the females are 'targetting' their body mass over the brooding period towards a mass which may be an optimum for the period of high nestling demand from day 8 to day 18 of the non-brooding phase. Such an optimal mass would minimise flight costs without necessarily jeopardising adult survival or impairing development of the brood. This interpretation is strengthened because although adult body masses were lightest during the period of maximal food delivery rate to the brood, no adult starved to death during the study, and swallow body masses could be forced to levels considerably lower than those experienced by nestling rearers through experimental manipulation of brood demands (Figure 8.12)

The evidence for a hypothesis of targetting towards an optimal mass accumulates when male and female masses are compared. During incubation, female swallows were significantly heavier than males (Chapter 7). By day 7 of nestling-rearing there was no significant difference between the masses of males and females (Figure 8.1, $t = 1.00$, ns). Males and females on average feed the brood at similar rates (section 8.3.8), and may benefit from a similar optimal mass during the period of high nestling demand.

Other bird species may target towards an optimal mass over the brooding phase. The mass range of female pied flycatchers shortly before fledging was less than half that recorded amongst incubating females, suggesting convergence towards a similar mass among females (Askenmo, 1982). Female and male pied flycatchers also attained similar masses shortly before the young fledged, although the females were significantly heavier than males during incubation (only females incubate) (Winkel and Winkel, 1976).

Although mass loss during the non-brooding phase in swallows is interpreted largely on an adaptive, programmed anorexia, body mass was correlated with food abundance, and excessive mass losses on days of low food availability could be costly to the female.

Because food abundance levels from day to day tend to be correlated (Chapter 7), then on any poor day the likelihood is that the next day will be poor. Hence it may pay female swallows to maintain reserves on poor days for insurance during the next day which is also likely to be poor, and targetting towards an optimal mass may be confounded by subsequent and predicted future weather conditions.

Mass losses during the non-brooding phase, when FDRs are high, probably have different ultimate causes than the mass losses during the brooding phase. Birds of both sexes lost more mass when feeding the brood at higher rates (Figure 8.10), and mass losses at high FDRs may represent body condition costs to the adults. The relationship between mass change and FDR was linear, as seen in blue tits (Nur, 1981, 1984b).

The effects of increasing FDRs on adult body condition are not straightforward however, since there was no significant tendency for adults rearing enlarged broods to lose more mass from day to day compared with adults rearing reduced or natural brood sizes (Figure 8.14). In starlings feeding experimentally manipulated broods, body mass was inversely related to brood mass only at the end of the nestling period, and only amongst males (Ricklefs and Hussell, 1984).

Parental responses to brood demands may differ between male and female birds (Howe 1979, Wittenberger, 1982). The responses of the two sexes of swallow to brood demands differ according to the level of food abundance. Females appear to be prepared to lose more mass than males during the non-brooding phase (Figure 8.23). Females also became lighter than their mates on days of low food abundance (Figure 8.24) as an eventual consequence of their higher feeding rates to the brood relative to males in poor conditions (Figure 8.26). Swallow parental investment has also been studied by quantifying mobbing responses - female swallows mob more intensively than do males, and mobbing is most intensive in bad weather (Møller, 1984b).

Female starlings lost more mass than males during the second half of the rearing period, and this was associated with higher feeding rates by the females (Ricklefs and Hussell, 1984). Hence

in starlings mass losses during the non-brooding phase may also reflect condition costs associated with different levels of reproductive effort by each sex.

Theoretical studies of parental investment predict that investment should be considered in relation to future expectations of offspring survival (Dawkins and Carlisle, 1976; Boucher, 1977). After the end of the brooding phase, future investment in current offspring is similar for male and female swallows, since both feed the brood at similar rates (Ball, 1983a). Hence why should female swallows appear to take greater risks than males in allowing their body masses to fall to lower levels when food is scarce, and seemingly commit the 'concordefallacy' (Dawkins and Carlisle, 1976)?

The answer may lie in consideration of future nesting attempts. Females probably need considerable time to attain a suitable reproductive condition for re-laying, whilst males may already be carrying viable sperm. A male swallow may thus easily breed again if his current offspring die, whilst a female may be incapable of affording time for investment in new eggs, and so may take bigger risks to ensure the survival of her current offspring compared with her mate. However, males may have difficulty in finding a mate to re-nest with, especially during second broods, and so different levels of investment between the sexes may also be associated with different overwinter survival probabilities for males and females. If females are more likely to incur an overwinter mortality cost of reproduction, as seems likely in house martins (Bryant, 1979), they may be prepared to invest more in current offspring than males, and such higher female investment could further increase their reproductive costs.

The effect of manipulating brood size on adult mass changes was small and insignificant (Figure 8.14), as also found in starlings (Ricklefs and Hussell, 1984). There is no obvious reason to expect that parent swallows rearing enlarged broods should have higher mortality rates than birds rearing smaller rates if a bird's chance of dying is related to its body mass during nestling-rearing. Any reduction in parental inclusive fitness through rearing enlarged brood sizes may also be influenced by the effects of brood size on nestling growth and survival. In this study brood size had a more obvious effect on nestling growth rates and peak masses than it did on adult mass changes (Tables 8.6, 8.7). Nestlings in enlarged brood sizes grew more slowly than chicks in control or reduced brood sizes, and nestling peak mass was negatively correlated with brood size. If nestling overwinter survival were related to chick peak mass or growth rate, the inclusive fitness of parents rearing enlarged broods may be reduced, even though enlarged broods fledged more young.

Nestlings often have lower survival rates as chicks in artificially enlarged broods (Newton, in Lack 1966; Perrins, 1964; Ward, 1965; Askenmo, 1977; Schifferli, 1978), although some species can rear more young than the number of eggs laid, and the masses of fledglings suggested no reduced post-fledging survival rates (Nelson, 1964; Harris and Plumb, 1965). House martins can also rear more nestlings than the natural clutch size, and the survival rate of young from enlarged brood sizes was no lower than that of young from natural brood sizes (Bryant, 1975; 1979). Nestlings in enlarged broods of tree swallows were only lighter if reared by yearling females, and mortality after fledging appeared to be independent of

brood size (De Steven, 1980). Swallows resemble kittiwakes, Rissa tridactyla, (Coulson in Lack, 1966) and Japanese grey starlings, Sturnus cineraceus (Kuroda, 1959) whereby more young are reared in enlarged broods, though such young show slower growth rates.

The significance of nestling peak mass or fledgling mass on subsequent survival is controversial. House sparrows that died within 10 days of fledging were significantly lighter as nestlings than those which survived (Dawson, 1972). However, the total lipid reserves of a fledgling great tit are estimated to only subsidise one day's energy expenditure (Garnett, 1981), so the benefits of fledging at increased mass may be small or short-lived, especially in aerial insectivores where fledging with heavy lipid reserves may be a liability (through increasing flight costs) if food is plentiful.

Why do swallows not rear brood sizes larger than those normally observed, especially since brood size seems to have an insignificant effect on adult mass changes during the non-brooding phase, and brood size effects on fledging overwinter survival appear to be small in hirundines?

It is possible that optimal brood size may be constrained by factors acting outside of the nestling rearing phase. Parents may encounter energetic bottlenecks at the end of the incubation period and during laying (Yom-Tov and Hilborn, 1981). Short-term clutch size enlargement experiments (Chapter 7) suggest, however, that female swallows can successfully incubate larger than normal clutches without suffering any deterioration in body mass, and enlarged clutches hatched successfully. The experiments were of brief duration however, and occurred in mainly good weather conditions - females may

not be capable of incubating enlarged clutches in poor feeding conditions.

Poor weather during nestling rearing may also constrain optimal brood size in swallows. In fine weather adult energy gains are theoretically high enough to supply the demands of an enlarged brood. However, in bad weather adult swallows may only collect sufficient food to nourish naturally occurring brood sizes adequately, so the effects of weather and feeding conditions may limit the upper brood size in swallows (Turner, 1983).

CHAPTER 9

'Natural selection will modify the structure of the young in relation to the parent, and of the parent in relation to the young.'

CHARLES DARWIN (1859)
The Origin of Species by
Means of Natural Selection.

9. GENERAL DISCUSSION

REPRODUCTIVE COSTS, REPRODUCTIVE EFFORT, AND PARENTAL INVESTMENT IN SWALLOWS

9.1 Definitions

'Reproductive effort' can be defined as the proportion of resources (for example time and energy) diverted to reproduction summed over the time interval in question (Stearns, 1976). Reproductive effort can be partitioned into two components (Low, 1978; Alexander and Borgia, 1979):

- a. Mating effort, that is, effort devoted to acquiring mates, and
- b. Parental effort, or effort invested in provisioning and rearing offspring.

'Parental investment' has been defined by Trivers (1972) as: 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence their reproductive success) at the cost of the parent's ability to invest in other offspring'. 'Parental effort' may also be defined as the sum of parental investment on each offspring over the time interval in question.

'Reproductive cost' has been defined, according to Hirshfield and Tinkle (1975), as: 'the cost of a given level of reproductive effort is the difference between residual reproductive value when reproductive effort equals zero, and that residual reproductive value accompanying that particular expenditure of effort'.

It is important to distinguish between reproductive effort and reproductive costs. Whereas most empirical studies measure repro-

ductive effort as energy values, it is through the reproductive costs of breeding that natural selection operates (Pianka, 1976, 1978).

The extent to which the energetic costs of breeding reflect the reproductive costs is fundamental for an understanding of life-history tactics (Clutton-Brock, 1984, section 9.2).

9.2 Body mass changes as an indicator of reproductive costs in birds

Several studies of the reproductive biology of birds have suggested that mass loss while rearing chicks is an index of the physiological stress imposed on parents through breeding (Nice, 1937; Hussell, 1972; Ricklefs, 1974). Only one study has conclusively related differences in mass loss to differences in mortality costs of reproduction, and then only in females (Nur, 1984a).

Although insufficient to account for differences in clutch size, the present study has shown that mass losses in birds rearing nestlings are complex, and may be the consequence of a programmed anorexia early in the rearing phase, while subsequently reflecting the cost of provisioning nestlings when chick demands are high (Chapter 8). Studies relating mass losses to the physiological stress of breeding should therefore be treated with caution, especially if mass changes were inferred as being costly over an early stage of the rearing period (Howe, 1979; De Steven, 1980).

The relationship of mass changes during nestling rearing to parental feeding rate was linear and of negative slope for male and female swallows in this study, and Nur (1984b) also showed a negative linear relationship between the mass of female blue tits and their feeding rates. In female blue tits, a threshold mass during breeding probably exists, below which subsequent overwinter survival is drastically reduced (Nur, 1984a). The relationship between brood

size and female survival in blue tits was 'concave-up' (second derivative positive), with survival rate decreasing as brood size increased (Nur, 1984a).

9.3 Life-history tactics and reproductive effort

Theories of life-history tactics generally predict that reproductive effort should increase towards the end of an individual's lifespan in those animal species in which reproductive value declines with age (Fisher, 1930; Williams, 1966a, b; Gadgil and Bossert, 1970; Charlesworth and Leon, 1976; Pianka, 1976). Alternative theories are given by Fagen (1972), Goodman (1974), Hirshfield and Tinkle (1975), and Charlesworth and Léon (1976). Individuals with a high probability of future reproductive success, that is a high residual reproductive value (Pianka and Parker, 1975; Williams, 1966b) should be expected to take fewer risks raising current offspring than should individuals with lower chances of reproducing in the future. This idea has been referred to as 'terminal investment theory' (Clutton-Brock et al., 1982; Clutton-Brock, 1984).

Empirical evidence to date lends little obvious support to the theory of terminal investment in birds. Most measures of reproductive performance, such as clutch size or frequency and fledgling survival usually remain constant or decline towards the end of the lifespan, though they may improve over the first few breeding attempts (Mills, 1973; Perrins and Moss, 1974; Crawford, 1977; Brooke, 1978; Ollason and Dunnet, 1978; Newton, Marquiss and Moss, 1981). One problem with quantifying reproductive effort in individuals of different ages is that an animal's foraging ability may improve as it becomes older (Groves 1978, Burger, 1980), even improving beyond the age of first breeding (Recher and Recher, 1969). Hence older

parents may rear more offspring than younger individuals simply because they are more efficient at collecting food for the young, and this increase in foraging ability would not necessarily reflect parents taking greater risks with age.

Although the evidence for terminal investment during an individual's lifespan is equivocal (Clutton-Brock, 1984), consideration of reproductive effort in ways other than clutch or brood size may provide greater insight into the problem. For example, older California gulls Larus californicus, fledge more offspring than young or middle aged parents, probably because they feed their chicks for longer, and more frequently (Pugesk, 1981). Offspring born to older red deer, Cervus elaphus, mothers may show improved body condition and survival (Clutton-Brock, 1984).

Although insufficient data were available to determine whether terminal investment occurred over the lifespan of swallows, the theory can be adapted and condensed over short time periods, such as one breeding attempt. Again, the expected future cumulative reproductive effort would be expected to influence current reproductive effort or parental investment. Individuals with high future cumulative investment during one breeding attempt or season may take lower risks during reproduction than individuals with lower future cumulative investment, because individuals with high future cumulative investment would have more time to reinvest should the current attempt fail (Dawkins and Carlisle, 1976; Boucher, 1977). Terminal investment theory applied to one breeding attempt may also be easier to analyse because it is likely to remove the confounding variable of adult age influencing provisioning ability which is inherent in studies of lifetime reproductive effort.

Terminal investment theory therefore makes several testable predictions concerning the allocation of parental effort. The predictions are based on the theory of Trivers (1972) modified by Dawkins and Carlisle (1976), and Boucher (1977).

(i) Individuals should take bigger risks when breeding later in the season, as the chances of renesting during that season decline.

(ii) Individuals should take bigger risks towards the end of any breeding attempt, since potential future cumulative investment declines as the breeding attempt progresses.

(iii) The sex with the lower probability of renesting should invest more in current offspring. Differential renesting probabilities should occur because anisogamy results in an asymmetry in early parental investment by the sexes. Eggs, because of their relatively large size, are more expensive to produce than the smaller sperm. Hence a female would take longer to attain reproductive condition after a breeding failure than a male, because for females, egg production may take several days (Ricklefs, 1974), while males may carry viable sperm throughout the breeding cycle. Females are therefore assumed to have a lower probability of renesting than males and expend a greater effort in renesting than their mates, and so should invest more in current offspring. Males may also attain some reproductive success in any season through mating promiscuously with females other than their mates (Chapter 6). Any potential increase in male reproductive success achieved by mating promiscuously is likely to be greater than an increase in female reproductive success by egg dumping (as seen in cliff swallows, Hirundo pyrrhonota, (Brown, 1984) and swallows (A. P. Møller, pers. comm.)) because males are likely to

produce far more sperm than females make eggs, and since females must presumably find a mate to help rear her own brood before dumping eggs elsewhere.

Howe (1979) elaborated Trivers' ideas and predicted three behavioural patterns in monogamous biparental species as a consequence of differences in reneating probabilities between sexes.

- (i) More frequent male than female desertion.
- (ii) Greater and less variable female than male effort.
- (iii) Exceptional male effort only when the young most need it.

How do the predictions arising from terminal investment theory over single breeding attempts stand up to tests? Firstly consider Dawkins' and Carlisle's theory that breeding individuals may be expected to accept greater risks to their survival at later stages of the breeding cycle when the relative difference between parents and offspring in expected future survival has decreased (Andersson, Wiklund, and Rundgren, 1980).

One measure of parental investment is the readiness with which a bird performs a distraction display, attracting the attention of a potential predator towards themselves and away from the offspring by feigning injury. The distance from the nest with which female alpine accentors, Prunella collaris, perform distraction displays decreased as chicks became older, and display conspicuousness increased with increasing age of eggs and nestlings (Barash, 1975).

Other plausible anti-predator behaviours which may be indices of parental investment such as alarm calling (Greig-Smith, 1980; East 1981), nest defence (Andersson et al., 1980), and mobbing behaviour

(Krunck, 1964; Curio, 1975; Smith and Graves, 1978; Møller, 1984b) all tend to increase in frequency or intensity as the breeding attempt progresses, although predator persistence or abundance may perhaps also increase over the breeding period.

Trivers' (1979) hypothesis of asymmetric investment by the two sexes during gamete production, resulting in differential investment in current offspring by males and females, has been criticised, largely because of uncertainties about the extent and costs of male investment as compared to egg production by females.

The cost of the meiotic stages necessary in producing sperm cells are unknown, and could be more substantial than generally assumed. Increasing sexual activity reduces longevity in male fruit flies, Drosophila melanogaster (Partridge and Farquhar, 1981). Fertilization rates achieved by male lemon tetras, Hyphessobrycon pulchripinnis, in laboratory conditions (Pisces; Characidae) decline with spawning frequency, and even when the number of females is not limited, males can only produce four times as many offspring as females (Nakatsuru and Kramer, 1982). Male birds may invest heavily in mating effort while females are producing eggs (Burger, 1981). Males may also courtship feed females during egg production (Royama, 1966b, Nisbet, 1973; Niebuhr, 1981). In many birds species males guard their mates from other males seeking promiscuous copulations during the female fertile period (Chapter 6). Mate-guarding is marked in sand martins (Beecher and Beecher, 1979, Chapter 6), but also occurs in swallows (Woods, 1982, pers. obs.), and guarding behaviour may decrease the time males have available for self-feeding. Male gannets, Sula bassana lose 6276 kJ of lipid while defending territories before incubation, whereas the single egg laid by the female costs only 590kJ (Montevecchi and Porter, 1980).

Nevertheless, although male swallows do mate guard, they will probably have a higher reneating probability than females. Even if they do not reneat, they may obtain promiscuous copulations with females other than their mate should their current offspring die. Reduced male relative to female investment is unlikely to result in increased male desertion rates if the ability of males to find and mate with other females is low (Maynard Smith, 1977; Grafen and Sibly, 1978). No unilateral male or female desertion was observed in this study.

Increases in the intensity of nest defence behaviours over the breeding cycle are thus generally explicable in terms of future cumulative investment prospects. The interpretation of sexual differences in parental investment is difficult, however, largely because of the problems in assessing the costs of different activities. Weatherhead (1979) believed that sexual differences in the nest defence behaviour of savannah sparrows, Passerculus sandwichensis, was best explained in terms of past rather than future cumulative investment. By manipulating the clutch sizes of red-winged blackbirds with the same amount of past investment, Robertson and Biermann (1979), showed that females defended nests with larger clutch sizes more vigorously than did females with smaller clutch size, suggesting that investment was allocated in terms of prospective cumulative investment.

Both sexes of the North American barn swallow usually incubate, yet when females were detained during incubation, males did not significantly increase their time spent incubating. However, during brooding males doubled their brooding rates when their mates were detained, and hence males may increase their parental investment through increasing brooding rates when future cumulative investment is reduced compared with incubation (Ball, 1983a).

Ball (1983a) also increased the brood size of swallows during late rearing when female past investment is higher than that of the male, but future cumulative investment is similar for both sexes. Since both sexes increased their feeding rates to enlarged broods at the same rates, Ball argued that selection was acting on expected payoffs rather than on past cumulative investment.

How do the data on swallow body condition obtained in this study accord with theories of parental investment and terminal investment?

(i) Increased investment at later stages of the breeding cycle.

A graphical model of parent:offspring resource allocation as a function of female body mass during nesting is presented in Figure 9.1.

During breeding body mass increases as food abundance increases (Chapters 7, 8) and an individual female's mass at any time will probably reflect resource availability on that day and for several preceding days (Chapter 8). The maximum mass attained by an incubating female swallow in the study was 27g, and this is assumed to be at or close to an economically imposed upper limit to mass (Chapter 6). The upper mass limit will actually depend on a female's body size (Chapters 7, 8), but is likely to be between 22g and 27g. From the equation of extractable lipid as a function of body mass (Chapter 5), it was calculated that a swallow weighing 13.6g would carry no fat reserves. Since about 1.3% of total body mass may be structural lipid (Ward, 1969a), it is estimated that swallows of mean size weighing about 14g were likely to die through starvation. The mean body masses of adult swallows which died through starvation at their wintering grounds in southern Africa was 13.0g in one study (Skead and Skead, 1970), and 13.6g as recorded by Broekhuysen (1953).

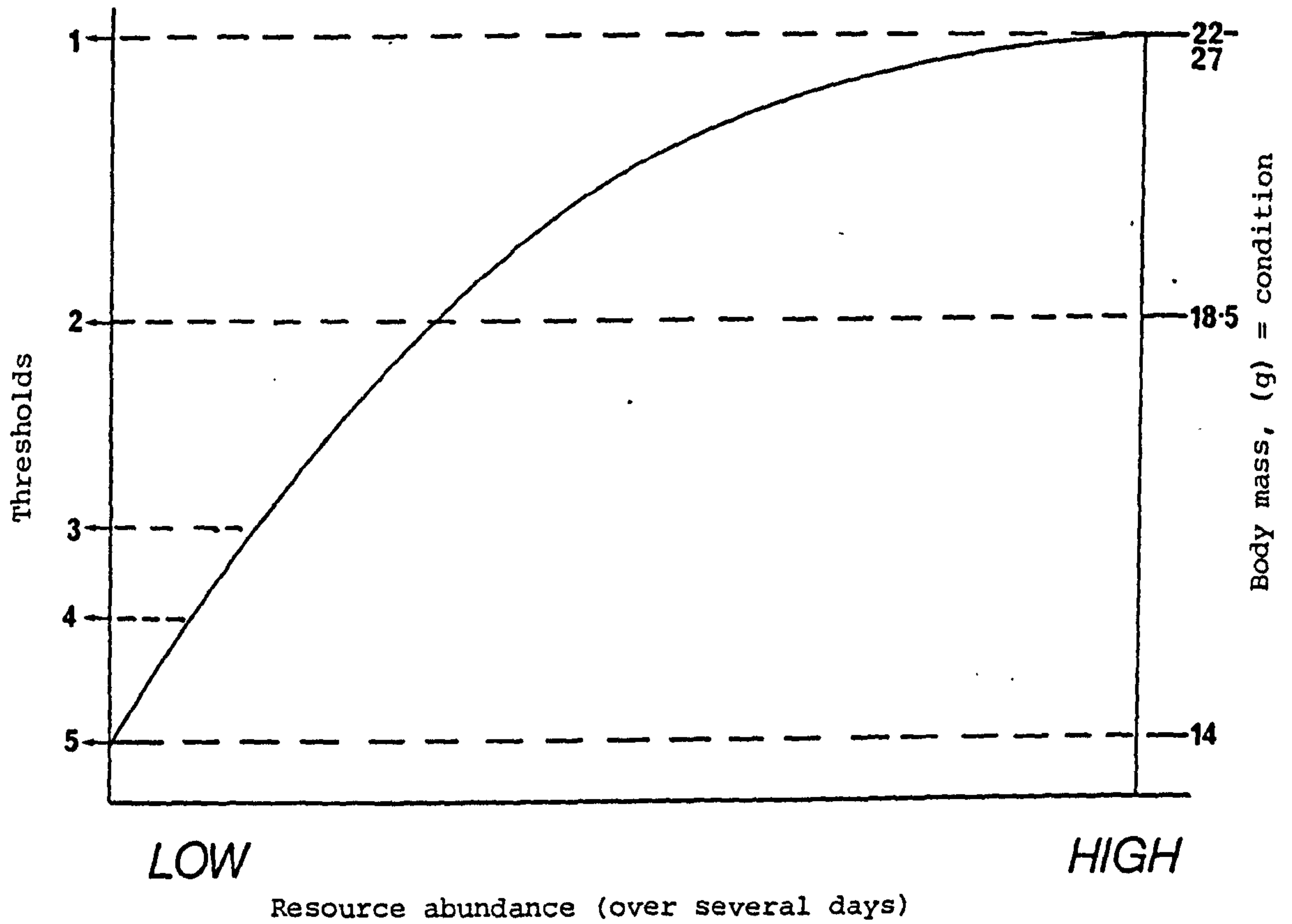


Figure 9.1

A theory of resource allocation decisions in female swallows, whereby decisions are made on the basis of body condition.

Thresholds are:

- 1 : maximal economical mass
- 2 : clutch desertion
- 3 : selective brood starvation
- 4 : total brood starvation
- 5 : self-starvation.

See text for explanation.

Since these dead birds will have lost some mass through dessication, 14g seems a reasonable assumption for the lower critical mass necessary for survival in swallows.

The rate of mass increase with increasing resource availability is assumed to decrease once the economical upper limit to mass is approached. Although extractable lipid was related to body mass in a linear fashion between 17g and 22g (Chapter 5), protein reserves may be metabolised once fat reserves are low (Houston, 1977), and since protein yields less energy per unit mass than lipid, the rate of mass decrease may accelerate at low food levels.

Within the upper and lower limits of body mass during incubation and nestling rearing, various body condition thresholds are likely to exist for a female's behavioural options. Incubating females were judged likely to desert eggs at about 18.5g - one female seemed close to desertion at this mass in bad weather. However, swallows of this mass were frequently observed rearing nestlings, so the condition threshold (i.e. critical body mass) for clutch desertion is probably greater than that for desertion of nestlings.

One female swallow was reduced in mass to 16g after a brood size enlargement followed a replacement experiment, but nevertheless successfully fledged six young. Since incubation is a relatively early stage of the breeding cycle, females may still have time to relay if they desert their clutch. Females may therefore desert at a relatively high body mass so that the energy investment in a new clutch would take less time and energy to accumulate than if they deserted with small energy reserves. The probability of relaying would be lower during nestling rearing since less time remains for future breeding attempts. Hence rearing females may allow their

body reserves to decline to lower levels than during incubation at the risk of extending the time to collect energy for a replacement clutch, because future cumulative investment in current offspring is lower in rearing than incubation.

Parents will put their own interests above those of the brood, since adults may have re-nesting opportunities but offspring will not survive without parental care. Hence the body condition threshold for a female to starve the brood will be greater than that for self-starvation, which is estimated at 14g. Moreover, at an intermediate stage, it is expected that the parents will selectively starve individual chicks (brood reduction) which contribute least to their inclusive fitness before starving the whole brood.

Obviously the above model is simple, and could be elaborated to consider the different thresholds for male and female desertion (males predicted to desert before females), for desertion by parents of different ages (older birds are predicted to risk body mass dropping to lower levels), and for deserting broods of different ages (younger broods deserted at a higher critical mass than older broods) on the basis of terminal investment theory. Moreover, the optimal female mass is lower during nestling rearing than during incubation (Chapters 7, 8), so the model should ideally involve deviations from the optimal mass (taking into account size differences between individuals) as criteria for making behavioural decisions.

(ii) Differential investment on current offspring by males and females

Female swallows in this study were prepared to lose more mass during the non-brooding phase than their mates when rearing natural brood sizes, seemingly because females fed their broods more than

males when food was scarce. However, both sexes increased the food delivery rates to larger broods at similar rates (Chapter 8). As yet, the analysis of parental investment in feeding nestlings has not considered investment in self-maintenance relative to concurrent allocation in provisioning offspring. This analysis is performed in Section 9.4, to elucidate differential investment in current offspring relative to self-maintenance by the two sexes of swallows.

9.4 Concurrent parent:offspring resource allocation in swallows

An individual swallow's body mass during the non-brooding phase can be used as a measure of self-investment since mass changes during late rearing are related to the work done in feeding the brood (Chapter 8). Investment in current offspring can be quantified by an individual's food delivery rate (FDR) to the broods. The ratio of body mass during the non-brooding phase/FDR can then be considered as an index of investment in self relative to investment in offspring. This index is referred to as the 'self-investment index', and high values indicate substantial investment in self-maintenance relative to investment in offspring.

(a) Food abundance effects

For both males and females, the self-investment index was negatively correlated with food abundance as determined by hand-net biomass males: $r = -0.38$, $P < 0.05$; females: $r = -0.47$, $P < 0.01$, $n = 34$ for both sexes). A tighter fit is obtained by plotting \log_e of the self-investment index against \log_e food abundance (males: $r = -0.59$, $P < 0.001$; females $r = -0.48$, $P < 0.001$) (Figure 9.2). Since both adult body mass and FDR were positively correlated with food abundance (Chapter 8), it is their ratio which is of interest.

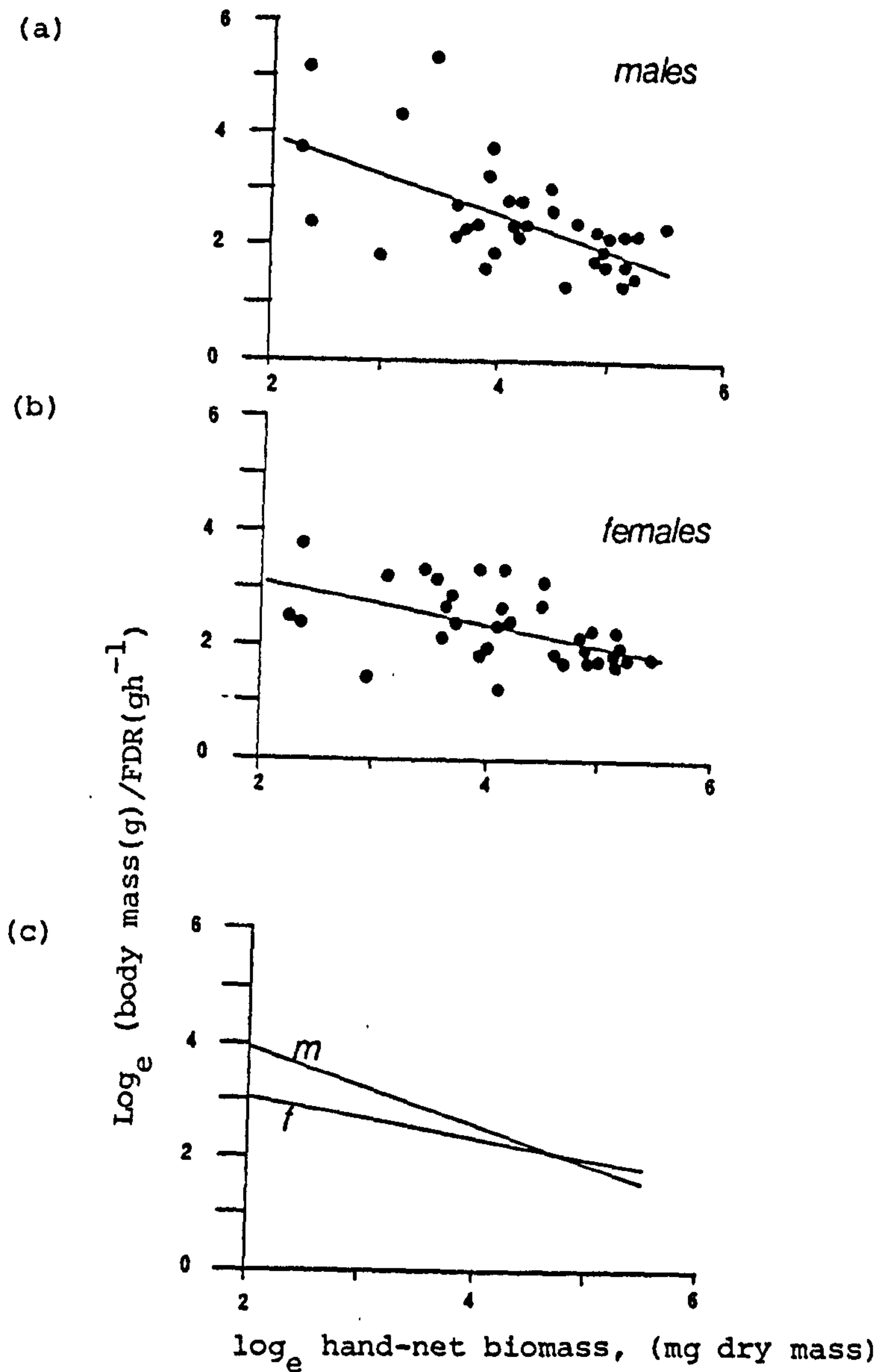


Figure 9.2

Self-investment indices as a function of food abundance for male and female swallows during the non-brooding phase.

(a) Males: $\ln y = 5.25 - 0.67 \ln x$;
 $r = -0.59, n = 34, P < 0.001$.

(b) Females: $\ln y = 3.76 - 0.36 \ln x$;
 $r = -0.48, n = 34, P < 0.001$

(c) Regression lines for males (m) and females (f).

Includes data from control and experimental brood sizes.

For both sexes, the negative correlation between variables indicates greater investment in self relative to investment in offspring when food was scarce, yet the slopes of the relationships for males and females are significantly different (analysis of covariance, $t = 7.7$, $n = 68$, $P < 0.001$). Males invest more in 'self', relative to 'offspring', than do females when food is scarce.

The negative correlations between self-investment indices and food abundance could reflect seasonal changes in parent:offspring resource allocation, since food abundance was low early in the season (Chapter 3), and parental investment theory would predict higher self-investment indices (and lower investment in offspring) earlier in the season when the chances of renesting are higher.

The logarithm_e of the investment indices was entered as the dependent variable in a stepdown multiple regression analysis where the natural logarithms of food abundance and date (days after June 1st) were entered as independent variables. For both sexes, food abundance entered as a significant variable (males $t = 3.6$, $P < 0.01$, females $t = 3.0$, $P < 0.01$), whereas date did not significantly influence the self-investment indices. However, data for late first and early second broods were mixed in the analysis and it remains possible that investment indices differed between first and second broods, though insufficient data were available to test this.

Hence the prediction that investment in offspring relative to investment in self should increase as the breeding season progressed was not substantiated in this data set. House martins, however, increased their average daily metabolic rates when feeding second broods, suggesting a rise in reproductive effort later in the season (Hails and Bryant, 1979).

Both sexes of swallow invested more in 'self' relative to 'offspring' when food was scarce, however, males to a greater extent than females. Males may accept lower risks to their survival than their mates when food is scarce, since male reneating probabilities may be greater, and females may pay greater mortality costs of reproduction in the wintering grounds (Bryant, 1979).

(b) The effects of brood mass

In the analysis described below, metabolic brood mass ($\text{mass}^{0.66}$) of broods aged 8-16 days was used as an approximation of brood food requirements. Both sexes increased their FDRs to larger brood masses at similar rates, although birds feeding enlarged broods did not lose significantly more mass on a daily basis than individuals rearing natural or reduced brood sizes during the non-brooding phase (Chapter 8). Hence, although investment in 'self' may remain constant for parents rearing different brood sizes, investment in self relative to investment in offspring may be reduced at large brood masses because of the higher FDRs to the larger broods.

The most significant relationship of self-investment index and metabolic brood mass occurs when the investment index alone is transformed to natural logarithms (males: $r = -0.58$, $P < 0.001$; females $r = -0.75$, $P < 0.001$, $n = 34$ for both sexes). For both sexes investment in self relative to investment in offspring is greater at lower brood masses (Figure 9.3). Parents rearing larger broods (with heavier brood masses) have greater future benefits since they may fledge more young than parents rearing smaller broods. Hence parental investment theory successfully predicts greater investment in 'offspring' relative to 'self' in swallows for larger brood sizes.

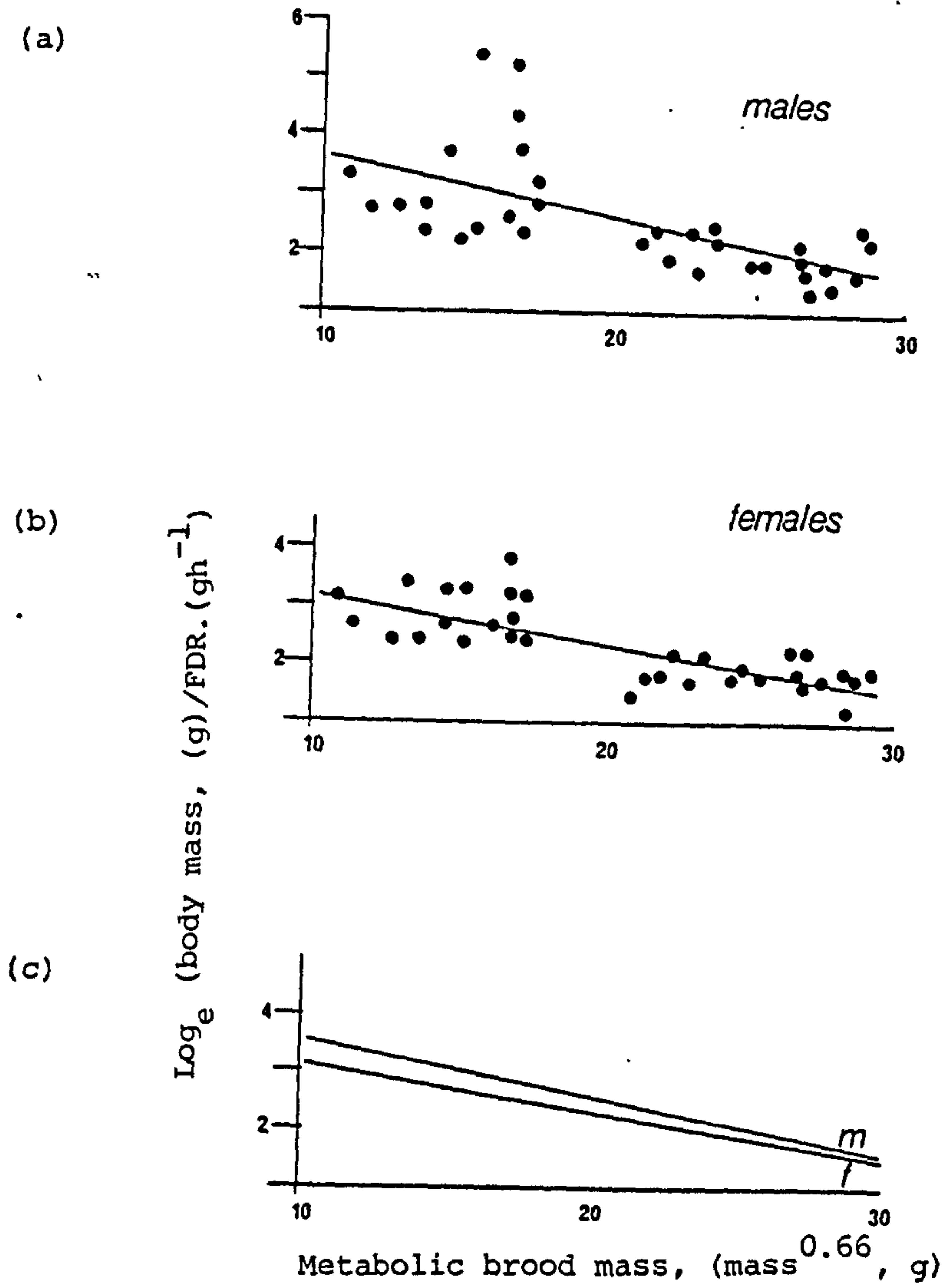


Figure 9.3

Self-investment indices as a function of metabolic brood mass for male and female swallows during the non-brooding phase.

(a) Males: $\ln y = 4.54 - 0.1x$; $r = -0.58$, $n = 34$, $P < 0.001$

(b) Females: $\ln y = 4.02 - 0.085x$;
 $r = -0.75$, $n = 34$, $P < 0.001$

(c) Regression lines for males (*m*) and females (*f*).

Includes data for control and experimental brood sizes.

The slopes of the relationships for males and females were significantly different (analysis of covariance, $t = 2.0$, $P < 0.05$), suggesting that males invest more in 'self' relative to 'offspring' when rearing broods of low mass. Hence female self-investment indices are lower than those of males even when expected future benefits are relatively low.

Previous work on parental investment in birds has generally attempted to quantify 'investment' through monitoring anti-predator behaviours (e.g. Barash, 1975; Andersson et al., 1980; Robertson and Biermann, 1979; Weatherhead, 1979; Greig-Smith, 1980; East, 1981), and such studies experience problems in that changes in predation pressure over the breeding season confound the quantification of anti-predator behaviours. Studies using precision automated nest balances, based on a sound knowledge of the causes and consequences of mass changes during breeding provide a reliable measure of reproductive investment in birds, and also allow simultaneous quantification of resource allocation in 'self' and 'offspring'.

The scope for future work on reproductive investment measured by mass changes is promising. For example, investment by one sex could be experimentally manipulated by mate detention experiments. The study of parental investment in birds of different ages using precision nest balances remains as a challenging prospect, and the use of such balances would greatly increase knowledge of short term resource allocation decisions in parent birds collecting food for their nestlings.

SUMMARY AND CONCLUSIONS

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1. The distribution and abundance of sand martins in the Stirling Region was estimated by burrow counts at 27 sites between 1982 and 1984 inclusive. Eighty-one percent of pairs nested in sand and gravel quarries. A population crash over the study period reduced 1984 numbers to 24.9% of 1983 numbers, 18.9% of the 1982 total. The dramatic reduction in the breeding population of sand martins, both locally and throughout the U.K., was probably largely attributable to drought conditions in the wintering ground and poor weather encountered on migration.

The mean body size of sand martins, as determined by keel-length, decreased significantly between 1983 and 1984 when overwinter mortality was assumed to be exceptionally high. Selection for smaller individuals appears to have occurred in the wintering ground, and an adaptive advantage for small body size in severe climatic conditions is proposed. Selection acting on size in the wintering grounds will constrain the distribution of body sizes during the breeding season, and birds of a size which maximises overwinter survival prospects may not be of a size which maximises breeding success.

Wing-length increased with adult age in sand martins, and was not consistently correlated with body mass. Older birds returned to the main study colony before first-year individuals, and thus had the widest choice of subcolony in which to nest. A model of colony settlement was developed which assumed that individuals nested in subcolonies where their reproductive success was maximised. The costs and benefits of early arrival at the breeding colony were discussed.

2. Resources available for breeding hirundines were measured by hand-net sampling over short time periods, and by a 12.2 metre suction trap which sampled over an entire day. Suction trap catches increased during the spring, generally providing a high level of food abundance between June and early September, except in periods of poor weather. Hand-net catches peaked during July in 1983, when sampling was performed on most days between June and September. Temperature and season significantly influenced the level of insect abundance. Net catches were correlated with suction trap catches. A consistently greater volume of insects was captured by the suction trap in 1982 than during 1983.
3. Short-term body mass changes of canaries and sand martins were investigated in the laboratory using precision automated electronic balances. Diurnal body mass changes of canaries could be accurately estimated by time budgeting birds and from knowledge of rates of mass changes associated with different activities. Mass gains occurred through foraging and drinking, instantaneous mass losses resulted from defaecations. Continuous mass losses were attributable to evaporative water loss, which varied with temperature and activity. An understanding of short term mass changes for swallows in the field was developed in the light of laboratory investigations, so that conclusions about more substantial mass changes during breeding could be reached. The use of precision balances in studies of avian ecology and physiology was discussed.
4. The body condition of breeding adult sand martins was investigated by carcass analysis. Body component lipid indices were poor predictors of total extractable lipid, though the mass of lipid in the tracheal pit was strongly correlated with total body lipid.

Field estimates of lipid condition by fat scoring correlated with lipid indices and lipid content determined by carcass analysis in both sand martins and swallows. Body mass changes of breeding sand martins were related to changes in lipid and protein reserves, water content, and the mass of reproductive structures. Mass changes were largely attributable to changes in the birds' lipid reserves, except in laying and pre-laying females which carried considerable reproductive material. Small changes in pectoralis lean dry mass were correlated with changes in lipid content, though the significance of protein reserves as an energy reserve during breeding was slight. The body condition of adult sand martins was compared with that of fledglings.

Changes in the condition of nestling sand martins were related to age. Body component development and the lipid content of components in chicks were described. The lipid content of nestling body components was generally a good predictor of total body lipid. Lipid index hierarchies within broods were investigated, and it was concluded that hierarchies exist partly because of pre-hatching factors. The oldest chick in a brood usually had a higher lipid index than the youngest, though neither the youngest nestling nor the chick with the lowest lipid index in a brood was consistently under-nourished.

Maturing nestling sand martins can potentially live for considerably longer from their energy reserves than adults in the absence of food, so the selective premium on adult self-maintenance behaviours in poor feeding conditions was considered to be great.

5. Because female sand martins became exceptionally heavy when they were most likely to be fertile, their increased mass was likely to

present cues during flight to males seeking promiscuous copulations. Heavy female sand martins released from the hand were selectively chased in sexual chases. Breeding females were heaviest during laying and pre-laying, exceeding any masses normally achieved by breeding males. Experimental manipulation of flight feathers suggested that flight behaviour influenced the probability of being chased. A sample of naturally heavy females and birds whose mass had been experimentally increased to that of laying and pre-laying females took longer to reach ascending flight, as determined by analysis of video recordings, than a sample of lighter birds. It was concluded that this and other flight cues may be detected by males so that they may achieve promiscuous copulations and increase their reproductive success. The relationship of mate-guarding behaviour to colonial breeding in birds was discussed.

6. An optimality model was developed for bird species where one sex incubates. The model assumed that fitness was increased in individuals which maximised time on the nest by maximising the net benefit of metabolizable energy gained while foraging - energy cost of reheating eggs, during inattentive periods. Using laboratory data on egg cooling rates, and field information on instantaneous mass changes while foraging, and hence energy gains, the predicted optimal inattentive period was found to correspond closely with that most frequently observed. Inattentive periods longer than the predicted optimum were calculated to be energetically relatively profitable, but were avoided by swallows probably because of risks of embryo maldevelopment resulting from frequent inattentiveness and chilling of eggs.

The effects of changing costs and benefits on the model of an

optimal inattentive period were considered, and investigated by experimental manipulation of clutch size. Females did not significantly reduce the length of inattentive periods, as predicted by the model, when clutch size was increased, probably because repeated and brief foraging times are likely to jeopardise body condition and hence survival prospects. The effect of increasing clutch size on female body mass was described to provide insight into whether the upper limit to brood size in swallows was limited by incubation constraints. Clutches of eight eggs were successfully incubated in fine weather by two females without any deleterious consequences for their body condition, so it was concluded that incubation constraints do not limit brood size, at least when food is abundant.

Female swallows incubated for longer bouts if their preceding foraging period was relatively long, but neither mass gain nor rate of mass gain while foraging significantly influenced the duration of incubation stints.

Female swallows maintained a relatively heavy body mass during incubation, and mass was positively correlated with ambient temperature. The time constraints of incubating caused female body condition to deteriorate in poor weather conditions. Females spent less time incubating at high ambient temperatures, and when their body condition was poor.

7. Body mass changes of swallows during nestling rearing were analysed to determine whether mass losses reflected the costs of feeding or brooding nestlings. Females lost mass most rapidly when brooding young chicks, before the peak food requirements of the brood were attained. This rapid mass loss was not caused by the cost of feeding nestlings. Since females did not significantly lose mass

when their brooding time was experimentally increased, and since mass changes while foraging were on average relatively low or negative during the late brooding phase, rapid mass loss during brooding was interpreted largely as a 'programmed' anorexia, whereby females targetted their condition towards an optimal mass in time for a period of high nestling demand. Such an optimal mass probably minimised flight costs and allowed energy release for work without jeopardising female survival.

Rapid foraging after termination of the brooding phase was potentially costly for both males and females in that mass changes were negatively and linearly related to food delivery rates. Experimental manipulation of brood size showed no significant tendency for parental mass changes to be related to brood size however, although nestlings in larger brood sizes grew more slowly and attained lower peak masses than chicks in smaller broods.

8. Female swallows were prepared to lose more mass than their mates after termination of daytime brooding. Females fed broods at a faster rate than males when food was scarce, and this probably resulted in the ratio of female mass/mate mass decreasing at low levels of food abundance. Both sexes increased their feeding rates to larger brood masses at similar rates.

9. The implications of body mass changes in breeding swallows for theories of life-history tactics and parental investment were discussed by considering parental self-investment and investment in offspring simultaneously. Self-investment indices were derived by dividing parental body mass during the non-brooding phase by food delivery rates to the brood. Both sexes invested more in self-maintenance relative to offspring allocation when food was scarce,

and when feeding broods of low metabolic mass. Self-investment indices were higher for males than females at low levels of food abundance and at low metabolic broods masses, as predicted by parental investment theory.

10. Overall, it was concluded that the use of precision balances can be of great value in studies of avian behavioural ecology and physiology. Body mass changes in the field could be monitored to a degree of precision not previously attained, and short term mass changes can be useful measures of energetic costs and benefits in determining optimal reproductive tactics. A detailed knowledge of the causes of mass changes allows accurate quantification of reproductive costs and parental investment, and an understanding of behavioural decisions made by adult birds during breeding.

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APPENDICES

APPENDIX I

Sand Martin colonies in the Stirling Region,

1982 - 1984

APPENDIX I

Estimated maximum number of pairs attempting first broods

Site No.	DISTRICT/nature of site	Name of site	Grid Reference			
			1982	1983	1984	1984
STIRLING						
1	artificial, gravel pit	Cambusmore GP, nr. Callander	NN 649062	34	322 [†]	70
2	artificial, sand pit/gravel pit	Cambusbeg S + GP, nr. Callander	NN 665052	530	423	75
3	artificial, sand/gravel pit	Blair Drummond sand + gravel pit	NS 732003	40	5	0
4	artificial, sand/gravel pit	Kinbuck sand + gravel pit	NN 795048	501	207	55
5	artificial sand/gravel pit	Barbush, nr. Dunblane, sand + gravel pit	NN 787026	918	577	115
6	artificial, sand/gravel pit	Drumbeg, S + GP, Drymen	NS 478881	600 ¹	334	197
7	artificial, gravel pit	Cowie GP	NS 822899	NC	2 [‡]	0
8	natural, river bank	Allan Water, Kinbuck-Greenloaning	NN 805060	356	185	15
9	natural, river bank	River Teith, Greenocks, Lecropt	NS 765964	15	NC	
10	natural, river bank	River Teith, Callander	NN 623075	46	18	8
11	natural, river bank	River Balvag, Strathyre	NN 562192	10	NC	0
12	natural, river bank	River Endrick, county boundary below Catterburn	NS 470873	NC	61	58*

Site No.	DISTRICT/nature of site	Name of site	Grid Reference			
			1982	1983	1984	1984
STIRLING						
13	natural, river bank	River Forth, Gargunnoch-Kippen	NS 695968	NC	NC	10
14	natural, glacial esker	Strath a Ghlinne, Glen Artney	NS 680170	NC	50	35
FALKIRK						
15	artificial, sand + gravel pit	Scottish Aggregates, nr. Linlithgow	NS 969784	72	0	0
16	artificial, gravel extraction	Whitecross	NS 964778	6	0 ^Y	0
17	artificial, sand + gravel quarry	Alva Glen S + GP	NS 955784	25	91 ^Z	53 ^Z
18	artificial, sand + gravel quarry	Roughmute S + GP	NS 832810	366	10 ^Y	0
19	artificial, sand + gravel quarry	Castle Rankine Glen, nr. Denny	NS 792823	48	48	3 ^{Y,Z}
20	artificial, sand pile	Northfield quarry, nr. Denny	NS 800854	NC	1	0
21	artificial	Dunipace Cemetery	NS 83818	NC	15 [†]	7
CLACKMANNAN						
22	golf course	Muckhart golf course	NN 002002	4+ ²	NC	50 ²
23	sand bank	Tillicoultry quarry	NS 912978		19 [†]	19
24	natural, river bank	Dunning Glen	NN 005030	15 ^{†2}	NC	3 ²
25	natural, river bank	River Devon, Menstrie+Alva	NS 874963	6	2	1

Site No	DISTRICT/nature of site	Name of site	Grid Reference			
			1982	1983	1984	1984
	CLACKMANNAN					
26	natural, river bank	River Devon, Alva→Tillicoultry	NS 903965	106	123	84
27	natural, river bank	River Devon, Tillicoultry→Dollar	NS 940974	52	103	50

KEY: † probably some movement here from Cambusbeg

‡ probably first year of use

* more thorough survey in 1984

Y decline probably attributable to poorer quality sand faces being available

Z better quality sand faces probably available

1 Count from J. Mitchell, N.C.C.

2 Count from D. M. Bryant

GP : gravel pit

S + GP : sand and gravel pit

APPENDIX II

BODY COMPONENT ANALYSIS FOR
ADULT AND FLEDGLING SAND MARTINS

APPENDIX II a. Mean dry masses, lean dry masses, and lipid indices of dissected body components of adult and fledgling sand martins

Component	Males				Females				Lipid Index
	Dry mass g	n	Lean dry mass, g	Lipid index	Dry mass, g	n	Lean dry mass, g	Lipid Index	
Tail feathers	0.0645 ± 0.0092	(13)	0.0653 ± 0.0087	0*	0.0610 ± 0.0116	(18)	0.0597 ± 0.0110	2.2	
Wing feathers	0.3146 ± 0.0203	(13)	0.3185 ± 0.0237	0*	0.3059 ± 0.0208	(18)	0.3105 ± 0.0241	0*	
Skin and contour feathers	1.0648 ± 0.1398	(13)	0.7730 ± 0.0538	37.7	1.0610 ± 0.1768	(19)	0.7533 ± 0.0776	40.8	
Legs	0.3115 ± 0.0488	(13)	0.2016 ± 0.0203	54.5	0.3292 ± 0.0699	(19)	0.2082 ± 0.0300	58.1	
Wings	0.4080 ± 0.0359	(13)	0.2782 ± 0.0221	46.7	0.4261 ± 0.0495	(19)	0.3028 ± 0.0465	40.7	
Pectoralis Major	0.6732 ± 0.0702	(13)	0.5832 ± 0.0599	15.4	0.6426 ± 0.0682	(19)	0.5554 ± 0.0569	15.7	
Pectoralis Minor	0.0356 ± 0.0090	(13)	0.0304 ± 0.0082	17.1	0.0503 ± 0.0234	(18)	0.0437 ± 0.0208	15.1	
Body shell	0.8528 ± 0.1487	(13)	0.5434 ± 0.0551	56.9	0.8682 ± 0.2315	(19)	0.5655 ± 0.0855	53.5	
Head	0.4170 ± 0.0166	(13)	0.3224 ± 0.0126	29.3	0.4008 ± 0.0284	(19)	0.3100 ± 0.0189	29.3	
Neck	0.1140 ± 0.0169	(13)	0.0841 ± 0.0129	35.6	0.1158 ± 0.0153	(19)	0.0861 ± 0.0101	34.5	
Oesophagus and Gizzard	0.1680 ± 0.0439	(13)	0.1452 ± 0.0410	15.7	0.1945 ± 0.0384	(19)	0.1651 ± 0.0351	17.8	
Lung	0.0600 ± 0.0077	(12)	0.0539 ± 0.0071	11.3	0.0571 ± 0.0074	(18)	0.0521 ± 0.0068	9.6	
Heart	0.0717 ± 0.0107	(13)	0.0611 ± 0.0095	17.3	0.0729 ± 0.0112	(19)	0.0615 ± 0.0097	18.5	
Liver	0.2896 ± 0.0786	(13)	0.2050 ± 0.0356	41.3	0.2812 ± 0.0419	(19)	0.2056 ± 0.0320	36.8	
Gut	0.2419 ± 0.0413	(13)	0.1773 ± 0.0228	36.4	0.2343 ± 0.0673	(19)	0.1670 ± 0.0413	40.3	
Kidneys	0.0631 ± 0.0164	(13)	0.0510 ± 0.0124	23.7	0.0650 ± 0.0131	(12)	0.0498 ± 0.0101	30.5	
Gonads	0.0160 ± 0.0075	(11)	0.0117 ± 0.0071	36.8	0.1978 ± 0.2964	(12)	0.1222 ± 0.1866	61.9	
Tracheal fat	0.0689 ± 0.0454	(12)	0.0041 ± 0.0023	1580.5	0.0964 ± 0.0580	(17)	0.0133 ± 0.0141	753.1	

* feathers occasionally increased in dry mass after lipid extraction, probably because of water absorption in the short time before weighing.

APPENDIX II a. (cont.)

Component	Adults				Fledglings				Lipid	
	Dry mass, g	n	Lean dry mass, g	Lipid Index	Dry mass, g	n	Lean dry mass, g	Lipid Index	Lean dry mass, g	Lipid Index
Tail feathers	0.0626 ± 0.0105	(32)	0.0619 ± 0.0102	1.1	0.0544 ± 0.0043	(6)	0.0532 ± 0.0039	2.3	0.0532 ± 0.0039	2.3
Wing feathers	0.3094 ± 0.0204	(32)	0.3133 ± 0.0237	0*	0.2540 ± 0.0185	(6)	0.2521 ± 0.0186	0.8	0.2521 ± 0.0186	0.8
Skin and contour feathers	1.0602 ± 0.1584	(33)	0.7622 ± 0.0678	39.1	1.0579 ± 0.2824	(6)	0.6716 ± 0.0944	57.5	0.6716 ± 0.0944	57.5
Legs	0.3198 ± 0.0624	(33)	0.2049 ± 0.0261	56.1	0.3003 ± 0.0180	(6)	0.1730 ± 0.0119	73.6	0.1730 ± 0.0119	73.6
Wings	0.4190 ± 0.0440	(33)	0.2934 ± 0.0395	42.8	0.3389 ± 0.0189	(6)	0.2412 ± 0.0121	40.5	0.2412 ± 0.0121	40.5
Pectoralis major	0.6547 ± 0.0685	(33)	0.5666 ± 0.0579	15.5	0.6546 ± 0.0528	(6)	0.5446 ± 0.0413	20.2	0.5446 ± 0.0413	20.2
Pectoralis minor	0.0443 ± 0.0198	(32)	0.0381 ± 0.0178	16.3	0.0323 ± 0.0075	(6)	0.0266 ± 0.0072	21.4	0.0266 ± 0.0072	21.4
Body shell	0.8535 ± 0.2021	(33)	0.5539 ± 0.0747	54.1	0.7946 ± 0.0996	(6)	0.4755 ± 0.0178	67.1	0.4755 ± 0.0178	67.1
Head	0.4067 ± 0.0252	(33)	0.3146 ± 0.0174	29.3	0.3395 ± 0.0201	(6)	0.2634 ± 0.0108	28.9	0.2634 ± 0.0108	28.9
Neck	0.1144 ± 0.0159	(33)	0.0850 ± 0.0111	34.6	0.1033 ± 0.0205	(6)	0.0772 ± 0.0169	33.8	0.0772 ± 0.0169	33.8
Oesophagus and Gizzard	0.1826 ± 0.0421	(33)	0.1562 ± 0.0379	16.9	0.2119 ± 0.0309	(6)	0.1431 ± 0.0174	48.1	0.1431 ± 0.0174	48.1
Lung	0.0580 ± 0.0076	(31)	0.0527 ± 0.0068	10.1	0.0557 ± 0.0103	(6)	0.0498 ± 0.0085	11.8	0.0498 ± 0.0085	11.8
Heart	0.0726 ± 0.0107	(33)	0.0616 ± 0.0094	17.9	0.0848 ± 0.0133	(5)	0.0739 ± 0.0090	14.7	0.0739 ± 0.0090	14.7
Liver	0.2846 ± 0.0586	(32)	0.2053 ± 0.0330	38.6	0.2052 ± 0.0279	(6)	0.1585 ± 0.0158	29.5	0.1585 ± 0.0158	29.5
Gut	0.2334 ± 0.0610	(33)	0.1692 ± 0.0362	37.9	0.2223 ± 0.0369	(6)	0.1571 ± 0.0222	41.5	0.1571 ± 0.0222	41.5
Kidneys	0.0640 ± 0.0147	(25)	0.0504 ± 0.0111	27.0	0.0541 ± 0.0062	(6)	0.0420 ± 0.0055	28.8	0.0420 ± 0.0055	28.8
Gonads	0.1108 ± 0.2293	(23)	0.0694 ± 0.1436	59.7						
Tracheal fat	0.0850 ± 0.0541	(29)	0.0084 ± 0.0014	911.9	0.1071 ± 0.0293	(6)	0.0057 ± 0.0014	1778.9	0.0057 ± 0.0014	1778.9

* feathers occasionally increased in dry mass after lipid extraction, probably because of water absorption in the short time before weighing.

APPENDIX II

b. A comparison of DM and LDM of adult male and female sand martin body components.

Tabulated values are 't'.

Data from Appendix II(a)

* : $P < 0.05$

ns : not statistically significant

	<u>dry mass</u>	<u>lean dry mass</u>
tail feathers	0.90 ns	1.52 ns
wing feathers	1.16 ns	0.92 ns
skin and contour feathers	0.06 ns	0.79 ns
legs	0.79 ns	0.69 ns
wings	1.13 ns	1.79 ns
pectoralis muscles	0.67 ns	0.72 ns
body shell	0.21 ns	0.82 ns
head	1.85 ns	2.07*
neck	0.31 ns	0.49 ns
oesophagus and gizzard	1.81 ns	1.47 ns
lung	1.03 ns	0.71 ns
heart	0.30 ns	0.12 ns
liver	0.39 ns	0.05 ns
gut	0.36 ns	0.82 ns
kidneys	0.02 ns	0.26 ns
gonads	2.03 ns	1.96 ns
tracheal fat	1.37 ns	1.74 ns

APPENDIX II

c. A comparison of DM and LDM of adult and fledgling sand martin body components.
 Tabulated values are 't'.
 Data from Appendix II(a)

* : P < 0.05

** : P < 0.01

*** : P < 0.001

ns : not statistically significant

	<u>dry mass (DM)</u>	<u>lean dry mass (LDM)</u>
tail feathers	1.84 ns	2.04 *
wing feathers	6.09 ***	5.97 ***
skin and contour feathers	0.03 ns	2.84 **
legs	0.75 ns	2.91 ***
wings	4.35 ***	3.18 **
pectoralis muscles	0.47 ns	1.42 ns
body shell	0.69 ns	2.53 *
head	6.16 ***	6.92 ***
neck	1.51 ns	1.46 ns
oesophagus and gizzard	1.62 ns	0.82 ns
lung	0.64 ns	0.92 ns
heart	2.31 *	2.74 *
liver	3.22 **	3.37 **
gut	0.43 ns	0.79 ns
kidneys	1.60 ns	1.78 ns
gonads	∞ ***	∞ ***
tracheal fat	0.96 ns	0.57 ns

APPENDIX III

BODY COMPONENT ANALYSIS FOR
ADULT AND FLEDGLING SWALLOWS

APPENDIX III

Mean dry masses, lean dry masses, and lipid indices of dissected body components of adult and fledgling swallows

Component	ADULTS n = 6		Lipid Index
	Dry mass (g)	Lean dry mass(g)	
Tail feathers	0.1127 ± 0.0216	0.1139 ± 0.0190	0
Wing feathers	0.4966 ± 0.0140	0.4954 ± 0.0102	0.2
Skin and contour feathers	1.3561 ± 0.1481	1.1047 ± 0.0698	22.8
Legs	0.3553 ± 0.0516	0.2481 ± 0.0168	43.2
Wings	0.5968 ± 0.0639	0.4562 ± 0.0211	30.8
Pectoralis major + minor	0.9708 ± 0.0422	0.8674 ± 0.0176	11.9
Body shell	1.1716 ± 0.1531	0.8836 ± 0.0540	32.6
Head	0.5492 ± 0.0350	0.4565 ± 0.0140	20.3
Neck	0.1722 ± 0.0252	0.1473 ± 0.0229	16.9
Oesophagus + gizzard	0.2156 ± 0.0260	0.1904 ± 0.0241	13.2
Lung	0.0964 ± 0.0192	0.0863 ± 0.0160	11.7
Heart	0.0914 ± 0.0119	0.0796 ± 0.0099	14.8
Liver	0.2723 ± 0.0715	0.2163 ± 0.0495	25.9
Gut	0.2289 ± 0.1063	0.1706 ± 0.0730	34.2
Kidneys	0.0684 ± 0.0197	0.0560 ± 0.0173	22.1
Gonads*	0.1121 ± 0.2090	0.0995 ± 0.1861	12.7
Tracheal fat	0.0245 ± 0.0178	0.0029 ± 0.0016	744.8

* : mean testis dry mass = 0.0186 ± 0.0075g (n = 4)

LDM = 0.0163 ± 0.0064

adult sample also includes one female, 2 eggs laid:

gonad dry mass = 0.4858g

LDM = 0.4323g

APPENDIX III (cont.)

FLEDGLINGS n = 3

Component	Dry mass (g)	Lean dry mass(g)	Lipid Index
Tail feathers	0.0904 \pm 0.0010	0.0896 \pm 0.0011	0.9
Wing feathers	0.4287 \pm 0.0164	0.4272 \pm 0.0169	0.4
Skin and contour feathers	1.5128 \pm 0.2535	1.0267 \pm 0.0575	47.3
Legs	0.4534 \pm 0.0575	0.2689 \pm 0.0203	68.6
Wings	0.6301 \pm 0.0723	0.4515 \pm 0.0269	39.6
Pectoralis Major + Minor	0.8548 \pm 0.0999	0.7449 \pm 0.0924	14.8
Body shell	1.3263 \pm 0.2436	0.8324 \pm 0.0560	60.0
Head	0.4920 \pm 0.0581	0.3937 \pm 0.0494	25.0
Neck	0.1732 \pm 0.0260	0.1392 \pm 0.0133	24.3
Oesophagus + Gizzard	0.2549 \pm 0.0290	0.2020 \pm 0.0215	26.2
Lung	0.0832 \pm 0.0158	0.0735 \pm 0.0160	13.2
Heart	0.0830 \pm 0.0050	0.0703 \pm 0.0079	18.1
Liver	0.2707 \pm 0.0195	0.2371 \pm 0.0198	14.2
Gut	0.3020 \pm 0.0768	0.1852 \pm 0.0117	63.1
Kidneys	0.0750 \pm 0.0171	0.0619 \pm 0.0129	21.2
Gonads			
Tracheal fat	0.0812 \pm 0.0480	0.0056 \pm 0.0034	1350

APPENDIX III (cont.)

ADULTS & FLEDGLINGS n = 9

Component	Dry mass (g)	Lean dry mass(g)	Lipid Index
Tail feathers	0.1053 ± 0.0204	0.1058 ± 0.0193	0
Wing feathers	0.4739 ± 0.0366	0.4723 ± 0.0361	0.3
Skin and contour feathers	1.4083 ± 0.1895	1.0787 ± 0.0734	30.6
Legs	0.3880 ± 0.0699	0.2550 ± 0.0197	52.2
Wings	0.6079 ± 0.0643	0.4546 ± 0.0216	33.7
Pectoralis major + minor	0.9322 ± 0.0835	0.8266 ± 0.0780	12.8
Body shell	1.2232 ± 0.1883	0.8665 ± 0.0571	41.2
Head	0.5301 ± 0.0493	0.4355 ± 0.0414	21.7
Neck	0.1726 ± 0.0238	0.1447 ± 0.0197	19.3
Oesophagus + Gizzard	0.2287 ± 0.0319	0.1943 ± 0.0226	17.7
Lung	0.0920 ± 0.0184	0.0820 ± 0.0163	12.2
Heart	0.0886 ± 0.0106	0.0768 ± 0.0099	15.4
Liver	0.2718 ± 0.0573	0.02233 ± 0.0417	21.7
Gut	0.2532 ± 0.0994	0.1754 ± 0.0585	44.4
Kidneys	0.0706 ± 0.0181	0.0580 ± 0.0154	21.7
Gonads*			12.7
Tracheal fat	0.0434 ± 0.0397	0.0038 ± 0.0026	1042

* : mean testis dry mass = 0.0186 ± 0.0075g (n = 4)

LDM = 0.0163 ± 0.0064 (n = 4)

adult sample also includes one female, 2 eggs laid:

gonad dry mass = 0.4858g

LDM = 0.4323g

APPENDIX IV

Body mass changes of control pairs
of swallows and their broods

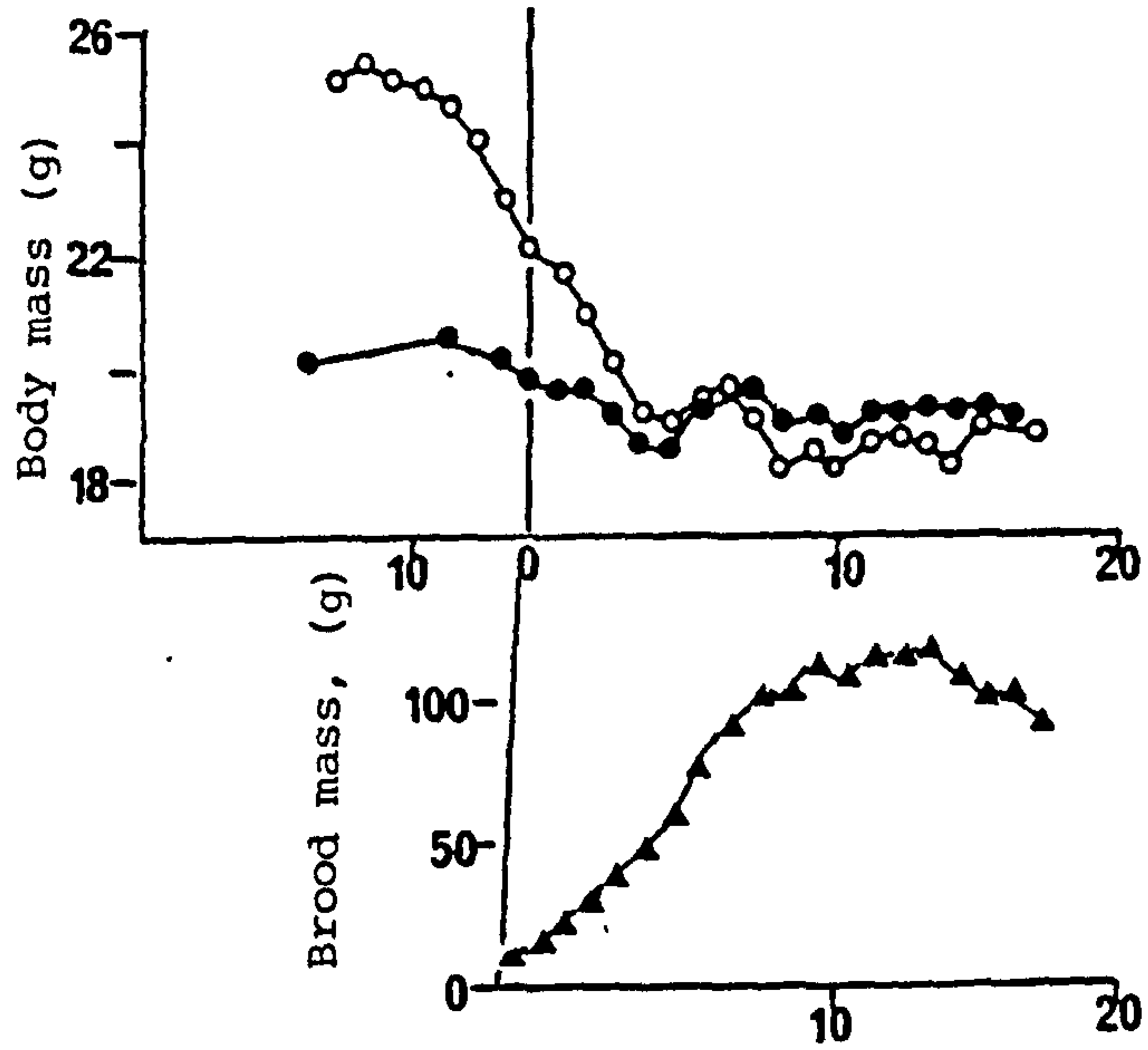
Open circles - female masses

Closed circles - male masses

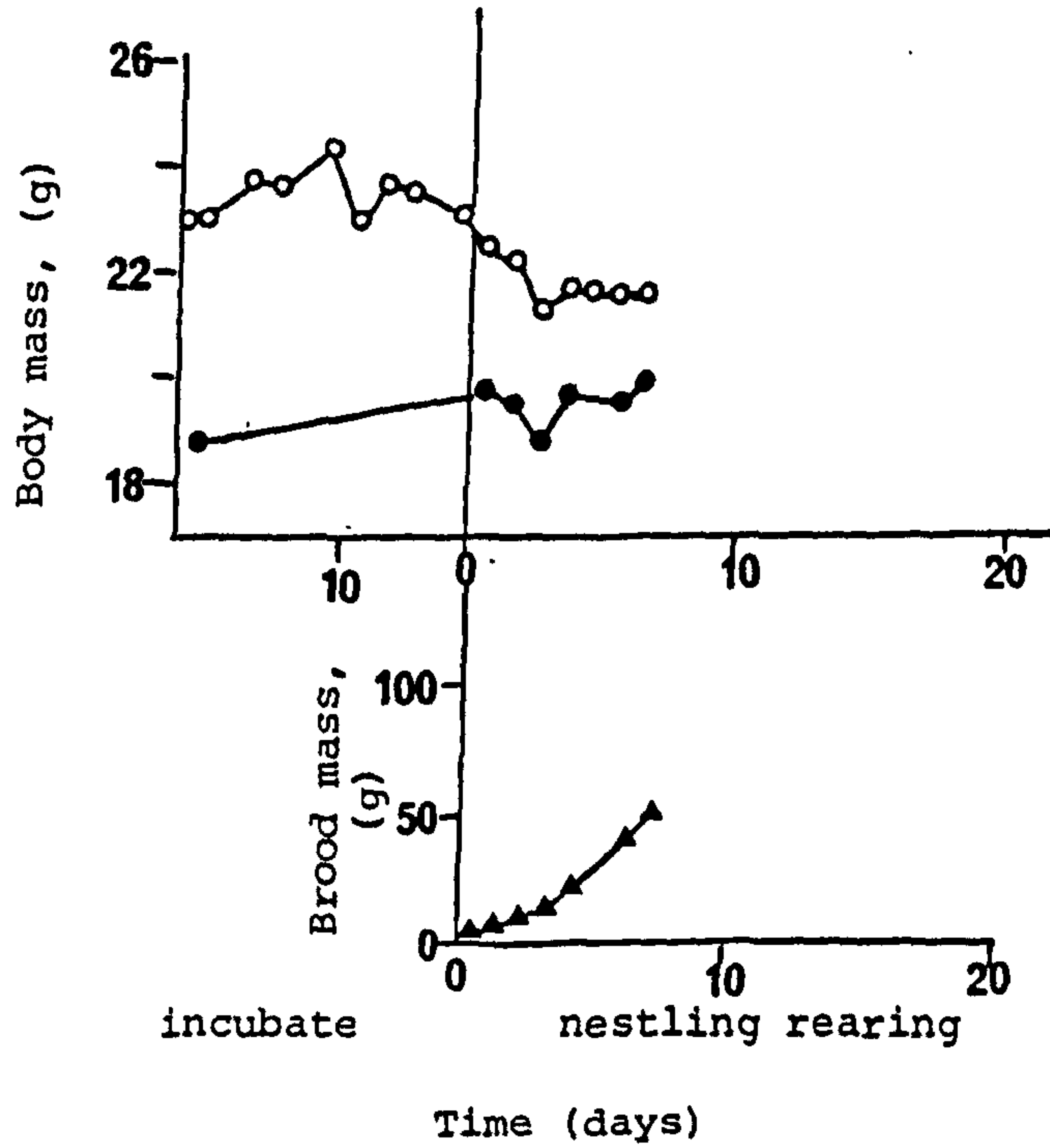
Closed triangles - brood masses

All masses are means of afternoon sampling
period.

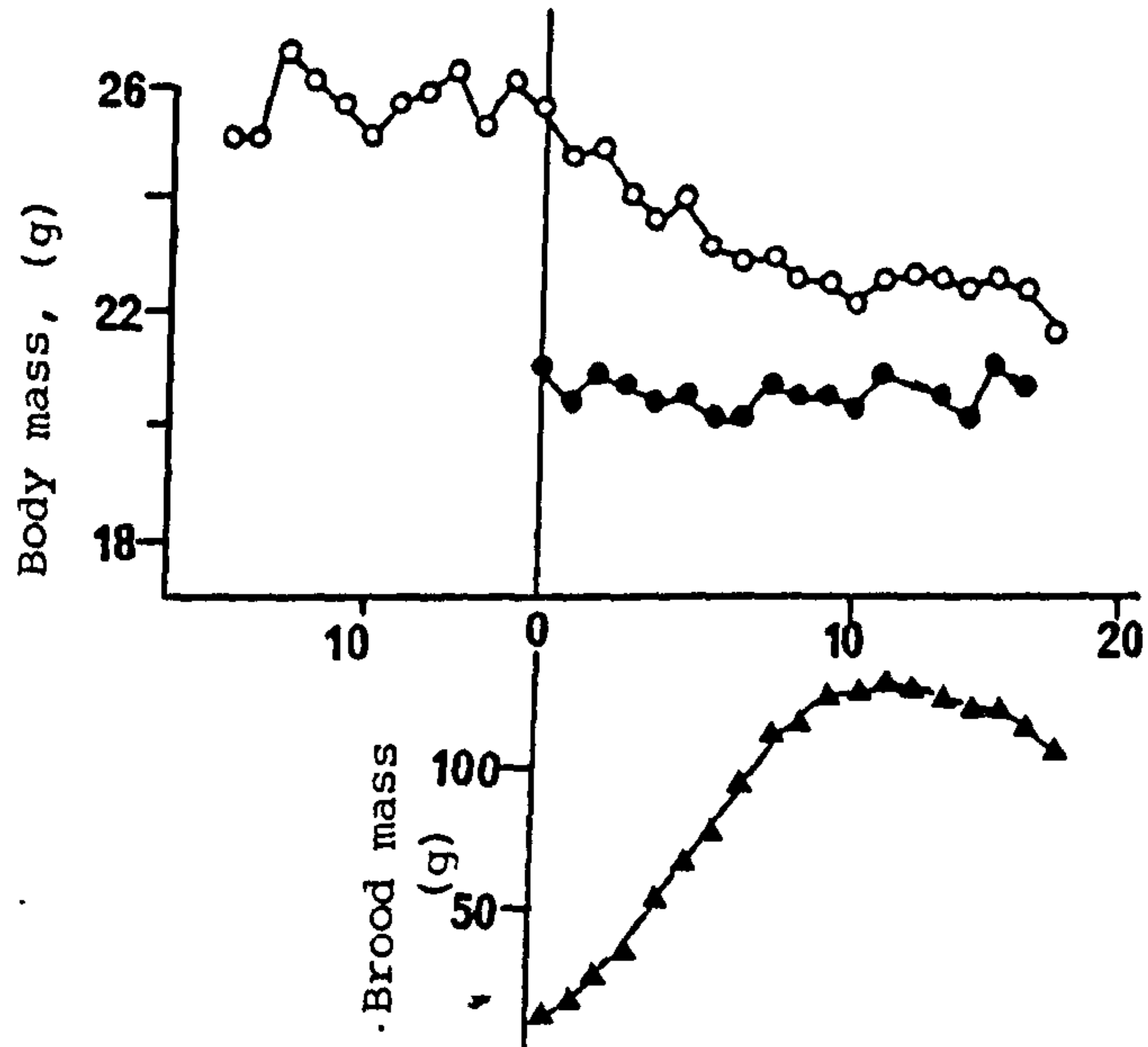
(a) M/C A82, brood size 5



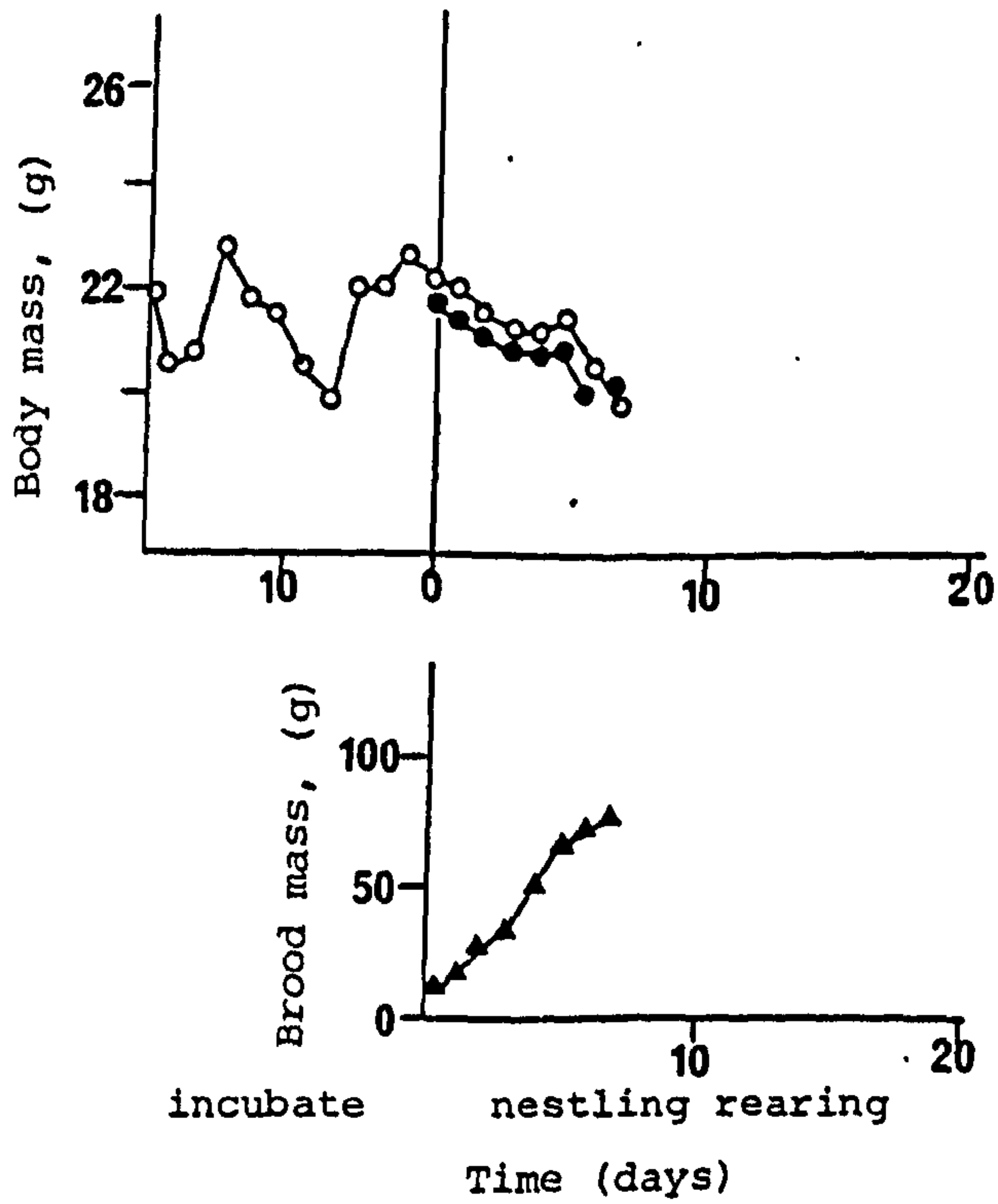
(b) M/C B82, brood size 4



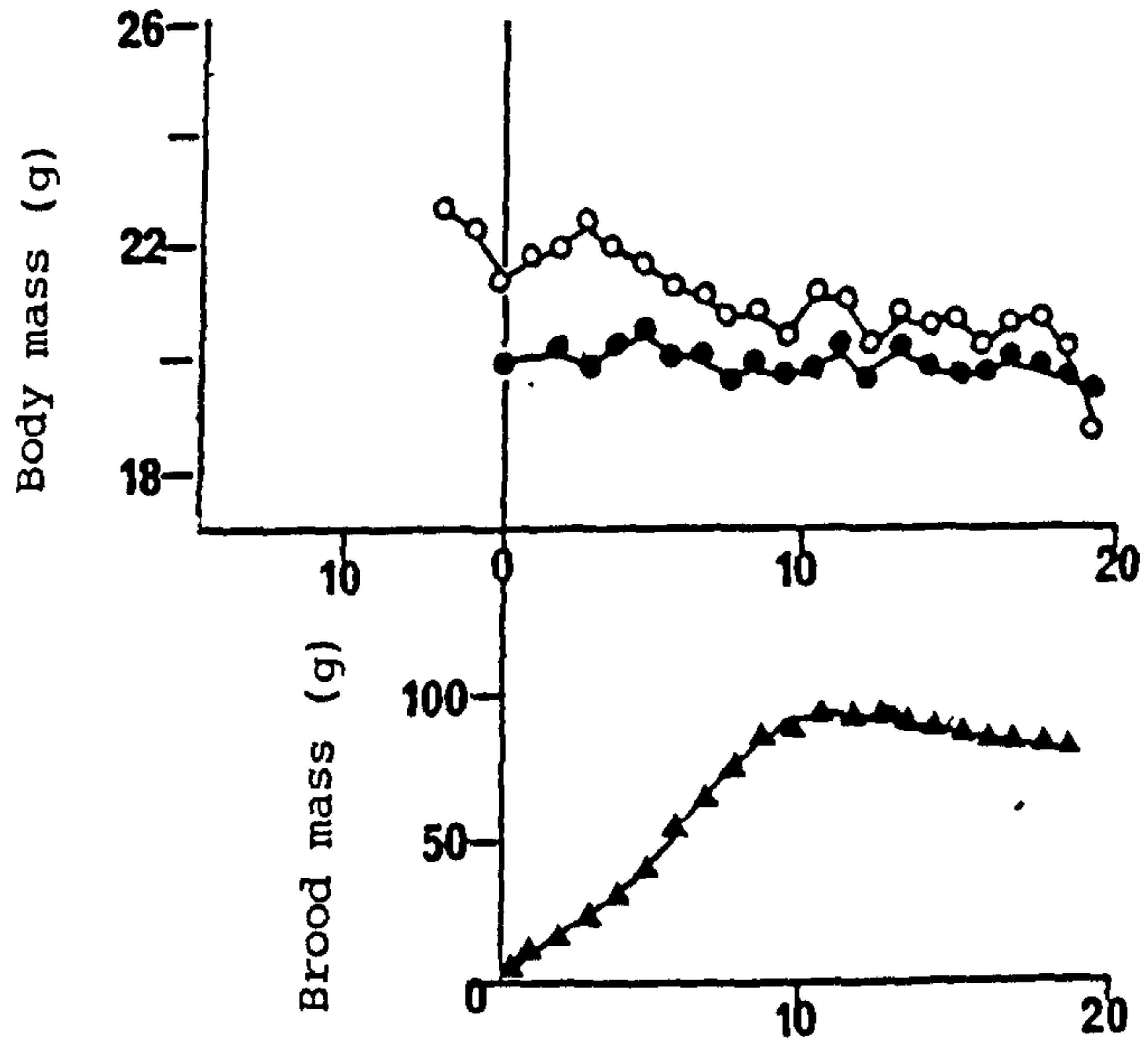
(c) M/C g 83, brood size 5



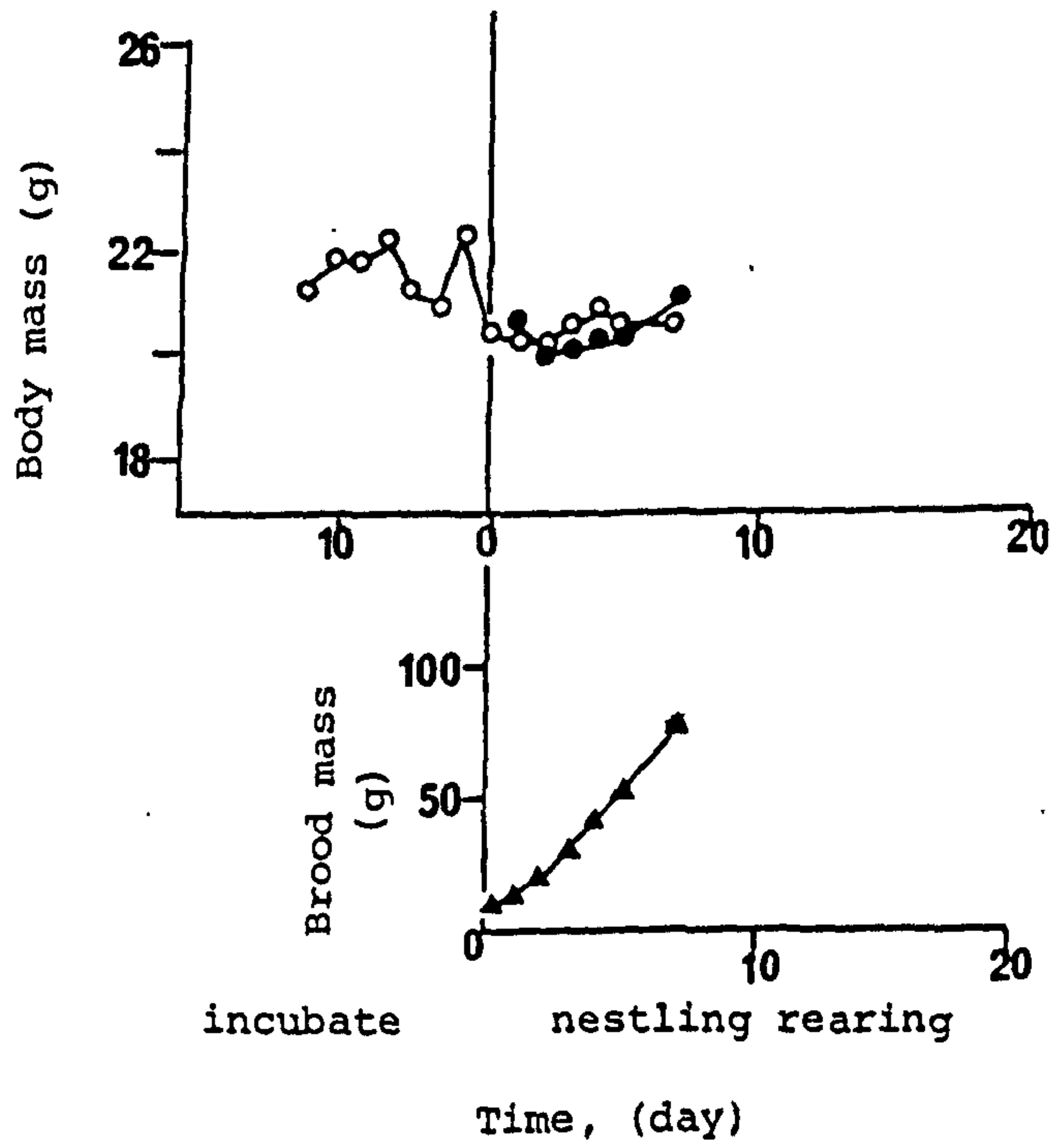
(d) M/C A83, brood size 6



(e) M/C K83, brood size 4



(f) M/C G83, brood size 5



APPENDIX V

1. A comparison of energy balance data collected from the use of Mettler electronic balances with other techniques used previously on swallows in the same study area

Energy balance data collected through the use of Mettler electronic balances should be directly comparable with results obtained from techniques previously used with breeding swallows.

(a) Brood energy requirements

In Figure 8.22, the predicted load mass at the mean round trip length is 125 mg. Such a load would yield $(0.125 \times 0.27 \times 22.84 \times 0.7)$ kJ, where 22.84 is the calorific density of insect prey, kJ g^{-1} dry mass, 0.27 is the proportion of insect prey which is dry mass, 0.7 is the assimilation efficiency of swallow nestlings (Turner, 1980).

With these assumptions, one swallow load of 125 mg would yield 539.6J. The daily feeding rate of swallow broods containing five chicks ≥ 10 days old is 403 ± 117 feeds day^{-1} (Turner, 1980). Such a daily feeding rate would result in 217.46 kJ delivered to a brood of five swallow nestlings per day, assuming load mass to be constant at 125 mg over the entire day.

Using four different methods, Turner (1983) calculated daily metabolized energy of five nestling swallows as 180-290 kJ day^{-1} . Hence the brood energy requirements calculated using food delivery rates obtained with Mettler balances lies within the range of requirements calculated from four other techniques.

The daily metabolized energy of a brood of five swallow nestlings was calculated as 250 kJ day^{-1} from multiplying feeding rate by bolus assimilable energy content (Turner, 1983). Boluses were obtained by collaring nestlings in Turner's study, and the brood

energy requirement calculation, as determined by measuring feeding rate, probably exceeded that obtained in this project because of differences in load masses between the two studies.

The mean load dry mass of swallows determined by collaring nestlings was 73.38 ± 31.90 mg (Bryant and Turner, 1982). Assuming insect prey to contain 73% water (Turner, 1980), the mean load dry masses in this study can be calculated as 31.05 mg (males) and 36.99 mg (females) (Section 8.3.7).

Differences in load masses between the two studies could arise for several reasons: load size has been shown to vary seasonally, between sexes, and between individual swallows (Section 8.3.7), and also varies according to food abundance and weather (Bryant and Turner, 1982). Moreover, load masses obtained from the collaring technique could be greater than those normally delivered by the parents (Johnson et al. 1980), especially if adults are reducing visitation rates to nests after periods of interference associated with collaring nestlings.

(b) Minimal energy requirement collected on a foraging recess during incubation

The daily energy expenditure (DEE) of a female swallow during incubation has been determined as $120.59 \text{ kJ day}^{-1}$ (Westerterp and Bryant, 1984). To meet this expenditure, a swallow must accumulate the same quantity of energy over the course of a day during foraging recesses.

The mean length of a foraging recess during this study was 4.107 ± 2.624 minutes ($n = 293$). In foraging recesses of 4-5 minutes, female swallows on average gained 960J, or 213.3 J min^{-1} through capture of insect prey (Figure 7.14b). Female swallows

on average spend 84.21% of a day sitting on eggs during the incubation period (Turner, 1982a), leaving 3.79h to feed. Using the data presented in Figure 7.14 (showing a foraging rate of 213.3J min^{-1}) a female could theoretically gain only 48.50 kJ day^{-1} , and hence would not meet her DEE during incubation.

The incongruence between the calculated energy gains from body mass increments and energy expenditure measured by the D_2O^{18} technique presumably results from invalid assumptions about defaecation rates in Figure 7.14. If it is assumed that a female swallow defaecates once during every foraging trip of average length, the following energy gains can be calculated.

An average faecal pellet weights 397.3 mg (page 92). If a swallow increased in mass by this amount during every 4-5 minute recess by ingesting insects, an extra 1.715 kJ of energy would be gained per recess. If the swallow's average of 3.79h of foraging time during incubation were divided into 4.5 minute recesses, 50.53 recesses would be made on average each day, amounting to an extra 86.66 kJ of ingested assimilable energy. Hence a total assimilable energy gain of $135.16\text{ kJ day}^{-1}$ is now calculated overall, this corresponding closely with the directly measured DEE of $120.59\text{ kJ day}^{-1}$ (Westerterp and Bryant, 1984). Even if defaecation were not a feature of each departure, a DEE between 48.50 kJ day^{-1} and $131.16\text{ kJ day}^{-1}$ would probably closely correspond with Turner's (1982a) estimate of DEE (76.69 kJ day^{-1}), which was based on time budget and D_2O^{18} information on incubating swallows.

Assumptions about defaecation rate in relation to recess lengths are likely to influence the predictions of the optimality

model developed in Figure 7.14. If a female always defaecates once per recess regardless of recess duration, the net energy gain curve of Figure 7.14b would be elevated by a constant amount over the complete range of foraging periods, and the predictions of the model remain unaltered. If, however, defaecations only occur at longer recesses, elevation of the net gain curve will only occur at relatively long foraging times and benefits (foraging energy gains - reheating costs) will increase only at longer recesses. Thus longer recesses would become even more profitable, make the model of value only for predicting why short recesses (when defaecations do not occur) are avoided.

2. The rationale behind the choice of suction trap and hand-net catch information in the various analyses

As described in Section 3.2, the suction trap sampled insects available at a height favoured by foraging sand martins, and sampled over an entire day. Hand net sampling was performed over short time intervals (about 20 minutes) in swallow feeding sites, at heights normally exploited by foraging swallows.

Suction trap catches were used for all analyses of sand martin masses. During 1983 the patterns of suction trap volume and hand net catch parameters differed over the season, with suction trap volume reaching a May-September plateau, whilst hand-net catches peaked in mid season (July) (Figures 3.2, 3.4). The use of suction trap data in analyses of swallow breeding biology could be questioned in view of these differences in seasonal abundance between sampling methods. Nevertheless, both sampling methods produced results which were significantly positively correlated in 1983 (Figure 3.6b).

Suction trap data were usually used in analyses of swallow daily body mass changes (e.g. Figures 7.3, 7.7, 8.2) because it was reasoned that daily mass changes were likely to reflect relatively long-term measurements of food abundance, which were best assessed by the suction trap.

In correlations and multiple regressions of swallow daily masses, all measures of insect abundance were entered for each analysis, and the insect abundance measurement which contributed the highest r^2 value was presented in the tables. Hence sweep net biomass was used as a predictor of swallow afternoon mass in Tables 8.1 and 8.5 because inclusion of biomass as an independent variable in the multiple regression resulted in a higher coefficient of determination than if either suction trap volume, number of items in the handnet, or number of large items in the hand net was entered as an independent variable in the analysis. The chosen measure of insect abundance always correlated with body mass in the same direction as all other abundance measurements considered, and it was reasoned that choice of the measurement which contributed the greatest coefficient of determination value could provide the best predictive model of body mass.

Hand net catches were always used for analyses of swallow food delivery rates (e.g. Figures 8.25, 8.26, 9.2, 9.3) since a swallow's foraging rate was reasoned to be more strongly influenced by immediate food availability as determined by the hand net than by longer term measures of insect abundance.