

Reproductive Effort Strategies in Passerine Birds: the role of body state.

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Abstract

State-dependent life history theory predicts a trade-off between an individual's state and reproductive effort. The identification and effects of key state variables, however, have not been explored empirically in depth. Although there are some studies which have provided evidence that state-dependent behaviour indeed occurs, the bulk of this work is neither experimental, nor related to reproduction. Furthermore, the quantitative effects of manipulations of specific state variables are invariably unknown (McNamara & Houston 1996).

This thesis explores potential trade-offs between state and behaviour and determines if energy reserves can be employed as a useful state variable. In contrast to other empirical studies, parental states (energy reserve at dawn) were experimentally manipulated using a direct method, namely changes in overnight temperature (Warming, Chilling and Control). The effects of these temperature changes were quantified using indirect calorimetry. Responses to these experimental manipulations were measured by behavioural observations, a common method in behavioural ecology, but were also quantified in terms of energy expenditure, with the aid of the doubly labelled water technique. Thus, this thesis provides a unique quantitative approach, in that it measures both manipulations and responses in the currency of energy.

Individual energy reserves at dawn significantly affected resource allocation decisions the subsequent day. Birds with surplus energy upon release increased the number of feeding visits to their nestlings whilst in parallel increasing energy expenditure. Those with an energy deficit at dawn, conversely decreased nest visitation rates along with energy expenditure. There were no effects of temperature manipulations upon mass or fat score changes over the trial period, suggesting a regulation of somatic investment at a threshold level, whilst reproductive effort was varied depending on parental state. The responses to positive manipulations (warming) were congruent across two species with differing foraging ecologies: the swallow, an aerial feeder foraging in a variable environment; and the great tit, foraging in relatively stable woodland. Thus, the behavioural and energetic responses seen here were not the result of species-specific strategies. This points the way towards a general rule within state-dependent behaviour.

The trade-off identified here implies that reproduction carries a cost, and that reproductive effort will be reduced if an animal's survival is jeopardized and *vice versa*:

a life history response, mediated by an individual's body-state. Furthermore, the response of birds to positive and negative manipulations was large enough to be readily detected, even amongst the considerable variation in energy expenditure related to individual differences. This, suggests that body-state not only plays a key role in allocation decisions, but that it is comparable in the scale of its effects to other major influences on energy expenditure of free-living animals.

Declaration

The work described here was carried out in the Institute of Biological Sciences at the University of Stirling. All the work is my own, unless stated otherwise, and it has not been submitted previously for a degree at this or any other institution.

Signed..... Date.....

1 General Introduction

1.1 *Life History Theory*

1.1.1 Demography and its role in life history theory

Organisms show a high degree of diversity in the strategies used to maximise the contribution of their genes to the next generation. This life cycle or life history consists of several components, which may vary and ultimately determine individual fitness. The analysis of the evolution of these fitness components or traits is known as Life History Theory (LHT). The traditional view of LHT asserts that the phenotype consists of several traits including age, size at maturity, and number and size of offspring (Charlesworth 1980, Stearns 1992). Demographic LHT assumes age-specific mortality rates are constant in space and time, causing a stable age distribution. It thus assumes that fitness is more sensitive to changes in mortality or fecundity at younger age classes than in older ones. The interaction between these traits, over an individual's lifetime determines its level of fitness. Individuals should, according to theory, attempt to maximise their fitness over their full lifetime (Stearns 1992), and the strategy adopted will differ depending upon the life history of the individual, e.g. semelparous or iteroparous. Semelparous organisms only survive to reproduce once, and consequently all their 'effort' is placed into maximising success in a single reproductive event. Iteroparous individuals, in contrast, are more likely to attempt more than one reproductive event within their lifetime. This leads to a more complex distribution of 'effort'. Life History Theory is, ultimately, an attempt to supply explanations for the life cycles of all species under all circumstances.

1.2 *State-dependent Life History Theory*

1.1.2 Rationale and Stochastic Dynamic programming

Stochastic dynamic programming (SDP) is a relatively recent method of modelling the patterns of reproductive behaviour of an individual over its lifetime. The theory hinges on the observation that an individual's state, which can be defined by a number of variables, determines survival and fecundity (Mangel & Clark 1988; McNamara & Houston 1992; 1996; Houston & McNamara 1999). Whereas traditional models of life history evolution are based on the assumption that survival and fecundity vary only with age (Stearns 1992). State variables can describe many aspects of an individual, (e.g. energy reserves, parasite load, body temperature) but they can also describe an individual's extended phenotype (e.g. offspring condition or territory quality). SDP is used to characterise an individual's state. These models split time into discrete periods, within each of which an individual will 'choose' an action. This action interacts with its state and will determine the probability

that an individual will survive to the next time period, it will also affect the individual's state and the state and number of offspring produced in the next time period. The aim of this method of programming is to quantify the optimal behaviour given what is to be maximised in the long-term. To achieve this, the model works backwards to calculate the 'optimal policy'.

1.1.3 Comparison of demographic and state-dependent models of Life History Theory

In the traditional age-based models of Life History Theory, survival and fecundity vary due to the age class of the individual, however, individuals of the same age vary greatly in terms of condition, e.g. mass, fat score or energy reserves, etc. These condition indices, although potentially correlated with age, may affect survival and reproduction, the two components at the heart of Life History Theory. It is not enough then to simply assume life history changes are due only to the age of the individual, as condition indices can fluctuate positively or negatively over a lifetime, whereas, age change is fixed. Age-specific mortality has been shown to affect life history traits (Hutchings 1993; Tatar & Promislow 1997; Wiebe & Martin 1998). Alerstam & Höegstedt (1983) found that the higher the probability of survival from birth to independence in birds and mammal species, the increased number of offspring they attempted to rear in a single reproductive event. There is, however, some empirical evidence that individuals of the same age vary widely in life history traits. Wendeln & Becker (1999) presented a correlative study where the body condition of adult breeding common terns was found to be independent of age, and reproductive success was linked to body condition and not age. Berube *et al.* (1999), however, found mixed evidence for a relationship between age and weaning success in Bighorn sheep (*Ovis canadensis*), where only one out of two populations showed an age-specific correlation. Thus, the state variable in question within these populations may have been body condition.

1.2.1 Defining Fitness

Fitness measures are based on a number of assumptions, and for this reason, there is no one generally agreed definition of fitness. Demographic models have produced several measures: R_0 , the net reproductive rate, a combination of age-specific survival and reproduction rates has been used to good effect by biologists (Gross & Charnov 1980; Kozlowski & Wiegert 1987; Clutton-Brock *et al.* 1988). R_0 is concerned with the total number of offspring produced in a lifetime. There are, however, certain problems with this approach, as it may not be optimal to produce a large amount of offspring, but fewer of higher quality. The timing of offspring production may be crucial. Thus, a measure which

does not encompass the probability of offspring to reproduce and contribute to future generations, does not fully capture fitness. As R_0 is a per generation rate, it cannot be used to compare across populations, and thus 'r', the Malthusian parameter, was developed (Fisher 1930) to measure the fitness of genotypes. 'r', the intrinsic rate of natural increase. This only holds in a homogeneous environment with no density dependence, but was successfully applied to the evolution of age at maturity (Cole 1954) and the age distribution of reproductive effort (Lewontin 1965). Nevertheless, 'r', although used widely in traditional life history theory, has the same constraint as R_0 , as it does not account for offspring quality or parental state.

In state-dependent life history, fitness is treated slightly differently than in demography models. If all individuals possess the same 'state' in a single time period then fitness in an iteroparous organism with sexual reproduction, is the number of offspring expected to survive, scaled to control for relatedness to parents, plus the probability that the parent will survive into the next time period (Caswell 1989). This measure of fitness, analogous to those in demographic models, still does not account for density-dependence, environmental fluctuations or the fact that all individuals do not share the same state. Thus a more proper measure of fitness, as used by SDP models, encompasses: i) survival of the parent until the next time period, ii) the state of this focal individual, iii) the number of offspring produced which survive to the next time period (scaled for relatedness), and iv) the state of these offspring in the next time period (Houston & McNamara 1999). This is known as the reproductive value of an individual (V).

1.3 Trade-offs

1.3.1 Introduction

The interactions between life history traits constrain the simultaneous evolution of two or more traits, as a benefit to one trait has to be paid via a cost to another linked trait. The best example of this connection is the trade-off between reproduction and survival. With a limited amount of resources, any increase in investment in reproduction will result in a decrease in investment towards survival. Both these parameters have consequences for fitness and thus any resource allocation strategy 'chosen' by an individual must strive to maximise fitness and balance reproductive and survival investment. This follows the Principle of Allocation (Levins 1968; Sibly & Calow 1986). Thus trade-offs are central to life history theory. Stearns (1992) reported 45 trade-offs studied in the literature, with current vs. future reproduction, current reproduction vs. survival, reproduction vs. growth, reproduction vs. condition and the number vs. quality of offspring receiving the most

attention. Trade-offs have been measured in several ways. Most trade-offs have been measured as phenotypic correlations in the field (Cassai & Prevedelli 1998; Richner & Heeb 1995; Sorci *et al.* 1996). However, some workers have manipulated phenotypic traits and determined changes in other traits in response to these manipulations (Blondel *et al.* 1998; Bolton 1995; de Lope *et al.* 1998; Hillstrom 1995; Loonen *et al.* 1999; Sinervo & Licht 1991). Genetic correlations between traits have also been measured, using selection experiments to manipulate a specific trait (Chippindale *et al.* 1997; Graves 1993; Sinervo & Svensson 1998; Swallow *et al.* 1999). In some cases these differing methods can yield the same answer. Phenotypic manipulation in *Drosophila melanogaster* uncovered a trade-off between fecundity and longevity. Individuals deprived of yeast in their diet showed decreased daily fecundity, and increased longevity (Leroi *et al.* 1994). In an earlier study *Drosophila* populations selected for late-life fecundity, showed increased longevity (Rose & Charlesworth 1981).

Trade-offs may not always be revealed by empirical tests for several reasons. If a fixed amount of energy is always allocated to a certain function, then only the residual reserves can trade-off, this may mean that a trade-off only becomes apparent in years of low food availability or high predation (Bryan 1996). Energy may be a limiting factor, but functions may vary in their sensitivity to changes in allocation, thus some variables may show a large trade-off, whilst others a weak relationship (Tuomi 1983). There is one other problem with the empirical measurement of trade-offs. Observers must take care to measure traits and fitness components in the most effective way possible. Siikamaki *et al.* (1997) measured the survival consequences for male Pied Flycatchers (*Ficedula hypoleuca*) of increased reproductive effort, induced via brood manipulations, and suggested that males with enlarged broods incurred higher mortality rates due to the increased costs of reproduction. Survival was measured using return rates, a common method in ecology, but there has been criticism of this method as the assumptions involved are potentially invalid. These return rates are based on the probability of survival and the probability of recapture or re-sighting which may bias the results (Martin *et al.* 1995). In state-dependent theory, where a trade-off exists a range of allocation strategies are available, and this range is dependent upon that individual's state in a single time period, and the time period preceding.

1.4 State-dependent behaviour

Empirical examples of behaviour mediated by state invariably only deal with one or two state variables, such as energy reserves, body size, body mass, season or territory quality. A recent suggestion has been that workers should focus on more composite state variables

for simplification (Morris 1998), even though single state variables are more easily manipulated and analysed. A similar methodology is often used in SDP models of such behaviour in an attempt to obtain the simplest possible description of the observed behaviour (Anderson & Roitberg 1999; Fiksen & Carlotti 1998; Houston 1998; Houston & McNamara 1999; Mangel & Clark 1988; Marrow *et al.* 1996; McNamara & Houston 1992). Few studies have yet realised the potential of state-dependent life-history, even though in many studies the variables being tested could be termed 'state variables'. There are, however, areas of work, which have addressed 'state', the majority via phenotypic correlations and some via experimental manipulations (e.g. Godfrey & Bryant 2000; Gotthard *et al.* 1999; Metcalfe *et al.* 1998; Olsson 1997; Reinhardt & Healey 1999; Damsgard *et al.* 1997; Tannerfeldt & Angerbjorn 1996).

1.4.1 Phenotypic plasticity in variable environments

Individuals normally have to make a decision before environmental conditions are fully known. In this case the interaction between any state-dependent decision and the environment in which an individual lives will determine fitness. One of the best examples of a test of environmental interactions and life history traits is seen in Trinidad guppies. Reznick (1996) describes an experimental manipulation of guppies transplanted from a high predation risk area to a low risk area. Guppies in high predation areas show high mortality rates, fast maturity, and large numbers of small offspring. Following transportation to a low predation area guppies showed a plastic response as maturity became delayed and the proportion of resources allocated to reproduction decreased, and life history traits evolved to resemble those of guppies reared at low risk sites. Some traits were seen to change within six generations post-manipulation. This study provides evidence that predation and mortality play a significant role in life history evolution, however, this need not be driven by age-specific fecundity or mortality. Maurer (1996) has shown that state-dependent decisions do not just have a short-term basis. Small-mouthed salamander larvae were reared individually at either low or high prey densities. Those reared in low densities developed significantly smaller body sizes than those in high densities and treatment had a significant effect on larval feeding rates and behaviour, proving that environmental background has a significant effect on life history.

1.5 Aims and objectives of current study

The aim of this study was to experimentally manipulate adult body state to determine if a trade-off exists between body-state and reproductive effort. This is the first manipulation of its kind which focuses on reproduction, although similar methods were used by Godfrey

and Bryant (2000) in a study of the European robin (*Erithacus rubecula*) to investigate state-dependent winter foraging and territorial behaviour. The studies which contribute to this thesis measured the energy expenditure of individual birds following either a positive or negative body-state manipulation and compared this with energy expenditure of a control group of birds. Alongside this provisioning rate and mass and fat score were monitored for all groups. Thus any changes in energy expenditure, above the level of a Control, could be related to changes in reproductive behaviour.

The state variable of interest in this study is individual energy reserves at dawn, since individuals may use this as a cue upon which to base their short-term resource allocation decisions. Thus an individual with lower than expected reserves at dawn (negative state), may 'decide' to reduce the amount of energy devoted to provisioning offspring and use any surplus power to regain the lost reserves, or maintain its past level of provisioning and potentially be in energy deficit at the end of the foraging period. This latter strategy would mean the individual was in a negative state the following morning and would also increase the potential overnight mortality risk. If an individual is, however, in a positive state with higher than expected reserves at dawn then it has excess energy to allocate either to reproduction or survival (somatic investment). Thus in a positive state an individual may increase offspring provisioning to a certain level, whilst still maintaining its usual level of self investment, or, if reproduction does not trade-off against survival, it may allocate the excess energy to itself and maintain its past provisioning effort. To determine the relationship between these traits experimental manipulations of body state were used in two species of passerine birds whilst brood rearing: the swallow (*Hirundo rustica*) and the great tit (*Parus major*).

1.5.1 Manipulations

Phenotypic manipulation is the most appropriate method of measuring a trade-off between life history traits. This method overcomes many problems of purely correlative measures. Correlative measures rely upon the naturally existing range of phenotypes, and in some populations this range may not be enough to demonstrate the trade-off, or may even show a relationship in the opposite direction to that normally seen (Stearns 1992), even though in other populations the range is larger. Also, if we accept that individuals allocate their optimal resources to reproduction, for example, then by manipulating their allocation we can obtain a direct estimation of the response to the manipulation, and not just a general trend within a population. Thus overnight manipulation of body state due to exposure to

different overnight temperatures were used in this study, and these experimental groups were compared with Control groups in order to quantify the responses.

1.5.2 Measuring optima

Trade-offs represent a relationship between current reproduction and future reproductive value and the function can take several different shapes depending upon the broad life history of the individual (Stearns 1976). The Euler-Lotka equation, which is based on a stable age distribution model, can be used to determine 'lines of equal fitness' with a slope of negative residual reproductive value (-RRV). The optimal schedule for allocation to reproduction and survival can be obtained by imposing the tangent of the lines of equal fitness on the trade-off function (Figure 1.1).

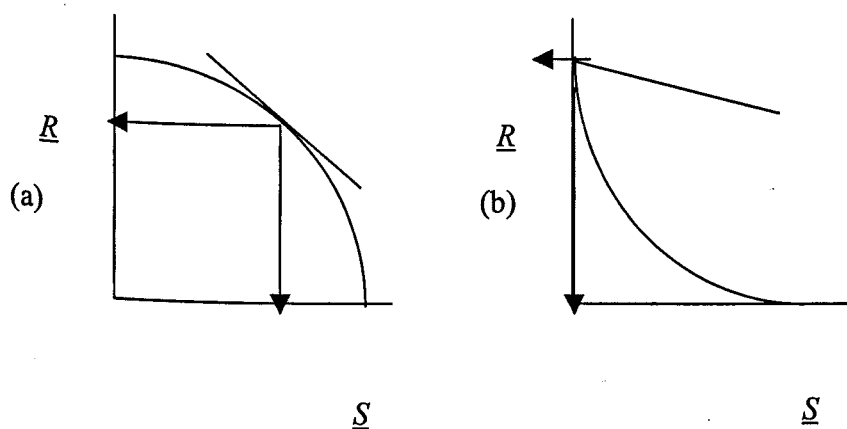


Figure 1.1 (a & b). The trade-off functions between reproduction (R) and survival (S), and lines of equal fitness, which form a tangent with each function. (a) represents the iteroparous situation and (b) the semelparous.

Figure 1.1(a) shows the concave trade-off function for survival and optimal reproductive effort normally associated with iteroparous organisms, where the line of fitness forms a tangent with the trade-off function (Stearns 1992), and (b) shows a convex trade-off function depicting the semelparous situation, where reproduction is maximised in one instance and survival post-reproduction is nil. The line of fitness here has a very shallow slope as with high adult mortality residual reproductive value is very low. Figure 1.1(a) and derivatives of this model will be used in the proceeding chapters in an attempt to describe the relationship between body-state, reproduction and survival.

1.5.3 Doubly labelled water technique.

The DLW technique is a method of indirect calorimetry, which measures the CO₂ production of an individual (Lifson & McLintock 1966). The application involves the introduction of stable isotopes ²H and ¹⁸O into the body. These isotopes then reach

equilibrium with the naturally occurring isotopes of oxygen and hydrogen in the body water pool. Depletion of ^{18}O will occur via a combination of CO_2 production and water loss (urine, faeces and evaporation), whilst the depletion of ^2H is due to water loss alone. Thus, the difference in fractional turnover rates of ^{18}O and ^2H can be used to calculate the rate of CO_2 production. The technique relies on several assumptions, and the significance of infringements of these assumptions has been widely discussed (Nagy 1980; Nagy & Costa 1980; Speakman 1997) and are normally unimportant. DLW is now widely used in many areas of biology to address a wide range of questions, and has been validated many times (e.g. Hails & Bryant 1979; Kasarov 1981; Visser & Schekkerman 1999; Withers et al. 1998; Wolf et al. 1996). DLW represents a relatively non-invasive method of obtaining accurate measures of energy expenditure in free-living individuals. Thus, it was invaluable in this study where responses to physiological state manipulations were quantified using changes in energy expenditure and behaviour.

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2 Trade-offs and state-dependent behaviour in breeding barn swallows (*Hirundo rustica*): consequences for reproductive effort.

2.1 Summary

Life history theory offers an explanation for intraspecific variation in reproductive effort; increased levels of current reproductive success, for example, may trade-off against residual reproductive value. Even where such trade-offs have been demonstrated, however, much variation in effort remains unexplained and the underlying causes are usually obscure. Here we examine a specific factor which could moderate reproductive effort; namely body-state. Overnight-heating and cooling treatments were used to adjust dawn energy reserves in female swallows without impinging on their opportunities for foraging. To measure changes in reproductive effort we recorded 'daytime energy expenditure' (doubly labelled water technique) and the 'number of feeding visits' during brood rearing, which both relate positively to current reproductive success. Our experimental treatments and responses were then compared using the common currency of energy. In response to positive and negative state manipulations, female swallows increased and decreased, respectively, their daytime energy expenditure (and number of feeding visits). The recorded changes in energy expenditure by breeding swallows averaged 2 - 4.5 times the energy value of our heating or cooling treatments, although positive and negative changes were similar in scale. Hence, the induced energetic trade-offs were, respectively, disproportionate and possibly symmetrical. These responses to experimental manipulation of state provided evidence of a direct link between energy expenditure, life history and behaviour, which has hitherto proved elusive. They allow that energy supply and expenditure play a regulatory role in reproductive effort, and also indicate that units of energy expenditure are likely to carry fitness costs and benefits which are context-dependent.

2.2 Introduction

One of the fundamental issues in life history theory concerns the allocation of effort to reproduction and survival (Stearns 1992). It is generally thought that energy allocated to reproduction (here called reproductive effort) takes resources which might otherwise be destined for survival or subsequent reproduction (Williams 1966). Much unexplained variation can be seen in field studies of this trade-off, however, involving a range of possible fitness costs or benefits for a given level of effort (Nur 1986; Van Noordwijk *et*

al. 1981). Environmental factors, parasite loads or individual quality are often proposed as sources of this variability. In addition, recent dynamic models of resource allocation have suggested that an individual's physiological state (also called body-state or body condition) may play a role in life history decisions (McNamara & Houston 1992) and thereby affect reproductive effort. Yet, to date, only a few studies have provided evidence that state-dependent behaviour indeed occurs (Bouchon 1991; Damsgard *et al.* 1997; Olsson 1997) and the bulk of this work is neither experimental, nor related to reproduction. Furthermore, the quantitative effects of manipulations of specific state variables are invariably unknown (McNamara & Houston 1996). Accordingly, in this study we manipulated the energy reserves of adult female barn swallows, *Hirundo rustica*, during chick rearing, via overnight heating and chilling treatments which had known effects on physiological state, warming treatments conferring a 'positive' state, i.e. more energy at dawn relative to controls, and chilling treatments a 'negative state', or lower energy at dawn. Induced changes in reproductive effort were measured using the doubly labelled water (DLW) technique (Lifson & McClintock 1966) and were characterised by observations of provisioning at the nest. Any changes in energy expenditure and nest visitation compared to controls were used to determine the level of reproductive effort in the two manipulation groups. Somatic investment was determined using mass and fat score changes relative to controls.

To develop specific hypotheses concerning responses of swallows to experimental changes in state, we modified the familiar convex trade-off function relating reproduction and survival (Stearns 1992) so that it dealt with reproductive and somatic allocation of resources (Fig. 2.1). We assumed the relationship between reproductive and somatic allocation did not have to be symmetrical (Fig. 2.1(a)); hence, a bias may occur in either direction (Fig. 2.1(b) or (c)). Under the two treatments in this study, which involved positive and negative manipulations of body-state, we predicted different optimal allocation strategies depending upon the form of the trade-off function. Accordingly, we expected energetic and related behavioural responses under our contrasting manipulations to comply with one of the following:

H₀) **No trade-off.** All birds will show Control effort and maintenance levels. NB energy expenditure denotes energy expended the day following manipulation.

Warmed females	Chilled females
Energy expenditure = Controls	Energy expenditure = Controls
Nest visitation = Controls	Nest visitation = Controls
Mass and Fatscore changes =	Mass and Fatscore changes =

H_i) **Symmetrical trade-off.** Responses seen in both reproductive and somatic investment.

Warmed females	Chilled females
Energy expenditure > Controls	Energy expenditure < Controls
Nest visitation > Controls	Nest visitation < Controls
Mass and Fatscore > Controls	Mass and Fatscore < Controls

H_{ii}) **Biased trade-off 1:** variable somatic investment.

Warmed females	Chilled females
Energy expenditure > Controls	Energy expenditure < Controls
Nest visitation = Controls	Nest visitation = Controls
Mass and Fatscore > Controls	Mass and Fatscore < Controls

H_{iii}) **Biased trade-off 2:** variable reproductive effort.

Warmed females	Chilled females
Energy expenditure > Controls	Energy expenditure < Controls
Nest visitation > Controls	Nest visitation < Controls
Mass and Fatscore = Controls	Mass and Fatscore = Controls

Overnight manipulations either donate or withhold a finite amount of energy from the experimental birds. If energetic and behavioural responses are proportional to this amount of energy then the trade-off will be biased. An individual with substantial energy reserves, implying favourable conditions, would be expected to allocate more energy to current reproduction (H_i & H_{iii}). Equally, those with diminished reserves would show a reduced reproductive effort until some notional optimal body-state was recovered. In H_{ii} reproductive investment remains constant, and birds vary their somatic investment. In H_{iii} , the converse is true, whereby birds maintain their somatic investment whilst increasing or decreasing investment in reproduction, depending upon treatment.

We justify our assumption that body state manipulations which increased the swallow's reserves relative to controls are favourable (i.e. positive), as follows. Jones (1987) showed that female swallows have a 'programmed' mass loss (Freed 1981) which continues throughout incubation and into the early brooding period (nestling day 0 - 7). After this, body mass tends to stay constant, although rising in response to greater food abundance

and favourable weather, in unison with provisioning rates, and *vice versa*. So, while there may be an optimal mass within this latter period (the time of our observations), it is clear that environmental factors also induce mass changes.

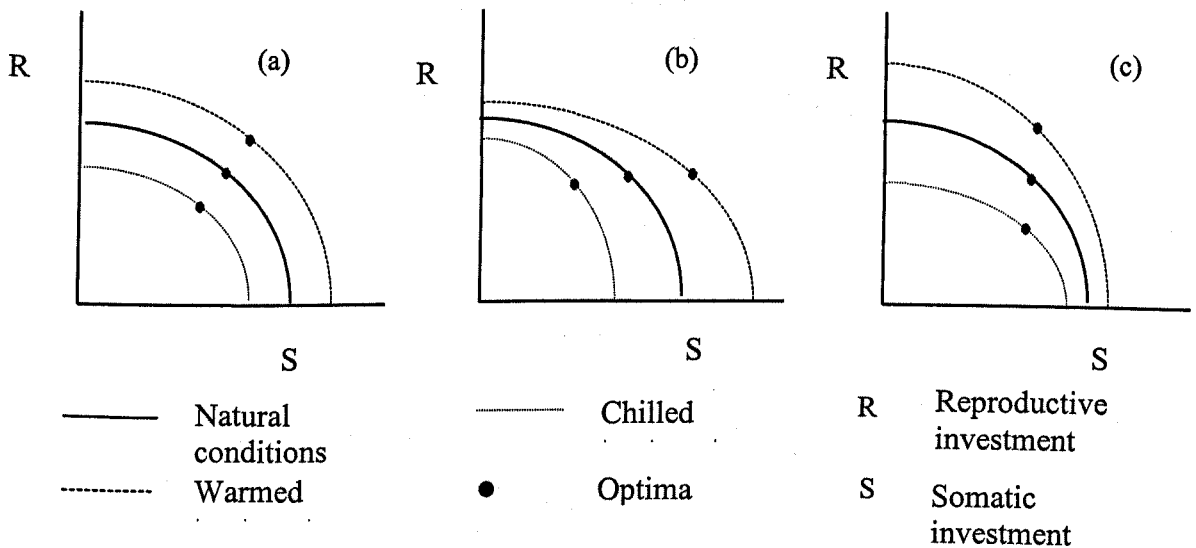


Figure 2.1. Allocation of energy between reproductive and somatic investment is usually assumed to be symmetrical (a). This need not apply, however, as there may be a bias toward either somatic investment (b) or reproductive investment (c). The area under each curve is constant and represents the amount of energy acquired by an individual under each treatment group. The optimal allocation for an individual changes with each treatment, but there is also a shift in position within treatment groups under the two different bias hypotheses (Hii & iii).

2.3 Methods

2.3.1 Manipulations

The experiments were undertaken near Stirling in Central Scotland (56°8'N, 3°54'W) during 18th June to 21st August of 1997/98. They involved swallows rearing chicks aged 10 - 14d. Swallows were caught using mist nets between 17.00 - 19.30h at local farms. Sex, mass and fat score were recorded. Fat score was recorded as a rank score (0 - 5) of visible fat deposits in the inter-clavicular pit (Krementz & Pendelton 1990; Scott *et al.* 1995); a method used reliably with breeding Hirundines (Bryan 1996; Bryant & Westerterp 1983). Breeding pairs were randomly assigned to one of three groups; Warmed, Chilled and Control (Table 2.1.) to induce differences in body-state. In Warmed and Chilled groups only females underwent manipulations. Thermostatic energy expenditure would be lowered by the warm treatments, leading to relatively high residual energy reserves at

dawn. The converse applies after chilling, due to the effect of temperatures, below the lower-critical temperature ($^{\circ}T_{lc}$), thereby increasing catabolism of energy substrates. Once initial blood samples had been taken in the laboratory for DLW studies (see below), our treatments were performed overnight, typically from 20:00 - 03:30h. During this time, birds were kept in 4.4 l containers equipped with a perch, allowing a normal posture and space for the wings to be fully spread. Warmed females were placed in an incubator (Sanyo™) in the dark at 29°C (within thermoneutral zone, Kendeigh *et al.* 1977), while their male partners were kept outside under the same conditions as Control birds. Chilled females were placed in an incubator programmed to start at 15°C for 1h, to decline to 7°C over 1h, and then remain at that temperature for the remainder of the night. Once again, their male partners were kept as Controls. All males and the Control females were placed in an outdoor shelter (average night-treatment period across groups was 7.2 ± 0.5 h s.d.) and therefore experienced prevailing ambient temperatures (13.8 ± 2.0 °C s.d.), which were recorded using a data-logger (Psion™) equipped with a thermocouple, logging every 15 min.

Table 2.1.(a). Temperature treatments for the two experimental groups and Controls. Only females were manipulated; male partners served as Controls for all treatment groups. (b) shows sample sizes for each analysis performed. M_{rel} and Fs_{rel} are mass and fat score changes during the release period; AEE is active energy expenditure; and VR represents visiting rate.

(a)	Treatment	Temperature °C	
			Male
	Warmed	29	14
	Chilled	7	14
	Control	14	14
		sample size (n)	
(b)	$M_{rel} + FS_{rel}$		Male
	Warmed	8	5
	Chilled	5	4
	Control	8	8
	AEE		Male
	Warmed	8	5
	Chilled	5	3
	Control	8	7
	VR		Male
	Warmed	7	7
	Chilled	5	5
	Control	15	15

Birds were released at dawn (ranging from 03:30h to 04:00h) to ensure a normal foraging period: mass and fat score were recorded again at this point. This information was not obtained from all birds due to accidental release (Table 2.1.). During the release period (mean time to recapture: 16.4 ± 1.5 h), pairs were observed, using video cameras (Panasonic, model NB-585B) at the nest to obtain 'feeding visit rates' (observations lasted 1.4 ± 0.4 h per nest), and from this visits h^{-1} was calculated. Visitation rates for one pair of birds was lost due to video damage. Approximately 65% of dosed birds were recaptured and final blood samples taken approximately 24h (23.6 ± 1.3 h) after the initial blood samples. Mass and fat score were recorded once again.

The energetic costs of overnight treatments were quantified using indirect calorimetry with a sub-sample of birds, some of which were not drawn from experimental groups ($n = 15$). A VGTM quadrupole mass spectrometer was used to determine oxygen and carbon dioxide concentrations in an open-flow respirometer. From this we derived estimates of energy

expenditure overnight. Details of equipment and methods are given by Bryant & Furness (1995), where an identical approach was used. Food abundance was measured using a 12.2m Rothamsted suction trap situated at the University of Stirling (Macauley *et al.* 1988). Daily maximum and minimum temperatures were taken from the Parkhead weather station, sited on the University campus, within 15 km of all study sites. Also, during each pair-observation, local temperature, rainfall, and wind were recorded simultaneously near nest sites. Rainfall was recorded as the proportion of time within each observation period when precipitation occurred.

2.3.2 Doubly labelled water.

Doubly labelled water (DLW) was used to measure the energy expenditure of swallows (Lifson & McClintock 1966; Tatner & Bryant 1989). Birds were given intraperitoneal injections of DLW ($10\mu\text{l g}^{-1}$ body mass). The injectate was prepared by adding 0.37g of 99.9 APE deuterium (^2H) to 5ml of 20 APE oxygen-18 water (H_2^{18}O). Once injected, the birds were kept in a bag for 1h to allow the isotopes to reach equilibrium with the body water (Bryant & Westerterp 1982). Blood samples were then taken in capillaries (Vitrex™) from the femoral vein and immediately flame-sealed. Six to ten capillaries, each with $5\mu\text{l}$ of blood, was taken from each bird at the time of 'initial' and 'final' samples. Background isotope levels were obtained from blood samples of non-experimental birds ($n=2$ (1997), $n=3$ (1998)). Background levels were found to be 1995.5 ± 7.1 (s.d.) for ^{18}O and 146.0 ± 4.0 (s.d.) for ^2D . Isotope concentrations were determined from duplicate samples by mass spectrometry and a mean value was used in subsequent calculations (Tatner & Bryant 1989; Speakman 1997a). Samples for two birds were lost during processing.

2.3.3 Calculation of energy expenditure

Daily energy expenditure (DEE, kJ d^{-1}) was calculated as described by Tatner & Bryant (1989) and Lifson & McLintock (1966), using an RQ of 0.75. The body water pool was derived using Bryant & Westerterp's (1982) equation for a closely related species (house martin, *Delichon urbica*) during the breeding season. Overnight metabolic cost was obtained from the respirometry results (Gessaman 1987) and a mean obtained for each treatment group (E_{resp} $\text{kJ g}^{-1} \text{h}^{-1}$). From this the cost of the overnight period ($E_{\text{overnight}}$) was calculated using Equation 1 (W = mean overnight body mass, g; $t_{\text{overnight}}$ represents the hours a bird spent in the incubator). $E_{\text{overnight}}$ was then used to calculate, by difference from the daily energy expenditure (DEE), the 'active' energy expenditure (AEE) of each individual during the release period (Equation 2.2).

$$E_{\text{overnight}}(\text{kJ}) = E_{\text{resp}} * W * t_{\text{overnight}} \quad \text{Equation 2.1.}$$

$$\text{AEE (kJ)} = \text{DEE (kJ)} - E_{\text{overnight}}(\text{kJ}) \quad \text{Equation 2.2}$$

$$\text{MI} = E_{\text{overnight}}(\text{kJ}) / \text{BMR} \quad \text{Equation 2.3.}$$

Basal metabolic rates (BMR) were derived from the passerine equation of Aschoff & Pohl (1970), resting phase, and used to provide a standard for comparisons between individuals (called Metabolic intensity, MI, Equation 2.3.).

2.3.4 Statistical analysis

Data were collected over two years. Hence, to control for random year effects and non-orthogonality due to different treatments each year (Warmed in 1997 and Chilled in 1998, Controls were available for both years), Residual Maximum Likelihood (REML) analysis was used to explain variation in energy expenditure, visiting rate, fat score and body mass data. REML is a linear mixed model able to analyse unbalanced, non-orthogonal data (Patterson & Thompson 1971), a similar approach to this has been used recently by Kruuk et al. (1999). Stepwise deletion of fixed variables from the minimal adequate model was performed. The random model controlled for the year in which the treatment was performed and the date of the trial within each year. The significance of fixed variables was estimated using the Wald statistic, which is asymptotically distributed as χ^2 (Genstat 5 Committee 1992). Post-hoc analysis was undertaken using a ratio of the estimated effects and standard errors of the difference between pairs (distributed as t). Overnight mass change and respirometry results were analysed using ANCOVA (Minitab 1997). Analysis of overnight energy costs was performed upon reciprocal transformed, $\frac{1}{(x-1)}$, energy expenditure (E_{resp}) to normalise residuals and to control homogeneity of variance. Predicted means were back-transformed and converted to MI data (Equation 2.3). Sample sizes for all analyses are given in Table 2.1. All residuals were checked for normality and homogeneity of variance. Predicted means \pm standard error from statistical analysis (REML, ANCOVA) are quoted in text and figures.

2.4 **Results**

2.4.1 Overnight energy expenditures.

Body-state manipulations affected the overnight energetic costs of birds. Warmed birds had the lowest costs (MI=1.1 x BMR), and Chilled the highest (MI=2.6 x BMR). Control birds had an intermediate overnight cost of 2.1 x BMR. There was a significant difference

between treatment groups with respect to energy expenditure, but there was no effect of treatment on mass loss overnight.

2.4.2 Active energy expenditure

Thirty-six swallows were available for analysis of 'active' energy expenditure (21 from 1997, and 15 from 1998). Covariates which have been shown to, or were likely to affect swallow foraging strategy and parental effort, such as food abundance and daily temperature (Bryant & Turner 1982; Jones 1987), were included in this analysis, but none explained a significant amount of variation (Table 2.2). Visiting rate to the nest, however, showed significant interactions with both treatment group ($\chi^2_{(2)} = 7.10$, $p = 0.029$) and sex ($\chi^2_{(1)} = 3.57$, $p = 0.059$). Visiting rate showed a significant decrease in the Chilled group, possibly due to the decrease in visiting rate of both members of Chilled pairs. A significant increase was not seen in the Warmed group. Males tended to show a higher visiting rate than females within this analysis. Although the above interactions explained a significant amount of variation and thus were retained, this was only a subsample (65%) of visiting rate data and a more complete data set is examined below. The model (Figure 2.2(a)) shows that imposing a different energy state upon an individual causes an energetic response (Treatment x sex interaction: $\chi^2_{(2)} = 19.80$, $p < 0.0001$). Control males and females showed very similar levels of expenditure (predicted means: 53.2 ± 3.0 kJ (female), and 51.5 ± 3.2 kJ (male)). Warmed females, however, increased their energy expenditure to 66.1 ± 3.0 kJ in response to their treatments. An opposite response can be seen in the Chilled females, which decreased their energy expenditure after treatment to 28.0 ± 6.8 kJ. *Post-hoc* analysis within REML, revealed a significant increase in active energy expenditure by Warmed females ($t_{(25)} = 3.09$, $p = 0.003$) and a contrary and significant response in Chilled females ($t_{(25)} = 3.36$, $p = 0.013$). These results were consistent with H_i , H_{ii} and H_{iii} , but not with H_0 . The active energy expenditure of the Chilled pair males was significantly higher than controls (57.7 ± 4.6 kJ: $t_{(25)} = 3.31$, $p = 0.0015$), whereas Warmed pair-males only showed a trend towards increased energy expenditure (53.0 ± 4.8 kJ: $t_{(25)} = 1.38$, $p = 0.180$). Since a mean overnight cost was used to calculate AEE sensitivity analysis was performed to validate this method. Two REML analyses were run, one using AEEs generated using the lowest control (mean - s.d.) and the highest chilled (mean + s.d.) overnight costs, and another using the highest Control and lowest warmed costs. This was an attempt to determine if significant treatment*sex interactions occurred at the limits of the group distributions. Both analyses revealed a

significant interaction term, and *post-hoc* analysis indicated the significant increase of warmed females and decrease in chilled females held. Thus, we assert that, although not ideal, the use of means is acceptable in this case.

2.4.3 Feeding visits to the nest.

Fifty-four swallows were involved in the analysis of feeding visits to the nest ($n = 35$ in 1997, $n = 18$ in 1998). Weather variables and food abundance proved non-significant terms (Table 2.2), but birds with larger broods tended to visit more often than those with relatively smaller broods ($\chi^2_{(1)} = 5.63$, $p = 0.018$). The model (Treatment x sex interaction $\chi^2_{(2)} = 32.21$, $p < 0.0001$) indicates similar patterns as for energy expenditure (Figure 2.2(b)), with Control pairs having similar rates, although males seemed to show a slightly higher visiting rate (female: 11 ± 1 , male: 13 ± 1 visits h^{-1}). Warmed females increased their visits (to 18 ± 2 h^{-1}), and females decreased their visits (to 4 ± 3 h^{-1}) in response to the chill treatment. The visiting rates of pair males from both Warmed and Chilled groups were not significantly different from Controls (13 ± 2 and 10 ± 3 h^{-1} , respectively). *Post-hoc* tests revealed that the changes in visiting rate seen in Warmed and Chilled females differed from Controls ($t_{(46)} = 4.75$, $p < 0.0001$, and $t_{(46)} = 2.19$, $p = 0.033$, respectively). These results were consistent with those for energy expenditure, and provided support for H_i and H_{iii} .

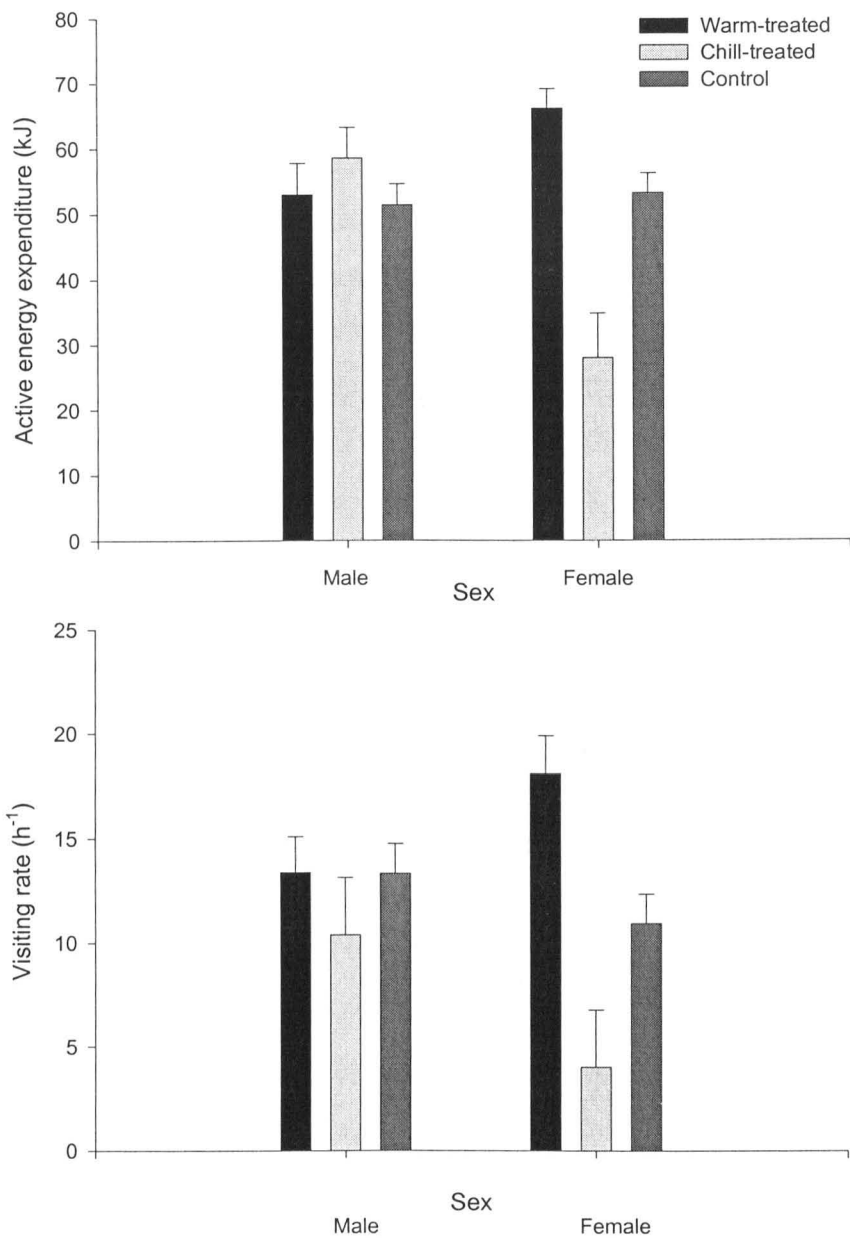


Figure 2.2(a). Predicted means \pm standard error (REML) for males and females showing AEE (i.e. energy expended (kJ) during the release period, 16 ± 1.5 h), for Control and treatment groups. Figure 2(b). Predicted mean visiting rates \pm standard error (h^{-1}) to nests by males and females of Control and treatment groups.

2.4.4 Symmetry of 'input' and 'output' energy values

The mean energy value of inputs was calculated from the model constructed (ANCOVA) to explain energy expenditure overnight: $E_{\text{overnight}}$ (kJ) (same variables used as Table 2.2). The predicted mean overnight cost for Control females (17.0 ± 0.7 kJ) was then subtracted

from all overnight energy expenditure data, in order to obtain a relative difference for treatment females. The analysis was then repeated using these differences as the dependent variable, and the resultant fitted means were used as input estimates, i.e. an energy saving of 8.0 ± 0.8 kJ for Warmed females, and a similar extra cost of 5.4 ± 0.9 kJ for Chilled females. Output was calculated in a similar way, using a REML model to explain AEE (kJ) (Table 2.2) for all data. The mean fitted value for Control females was again subtracted from the AEE data and the analysis repeated. This gave an increased energy expenditure amongst Warmed females of 13.0 ± 3.0 kJ ($0.5 \times \text{BMR}$), and a decrease of 25.2 ± 6.8 kJ ($0.9 \times \text{BMR}$) for Chilled females. *Post-hoc* analysis showed no significant difference between the absolute values of these two output expenditures ($t_{(24)} = 1.64$, $p = 0.114$). Accordingly, we interpret these responses as symmetrical with respect to the Control and each other, although the power of this analysis was only 43%.

In contrast, energetic input and output values were not equal. Hence, the response to our manipulations involved apparent overcompensation in relation to the energy that was either made available or withdrawn from reserves due to our treatments. The output:input ratios ranged from c. 2, in Warmed females, to c. 4.5 in Chilled females. This latter figure accounts for approximately 30% of the DEE of our swallows.

2.4.5 Mass and fatscore changes.

There was no effect of treatment, release period or weather variables on mass changes in experimental swallows over the trial period (Table 2.2). There was, however, a significant effect of initial mass on mass change ($\chi^2_{(1)} = 5.52$, $p = 0.019$) showing that heavier birds lost more mass over the trial period. Birds with larger broods showed a significantly greater mass loss ($\chi^2_{(1)} = 6.46$, $p = 0.011$). Fatscore changes were significantly affected by the initial fatscore ($\chi^2_{(1)} = 9.26$, $p = 0.002$). No other variable entered into the model, including treatment, explained any significant variation (Table 2.2). Both the mass and fatscore analyses held a statistical power of $>80\%$, to detect a mean change of 0.5 of a standard deviation of their respective distribution. This is equal to approximately 0.4g in terms of mass. The absence of treatment effects on mass or fatscore suggested that H_i should be rejected and provides evidence for H_{iii} .

Table 2.2.. Results of REML analyses. All significant terms ($p < 0.05$) are in **bold**, those showing a strong trend are in *italics*. Minimal adequate model is shown along with terms which were excluded from the analysis due to insignificance.

Adult mass changes	χ^2 statistic	d.f	p value
<i>Minimal adequate model</i>			
brood size	6.46	1	0.011
initial mass	5.52	1	0.019
<i>Excluded terms</i>			
local temperature	0.20	1	0.655
average precipitation	1.39	1	0.239
release period	0.53	1	0.467
treatment	0.03	2	0.986
sex	0.19	1	0.663
treatment*sex	4.11	2	0.128
residual d.f.		34	
Adult fatscore changes	χ^2 statistic	d.f	p value
<i>Minimal adequate model</i>			
initial fatscore	9.26	1	0.002
<i>Excluded terms</i>			
local temperature	0.37	1	0.546
average precipitation	0.15	1	0.702
release period	0.90	1	0.355
brood size	1.37	1	0.242
treatment	0.75	2	0.688
sex	0.16	1	0.690
treatment*sex	1.31	2	0.519
residual d.f.		35	
Active energy expenditure	χ^2 statistic	d.f	p value
<i>Minimal adequate model</i>			
treatment	4.52	2	0.104
sex	0.46	1	0.497
visiting rate		1	
treatment*sex	19.80	2	<0.0001
treatment*visiting rate	7.10	2	0.029
<i>sex*visiting rate</i>	<i>3.57</i>	<i>1</i>	<i>0.059</i>
<i>Excluded terms</i>			
Mass	1.24	1	0.265
local temperature	0.06	1	0.804
average rainfall	1.93	1	0.165
release period	0.86	1	0.394
brood size	1.27	1	0.260
treatment*sex*visiting rate	1.55	2	0.460
residual d.f.		25	
Continued overleaf...			

Visiting rate	χ^2 statistic	d.f	p value
<i>Minimal adequate model</i>			
brood size	5.63	1	0.018
treatment	6.68	2	0.035
sex	2.24	1	0.134
treatment*sex	32.21	2	<0.0001
<i>Excluded terms</i>			
local temperature	1.29	1	0.255
average precipitation	1.79	1	0.181
food abundance	1.33	1	0.248
residual d.f.		46	

NB. Release period refers to the period over which AEE was measured.

2.5 Discussion

Our experiments demonstrated a strong association between body-state and energy expenditure during reproduction in swallows. Therefore, we rejected H_0 and H_i . Under normal circumstances an individual can only increase reproductive effort in this way at the cost of future breeding success or survival (Williams 1966; Nur 1984; Partridge & Harvey 1985; Partridge 1992; Jacobsen *et al.* 1995; Henderson & Hart 1993). By manipulating body-state, however, and hence by implication the probability of future survival, we induced short-term changes in reproductive effort, measured in two complementary ways. Since positive state manipulations induced additional effort, and negative manipulations led to a reduced effort, we conclude that somatic energy storage (and associated survival risks) traded-off against the work done on provisioning the brood. This result was consistent with H_i and H_{iii} , whereby body state regulates metabolism and behaviour during breeding.

Although there are no other studies of the effects of body-state manipulations on energy expenditure by breeding birds, analogous experiments on an iguanid, *Uta stansburiana*, allow certain comparisons to be made. Follicle ablation in gravid females, leading to reduced clutch size and mass, was considered to moderate 'foraging effort and yolk synthesis' (Sinervo & DeNardo 1996), which in turn lowered energy expenditure. This allowed post-laying body condition of females to increase, along with their survival. Equally ovarian stimulation using exogenous hormones had the reverse effect, with energy expenditure increasing as a result. These responses to manipulations of egg mass comply with ours for swallows, in that experimental reductions and increases in reserves within lizards during breeding had knock-on effects on parental energy expenditure.

Warmed females will have had a positive energy balance at dawn, relative to Controls. We assume this energy could be allocated according to a notional 'effort strategy'. The strategy would derive from selective pressures to deliver optimally the energy required by nestlings, with spare time being allocated to other activities which could enhance fitness but which were not connected to parental duties, such as self-feeding (Kacelnik & Cuthill 1990). Energy available to Warmed females, surplus to that devoted to provisioning, might have been used to enhance somatic investment (H_{ii}). However, this type of response was not detected in this study, where all of the energy 'donated' to the swallow was evidently used to increase nest visitation. Indeed, birds not only expended the donated energy, but expended more energy than afforded by the treatment. The disproportionate output response relative to inputs via our treatments implies that the fitness implications of units of energy differed according to whether they represented short-term gains or losses. Alternatively adult swallows may choose not to, or be obliged not to, balance energy completely in a 24 h period.

If adult swallows maintain an optimal mass (i.e. at dawn) for brood rearing in order to minimise flight costs over this busy period (Freed 1981; Norberg 1981; Jones 1987; Cavitt & Thompson 1997), then 'donating' energy via treatments could be manifest, via an increased mass, as a greater wing-loading at dawn than 'expected'. On this view, greater reserves at dawn could be regarded as a 'negative' manipulation because flight costs would increase. In practice, there was no difference in mass loss overnight across all three groups, however, so all birds had the same starting mass at dawn, even though there would have been treatment differences in overnight substrate use and water loss. We infer that it was these differences which proximately gave rise to the observed changes in energy expenditure and associated behaviour, and this did not occur due to obligatory changes in mass-dependent flight costs.

The model outputs of energy expenditure and visiting rates were very similar (Figure 2.2(a) and (b)), and visiting rate played a significant role in explaining the variation seen in our energy expenditure data. Visiting rate in this study only provided a snapshot of behaviour, however longer observation period have revealed similar patterns (Chapter 3). Although some studies have found no relationship between energy expenditure and reproductive activities, such as visiting rate (Westerterp & Bryant 1984; Bryant 1988; Galbraith *et al.* 1999); field metabolic rates (FMR) and nest provisioning rates were positively related in studies by Williams (1988) and Siegel *et al.* (1999). These relationships, and the one identified in this study, suggest that nest-provisioning rates can

indeed be a reliable index of reproductive effort (and also reproductive investment) in some species (Daan *et al.* 1996).

There were no differences in mass or fat score changes amongst the three groups over the trial period; thus experimental birds returned to an equivalent mass or fat score by the end. The only parameter to affect fat score changes was initial fat score, potentially pointing to an individual optimum during brood rearing. Hence, if energy expenditure was normally increasing in parallel with visiting rate, and somatic investment did not vary substantially between treatment groups, we can infer the trade-off between body-state and reproductive effort. Thus, when evaluating our hypotheses with regard to changes in energetic state following treatments, the results were only consistent with Hypotheses H_{iii} . Specifically, following our manipulations of body-state, the subsequent response showed a bias towards reproduction, and no impact on mass or fat storage, implying a skewed underlying fitness function relating reproduction and somatic investment (Fig 2.1c). Therefore, reproductive effort is the parameter most likely to be sacrificed or boosted by barn swallows when their body-state is perturbed, with energy being a currency which is integral to both the perturbation and the response.

This study has shown that the effort devoted to reproduction is state-dependent. Even so, it is unclear if physiological state alone provides the cues. Aerial-feeding birds live in a highly variable environment (Martins & Wright 1993) and it has been found that swallows will feed their broods more often in good weather, and also respond to differences in brood size (Bryant & Turner 1982; Jones 1987). Hence, the swallow may adopt a strategy which allows it to be sensitive to its state, while also responding to other cues, such as chick begging rates and food availability (Godfray 1991). Responses to environmental cues, however, could be relatively unimportant (Cooch & Ricklefs 1994); a pattern consistent with the results of this study. Alternatively, the effects of environmental factors may have been relatively difficult to detect using our study methods. There was also a trend for Chilled birds to overcompensate for the manipulation more than Warmed ones. This occurred in spite of the smaller temperature difference imposed on Chilled birds. It may be due to a ceiling on energy expenditure (Drent & Daan 1980; Hammond & Diamond 1997), which could place an upper limit on the energy expenditure of Warmed birds. Therefore Warmed birds may not overcompensate because by doing so they may put their survival at risk. In contrast, with a Chilled bird, a decrease in expenditure is not liable to the same survival penalty, and so a fall in the energy allocated to breeding should be unconstrained

in this respect. If this applies, then symmetrical trade-offs (i.e. H_{iii}) should only be noted at relatively low levels of energy expenditure.

The trade-off identified here implies that reproduction carries a cost, and that reproductive effort will be reduced if an animal's survival is jeopardized and *vice versa*: a life history response, mediated by an individual's body-state. Furthermore, the response of swallows to positive and negative manipulations was large enough to be readily detected, even amongst the variation in energy expenditure related to individual differences and other factors. This, plus the disproportionate expenditure on outputs compared to inputs, suggests that body-state not only plays a key role in allocation decisions, but that it is comparable in the scale of its effects to other major influences on energy expenditure of free-living animals (Bryant 1997; Speakman 1997b).

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3 Sex related foraging differences in response to body state manipulations in the Barn Swallow (*Hirundo rustica*).

3.1 Introduction.

The trade-off between reproductive effort and survival is well documented (Stearns 1992). Recently the physiological state of an individual has been identified as a means of mediating this trade-off, by both dynamic models and empirical studies (Damsgard *et al.* 1997; McNamara & Houston 1992, 1996; Olsson 1997; Chapter 2). Chapter 2 described an experimental manipulation of adult body state using overnight temperature in brood rearing swallows. This showed that birds with an excess of energy at dawn, and thus in a positive state, increased their energy expenditure and visitation rates to the nest, thus increasing reproductive effort. This asymmetrical allocation of energy between reproduction and survival was robust enough to be picked up by DLW and not only was all the energy 'gifted' to the birds by the manipulation used to increase reproductive effort, but extra energy (between 2 and 4 times 'gift') was expended. This suggests that state is an important factor in the reproduction vs. survival trade-off, and indeed itself trades off against reproductive effort. However, no study has manipulated both males and females to investigate sex differences in response to physiological state. This study attempts this by manipulating females and males from different pairs and comparing their behaviour and energy expenditure with that of a Control group.

In swallows the female performs the incubation alone with frequent visits from the pair male (Jones 1987b). When brood rearing begins however, the pair take an equal share of the load, provisioning the brood at similar rates and expending a similar amount of energy (Jones 1987a; Chapter 2). Since this study took place when brood rearing was more than half way through (day 11-14), we would expect effort levels to be similar for both Control males and females. We would also expect females and males who have undergone a positive manipulation to respond in the same way and to the same extent as each other, simply as at this point in their breeding cycle they have the same role and bear the load equally. Sex differences in foraging and other behaviours have been seen in many bird species (Lombardo 1991; Salamolard &

Weimerskirch 1993; Siikamaki *et al.* 1998), and this is not just limited to the reproductive period (Ardia & Bildstein 1997; Figuerola & Bertolero 1998)

Male removal studies have often shown that females will incompletely compensate, in terms of provisioning of chicks, for the loss of their partner, although increases in feeding rates are observed (Bjornstad & Lifjeld 1996; Duckworth 1992; Markman *et al.* 1996; Whittingham *et al.* 1994). It has been argued that monogamy in birds is an evolutionarily stable strategy as long as each parent cannot totally compensate for the other member of a pair (Houston & Davies 1985). These studies have produced evidence supporting this theory. Most studies, be they mate removal or handicapping, have concentrated on manipulating the behaviour and effort levels of the female by removing the male. Two studies, however have manipulated male effort, with differing results. Markman *et al.* (1995) handicapped female Orange Tufted Sunbirds (*Nectarinia osea*) using tail weights and observed the changes in male behaviour. They found, in this predominantly female care centred bird, that males reduced their nest defence behaviour when faced with a handicapped female and used their time to provision the nestlings more than in Control nests. This provides evidence that males will attempt to compensate for low provisioning in their partner, and implies an important trade-off for bi-parental co-operation. However, Sanz *et al.* (2000) handicapped female Great Tits (*Parus major*) and found no change in male feeding rates at the nest. This was probably due to the fact that handicapped females did not reduce their feeding levels, at the expense of body condition. When males were handicapped, however, they significantly reduced nestling feeding and suffered no decline in body condition. We may expect, in this chapter, since only one member of a pair is manipulated, and is expected to respond to this accordingly, that pair members will also change behaviour and energy allocation when compared with controls.

Tolonen & Korpimaki (1996) performed brood size manipulations upon Eurasian Kestrels (*Falco tinnunculus*) in order to quantify male and female effort responses. Males showed no real responses to brood manipulations, whereas females showed highly significant responses. There are many reasons why males may not respond in the same way as females, e.g. perceived paternity. The rules governing male parental care and perceived paternity have received much attention and it has been suggested that males work to an 'all or nothing' rule, whereby if they are present during the females fertile period they will feed the nestlings, if they are absent during this period

then they will not provision the brood (Dickinson & Weathers 1999). This study was undertaken using Western Bluebirds, and since they tend to have very strong life-long pair bonds and be monogamous, these results are not too surprising. Lifjeld *et al.* (1998) found lower male parental care in the Pied Flycatcher (*Ficedula hypoleuca*), when males were replaced and paternity reduced. Sheldon *et al.* (1997) report similar findings by detaining laying female Collared Flycatchers (*Ficedula albicollis*) for 1h, and reducing male perceived paternity. Their results showed a weak effect and they suggest that paternity may be fixed at the start of laying in some species. In most studies nest visitation is used to determine male parental effort, and although an important component of reproductive effort, it may be unsuitable to define reproductive or parental effort in males. There are several components of reproductive effort which may have been relatively overlooked.

Birds with excess energy at dawn could increase several different effort components. Nest defence is energetically costly and has the potential to harm the parent bird, it is, therefore, thought to be a reliable indicator of parental effort. It is also a trait more likely attributable to males in some species (Hakkarainen *et al.* 1998; Lessells *et al.* 1998; Lombardo 1991). Male swallows may use their excess energy to increase mate guarding against extra-pair copulations, or may indeed increase their own level of extra-pair copulations (Currie *et al.* 1999; Magrath & Elgar 1997). Nest sanitation could also be increased as a method of reducing nest parasite load or nestling thermoregulation (Chapter 4; Christe *et al.* 1996; Lombardo 1991). Birds may change their foraging strategy to bring back larger or higher quality prey (Wright *et al.* 1998; Siikamaki *et al.* 1998), as a function of increased reproductive effort, without necessarily increasing nest visitation. In certain species, male responses to brood manipulations have been seen to equal the female's in terms of feeding rates (Conrad & Robertson 1993) or to even outweigh the female's with a change in bolus and prey size delivered to nestlings (Siikamaki *et al.* 1998). We would thus expect both male and female swallows to respond to positive body-state manipulations in similar ways. In this study nest visitation rate, parental energy expenditure and food quality are measured. The effect of the manipulations upon chick growth is also quantified.

Foraging strategy in birds has been seen to vary with experimental manipulation of brood size and environmental conditions (Siikamaki *et al.* 1998). Much work has been done to investigate foraging strategies of insectivorous predators and many have found

that adult birds provision their offspring with larger prey that is most readily available in the environment (Brodmann 1997; Burger *et al.* 1999). Optimal foraging theory predicts that birds will adjust their foraging strategy according to brood demand, in order to maximise net rates of energy gain (McNamara & Houston 1997; Welham & Beauchamp 1997). This change can manifest in a number of ways, either by changing flight speeds (de la Cueva & Blake 1997), habitat choice, load sizes (Bryant & Turner 1982) or prey type (Siikamaki *et al.* 1998). However, we would expect birds not to choose a strategy whereby their own fitness is compromised. Thus 'choice' of foraging strategy is possibly constrained by an individual's state. In this study, since adult energetic state has been manipulated, we would therefore expect birds who have undergone positive manipulations to respond by significantly shifting foraging strategy in order to provision their broods. With extra energy at dawn the birds are conferred an advantage over controls and their own partners. If they then choose to allocate this extra energy towards reproductive effort, and increase visiting rate to the nest, we may see two possible changes in prey delivery. (1) An increase in the amount of good quality, highly digestible prey, with higher fat content, or (2) no difference in prey choice, if swallows are opportunistic predators and just 'trawl' the air. In this case more prey would be delivered to the nest. Under prediction 1 the amount of faeces produced by nestlings would be lower than from Control nests, however, under prediction 2, warmed nests will produce more faeces than controls. There may also be changes in partners of manipulated birds strategies also.

There has been much debate concerning the currency individuals maximise whilst foraging. Welham & Beauchamp (1997) described the three main currencies proposed so far for provisioning parents: net rate of energy gain, which is constrained by the amount of time available for foraging; daily delivery rate, also time constrained; and efficiency, maximising a ratio of net energy gained against the energy costs of foraging, this is constrained by parental energy expenditure. Although once discarded, empirical studies have found that maximising efficiency can explain the strategies of individuals whilst provisioning young (Waite & Ydenberg 1994; Welham & Ydenberg 1988; Welham & Ydenberg 1993), and recent theoretical work has also highlighted efficiency (Welham & Beauchamp 1997; Ydenberg *et al.* 1994). State-dependent foraging models, however, have also been proposed, showing great affinity with the currency of efficiency (Houston 1995; Welham & Beauchamp 1997).

Several indices of reproductive effort have been utilised in this study, such as, energy expenditure relative to controls, prey quality, nestling faecal output, nestling mass changes, and visiting rate to the nest, in order to capture any foraging changes associated with a change in a provisioning parent's state.

3.2 Methods.

3.2.1 Manipulations.

Fieldwork took place over two breeding seasons, 1997 and 1998, in the Stirling area of Central Scotland (56°8'N, 3°54'W). Bird pairs were caught using mist nets between 17:00 and 19:30h, they were then randomly allocated to one of three groups: Warmed female, Warmed male, or Control. Mass, fat score and sex data were collected at this point. Fat score was recorded as a rank score (0 to 5) of visible fat deposits in the interclavicular pit. Although there is some controversy concerning the validity of this method (Krementz & Pendelton 1990; Scott *et al.* 1995), it has been used reliably in breeding Hirundines (Bryan 1996; Bryant & Westerterp 1983). Once initial blood samples had been taken (see next section) birds were placed within their respective manipulations. Control birds were placed in an outside shelter, overnight temperature being measured by a Psion™ datalogger at an interval of 15 minutes. This allowed us to control the manipulation period each group experienced, as it was usually still light when birds were placed in manipulations. Both warmed female (WF) and male (WM) groups were treated similarly, and placed in an incubator (Sanyo) at 29°C in the dark (thermoneutral zone, Kendeigh *et al.* 1977). The average overnight manipulation period across groups was 7.2h (± 0.5 s.d.). The male and female partners, respectively, of the Warmed groups were treated in the same way as controls (Table 3.1).

The energetic cost of each manipulation was recorded in a subsample of birds using direct respirometry. Since Control birds experienced an average overnight temperature of 14°C (13.8 ± 2.0) and this did not vary significantly between years ($F_{(1,27)} = 0.04$, $p = 0.85$), birds were placed in 14°C incubators to obtain respirometry results. Food abundance data was recorded using a 12.2m suction trap situated at the University of Stirling. Weather data was assessed in two ways. Suction trap samples were collected daily and analysed for volume of insects per day, which was used in statistical analyses. A breakdown of taxonomic families was also undertaken as part of a long term project (T.G. Benton and D.M. Bryant, personal communication), and these data

were used to calculate availability of certain insects whilst the study was ongoing. Daily maximum and minimum temperatures were taken from the Parkhead weather station, also based at the University, and during each pair observation, local temperature, rainfall, were recorded. Rainfall was scored as percentage of rainfall during an observation period.

3.2.2 Doubly labelled water.

DLW was used to obtain an accurate measure of energy expenditure (Lifson and McLintock 1966, Tatner and Bryant 1989). Birds received intraperitoneal injections of DLW (10 μ l g⁻¹ body mass). The injectate was prepared by adding 0.37g of 99.9 APE deuterium (²H) to 5ml of 20 APE water containing isotope 18 of oxygen (H₂¹⁸O). Once injected the birds were kept in a bird bag for 1h to allow the isotopes to reach an equilibrium with the body water (Bryant & Westerterp 1982). Initial blood samples were then taken from the femoral vein. Final samples were also taken from this area. Blood was collected using 10 μ l capillaries (Vitrex), each sample being approximately 5 μ l. These were immediately flame sealed post sampling. A maximum of 10 capillaries were taken from each bird. Background isotope levels were obtained from blood samples of non experimental birds (n=2 (1997), n=3 (1998)). Isotope concentrations were derived from mass spectrometry (Speakman 1997; Tatner & Bryant 1989).

3.2.3 Calculation of energy expenditure

Daily energy expenditure (DEE, kJ d⁻¹) was calculated as described by Tatner & Bryant (1989) and Lifson & McLintock (1966), using an RQ of 0.75. The body water pool was derived using Bryant & Westerterp's (1982) equation for a closely related species (house martin, *Delichon urbica*) during the breeding season. Overnight metabolic cost (E_{resp} : kJ g⁻¹ h⁻¹) was obtained from the respirometry results (Gessaman 1987) and a mean obtained for each treatment group (E_{resp}). From this the cost of the overnight period ($E_{overnight}$) was calculated using Equation 1 (W = mean overnight body mass, $t_{overnight}$ represents the time a bird spent in the incubator). $E_{overnight}$ was then used to calculate, by difference from the daily energy expenditure (DEE), the 'active' energy expenditure (AEE) of each individual during the release period (Equation 3.2).

$$E_{overnight}(\text{kJ}) = E_{resp} * W * t_{overnight}$$

Equation 3.1.

$$AEE \text{ (kJ)} = DEE \text{ (kJ)} - E_{\text{overnight}} \text{ (kJ)} \quad \text{Equation 3.2.}$$

$$MI = E_{\text{overnight}} \text{ (kJ)} / \text{BMR} \quad \text{Equation 3.3}$$

Basal metabolic rates were derived from the passerine equation of Aschoff & Pohl (1970), resting phase, to provide a standard for comparisons (called Metabolic intensity, MI, Equation 3.3.).

Nest visitation rates were monitored in the same way described in Chapter 2. An index of efficiency (I_e) was calculated for each sex within each treatment group (Equation 3.4.). This was done by obtaining the predicted visiting rate (h^{-1}) from statistical analysis (VR_m) and then dividing by the predicted mean active energy expenditure, already divided by the mean release period (t_{rel}), to convert energy expenditure to a hourly rate. This gives a ratio of potential energy gained for nestlings by energy costs of foraging (Ydenberg *et al.* 1994).

$$I_e = VR_m / [AEE_m \text{ (kJ)} / t_{rel} \text{ (h)}] \quad \text{Equation 3.4.}$$

3.2.4 Chick monitoring

Swallow nests were monitored from hatching date (day 0), wherever possible, however, if nests were found post-hatching chick age was estimated using plumage state and size. Trials were undertaken when chicks were between 10 and 14 days old. At the start of each trial, after the adults had been caught, chicks were removed from the nest and weighed using an electronic balance (Salter). Chicks were then placed back into the nest. A plastic sheet was then placed under the nest to cover the area where faeces fell. After recapture of the adults, chicks were again weighed to establish average brood mass. If recapture failed, chicks were still re-weighed. Some nests were built out of reach of the ladders and thus not every nest was measured in this way. Faeces was collected from all nests, although not all yielded useful samples as some faeces would build up on high beams, which were unable to be reached. These samples were not used in the analysis of faecal output, but were used to determine faecal content.

3.2.5 Faecal analysis

Once faecal samples were collected they were dried in an oven for at least 24h and immediately weighed to record dry mass of faeces produced by each nest over the trial period. Each sample was then placed in 70% ethanol and the faecal sacs broken down

to allow further analysis. A random amount of the faecal sample was then removed and the insect wings within it taken out and placed in a separate petri dish. At least 50 wings were collected from each sample (53 ± 2.8 s.d.). If less than 50 wings were found in the first subsample another random sample was taken and all the wings counted in this sample were added to those from before. Wing length was measured using a graticule, viewed with a binocular microscope (Figure 3.1). The percentage of the wing length represented by each fragment was estimated, mainly by comparing part wings with full ones. If wing fragments were less than 50% of a wing and no reference wing was available they were excluded from the size analysis. The phylogenetic order to which each fragment found belonged was also recorded. Within the Hymenopteran order it was also noted if the wings belonged to parasitic forms or not. The mean overall length of wings within each sample was calculated, along with the mean length of wings within each order. The proportion of wings belonging to each order within each sample was also calculated.

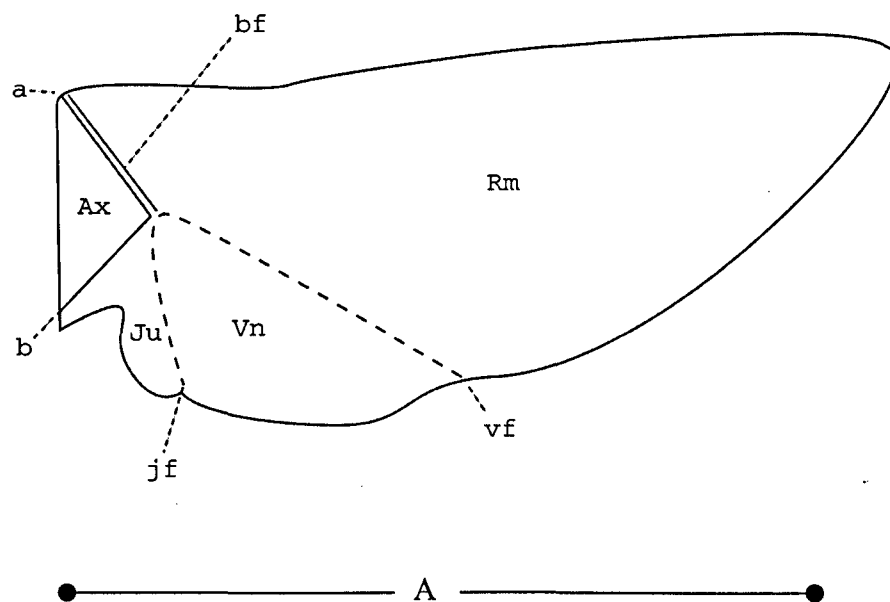


Figure 3.1. Schematic diagram of insect wing. Ax is the axillary region; bf, the basal fold; jf, the jugal fold; Ju, the jugum; vf, vannal fold; Vn, the vannus and Rm the remigium. The line a-b forms the main hinge of the wing to the body of the insect. The line A shows the ideal measurement for each wing in the analysis (100%). Since in

some were incomplete, a measurement was taken in the same plane as A and a percentage length of each wing fragment was estimated.

3.3 Statistical analysis

Data were collected over more than one year. Hence, to control for random year effects and non-orthogonality due to different treatments each year (Warmed females 1997 and Warmed males in 1998, controls were available for both years), Residual Maximum Likelihood (REML)(Genstat 5 Committee 1992) analysis was used to explain variation in energy expenditure, visiting rate, fatscore, body mass and faecal sample data. REML was also used to analyse the proportions of taxonomic orders within nestling faeces. These data were arcsine square root transformed to normalise residuals. Stepwise deletion of fixed variables from the minimal adequate model was performed. The random model controlled for the year in which the treatment was performed and the date of the trial within each year. The significance of fixed variables was estimated using the Wald statistic, which is asymptotically distributed as χ^2 (Genstat 5 Committee 1993). Overnight energy expenditure and faecal output were analysed using ANCOVA (Minitab 1997). Analysis of overnight energy costs was performed upon reciprocal transformed, $\frac{1}{(x-1)}$, energy expenditure (E_{resp}) to normalise residuals and to control homogeneity of variance. Predicted means were back-transformed and converted to metabolic intensity (MI) data (Equation 3.3). Changes in insect abundance over the two years of this project were analysed using log-transformed data in ANOVA (Minitab 1997), back-transformed data are shown in figures. Proportion of each taxonomic order was calculated for each year. Sample sizes for all analyses are given in Table 3.1. All residuals were checked for normality and homogeneity of variance. Predicted means \pm standard error are quoted from statistical models.

Table 3.1. Experimental design (a) and sample sizes for analysis of treatment and control groups (b). OV_{resp} = overnight costs of manipulations, M_{rel} = adult mass changes over trial, FS_{rel} = adult fat score changes over trial, AEE = active energy expenditure, VR = nest visiting rate, $M_{nestling}$ = mean brood mass changes over trial, F_{output} = faecal output, S^{wings} = insect wing size.

(a)

Treatment	Temperature °C	
	Male	female
Control	14	14
Warmed female (WF)	14	29
Warmed male (WM)	29	14

(b)

OV_{resp}		
Control	3	2
Warmed	2	3
$M_{rel} + FS_{rel}$		
Control	8	8
Warmed female (WF)	6	8
Warmed male (WM)	5	4
AEE		
Control	8	8
Warmed female (WF)	5	8
Warmed male (WM)	5	3
VR		
Control	14	14
Warmed female (WF)	7	7
Warmed male (WM)	5	5
$M_{nestling}$		
Control		10
Warmed female (WF)		10
Warmed male (WM)		2
F_{output}		
Control		13
Warmed female (WF)		8
Warmed male (WM)		7
S^{wings}		
Control		14
Warmed female (WF)		6
Warmed male (WM)		6

Table 3.2.. Results of all REML statistical analyses undertaken in this study, not quoted in main text. Wald statistic is quoted as test statistic, the relevant degrees of freedom (d.f.) and p values are quoted for both the minimal adequate model and all terms excluded due to insignificance. The residual number of degrees of freedom associated with the minimal adequate model are also presented. Column headings relate to abbreviations in Table 1. Significant terms are in **bold**, terms showing a strong trend are in *italics*.

Variable	Wald statistic	d.f.	probability
AEE			
Minimal adequate model			
Release period	6.40	1	0.007
Treatment	8.83	2	0.012
Sex	0.28	1	0.394
Treatment*sex	9.52	2	0.009
Excluded terms			
Mass	1.66	1	0.265
Average precipitation	0.01	1	0.912
Local temperature	0.03	1	0.867
Food abundance	0.03	1	0.869
Brood size	0.58	1	0.446
Visiting rate	0.69	1	0.407
Treatment*visiting rate	1.42	1	0.492
Sex*visiting rate	1.32	1	0.251
Residual d.f.		28	
VR			
Minimal adequate model			
Treatment	6.09	2	0.048
Sex	0.93	1	0.336
Treatment*sex	19.05	2	<0.0001
Brood size	4.62	1	0.032
Excluded terms			
Average precipitation	1.91	1	0.166
Local temperature	0.12	1	0.728
Food abundance	0.89	1	0.410
Time day obs (am/pm)	0.07	1	0.786
Residual d.f.		42	
Mass			
Minimal adequate model			
Initial mass (adult)	12.12	1	<0.0001
Excluded terms			
Release period	0.03	1	0.859
Average precipitation	1.66	1	0.197
Local temperature	0.00	1	0.985
Brood size	1.85	1	0.173
Treatment	0.37	2	0.833
Sex	1.30	1	0.253
Treatment*sex	1.34	2	0.511
Residual d.f.		35	

Table 3.2. cont.

Fat			
Minimal adequate model			
Release period	4.25	1	0.039
<i>Initial fat</i>	<i>3.52</i>	<i>1</i>	<i>0.061</i>
Excluded terms			
Average precipitation	0.78	1	0.378
Local temperature	0.87	1	0.352
Brood size	1.31	1	0.252
Treatment	3.61	2	0.165
Sex	0.46	1	0.499
Treatment*sex	1.42	<u>2</u>	0.492
Residual d.f.		34	
Mnest			
Minimal adequate model			
<i>Initial mass (brood)</i>	<i>3.69</i>	<i>1</i>	<i>0.055</i>
Excluded terms			
Release period	0.56	1	0.450
Average precipitation	3.67	1	0.055
Local temperature	0.02	1	0.902
Brood size	0.78	1	0.376
Treatment	1.85	2	0.397
Nestling age	0.67	<u>1</u>	0.519
Residual d.f.		15	

3.4 Results

3.4.1 Overnight cost of manipulation

The subsample of birds used to determine overnight costs showed significant differences between the Warmed and Control groups ($F_{(1,10)} = 37.23$, $p < 0.0001$). There were no differences due to sex ($F_{(1,10)} = 1.2$, $p = 0.305$). Warmed birds expend approximately basal metabolic rate overnight ($1.1 \times \text{BMR}$), where Control birds expended $2.1 \times \text{BMR}$. There was no effect of manipulation temperature or sex upon mass changes overnight ($F_{(1,52)} = 0.15$, $p = 0.70$). The model controlled for initial mass and overnight time period.

3.4.2 Body mass and fatscore variation

Brood size had no effect on adult mass changes over the trial period (Table 3.2.). There was also no effect of the manipulations or sex on mass changes. Initial mass was the only parameter to show a significant positive relationship with mass changes across groups. Fatscore also showed no treatment, sex or brood size effects (Table 3.2.). Initial fatscore was the only significant term tested. Neither mass or fatscore changes were affected by environmental variables (Table 3.2.).

3.4.3 Active energy expenditure (AEE)

Weather variables, known to affect swallow foraging behaviour (Jones 1987a) were placed in the model, however none proved significant (Table 3.2.). Visiting rate and brood size also had no effect on AEE. The predicted means for the model (Figure 3.2.), clearly showed an effect of the manipulation on energy expenditure. Warmed females (WF) showed a mean AEE of 65.3 ± 2.7 kJ, this is significantly higher than the Control females expenditure of 53.4 ± 2.8 kJ ($t_{(29)} = 3.1$, $p = 0.004$). Warmed males (WM) responded in a similar way, increasing AEE to 67.9 ± 3.7 kJ, compared with Control males at 52.9 ± 2.7 kJ. This increase is also significant ($t_{(29)} = 2.3$, $p = 0.03$). There was no difference detected between Control males and females energy expenditure ($t_{(29)} = 0.13$, $p = 0.898$). The female partners of Warmed males (WM) show slightly elevated expenditures compared with that of controls (59.5 ± 4.5 kJ), this increase is insignificant ($t_{(25)} = 1.2$, $p = 0.240$). Male partners of Warmed females showed no change in energy expenditure to 52.9 ± 3.6 kJ ($t_{(29)} = 0.02$, $p = 0.984$).

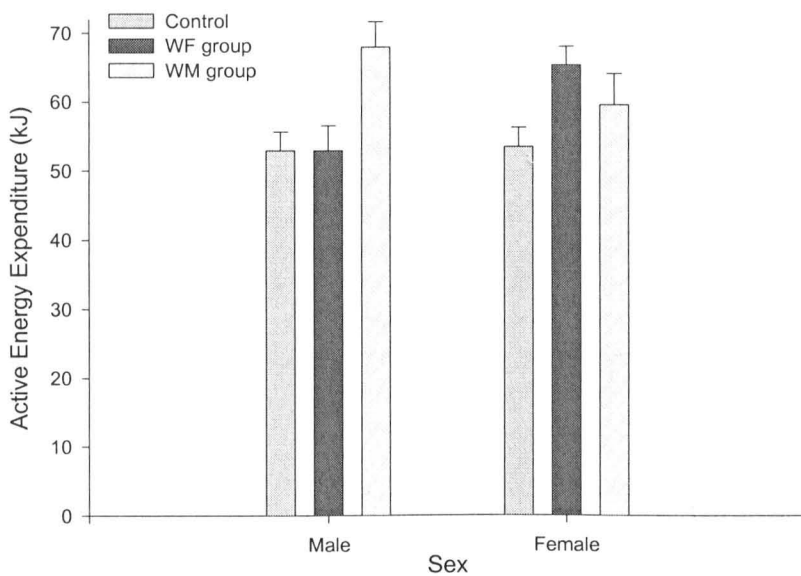


Figure 3.2.. Predicted mean active energy expenditure (AEE) over the release period ($h \pm sd$) by adult swallows within treatment and Control groups.

3.4.4 Feeding visits to the nest.

This analysis used data from fifty-one birds in order to discover the effect of treatment on the visiting rate of the adult swallows. Environmental factors, such as local rainfall and temperature showed no significant effects. There was no effect of time of day of the behavioural observations on visiting rate. Birds with larger brood sizes showed a higher visiting rate. There was a significant interaction between treatment and sex (Figure 3.3.), revealing an obvious effect of the manipulations upon the visiting rate of the Warmed female, showing a rate of 18.4 ± 1.8 vh-1, compared with Control females at 11.5 ± 1.4 vh-1 ($t_{(42)} = 4.1$, $p = 0.0001$). Warmed males also show a response in the same direction as Warmed females, with a visiting rate of 19.8 ± 2.5 vh-1, compared to 13.9 ± 1.4 vh-1 in Control males ($t_{(42)} = 2.8$, $p = 0.008$). Control pairs show similar levels of effort ($t_{(42)} = 1.7$, $p = 0.100$). Male partners of Warmed females show visiting rates non-significant from controls, however, there is a trend for their counterparts in the Warmed male group to increase visiting rate to 15.5 ± 2.5 vh-1, this response is insignificant ($t_{(42)} = 1.6$, $p = 0.123$).

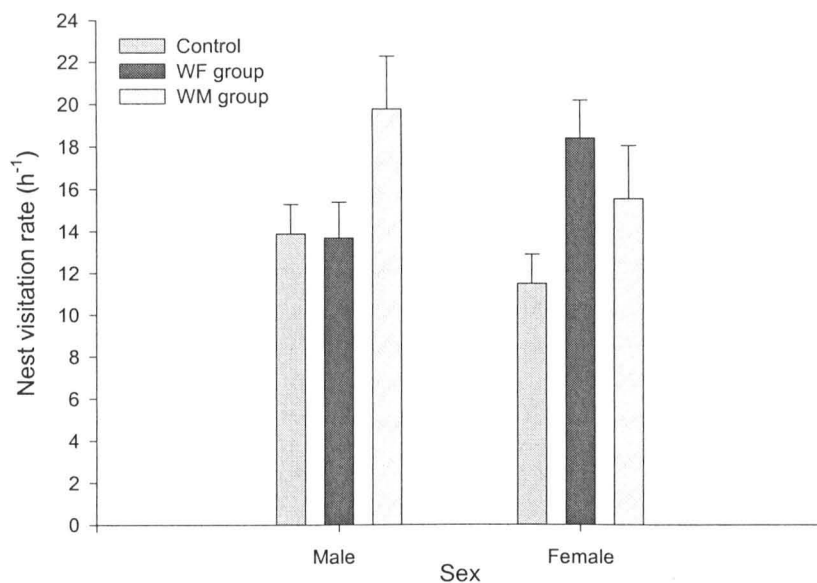


Figure 3.3.. Predicted mean visiting rate \pm standard error, to the nest from REML analysis, by adult swallows within Control and manipulation groups.

3.4.5 Index of efficiency.

Birds which had undergone a warming treatment showed the highest efficiency, i.e. net energy gains / energy costs. Warmed males (4.8) showing a slightly higher efficiency than females (4.6). Males tended to show the highest efficiencies. Control males and males in the WF group shared the same efficiency index of 4.1. Females in the WM group (3.9) showed a similar index to Control females (3.7).

3.4.6 Chick mass changes

Data from 22 nests was available for this analysis. There was no effect of local temperature on chick mass changes over the trial, but local rainfall had a significant effect, higher rainfall associated with higher mass loss in broods (Figure 3.4(a)). Brood size had no effect on chick mass changes. Initial average brood mass showed a significant positive relationship with chick mass loss. There was also no effect of treatment group on chick mass changes (Figure 3.4(b).), although there was a trend for broods assigned to the control group to lose more mass ($1.16 \pm 0.51\text{g}$) than either the Warmed female group ($0.90 \pm 0.25\text{g}$), or the Warmed male group ($0.89 \pm 0.24\text{g}$).

However, manipulated nests show no significant differences from controls ($t_{(16)} = 1.38$, $p = 0.187$).

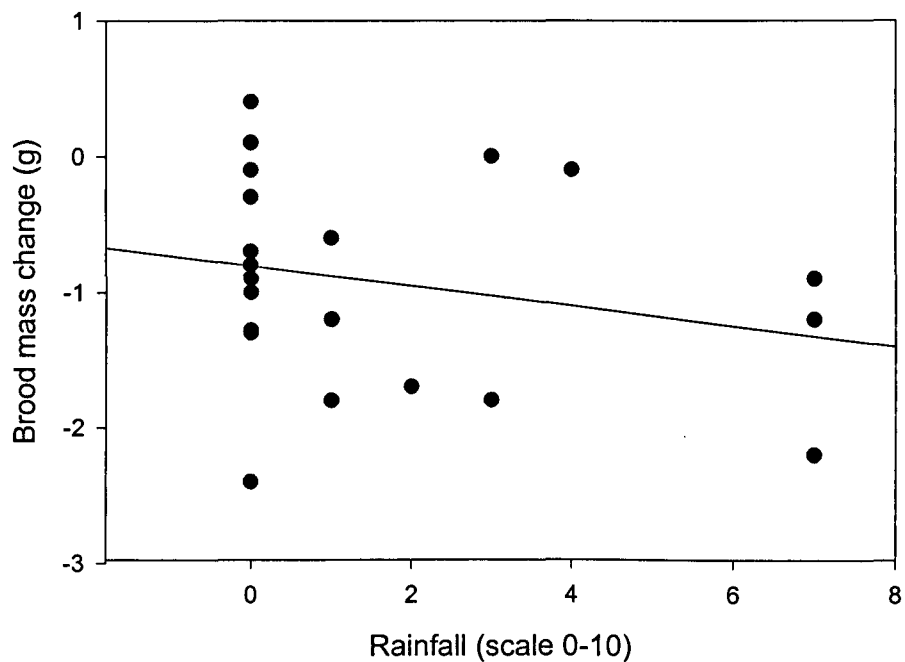


Figure 3.4(a).. Effect of precipitation (% of observation period) on mean brood mass changes (g) over the trial period across Control and manipulation groups.

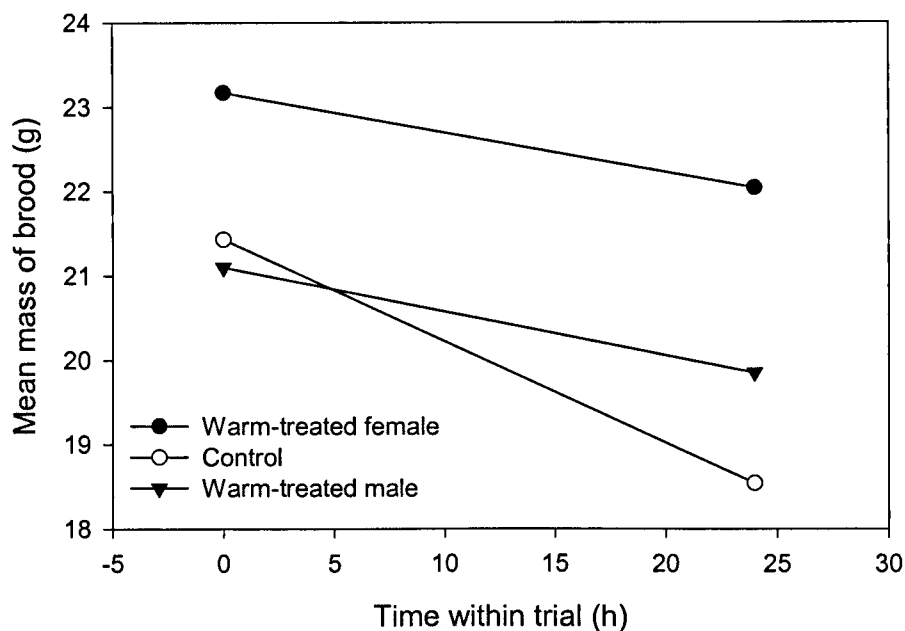


Figure 3.4(b). Nestling mass changes (g) over the trial period (0 to 24 h) within Control and manipulation groups. Mean mass is shown at start and end of trial period for each group.

3.4.7 Chick faecal output

The faecal output of each brood is defined as the dry mass of faeces produced over the trial period, and 28 nests were analysed in order to compare this between treatment groups. Brood size significantly affected total faecal output (Figure 3.5(a)), with a larger brood size causing a larger output. Chick age showed no effects. Weather data showed no significant effects. There was a significant effect of treatment on faecal output (Figure 3.5(b)). The Warmed female group show a significantly lower output, 1.21g, than that of controls, 2.27g ($t_{(23)} = 2.5$, $p = 0.02$). Broods in the Warmed male group show an opposite trend, with a mean output of 2.66g, but this increase is insignificant ($t_{(23)} = 0.9$, $p = 0.37$).

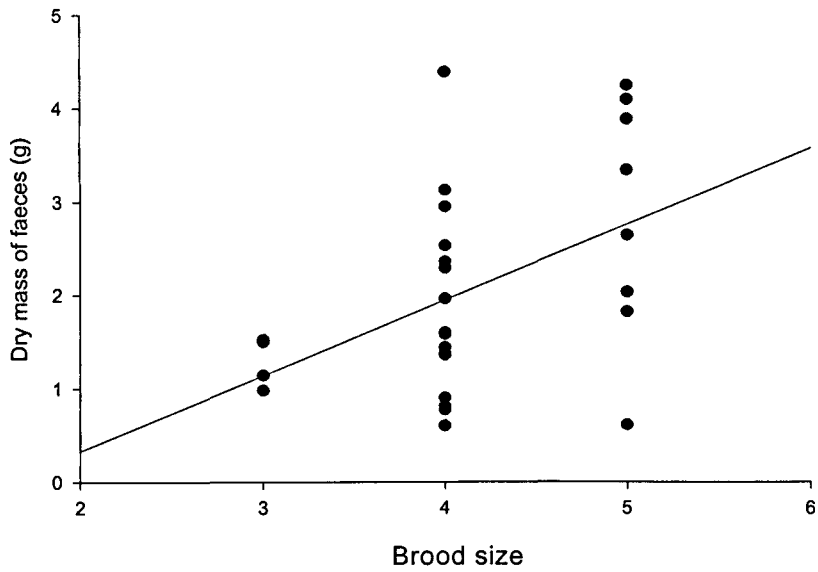


Figure 3.5(a). Effects of brood size on nestling faecal output over the trial period across Control and manipulation groups.

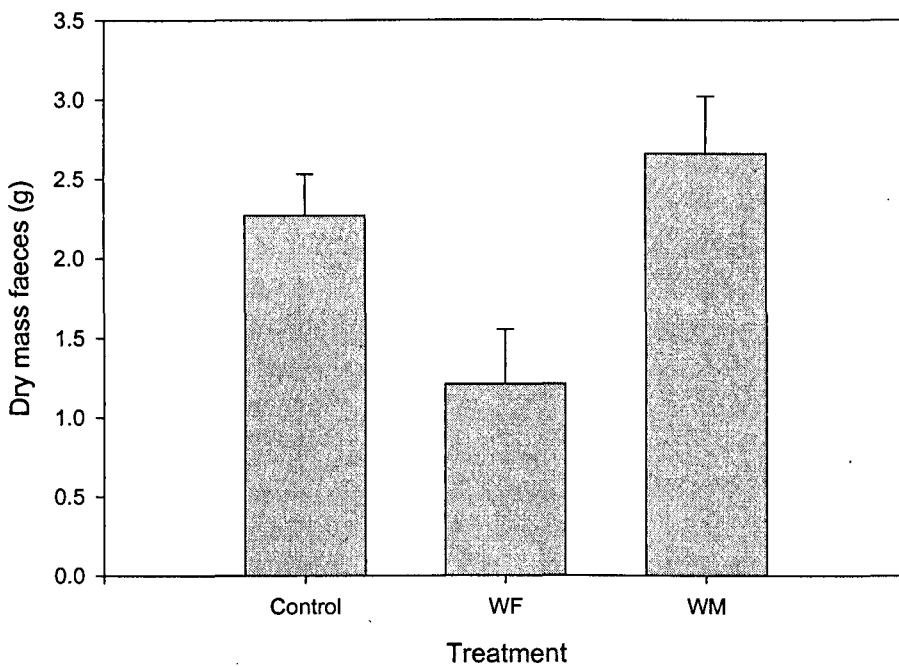


Figure 3.5(a). Effect of treatment group on faecal output (dry mass of faeces (g)) of nestlings over the trial period. Mean output \pm standard error are presented.

3.4.8 Nestling faecal analysis.

3.4.8.1 *Size of prey delivered to nest.*

When the mean wing length, regardless of Order, was analysed there was no effect of treatment on wing length (Figure 3.6(a).) ($\chi^2_{(2)} = 1.72$, $p = 0.424$). There was also no effect of brood size ($\chi^2_{(1)} = 0.06$, $p = 0.812$). When wing length was split by Order, however, certain patterns appeared. There was a significant treatment effect on the wing length of hymenopteran prey ($\chi^2_{(2)} = 6.92$, $p = 0.031$). *Post-hoc* analysis revealed that faeces from the WF group contained significantly smaller hymenopteran wings : $t_{(21)} = 2.62$, $p = 0.016$, Figure 3.6(b). than controls. There was no difference in hymenopteran wing size between the Control and WM group ($t_{(21)} = 1.10$, $p = 0.280$). When homopteran wings were analysed (Figure 3.6(b).), there was again a significant effect of treatment ($\chi^2_{(2)} = 7.15$, $p = 0.028$). Faeces from the WM group nests showed significantly larger winged homopteran prey than the Control group ($t_{(17)} = 2.64$, $p = 0.017$). There was no difference between Control and WF groups ($t_{(17)} = 0.05$, $p = 0.961$). Nest containing more nestlings showed larger wing lengths with respect to homopteran prey ($\chi^2_{(1)} = 9.60$, $p = 0.002$). There were no treatment or brood size effects upon the wing length of dipteran prey found in nestling faeces.

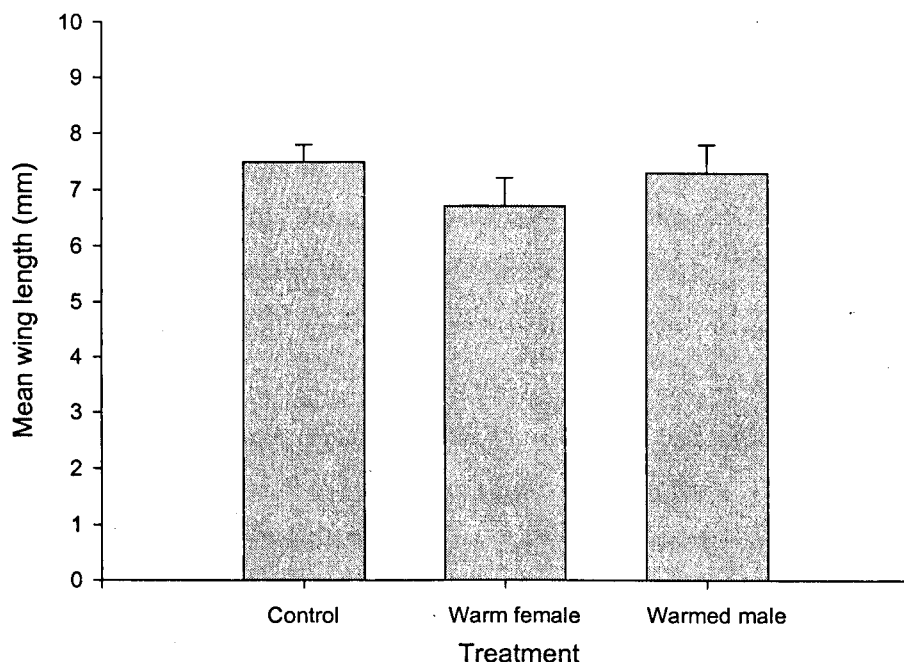


Figure 3.6(a).. Treatments effects on overall mean wing length (mm) \pm standard error, of wings found in nestling faeces over the trial period, regardless of Order.

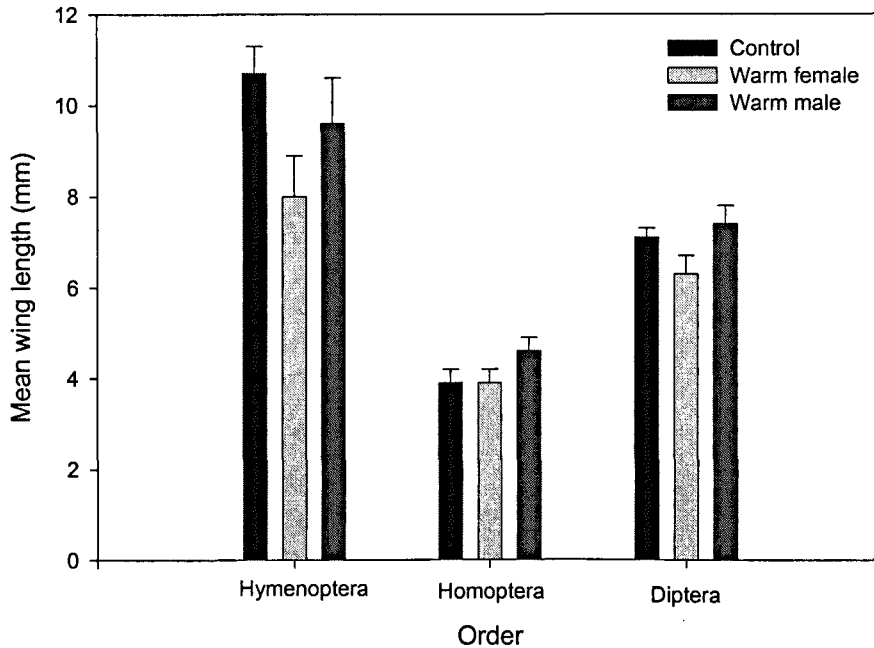


Figure 3.6(b). Taxonomic breakdown of mean wing lengths (mm) \pm standard error, found in nestling faeces over trial period, for Control and manipulation groups.

3.4.8.2 *Relative abundance of insect Orders in nestling faeces.*

There was a significant effect of treatment group on the proportions of hymenoptera and diptera found in nestling faeces. There was no effect of treatment on homopteran proportions. Control broods showed the preferred Order of adult swallows provisioning nestlings in this study was Diptera, which comprised 68% of the wings counted in Control faecal samples. 20% of the diet of Control broods was hymenopteran prey, with homopteran wings totalling 12% (Figure 3.6(c)). The Warmed female (WF) group showed a significant shift from the Control ratios, with an increased proportion of of hymenopteran (37%; $t_{(21)} = 2.13$, $p = 0.045$), the proportion of homopteran wings remaining the same (14%) and dipteran prey being taken less often (49%), this decline is almost significant ($t_{(21)} = 1.77$, $p = 0.091$). WM groups show a shift in a different direction to the WF group. The proportion of dipteran wings in WM faecal samples increased to 82%, this is an insignificant increase, however ($t_{(21)} = 1.34$, $p = 0.195$), with homopteran and hymenopteran wings decreasing to 5% and 13%, respectively. The observed decrease in hymenopteran wings is not significant ($t_{(21)} = 1.43$, $p = 0.167$).

There was a significant treatment effect on the proportion of hymenopteran wings classified as parasitic ($\chi^2_{(2)} = 7.35$, $p = 0.025$), with a significantly higher proportion being found in nests within the WF group ($t_{(22)} = 2.71$, $p = 0.013$, Figure 3.6(d)). Control and WM groups showed a similar proportion of parasitic hymenopteran wings ($t_{(22)} = 0.56$, $p = 0.581$). Figure 3.6(e) shows the numbers of each order just for 1997. WF nests show a steeper decline in the number of dipteran prey than an increase in hymenoptera.

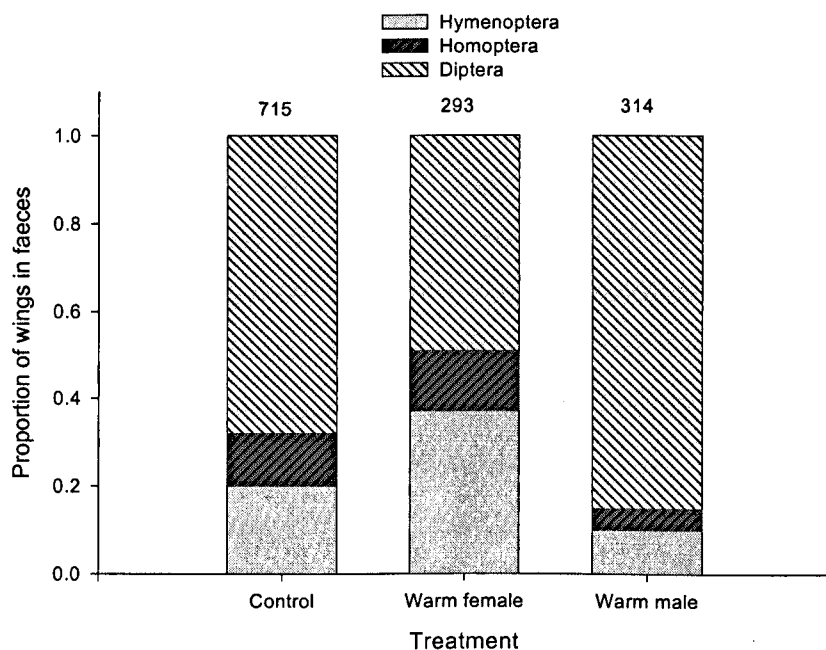


Figure 3.6(c).. Treatment effects on the proportion of each Order found in nestling faecal samples over the trial period. The total number of wings counted for each treatment is placed above the appropriate column.

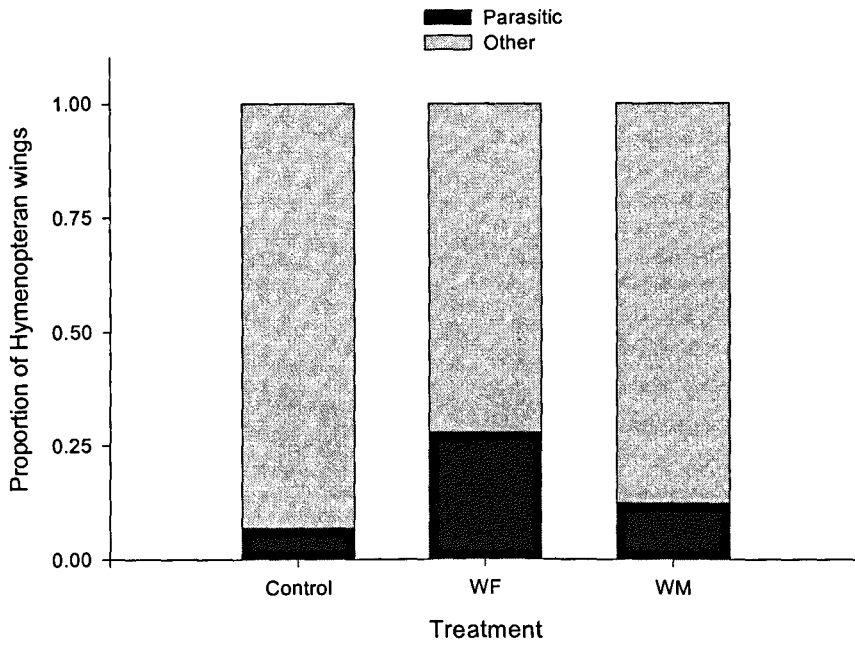


Figure 3.6(d). Treatment effects of the proportion of parasitic Hymenopteran wings found within the total number of Hymenopteran wings counted in nestling faeces over the trial period.

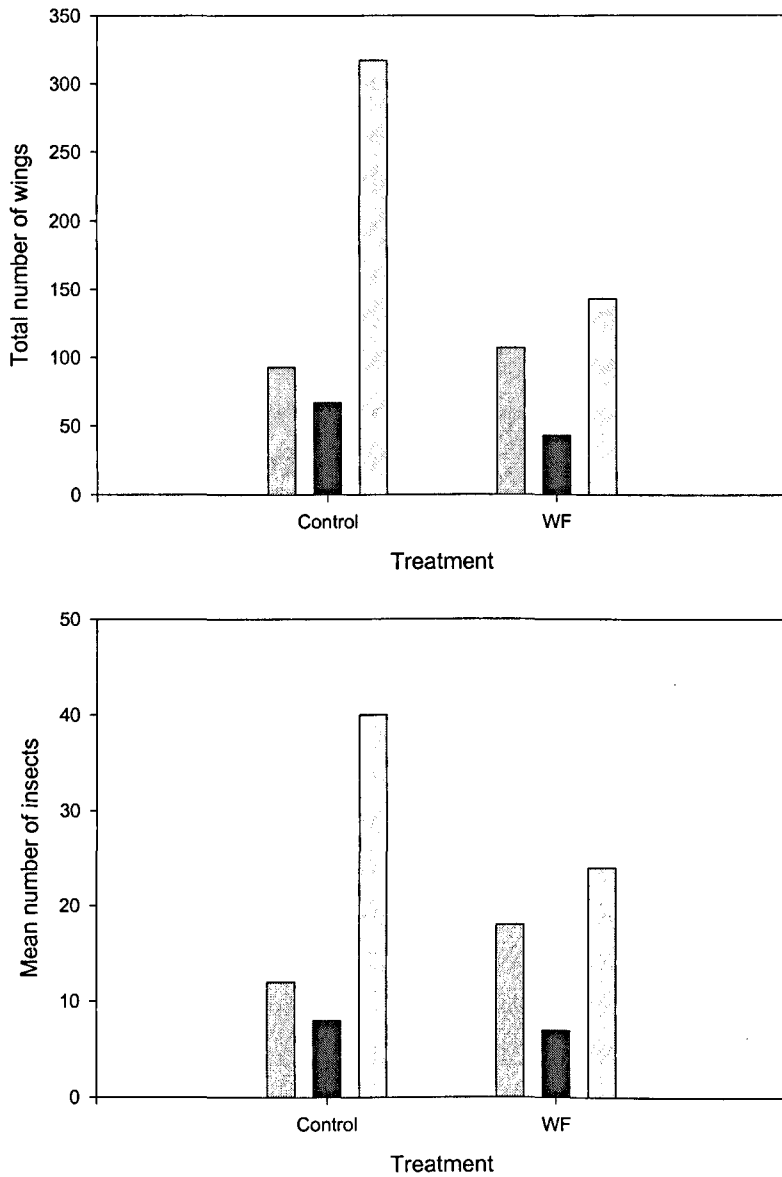


Figure 3.6(e)(i). Total numbers of each insect order within all samples from 1997 for Control and WF group. (ii) Mean number of each order in each sample in 1997 for Control and WF groups. Grey denotes Hymenoptera, Hatched dark grey is Homoptera and light grey hatched is Diptera.

3.5 *Insect abundance available in the environment.*

There were no year effects on the number of Diptera present in suction trap samples, however, both homopteran and hymenopteran abundance was affected by year (Figure 3.7.1(top)). 1997 shows higher numbers of both homopteran and hymenopteran prey than 1998. When the proportion each order were calculated from the total suction trap numbers, however, we found no difference between years in homoptera or hymenoptera (Figure 3.7.1(middle)). This may be due to lower overall numbers in 1998. The higher abundance of hymenoptera in 1997 is mainly due to a burst in numbers starting in July and peaking in August (Figure 3.7.1(bottom)). This can be partially explained by the emergence of ants, which only start to appear in the samples in July and peak in August (Figure 3.7.2(top)). These peaks are not seen in 1998 data.

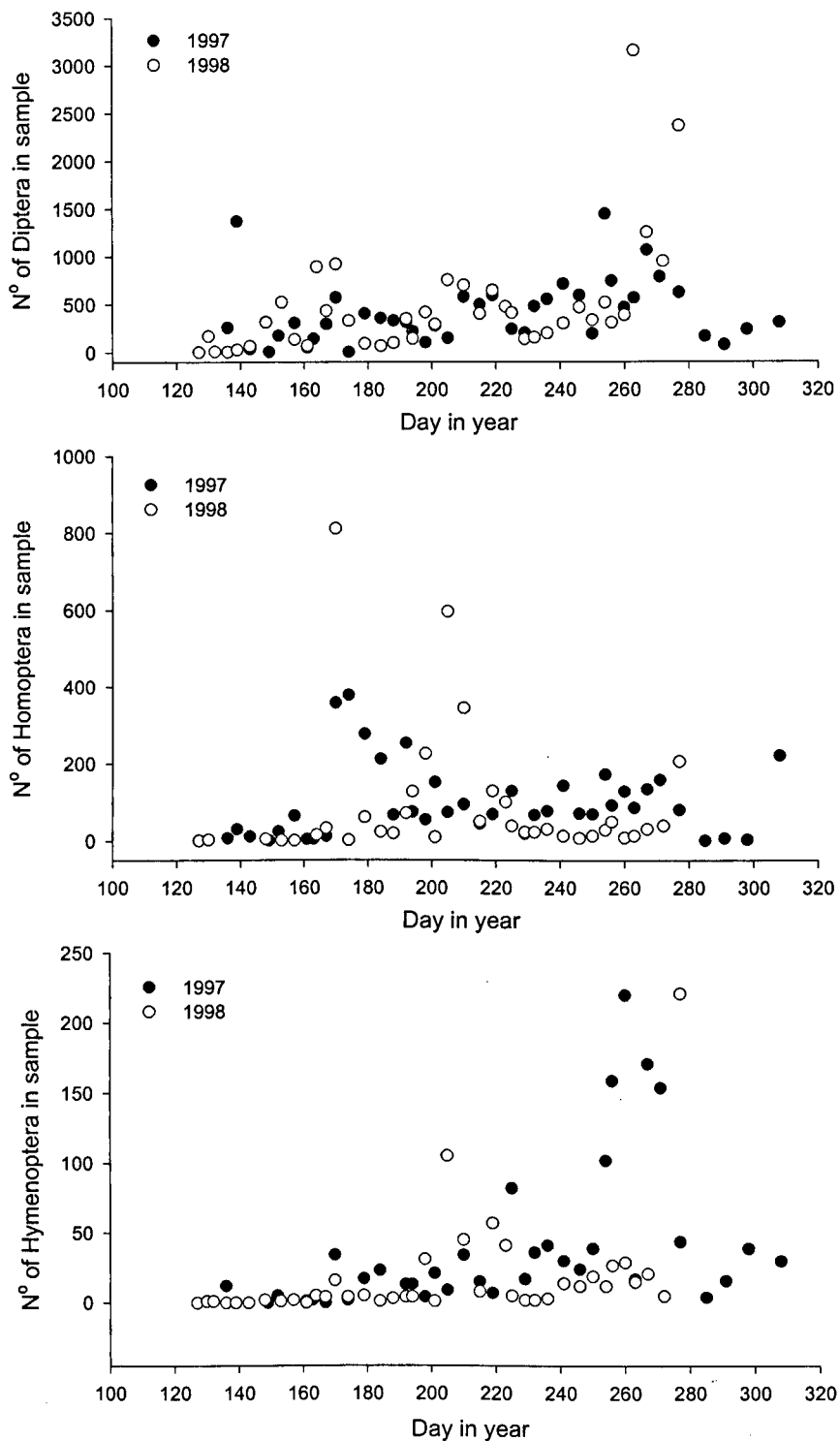


Figure 3.7.1. Suction trap data for the years 1997 and 1998. (top) shows the number of dipteran prey found in samples, (middle) the number of homoptera, and (bottom) the number of hymenopteran prey. The x axis on each graph indicates the day in the year to which samples belong.

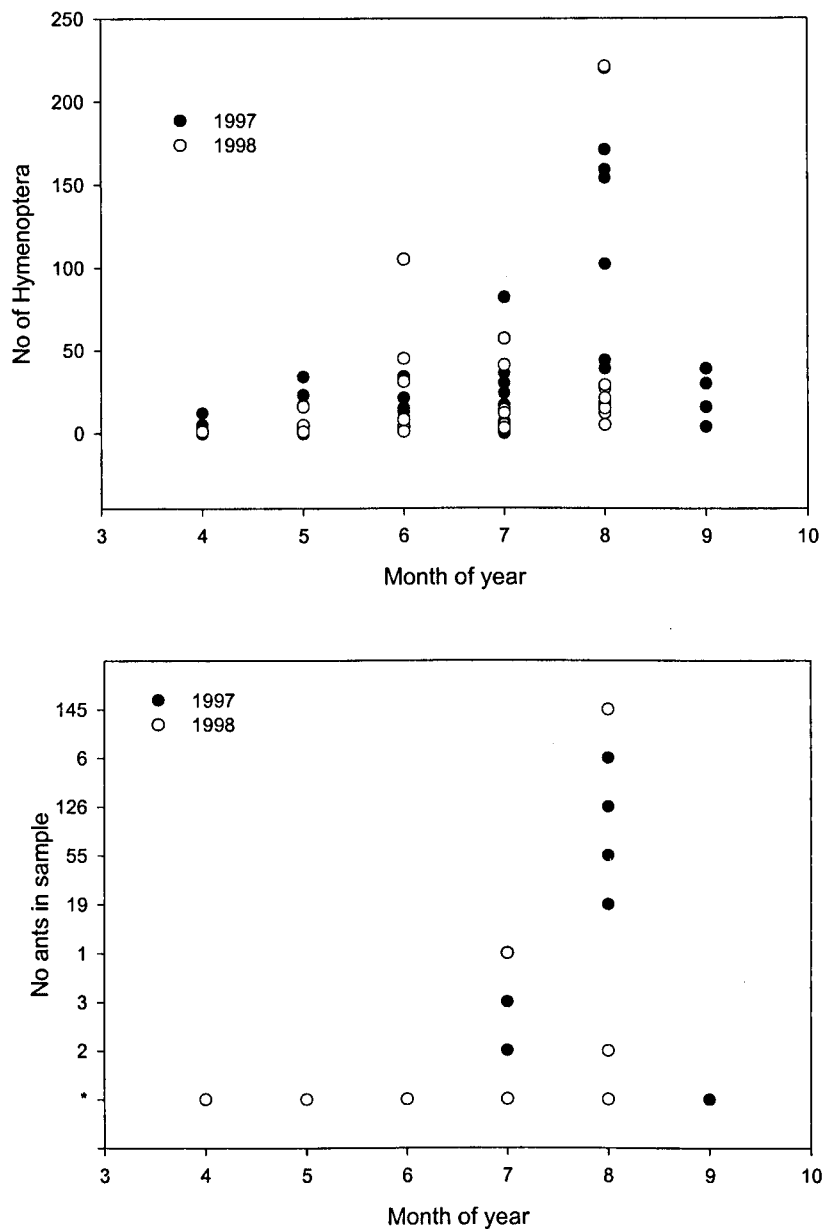


Figure 3.7.2 continued. (top) represents the sample sizes of hymenoptera found each month in 1997 and 1998. (bottom) shows the number of ants found in monthly samples during 1997 and 1998.

3.6 Discussion

3.6.1 State-dependent resource allocation.

Overnight warming treatments, considered to be a 'positive' manipulation in this study, have an effect upon the active energy expenditure of adult swallows, exposing the trade-off between body state and reproductive effort (Chapter 2). There was a

significant increase in energy expenditure in warmed female swallows (WF) and warmed males (WM) above that of their corresponding Control birds. The results presented here prove that male and female swallows share very similar strategies of energy allocation when gifted excess energy at dawn. Thus an individual's state provides an important cue upon which that individual will base short-term resource allocation decisions. The state manipulations performed here are only short-term and the effect probably only lasts until the next dawn, but there is scope that state can also play a part in longer term decisions (Maurer 1996).

This pattern of energetic responses was repeated in the nest visitation rates observed during the release period. Visiting rate (h^{-1}) increased along with brood size, this has been seen in many studies with a wide variety of species (Tolonen & Korpimäki 1994; Markman *et al.* 1995; Moreno *et al.* 1999; Sanz 1997; Sanz & Tinbergen 1999; Verhulst & Tinbergen 1997). The results of this model mimic those found in Chapter 2, when comparing the responses of females to warming and chilling treatments, where visiting rates confirm the active energy expenditure patterns. Hence, warmed females and males in this study conform to the model proposed in Chapter 2 of biased energy allocation towards reproductive effort, since all the energy gifted to warmed birds is used to increase behaviour aimed at reproduction, in this case, nest visitation rate. Energy reserves at dawn represent an important state variable which has been overlooked in many empirical studies.

The presence of significant energetic and behavioural responses indicates swallows are very sensitive to changes in state. Many DLW studies have shown great inter-individual variation (Peterson 1996; Speakman *et al.* 1994). This may be due to their unpredictable environment promoting greater plasticity, however similar results have been found in birds with more stable food supplies (Chapter 5). This also suggests that in the swallow changes in energy expenditure and nest visitation rate can be thought of as a good indicator of reproductive effort (Siegel *et al.* 1999). Although some studies have shown that male and female birds may have different responses to brood manipulations, our results tend to agree with other studies which show a symmetry between male and female energy allocation, which we would expect if both members of a pair are assuming the same roles.

3.6.2 Within pair compensation and reproductive effort.

The partners of each manipulated sex show different strategies in response to the warming treatment and subsequent change in reproductive effort of their partner. The male partners of warmed females (WF) showed no changes in energy expenditure in the release period, and maintained a nest visitation rate similar to Control males. Within-pair compensation of has been reported in several studies (Wright & Cuthill 1990; Whittingham *et al.* 1994; Sandel *et al.* 1996; Freeman-Gallant 1998; Dickinson & Weathers 1999): a female may increase effort when a male partner is handicapped or absent. Therefore, we may have expected to see a decrease in nest visitation in WF pair-males, responding to the female's shift to increased visitation rates, however, the male would not have incurred increased costs by maintaining Control effort levels.

The female partners in the warmed male (WM) group, in contrast, show a trend to increase energy expenditure and visiting rate along with their partner. The lack of significance in these birds may be probably due to an energetic ceiling (Drent & Daan 1980; Hammond & Diamond 1997; Siikamaki 1996), whereby the individual cannot increase effort above a certain level without jeopardising an unacceptable degree of survival. Deerenberg & Overkamp (1999) have shown that Zebra Finches (*Taeniopygia guttata*) with experimentally increased workloads in the non-breeding period display delayed reproduction, and thus, incur a fitness cost.

The relative importance of an individual's mate as an indicator of how much effort to put into offspring has been debated in ecology, mainly in terms of mate quality. Since we assume that these birds are splitting the work of provisioning their brood evenly between them, there would obviously be a cost to reduced or no male parental care. Although some studies have shown that male parental care is not important for the current brood as females compensate for the reduced effort of their partner (Freeman-Gallant 1998; Qvarnstrom 1997), there is strong evidence that male parental care is important in many species, and can influence brood and fledging success (Bjornstad & Lifjeld 1996; Davies & Hatchwell 1992; Dickinson & Weathers 1999; Lifjeld *et al.* 1998; Sandel *et al.* 1996; Wolf *et al.* 1991). Thus, if male parental care can influence female fitness, females should prefer mates of high quality who will potentially provision the brood at high rates. Increased female reproductive effort has been linked to mate quality (Balzer & Williams 1998; Wedell 1996). In one study Freeman Gallant (1996) found that the extent to which male Savannah Sparrows (*Passerculus*

sanwicensis) provisioned their first broods positively affected their pair-females fidelity for the next brood. It is possible that the short-term changes in the warmed males (WM) visiting rate caused a similar increase in effort of his pair-female due to her perception of mate quality. Whatever the cause it would seem that the effort level of the mate has relatively high importance in the swallow.

3.6.3 Mass and Fatscore variation.

Adult mass was not affected by the manipulations, all birds regaining almost all of their mass by the end of the trial. This suggests that there may be an optimal mass at this point in brood rearing and these birds are attempting to recover that (Jones 1987). Or it may be that mass change is not a good indicator of resource allocation, since it comprises many components, including evaporative water loss, defecation loss as well as somatic allocation. Fatscore also showed no significant changes over the trial period between treatments, however, this is a subjective score. Somatic investment is hard to quantify in the field, however, we assert that these data suggests that all treatment groups invested similar amounts in soma, maintaining their optimal mass.

3.6.4 Effects of adult state and foraging on nestling condition.

Although there was some effect of treatments upon adult behaviour and energy expenditure there was no real effect on the chicks provisioned by the adults. Broods in all treatment groups lost mass over the trial period, swallow chicks tend to do this from 10 days onwards (Jones 1987a), as they are investing in protein stores and growth, rather than lipid stores, attempting to reach optimal fledging mass. There was no effect of treatment on this decline in mass however. The two warmed groups showed the same slope of line in decreasing mass over the trial period.

Brood mass change was the only parameter measured in this study to be affected by any weather variables. Increased rainfall was related to increased mass loss in all broods. Since weather variables were not found to affect adult energy expenditure or visitation rates, it would seem that environmental variation may not be as important when considering adult birds as has previously been thought (Cooch & Ricklefs 1994). However, since rainfall seems to affect chick mass, it would see that environmental factors may be more important to the chicks' welfare than the adults (Siikamaki 1996). Since precipitation is normally associated with lower temperatures, this may be a short term thermoregulatory constraint on nestling growth. Parental visits may also be

misleading as parents may not be able to feed well in the rain and may return to the nest with little or no food.

When considering faecal output as the mean dry mass of faeces produced by nestlings over the trial period, the WM group showed no significant difference from controls. WF nests however, produced significantly less faeces than controls. This occurred even though there was no difference in nestling mass changes within this group. Changes in adult foraging strategy and prey choice may account partially for this low output. WF nestling faeces showed a larger amount of smaller hymenopteran wings, hymenoptera making up 37% of the total faeces analysed. When this order was broken down into parasitic and non-parasitic wings, there was a significantly higher proportion of parasitic hymenopteran wings present in WF faeces. Parasitic hymenopterans tend to be smaller than non-parasitic forms. This would then account for the smaller mean wing size observed in WF nests.

Although the WF manipulation was carried out in 1997, when we saw a higher abundance of Hymenoptera in the suction trap data, the trial dates were spread out evenly over June - August, and not just done in times of high hymenopteran abundance. We assume here that our suction trap data provides a good indication of insect abundance. There is long-term evidence that data from this trap is correlated with swallow breeding success (T.G.Benton, personal communication). Thus, since trial date and year were controlled for in statistical analyses, we suggest this shift in prey choice is not just an artefact of the experiment, but may provide some evidence for a more profitable prey being taken to provision young. Since birds have low chitin digestibility (Akaki & Duke 1999; Weiser *et al.* 1997), parasitic hymenopteran may prove to be more profitable prey, as they would have a thinner layer of chitin, however, these insects tend to be very small, and if optimal foraging rules are to be followed then we may expect medium sized prey to be more beneficial (Kaspari & Joern 1993). One other possible explanation lies with warmed females preferring to take hymenopteran prey, they increased the amount fed to nestlings. Swallows in this study provisioned nestlings with a diet predominant in dipteran prey. Nests provisioned by the WM group showed non-significant trends towards an increased proportion of Diptera. Significantly larger homopteran prey were taken, even though this Order comprises the lowest proportion of the diet. Although WM birds were not taking larger Diptera than controls, the increased proportion fed to nestlings would

lead to an overall increase in the mean size of prey item, especially as larger homoptera are also being taken. Turner (1982) suggest that when feeding conditions are favourable swallows will take larger prey. The results here cannot support this, however food abundance was not manipulated here, but potentially the perception of more favourable conditions. One other possible reason for the increased number of small hymenopteran wings in the WF group may be due to swallows taking smaller items at the beginning of a trip, and since foraging trip times are reduced in this group, this would cause a bias.

The faecal analysis in this study can only determine which insect orders are fed to nestlings within treatment groups, it cannot distinguish between the sexes within treatments. Since males in the WF group did not change their visiting rate or energy expenditure it is possible that there was no corresponding change in prey quality, thus the changes seen in WF nestling diet may be due to foraging changes in the female only. However, in the WM group, as the female tends to increase effort levels the increase in dipteran prey, and change in foraging strategy, is probably due to the responses of both pair members.

Since nestlings which are provisioned more often show no advantage over Control broods and produce less faeces, the shift in parental provisioning may not confer an advantage on the brood, however, this may be an artefact of nestling age not picked up by the analysis. When considering the numbers of each order just within the 1997 samples, nests belonging to manipulated females showed a decline in dipteran prey, perhaps shifting from Diptera to Hymenoptera. Other factors, such as increased nest sanitation, may also have affected faecal output in the WF group (Chapter 4).

3.7 Conclusion.

Ydenberg *et al.* (1994) showed the necessity for parental self feeding constrains the proportion of available energy devoted to nest provisioning. If parental costs increase and thus self feeding increases, also then the amount of energy available for nest provisioning decreases, we would then expect a change in foraging strategy associated with this. Hence, the reverse is also true, if the need for parental self feeding decreases as costs are decreased following the positive state manipulation in this study, then there will be more energy available to allocate to foraging for nestlings. The manipulation removes either partially or wholly the energetic

constraints upon the adult birds in the short term. Males and females, which underwent positive state manipulations, showed a higher index of efficiency than controls. This was also the case for males in the WF groups. Welham & Beauchamp (1997) compared the three potential fitness maximising provisioning currencies with a state variable model of nest provisioning. They found that maximising efficiency and the state variable model proved to be the closest to empirical work, and provided the highest fitness outcomes under favourable conditions and in a varying environment. They did not attempt to define their state variable, e.g. as energy stored, however, my study provides evidence that one important state variable is energy status, thus the similarity between these two provisioning strategies is not unremarkable. In this study manipulated birds show a higher efficiency index than controls.

This study has provided evidence for the lack of sex related differences in responses to physiological state manipulations in adult swallows. Both males and females showing a biased trade-off towards reproductive effort. This result is intuitive as at the late brood rearing stage we would expect adult swallows regardless of sex to perform the same task with the same criterion. There were potential sex differences, however, in foraging strategy, nests provisioned by manipulated males showing slight diet differences from controls, whilst nests provisioned by manipulated females showed a shift towards a potentially more profitable prey. Chick collaring was not performed in this study and would have provided important information on sex specific foraging rules within each treatment. Flight parameters may also have changed, but these were not measured here.

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4 The importance of nest sanitation as a component of reproductive effort in breeding barn swallows.

4.1 Introduction.

Reproductive effort may often be a composite variable, encompassing behavioural and physiological components with varying effects on life history traits. Thus the proportion of energy that an individual allocates to reproductive functions will stem from these 'effort components'. Such components have received a varying amount of attention in the past, the most studied including brood provisioning (Henderson & Hart 1993; Sandel *et al.* 1996; Nour *et al.* 1998; Wright 1998), mate acquisition, and nest defence and vigilance (Laiolo *et al.* 1998; Lombardo 1991). In Chapter 2, adult swallow energy expenditure and nest provisioning rates were related, and methods of this kind represent a more appropriate measure of reproductive effort (Siegel *et al.* 1999). The earlier studies presented in this thesis have provided a nest provisioning rate which only shows a snapshot of behaviour, either by using a short observation period or by using a mean rate (Chapter 2 & 3). However, visitation rates could be used to determine short-term pair dynamics following a manipulation, such as the one undertaken in this study.

Although nest provisioning is often considered to be the most important effort component (Emms & Verbeek 1991; Tolonen & Korpimäki 1994), more than one component comes into play during a single reproductive event. The significance of evaluations of the relative importance of differing components of effort may play in any optimal strategy has been reviewed by Jonsson *et al.* (1995). However, some components have been less studied, especially with respect to experimental manipulations, included in this group is nest sanitation (Christe *et al.* 1996; Kepler *et al.* 1996; Markman *et al.* 1996). Why may nest sanitation be an important effort component? There are two main hypotheses which can be applied to the swallow:

1. Parasites draw their energy from their hosts, leading to a decrease in the amount of host energy available for maintenance or reproduction. Host-parasite interactions have been studied for many species and a link between avian parasites and a decline in host quality or reproductive success, has been shown in a variety of studies. Harper (1999) studied nine species of birds (e.g. *Parus major*, *Troglodytes troglodytes*) and found that with a high feather mite load (Acari, Proctophyllodidae) they grew duller feathers and relatively shorter wing feathers following a moult, implying an energetic cost of the parasites. Mite load was also associated with lower protein stores. Zuk *et al.* (1998)

studied the effect of nematode infections (*Ascaridia galli*) on female Junglefowl (*Gallus gallus*) and found that those females with a higher parasite load showed smaller comb sizes and lower mass when mature. These characteristics had a significant effect on the social rank of the birds, causing parasitised females to hold a lower rank, and having potential implications for reproductive success and survival. Parasites do not just affect morphology and social rank; behaviour can also be modified. Male Tengman's Owls (*Aegolius funereus*) spend significantly less time in nest defence when infected with Trypanosomal blood parasites (Hakkarainen *et al* 1998). Clayton and Tompkins (1995) have also shown dramatic effects of mites (Mesostigmatidiae) on Rock Dove (*Columba livia*) reproductive success, agitating adults to an extent which caused egg neglect, but no direct effects on adult condition. Merino & Potti (1996) discovered a deleterious effect of three avian parasites (protocalliphoria diptera, and calliphoridae) on the fitness of their hosts, by causing detrimental effects on nestling growth and pre-fledging survival. However, interestingly, the roles of each parasite species interact depending upon environmental variables, blowflies causing the most effects during warm years and fleas effecting broods most in wet and cold years. Møller (1993) showed direct effects on parental resource allocation when mite (*Ornithonyssus bursa*, *Berlese (Macronyssidae, Gamasida)*) load was experimentally manipulated in swallows (*H. rustica*) during the first brood. Birds with reduced mites showed earlier egg laying and significantly larger clutch and brood size. The experimental reduction also had implications for nestling body mass at fledging, a measure often used to determine probability of survival.

2. Parasites can thus affect a parent bird's fitness directly by constraining behaviour or condition, however, parasites are also present within the nest, and so can directly affect nestling condition, another drain on parental fitness. The naive immune system of young birds exposes them to greater consequences of being parasitised than adults and recently Szep & Møller (1999) showed that Sand Martin (*Riparia riparia*) nestlings in nests with experimentally enlarged tick loads (*Ixodes lividus*) showed an increased wing length and higher leucocyte and immunoglobulin levels than broods with normal load sizes. There was no effect of these manipulations on adult Sand Martins, but reproductive success was lowered.

Thus, anti-parasite behaviour that reduces parasite impact is favoured by natural selection, and the removal of nestling faecal sacs is a common behaviour amongst birds (Goodey &

Lill 1993; Dellomo *et al.* 1998; Wright *et al.* 1998). There is a link between nest sanitation of this kind, and a reduction in harmful parasites (Cotgreave & Clayton 1995), however, this activity is time consuming and may impinge on time set aside for self and brood foraging. Christie *et al.* (1996) found that parent Great Tits (*Parus major*) were not able to show increased sanitation responses to parasitised nests during daylight hours but birds used their 'sleep time' in order to sanitise experimentally parasitised nests at a higher rate.

There is also evidence that an unsanitised nest may increase nest parasite load (Eeva *et al.* 1994), and thus, a higher cost to parental fitness would be incurred in these 'dirty' nests (Møller 1993; Hurtrez Bousset *et al.* 1997; Tripet & Richner 1997). Thus, in all these studies described here there is a potentially negative effect upon nestlings, with an increasing parasite load affecting growth and potentially fledgling survival. This all relates to an indirect effect on adult fitness, even if some studies do not find an effect of parasites at the nest on adults. Thus, there is a cost to fitness incurred via two possible routes, reduced nestling survival and recruitment, or increased nestling demands due to high parasite load.

Nestlings need to maintain their body temperature, and do this within the nest partially by huddling with siblings, to reduce air-exposed surfaces, reduce cold stress and energy requirements. Since nestlings do not obtain a full complement of feathers much needed for insulation straight away (Buchholz 1996), huddling is a very important form of cost-cutting, but it also suggests that thermoregulation costs in nestlings is high (Gil Delgado *et al.* 1995; Pearson 1998; Sanz & Tinbergen 1999). Any factor which effects this equilibrium is bound to have energy costs for nestlings. One such factor is water, a major component of nestling faeces. Water increases thermoregulatory costs by either increasing evaporative heat loss or by reducing insulation properties of feathers (Webb & King 1984). Thus, if a nest is left with a high number of nestling faecal sacs, then increased nestling demands may also be incurred due to an increase in thermoregulatory costs of soiled nests. This hypothesis has not been explored in detail, but has been suggested by Westerterp *et al.* (1982), but may be more viable than the anti-parasite hypothesis in some species as it has not been shown that all ecto-parasites would thrive in 'dirty' nests, especially in the swallow. Nestlings with increased energy demands may affect parental fitness either via a direct decrease in reproductive success or as a drain parental effort, potentially endangering adult survival.

Each of these hypotheses presents a scenario where parental fitness is compromised, either by a direct reduction in parental condition, or by a reduction in the reproductive value of the current nest. It has also been suggested that faecal sac removal may also reduce the

conspicuousness of the nest to potential predators (Petit & Petit 1987; Petit *et al.* 1989), however, this is unlikely to be the case in barn swallows, where most of the nestling faeces fall to the ground below the nest (personal observation), acting almost like a flag, and indeed it is one of the best methods of nest-finding in this species.

In this study adult female swallows underwent body-state manipulations brought about by overnight-warming treatment. This allowed them extra energy at dawn (Chapter 2) and by observing visiting and faecal sac removal rates we were able to determine any response to a positive-state manipulation. Behavioural observations encompass three separate 1.5h over the course of a morning (equivalent to one trial 4.5h), this allowed us to investigate the short term dynamic changes in visiting rate which occur after a positive body-state manipulation. Nestling faecal output was also quantified. We assume nest sanitation is time consuming, and parent birds are constrained in their reproductive activities. Birds provided with extra energy may bias their energy allocation towards reproductive activities, and we may expect an increase in nest sanitation in these birds, in this study measured as faecal sac removal rate.

Swallow nestlings, after the age of 7 days, tend to manoeuvre themselves to the edge of the nest and expel most faecal sacs over the rim. However, on occasion, defecation may coincide with a parent's visit with food, and at this time the parent would be more likely to take the sac away, otherwise the sac would be lost into the nest cup during the ensuing sibling competition for food. Thus the system presented here is not akin to some other studies, where nestlings are unable to expel, or would find a large cost in expelling faeces from the nest, such as in hole nesters, where the adults perform complete nest sanitation.

4.2 Methods

4.2.1 Manipulations

The experiments were undertaken near Stirling in Central Scotland (56°8'N, 3°54'W) during June to August of 1999. They involved swallows rearing chicks aged 11 - 15d. Swallows were caught using mist nets between 17.00 and 19.30h at local farms. Sex, mass and fat score (scale of 0 to 5, Chapter 2) were recorded. Breeding pairs were randomly assigned to one of two groups; Warmed and Control (Table 4.1). Once caught birds were placed in their respective treatments overnight. During this time, birds were kept in 4.4 litre containers equipped with a perch, allowing a normal posture and space for the wings to be fully spread. Warmed females were placed in an incubator (Sanyo) in the dark at 29°C (within thermoneutral zone, Kendeigh *et al.* 1977), while their male partners were kept outside as

controls. All males and the Control females were placed in an outdoor shelter (average night-treatment period across groups = 8.3 ± 0.6 h) and therefore experienced prevailing ambient temperatures (13.9 ± 2.4 °C), which were recorded using a datalogger (Psion) equipped with a thermocouple, logging every 15 min. Our choice of mates as controls ensured that environmental conditions during the day were standardised for treatment-control comparisons. Birds were released at dawn to ensure a normal foraging period: mass was recorded again at this point.

Table 4.1. (a) Overnight temperature treatments of Warmed and Control groups. (b) Sample sizes used in analysis of visiting rates during observation period 1. (c) Sample sizes used in the analysis of visiting rates during observation periods 2 and 3, plus faecal sac removal (FSR).

(a)	Treatment	Overnight temperature oC	
		Female	Male
	Warmed	29	14
	Control	14	14

(b)		Obs period 1	
		Female	Male
	Warmed	4	4
	Control	4	4

(c)		Obs period 2&3 & FSR	
		Female	Male
	Warmed	4	4
	Control	5	5

The energetic costs of overnight treatments were quantified using indirect calorimetry with a sub-sample of birds during 1997 and 1998 field seasons (Chapter 2). Details of equipment and methods are given by Bryant & Furness (1995), where identical methods were used. Daily food abundance was measured using a 12.2m Rothamsted suction trap (Macauley *et al.* 1988) situated at the University of Stirling. During each pair-observation (see below), local temperature and rainfall were recorded simultaneously near nest sites. Rainfall was recorded as the proportion of time over each trial period when precipitation occurred.

4.2.2 Observations

Observations of experimental pairs were undertaken during three periods over the morning post release: 06:00-07:30h, 08:00-09:30h, 10:00-11:30h, each known as observation periods (Table 4.1). Birds were observed from a hide situated near the nest site. During this time the visiting rate of both pair members was recorded. Also the number of faecal sacs removed from the nest by each pair-member over the 4.5h period was noted, referred to here as the trial period, and a rate was calculated as faecal sac removal h^{-1} .

4.2.3 Chick monitoring

Swallow nests were monitored from hatching date (day 0), wherever possible, however, if nests were found post-hatching, chick age was estimated using plumage state and size. Trials were undertaken when chicks were aged 11 - 15 days. At the start of each trial, after the adults had been caught, a plastic sheet was placed under the nest to cover the area where faeces fell, the bag was removed at the end of the 4.5h trial period. Faeces was collected in this way from all nests. Faecal samples were dried in an oven for 24h and weighed to give faecal output data. The mean mass of a single faecal sac was calculated for each trial by weighing each sac present, and thus a predicted mean sac mass was obtained for each treatment group from the analysis described below. Total faecal output (F_{tot}) for each treatment group was then calculated from the mean faecal mass collected under the nest (F_{nest}) and the mean faecal sac mass (M_{sac}) multiplied by the faecal sac removal rate (FSR). This was done in order to determine if total faecal outputs were the same after taking into consideration the number of sac removals.

$$F_{tot} = F_{nest} + (M_{sac} * FSR)$$

Equation 4.1

4.3 **Statistical analysis**

Nest visitation rate was analysed using REML analysis (Genstat 5 Committee 1992), as the data involved unbalanced nesting of each observation period within each trial, due to one missing pair in observation period 1. REML is a linear mixed model able to analyse unbalanced, non-orthogonal data (Patterson & Thompson 1971), a similar approach to this has been used recently by Kruuk *et al.* (1999). Stepwise deletion of fixed variables from the minimal adequate model was performed. The random model controlled for the observation period within each trial and trial date. The significance of fixed variables was estimated using the Wald statistic, which is asymptotically distributed as χ^2 (Genstat 5 Committee

1992). Number of faecal sacs, and faecal output (f_{nest} , M_{sac}) data were analysed using ANCOVA (Minitab). Stepwise deletion of non-significant terms was performed and residuals were checked for normality and homogeneity of variance. Nest sanitation rate was analysed using a Generalised Linear Model (SPLUS), with Poisson errors, as faecal sac removal events were distributed as non-normal count data. Each term was rotated within the model and the χ^2 statistic was used to calculate significance when terms were first in the sequence. All means presented here are in the form of mean \pm standard error. Predicted means are quoted from statistical models.

4.4 Results

4.4.1 Visiting rate

There was an overall trend for mean visitation rate to increase throughout the morning, mainly due to the influence of the warmed female data. Brood size, nestling age and ambient temperature did not have any effects on adult visiting rate to the nest, however, birds tended to visit the nest less when rainfall was higher (Figure 4.1). Food abundance had no significant effects on nest visitation. Warmed females showed a significant increase in nest visitation throughout the trial period (treatment*sex interaction term, Table 4.2.). Observation period showed significant effects on the patterns of visitation rate:

4.4.1.1 Observation period 1: 6:00-7:30 am.

There was a trend for Warmed females to increase visiting rates 15.3 ± 2.3 visits h^{-1} , whilst Warmed males show levels similar to controls (9.3 ± 2.3 h^{-1}). Control males and females show similar levels of effort: males 10.4 ± 2.5 ; females 9.7 ± 2.5 visits h^{-1} .

4.4.1.2 Observation period 2: 8:00-9:30 am.

There is a clear effect of the manipulation on the Warmed females as they increased their provisioning rate to 20.2 ± 2.3 visits h^{-1} , compared to Control levels (male: 15.2 ± 2.1 ; female: 12.0 ± 2.1). Warmed males showed similar rates to controls: 13.2 ± 2.3 .

4.4.1.3 Observation period 3: 10:00-11:30 am.

The same pattern seen in the earlier observation periods was observed in period 3. There was a repeated significant increase in warmed females visiting rate (24.8 ± 2.3 h^{-1}). Control pairs, once again show similar levels of effort: male 12.5 ± 2.1 ; female: 12.1 ± 2.1 h^{-1}). Warmed males show a slightly elevated visiting rate of 17.0 ± 2.3 h^{-1} . This elevated rate is almost significant and follows the pattern of increased nest visits over the trial exhibited by the warmed female.

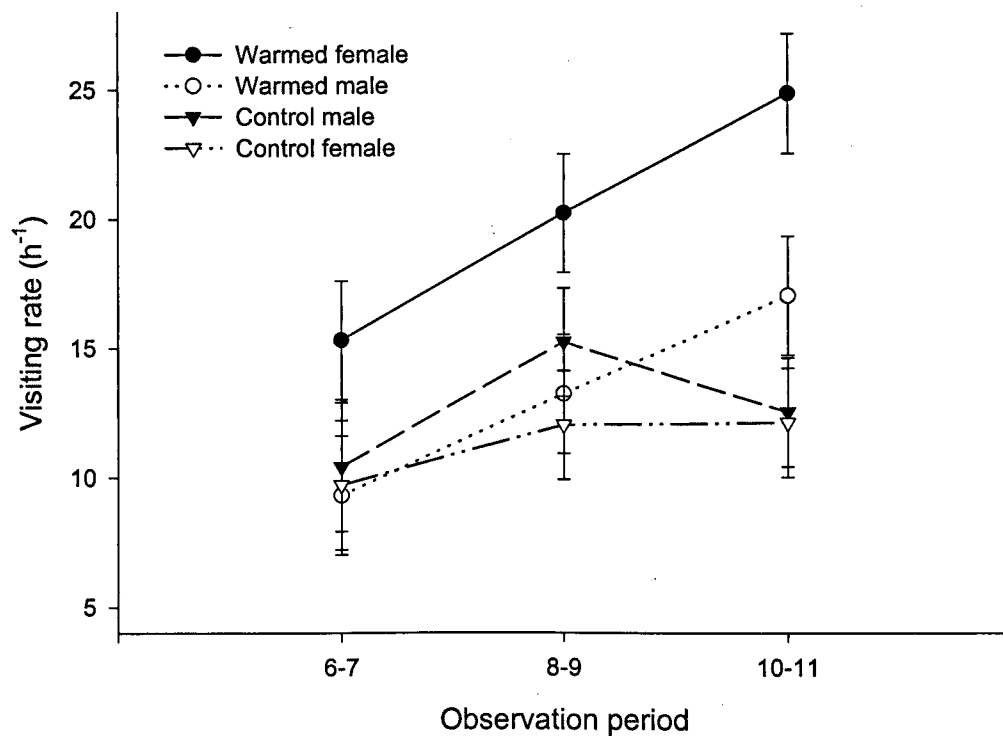


Figure 4.1. Predicted mean visiting rates \pm standard error, from REML analysis over three observation periods within trial period (4.5h), observation period 1 (6-7 am), observation period 2 (8-9 am), and observation period 3 (10-11 am). NB. Warmed male refers to males paired with warmed females.

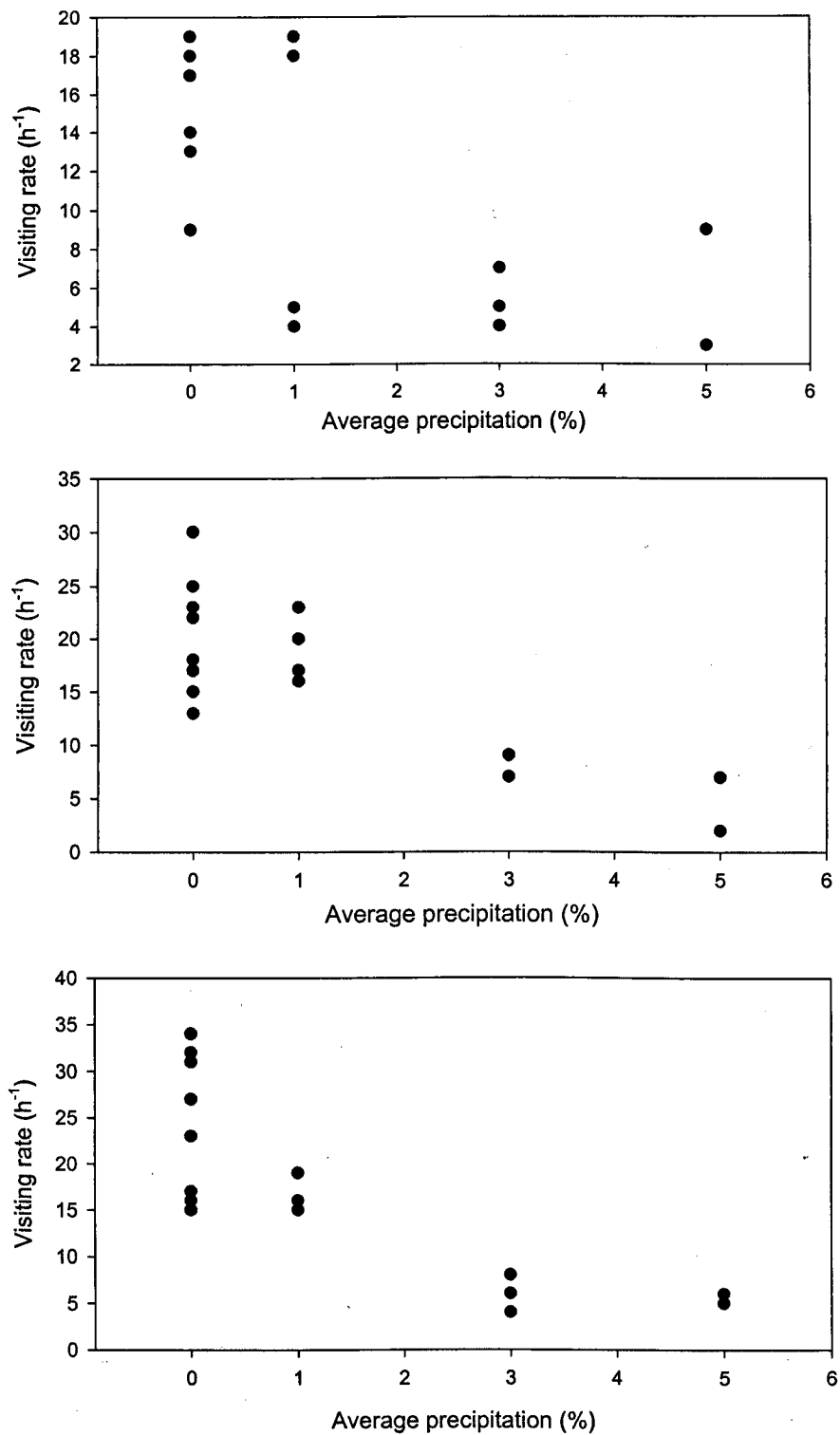


Figure 4.2. Effects of average precipitation on nest visitation rates. The upper graph represents observation period 1, the middle graph observation period 2, and the lower graph observation period 3.

Table 4.2. Statistical results of REML model for nest visitation rates in three observation periods. All significant ($p < 0.05$) terms are in bold and are shown as part of the maximal adequate model. Those terms which were excluded from the adequate model due to insignificance are also shown. The residual degrees of freedom are shown for adequate model.

Variable	Wald	d.f.	Probability (p)
Minimal adequate model			
Average precipitation	52.94	1	<0.0001
Treatment	8.46	1	<0.0001
Sex	3.92	1	0.048
Treatment*sex	18.43	1	<0.0001
Observation period	7.52	2	0.023
Excluded terms			
Brood size	0.21	1	0.643
Food abundance	0.29	1	0.606
Nestling age	0.87	1	0.351
Treatment*observation period	1.17	2	0.280
Sex*observation period	0.05	2	0.826
Treat*sex*OP	4.43	2	0.619
Average temperature	0.46	1	0.497
Residual d.f.		44	

4.4.2 Faecal sac removal (FSR).

There was a trend for Warmed females to take more faecal sacs away from the nest than controls, however there was no significant interaction between treatment and sex (Table 4.3). This may be due to the small sample sizes used in this study (power 17%). There was no effect of brood size or nestling age on sanitation rates (Table 4.3). Faecal sac removal was linked to visiting rate, however. Birds visiting the nest more often had a higher rate of faeces removal ($\chi^2_{(1)} = 9.07$, $p = 0.003$). There was also a significant effect of sex on removal rate, where females showed higher rates than males ($\chi^2_{(1)} = 12.47$, $p = 0.0004$).

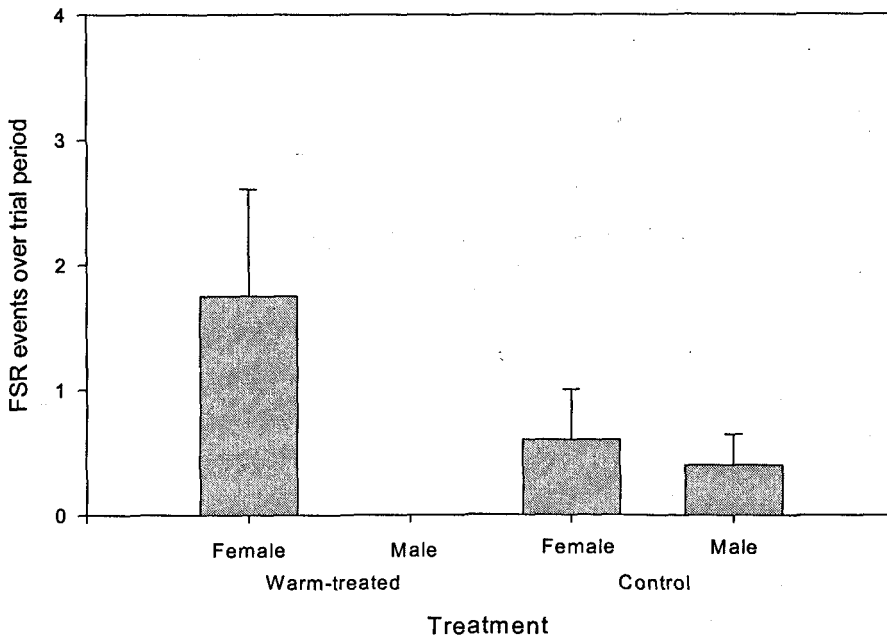


Figure 4.3. Mean faecal sac removal rates over the trial period (4.5h) \pm standard error, for males and females in treatment and Control groups.

Table 4.3. Results of Generalised Linear Model with Poisson errors, using rate of faecal sac removal as response variable. All terms in maximal adequate model are presented in **bold**, excluded terms and residual degrees of freedom are also shown.

Variable	χ^2	d.f.	p
Maximal adequate			
Sex	12.47	1	0.0004
mean visiting rate	9.07	1	0.003
Excluded terms			
brood size	0.94	1	0.329
nestling age	0.09	1	0.762
Treatment	1.63	1	0.201
treatment*sex	0.12	2	0.940
Residual d.f.		16	

4.4.3 Faecal output.

There was a non-significant trend for nests within the Warmed group to show a lower faecal output (F_{nest}) than those in the Control group, however treatment showed no significant effect (Table 4.4). When trial period was controlled for, i.e. the time period over which the faeces was collected, certain patterns were revealed, even though the sample sizes were

small. Larger broods showed a significantly higher faecal output than smaller broods (Table 4.4). There was also an effect of nestling age, with older nests producing more faeces (Table 4.4, Figure 4.4). No weather or date variables showed an effect of faecal output. There was no effect of treatment on the mean mass of faecal sacs produced by nestlings (Table 4.5), with Control groups showing masses in the range of 0.21 ± 0.03 g, and warmed nests 0.22 ± 0.04 g. As the mean FSR rate (males + females) in Control nests was 1 event, the total faecal output (F_{tot}) was 1.41g. In warmed nests FSR was higher at 1.8 events, however, F_{nest} was lower, thus F_{tot} in this group is still lower than controls, at 1.20g.

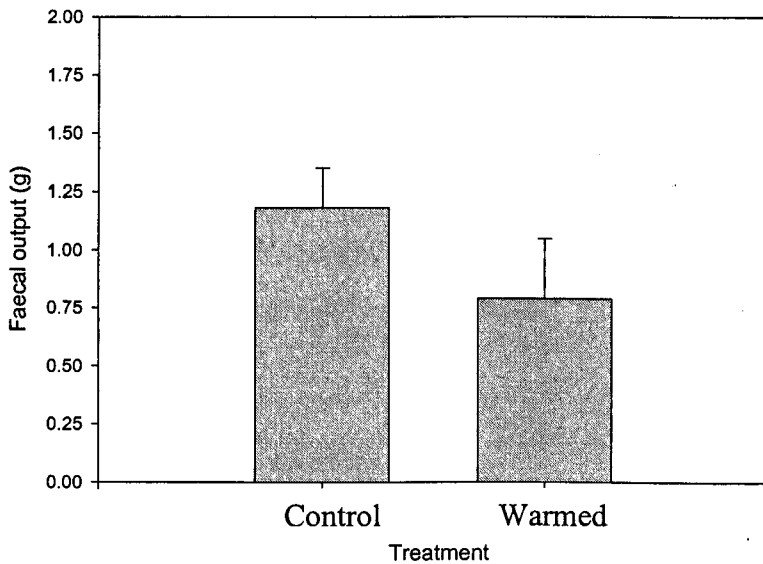


Figure 4.4. Effects of treatment on faecal output (dry mass of faeces g) period.

Table 4.4. Results of ANCOVA using dry mass of faeces (faecal output: g) as response variable.

Variable	F	d.f.	p value
Maximal adequate			
trial period	7.18	1,5	0.044
brood size	12.4	1,5	0.017
nestling age	9.29	1,5	0.028
Excluded terms			
Treatment	1.23	1,2	0.383
average temperature	3.61	1,4	0.130
average precipitation	0.00	1,1	0.981
trial date	5.12	1,3	0.109
food abundance	0.04	1,3	0.862

Table 4.5. Results of ANCOVA for mean mass of faecal sacs within each nest over the trial. All significant terms are presented in **bold**.

Variable	<i>F</i> ratio	d.f.	p value
Maximal adequate			
observation period	7.00	1,8	0.029
Excluded terms			
no. sacs	1.02	1,6	0.352
Date	0.32	1,5	0.595
Treatment	0.25	1,6	0.633

4.5 Discussion

There is a strong indication that the positive body-state imposed on Warmed females post treatment has a significant effect on reproductive investment, when measured using visiting rate as an indicator of reproductive effort (Chapter 2). During observation periods 2 and 3 warmed females show a significant increase in visiting rate above controls and Warmed males. This finding is in the same direction to that found in Chapter 2, and we can postulate that this would be matched by an increase in energy expenditure, suggesting a bias in the trade-off function in this case, towards reproductive investment as seen in Chapter 2. The lack of a significant increase in Warmed female effort in observation period 1 may be due to

lack of power, as small sample sizes were used in this study, but there is a definite trend for a response to the warming treatments. Over the three observation periods Control birds show similar patterns of visitation rates, with a slight increase in observation 2. This relatedness of visiting rate patterns within treatments is also seen in the Warmed group, both sexes showing an increase in feeding visits over time, although females show higher levels than males. These relationships suggest the reproductive effort level by one member of a breeding pair may be intrinsically linked to the behaviour of their mate. This is especially important when considering the Warmed group, where during observation period 1, females showed an elevated rate of visits, and males showed a Control level. This trend continued throughout the trial period (4.5h). This suggests that females responded to their manipulation, and hence level of energy balance, and not to some decreased effort of their partners.

Precipitation and temperature have shown strong relationships with visiting rate in this study, other studies have shown similar relationships in swallows (Jones 1987). Birds will visit the nest more often when weather is warmer and there is less rain. Rain may constrain foraging on aerial insects in two possible ways, by decreasing the availability and visibility of flying insects or by increasing the flight costs of adults. No relationship was found here with food abundance. Temperature has flight cost implications, a lower temperature increasing costs through increased thermoregulation. Therefore, swallow foraging decisions may be based on an evaluation of energy balance and a weighing up of the costs and benefits of foraging in different weather conditions, in order to maximise provisioning efficiency, whilst maintaining somatic investment.

Although nests within Warmed groups are visited more often than controls there is a trend for these nests to produce less faeces over the trial period. A similar, but significant effect, was seen in Chapter 2 using the same methods, but with a larger sample size. Certain factors or combinations of factors could come into play to explain this difference. Nests allocated to the Warmed female group in the 1997/98 study showed a greater proportion of small parasitic hymenopteran wings in the faeces of nestlings. This swing in prey choice could not explain the low faecal output alone, however, one explanation may be that it is the product of an interaction between prey choice and more faeces being removed from the nest for sanitation.

Nest sanitation can be quantified by faecal sac removal from the nest, as a large amount of faeces in the nest constitutes a 'dirty' nest. Faecal sac removal was closely linked to visiting rate to the nest (Table 4.3). A higher visiting rate extends the probability that nest sanitation would occur (Figure 4.3). This link suggests that birds in a positive state are more likely to remove faecal sacs from the nest, simply as they visit the nest more often, and this may be an opportunistic behaviour. Faecal sac removal and feeding rates have been linked together like this in the Tree Swallow (*Tachycineta bicolor*), where both increase as a response to larger brood sizes (Lombardo 1991). However the opposite trend has been noted in other species (Wright & Cuthill 1992; Westerterp *et al.* 1982), where sanitation decreased with brood size, as a larger proportion of time had to be spent foraging to provision the brood. Nest sanitation could then be a significant part of reproductive effort which is held at bay as it trades-off against the need to feed nestlings efficiently, in some species. However this study found no significant effects of the treatment on faecal sac removal rate, and thus no significant increase is seen in Warmed females that we would predict if Warmed females were allocating some of their extra energy to sanitation. There was, however, a trend for Warmed females to show a higher faecal sac removal rate than controls. Thus, possibly due to the low power of this study, we tentatively accept that nest sanitation is a relatively unimportant part of reproductive effort in breeding swallows, time or energy allocation is biased towards foraging. Total faecal output in this study was not equal across groups, thus, even when the amount of faeces removed through nest sanitation was compensated for Warmed nests still showed a trend towards a lower output. There were no differences in the mean mass of faecal sacs (M_{sac}) between Control and Warmed groups. This evidence suggests that the low output exhibited by Warmed groups is due to an interaction between nestling diet, and hence parental foraging strategy, and nest sanitation rates.

One problem encountered in the analysis of this data is the lack of or low frequency of faecal sac removal by breeding swallows in this study. This may be an effect of the capture and holding overnight, however this does not seem to have affected visiting rate significantly, if we compare this study with other swallow studies which recorded visiting rate without manipulation (Jones 1987a). Studies in this area have shown a decrease in faecal sac removal behaviour with nestling age (e.g. Lombardo 1991). This study was undertaken when chicks were in the late brood stage, as swallow nestlings fledge at day 19/20, and the lack of removal events may be linked to this. Other species, such as hole nesters, may provide a better subject for such a study.

Previous studies have shown that adults with larger brood sizes tend to remove faecal sacs more often. In this study no similar relationship was seen. A decline in faecal sac removal has also been documented elsewhere as brood age increases, but again no relationship was found here. This may be due to the increasing demand for food by the chicks as they attempt to attain an optimal fledging condition. It has been suggested that the brood size effect, and that of nestling age, may be partially due to the increase of activity in the nest, making it harder for the adults to remove faeces without wasting potentially precious time which could be spent foraging. This study cannot make definite conclusions concerning these issues, however. There were also significant sex differences found in this study, as females showed higher levels of sanitation. This finding agrees with other studies, where in the majority of cases females are the main sanitisers (e.g. Lombardo 1991).

Since an increase in faecal sac removal rate is associated closely with an increased nest visitation rate in this study, and no clear effects of body-state manipulation have been found here, it is likely that nest sanitation is an opportunistic behaviour in the barn swallow. Thus, nest sanitation is a relatively unimportant parameter of reproductive effort in these birds. This may be due to the overriding need to provision the brood, with excess energy being used to increase provisioning rate. If swallow nestlings in this study were not exposed to a high level of parasitism, or parents perceived there was no great effect of parasites, then there would be no increase in nest sanitation. Since swallow nestlings tend to eject the majority of faeces from the nest after day 7, the risk of parasitism maybe low, if there is a link with 'dirty nests'. The lack of response may also be due to a cost paid by the adults in either time or energy. As some studies have shown nest sanitation is time consuming, however, in this species the main time constraint is likely to be waiting for a faecal sac to appear at the nest, rather than searching for them in the nest cup. Hence, faecal sac removal may be an opportunistic behaviour bringing a potential fitness benefit to the parents. There may be another cost of faecal sac removal, however, and this is the potential for transmission from nestlings to parents, which may constrain the amount of nest sanitation in this study.

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5 Energetic and behavioural responses to positive body-state manipulations in the Great Tit, *Parus major*.

5.1 Introduction

The costs of reproduction have been documented for many species, especially birds, and this plays a central role in the evaluation of life history theory (Allander 1997; Calow 1979; Cichon *et al.* 1998; Nur 1988; Tinbergen 1987). The driving force behind avian life history evolution is often thought to be food limitation (Lack 1968; Brodmann *et al.* 1997; Drent & Daan 1980; Tinbergen & Dietz 1994), and it is likely that in striving for an optimal reproductive strategy, individuals recognise cues from environmental conditions, including food availability and nest predation, as well as their own state (level of energy balance). State-dependent behaviour during reproduction has been seen in a few recent studies (Olsson 1997; Chapter 2), where parental foraging decisions are made while taking their energy levels into account in order to maximise fitness. Parental foraging performance is a major determinant of reproductive success as nestlings rely completely upon parental provisioning, thus this is the main link between the environment and fitness.

Many studies of the Great Tit (*Parus major*), and related species, have found correlative relationships between food availability (mainly measured as caterpillar abundance) and certain reproduction parameters, such as reproductive success (Eeva *et al.* 1997; Riddington & Gosler 1995), and daily energy expenditure (Tinbergen & Dietz 1994). Great tits provision their young mainly with lepidopteran larvae (approx. 90% diet) and search the mid to high canopies of trees. Only when food is scarce do they spend more time feeding on the ground, where the risk of predation is increased (Diaz *et al.* 1998). Behavioural responses of this kind to a changing food supply suggests that, in this species, food availability is an important factor which may constrain parental foraging decisions and ultimately reproductive success. Thus in 'poor' food years, when compared to 'good' years, we may expect to see, not only differences in brood success, but also differences in the amount of energy parent birds devote to provisioning their nestlings. Seki & Takano (1998) found no relationship between lepidopteran caterpillar abundance and fledgling quality, as local environmental effects were compensated for by parental effort strategies. This did, however, result in significantly longer nestling

periods in territories with low food abundance. This suggests that in 'poor' food years parents will increase their provisioning effort in order to raise their broods. This may mean an increased feeding rate or a shift in foraging to provision better quality prey, focusing on current reproduction, however a significant increase in feeding rates may not be observed due to the potential constraints of search times in 'poor' food years (NaefDaenzer & Keller 1999). An increased provisioning rate may give nestlings an advantage, but potentially leave the parents with an energy deficit, leaving them unable to maintain mass or fat reserves. Thus, parent birds may 'choose' to allocate more of the energy gained from foraging to maintain their own energy balance at the expense of their brood, focusing on their own survival and ultimately future reproduction.

In this study adult Great Tits underwent positive body state manipulations, using overnight temperature, allowing them extra energy at dawn, and the consequences for reproductive behaviour were revealed. The flow of energy was followed over a 24 hour period, via behavioural and observational methods. The doubly labelled water technique was also used to quantify energy expenditure in provisioning parents. Since this study was undertaken over two years, including a marked contrast in food availability between these years, we would expect to be able to tease apart the interaction described above and follow the decisions made by provisioning adult Great Tits when food availability is relatively low.

The trade-off between reproduction and survival can be modified to demonstrate the likely relationship when an individual is in positive energy balance (Figure 5.1(a)). The amount of energy 'acquired' by an individual is greater following a warming manipulation, as less energy has been expended in overnight (Chapter 2). This extra energy can be used to enhance a number of activities, either reproduction-based, such as nest defence or provisioning rate (Figure 5.1(b), or survival based, e.g. self-feeding (Figure 5.1(c)). The strategy undertaken may depend upon the availability of food in the environment, and hence, the survival prospects of both adult and their brood.

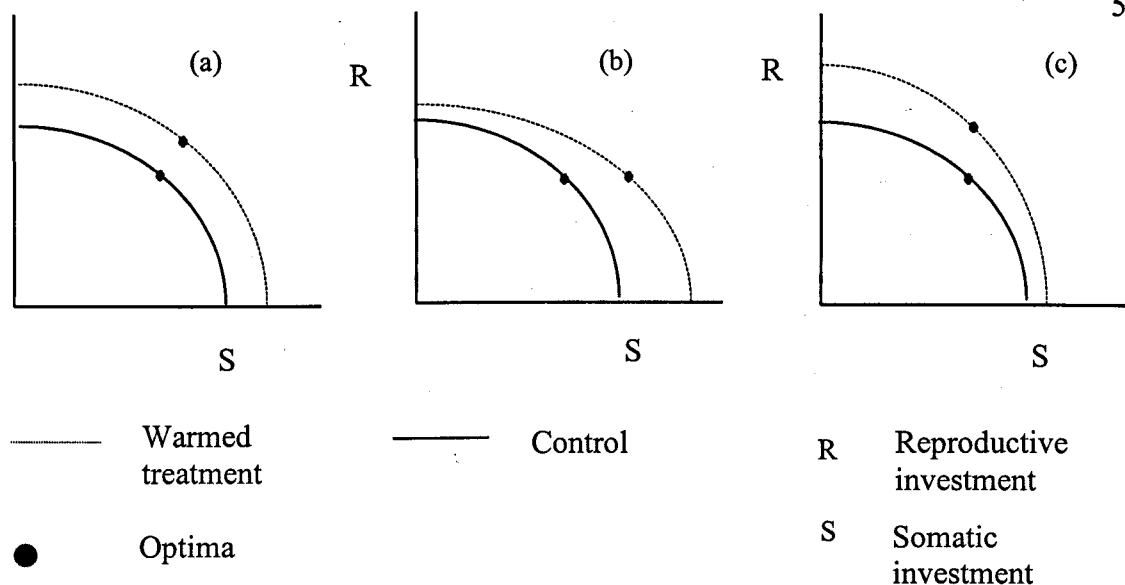


Figure 5.1. Allocation of energy between reproductive and somatic investment is usually assumed to be symmetrical (a). This need not apply, however, as there may be a bias toward either somatic investment (b) or reproductive investment (c). The area under each curve is constant and represents the amount of energy acquired by an individual under each treatment group. The optimal allocation for an individual changes with each treatment, but there is also a shift in position within treatment groups under the two different bias hypotheses.

Thus, when comparing responses to a positive body state in a 'poor' food year with those in a 'good' year there are two potential regimes under which we would predict different behavioural, energetic and foraging responses, combined with alternative nestling growth and mortality outcomes:

1. *energy allocation is biased towards current reproduction.*

- Increased parental energy expenditure
- increased or similar nest visitation rates
- increased loss of parental mass and fat reserve
- nestling mass changes similar to 'good' year
- no extra nestling mortality

2. *energy allocation is biased towards somatic investment (future reproduction)*

- increased parental energy expenditure
- decreased or similar nest visitation rates
- parental mass changes similar to 'good' year
- nestling mass loss more pronounced
- increased nestling mortality

Since all birds used in this study built nests in nestboxes, another potential constraint, nest predation, is not a source of 'noise' in this study, thus the effects of food can be seen quite clearly. This is not to say that nest predation does not constrain reproduction, for example in nest site selection (Martin & Roper 1988), but this was not tested here.

5.2 Methods

5.2.1 Manipulations

The experiments were undertaken near Stirling in Central Scotland (56°8'N, 3°54'W) during May in mixed woodland in 1997 and 1998. They involved Great Tits rearing chicks aged 10 - 12d. Birds were caught using nestbox-traps (Figure 5.2) between 17.00 and 19.30h. Sex, mass were recorded. Fatscore was recorded as a rank score (0 - 5) of visible fat deposits in the inter-clavicular pit (Krementz & Pendelton 1990; Scott *et al.* 1995). Breeding pairs were randomly assigned to one of two groups; warmed or Control, to induce differences in body-state. Thermostatic energy expenditure would be lowered by the warm treatments, leading to relatively high residual energy reserves at dawn. Once initial blood samples had been taken in the laboratory for DLW studies (see below), our treatments were performed overnight, typically from 20:00h to 03:30h. During this time, birds were kept in 4.4 litre containers equipped with a perch, allowing a normal posture and space for the wings to be fully spread. Warmed birds were placed in an incubator (Sanyo) in the dark at 29°C (within the thermoneutral zone, (Kendeigh *et al.* 1977). Control birds were placed in an outdoor shelter (average night-treatment period across groups was 7.9 ± 0.42 h s.d.) and therefore experienced prevailing ambient temperatures (6.0 ± 1.5 °C s.d.).

Birds were released at dawn (ranging from 03:30h to 04:00h) at their nest site, to ensure a normal foraging period: mass was recorded again at this point. Birds were recaptured and final blood samples taken approximately 24h (22.9 ± 1.2 h) after the initial blood samples. Mass and fatscore were recorded once again.

Overnight energetic costs over a range of overnight temperatures were quantified using indirect calorimetry with a sub-sample of birds ($n = 8$). A VG quadrupole mass spectrometer was used to determine oxygen and carbon dioxide concentrations in an open-flow respirometer. From this we derived estimates of energy expenditure

overnight. Details of equipment and methods are given by (Bryant & Furness 1995), where identical methods were used. Food abundance was measured using two 0.5m² frass traps, where frass was collected weekly over a four week period in 1997 and over three weeks in 1998. Four traps were originally set up in both years, however, samples of two trap were lost. Daily minimum temperatures and precipitation (mm) were taken from the Parkhead weather station, sited on the University campus, within 3 km of the study site.

5.2.2 Behavioural observations and prey quality

During the release period (mean time to recapture: 14.0 ± 1.2h), pairs were observed at the nest using video cameras (Panasonic) to obtain 'feeding visit rates' (observations lasted 0.9 ± 0.1 h per nest), and from this visits h⁻¹ was calculated. A metal cage was attached to the nestbox at least 3 days in advance of adult capture (Figure 5.2). This was equipped with a perch to enable the birds to enter the nestbox easily, however, the direction of entry was controlled, thus slowing the bird, which could be filmed at close range through the viewing window during the observation period. The video images of nine nests (Table 5.1) were analysed using NIH Image analysis package. Within each parental visit to the nest the length and width of each prey item (lepidopteran larvae) was measured. As the prey items tended not to lie straight in the bird's bill, a curve was fitted along the central axis of the length in order to gain a more accurate measurement. Multiple measurements of each caterpillar in different frames were taken wherever possible to gain a mean (range 1- 4). A mean volume was calculated for each caterpillar brought back to the nest (Equation 5.1). The cage window, which was of known length was used as a scale, however this was positioned approximately 6cm to the fore of the bird as it entered the nest. Thus the measurement and perspective errors involved in this method were quantified by recording and analysing five caterpillars of known size at a mock nestbox and cage setup. Each caterpillar was measured 10 times and a mean length and width calculated. These means were then used to calculate the percentage of real length/width represented by the image length/width, and the variation around that percentage (error). Image lengths were found to be 59% (± 2 s.d.) of the real lengths and image widths were 60% (± 2 s.d.) of real widths. Caterpillar dimensions gained from observation videos were scaled accordingly.

$$\text{Volume} = \pi * (\text{width}/2)^2 * \text{length}$$

Equation 5.1

Table 5.1. Sample sizes of warmed and Control treatment groups, used in statistical analyses in this study, in 1997 and 1998. (a) – (c) show number of individual birds, whereas (d) – (e) show number of nests. (a) Mass and fatscore changes (M_{rel} , FS_{rel}), (b) active energy expenditure (AEE), (c) nest visitation rate (VR), (d) nestling growth / mortality rates (N_{growth}), (e) prey quality (PQ).

	1997	1998
(a) $M_{\text{rel}} + FS_{\text{rel}}$		
Warmed	6	6
Control	8	6

	1997	1998
(b) AEE		
Warmed	6	5
Control	5	4

	1997	1998
(c) VR		
Warmed	6	6
Control	6	8

	1997	1998
(d) N_{growth}		
Warmed	3	3
Control	7	5

	1997	1998
(e) PQ		
Warmed	3	3
Control	0	4

(NB. The number of nests used to analyse prey quality was constrained by the quality of the video images, a proportion could not be used for this detailed work as the images were too blurred to make an accurate measurement, these videos were, however, successfully used to distinguish sex related visiting rate)

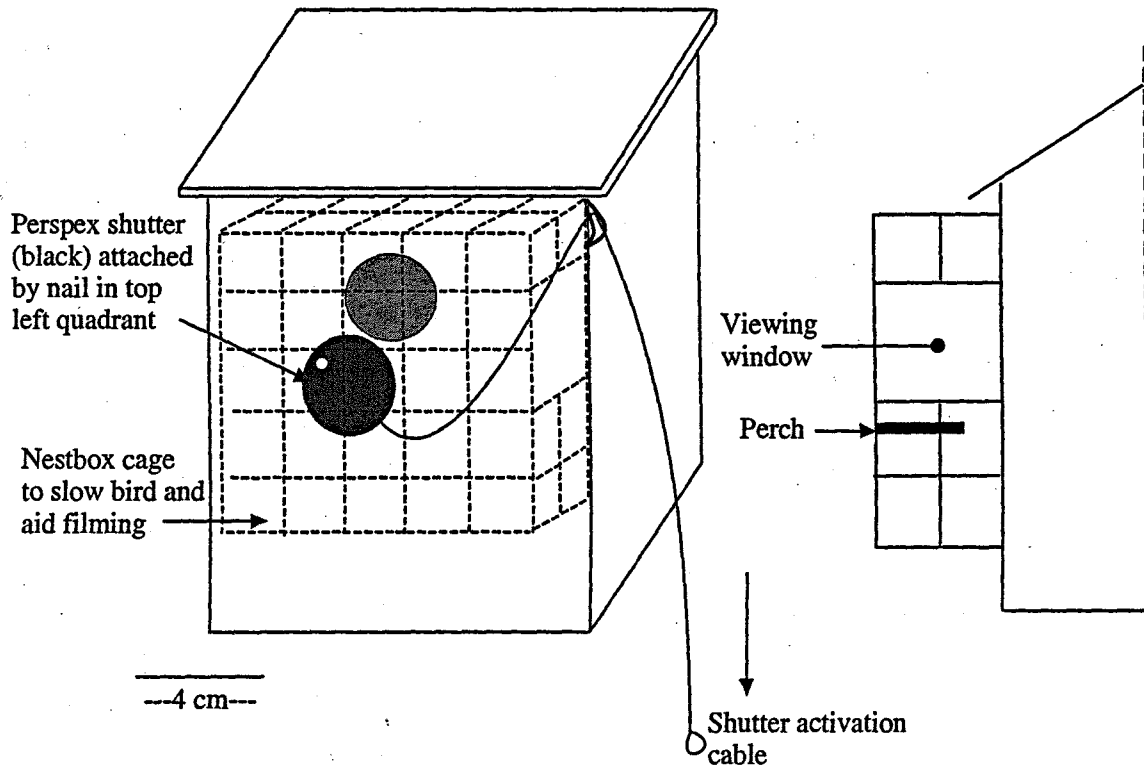


Figure 5.2. Apparatus used to catch and film adult Great Tits in this study. The cage and trap were placed on the nestbox at least three days before capture to allow conditioning, and to ensure normal behaviour. Upon capture a longer length of fishing wire was attached to the shutter activation cable to allow the observer to remain up to 25 m away. The cage window, covered with a mesh until capture to train birds to enter from the left, allowed filming to occur from a remote video camera, placed on a tripod approx. 2-3m from the nest.

5.2.3 Doubly labelled water.

Doubly labelled water (DLW) was used to measure energy expenditure by free-living Great Tits (Lifson & McLintock 1966; Tatner & Bryant 1989). Birds were given intraperitoneal injections of DLW (10 μ l g⁻¹ body mass). The injectate was prepared by adding 0.37g of 99.9 APE deuterium (²H) to 5ml of 20 APE oxygen-18 water (H₂¹⁸O). Once injected, the birds were kept in a bag for 1h to allow the isotopes to reach equilibrium with the body water (Bryant & Westerterp 1982). Blood samples were then taken in 10 μ l capillaries (Vitrex) from the femoral vein and immediately flame-sealed. Six to ten capillaries, each with 5 μ l of blood, was taken from each bird at the time of 'initial' and 'final' samples. Background isotope levels were obtained from blood samples of non-experimental birds (n=2 (1997), n=3 (1998)). Background levels were found to be 1995.5 \pm 7.1 (s.d.) for ¹⁸O and 146.0 \pm 4.0 (s.d.) for ²D. Isotope concentrations were determined from duplicate samples by mass spectrometry and a mean value was used in subsequent calculations (Tatner & Bryant 1989; Speakman 1997).

5.2.4 Calculation of energy expenditure

Daily energy expenditure (DEE, kJ d⁻¹) was calculated as described by Tatner & Bryant (1989) and Lifson & McClintock (1966), using an RQ of 0.75. An estimate of 66% was used as the body water pool (Mertens 1987). Overnight metabolic cost (E_{resp}: kJ g⁻¹ h⁻¹) was obtained from the respirometry results (Gessaman 1987) and a mean obtained for each treatment group (\times E_{resp}). From this the cost of the overnight period (E_{overnight}) was calculated using Equation 5.2 (t_{overnight} represents the time a bird spent in the incubator, W represents mass of the bird (g)). E_{overnight} was then used to calculate, by difference from the daily energy expenditure (DEE), the 'active' energy expenditure (AEE) of each individual during the release period (Equation 5.3).

$$E_{\text{overnight}} = \times E_{\text{resp}} * W * t_{\text{overnight}} \quad \text{Equation 5.2.}$$

$$AEE = DEE - E_{\text{overnight}} \quad \text{Equation 5.3.}$$

$$MI = E_{\text{overnight}} / \text{BMR} \quad \text{Equation 5.4.}$$

Basal metabolic rates were derived from the passerine equation of Aschoff & Pohl (1970), resting phase, to provide a standard for comparisons (called Metabolic intensity, MI, Equation 5.4.).

An index of provisioning was calculated according to Welham & Beauchamp (1997), as the ratio of energy delivered to the nest (here the mean number of visits to the nest) against the amount of energy expended on the foraging trip (Equation 5.5). VR represents the predicted mean visiting rate h^{-1} for each treatment in each year, AEE is the predicted mean active energy expenditure during the release period, and t_{rel} is the mean length of the release period for each treatment in each year.

$$I_e = VR/[AEE/t_{rel}]$$

Equation 5.5.

5.2.5 Nestling growth and mortality

Nestlings in each nestbox were weighed at the times of parental capture and recapture. From this mass data an average brood mass was calculated for the start and end of each trial, and mass changes were calculated by difference. All nests were monitored again at day 15-16, and at this time nestboxes were checked for mortality. Since Great Tits fledge at approx. day 18, this was used to derive brood mortality (number of nestlings dying / total number of nestlings).

5.2.6 Statistical analysis

Data were collected from different pairs over more than one year, however nestboxes were duplicated over the two years. Hence, to control for random nestbox effects and non-orthogonality Residual Maximum Likelihood (REML) analysis was used to explain variation in active energy expenditure, visiting rate, body mass and fat score changes, and nestling growth. Stepwise deletion of fixed variables from the minimal adequate model was performed. The random model controlled for the nestbox number within each year, in effect controlling for pairs. The significance of fixed variables was estimated using the Wald statistic, which is asymptotically distributed as χ^2 (Genstat 5 Committee 1992).

Differences in chick mortality between years was analysed using a logistic Generalised Linear Model (Genstat 5 Committee 1992), modelling binomial proportions. This was done by comparing the number of nestlings dying within a nest with the number available to die. A regression is performed and a ratio approximate to

the *F* ratio is calculated along with the associated probability. Overnight adult mass changes were analysed using ANCOVA (Minitab v12). Regression analysis of overnight energy costs was performed upon energy expenditure (E_{resp}) using CurveExpert 1.3 to determine the line of best fit. Prey quality (mean volume per caterpillar) was analysed using ANOVA (Minitab v12). Predicted means were converted to metabolic intensity (MI) data (Equation 5.4). Sample sizes for all analyses are given in Table 5.1. Residuals were checked for normality and homogeneity of variance, where appropriate. Predicted means \pm standard error from statistical tests are quoted for each analysis.

5.3 Results

5.3.1 Overnight costs of manipulation.

There was a significant effect of overnight temperature upon energy costs, explaining 98% of the variation in the data (Figure 5.3). The relationship was treated as curvilinear, and the best fit was obtained by a reciprocal quadratic function with the equation $R = 1/[5.58 + (0.48T) - (0.0066T^2)]$. Birds kept at warmer temperatures expended less energy than those at lower temperatures. Thus, Control birds, showed overnight costs of 2.0 x BMR, whereas, warmed birds had a resting metabolic rate of 1.2 x BMR. There were no treatment or sex related effects on overnight mass changes (Table 5.2(a)), however there was a significant interaction between these two terms, with Control females showing a strong trend towards higher mass loss ($t_{(16)} = 1.87$, $p = 0.08$).

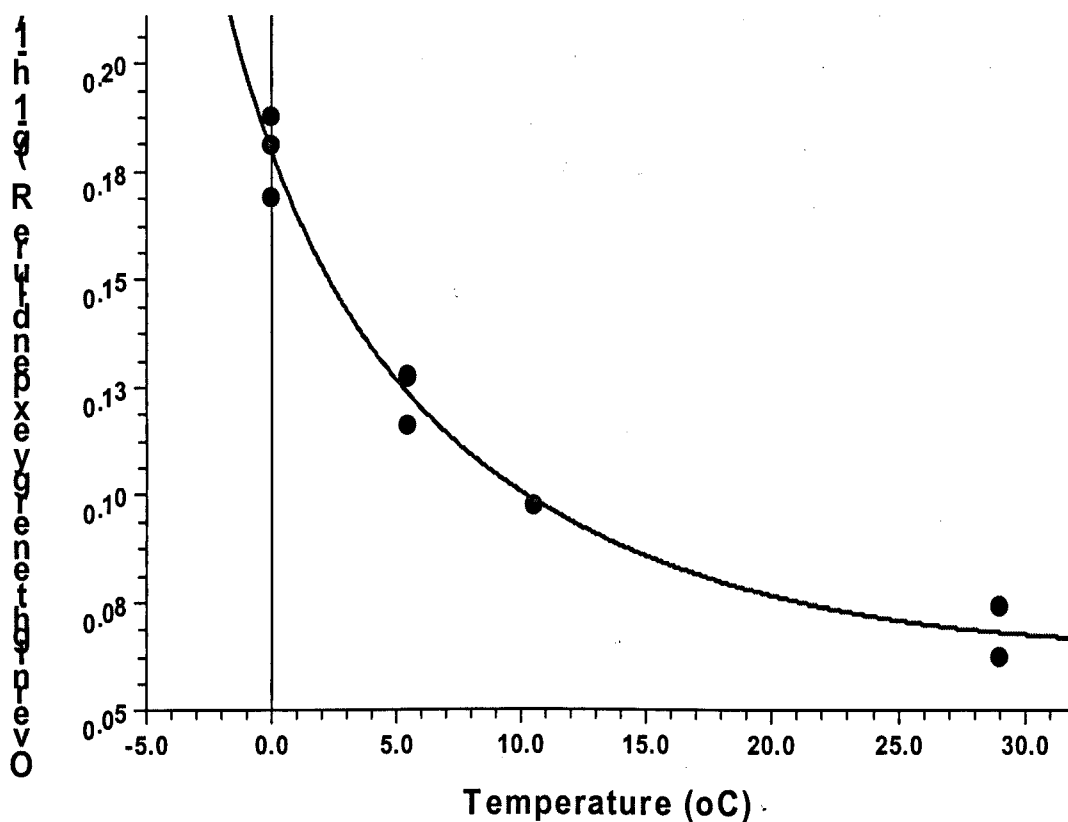


Figure 5.3. Inverse polynomial regression analysis of the effect of overnight temperature on energy costs in the Great Tit ($\text{kJ g}^{-1} \text{h}^{-1}$). Model accounts for 98% of the variation in data.

5.3.2 Mass and fat score changes

There were no effects of brood size or age upon adult mass changes over the trial period (Table 5.2(b)). Birds from all treatments tended to show the same mass change patterns over the trial. This was also the case for fat score changes, although there was a strong trend towards a sex-related difference, with females showing a higher rate of fat loss. There were, once again, no effects of brood size or age, but initial fat score proved to have a significant negative effect. Year showed no effects on mass or fat score changes, and there was no evidence of an interaction between year and treatment group (Table 5.2(b) & (c); Figure 5.4(a) & (b)).

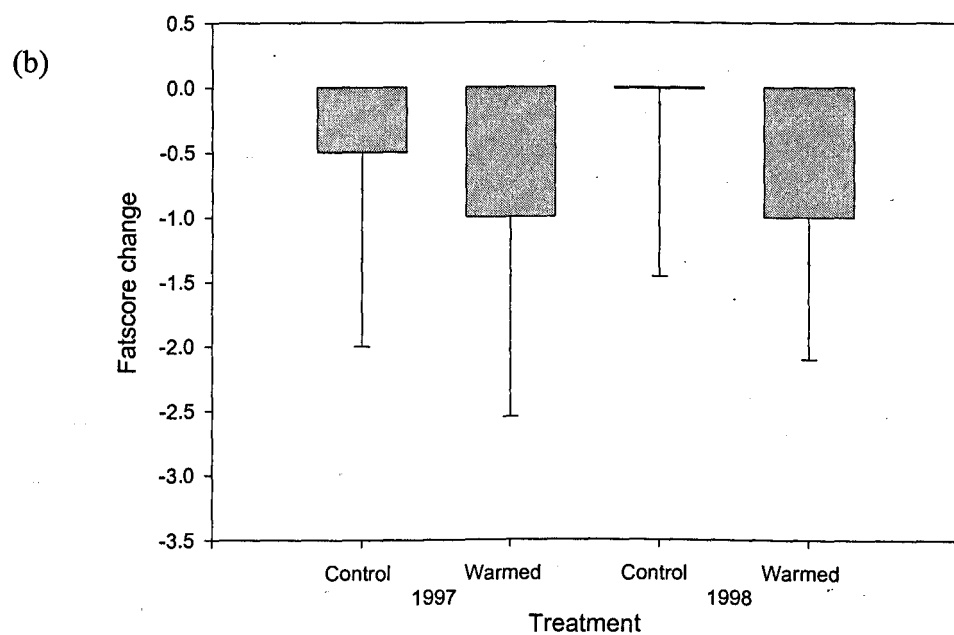
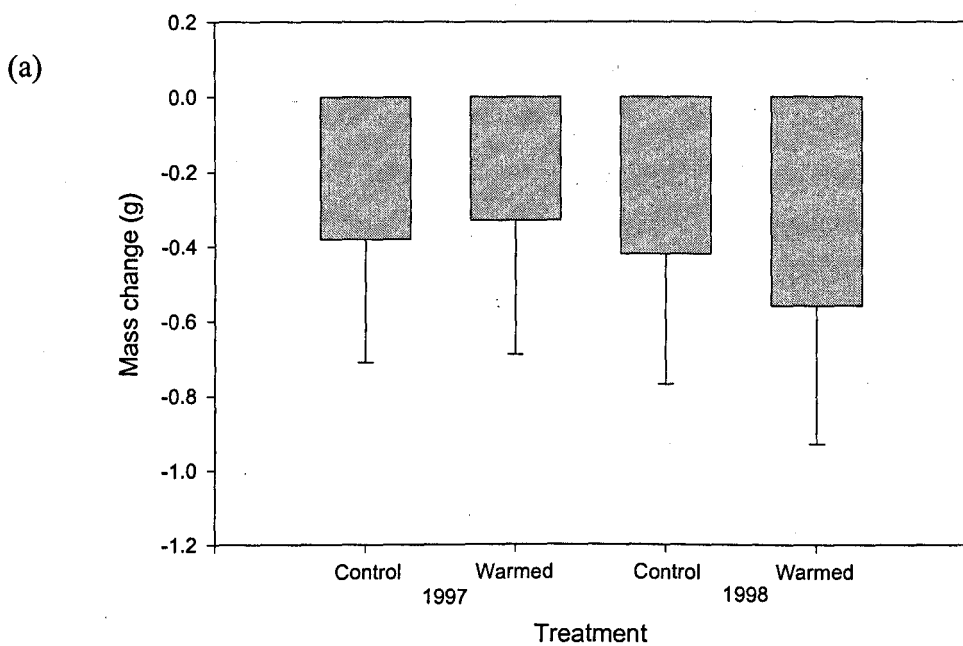


Figure 5.4. (a) Mean mass changes (final mass - initial mass) \pm standard error, over the trial period in 1997 and 1998, for Control and warmed treatment groups. (b) shows median fatscores \pm 95% confidence intervals for both Control and treatment groups.

5.3.3 Active energy expenditure

The mean daily energy expenditure (DEE) of adult birds in this study was 62.6 ± 12.6 (s.d.) kJd^{-1} . Brood size, food abundance and ambient temperature had no effects on the AEE of Great Tits in this study (Table 5.2(d)). Visiting rate to the nest also showed no effects, and there were no interactions between visiting rate and treatment. Males and females within each treatment group showed similar levels of expenditure i.e., Control male 39.1 ± 8.5 , and female 37.2 ± 6.8 kJ; warmed male 49.9 ± 7.2 , and female 55.7 ± 6.9 kJ. There was, however, a significant treatment effect on AEE. Birds assigned to the warmed group expended significantly more energy (53.1 ± 5.7 kJ) than controls (37.9 ± 5.9 kJ) over the release period (Figure 5.5(a)). There was no significant interaction between year and treatment group, however, birds in 1997 expended significantly less energy than those studied in 1998 (Table 5.2(d); 1997: 40.5 ± 3.1 kJ; 1998: 50.6 ± 3.4 kJ).

5.3.3.1 Asymmetry of energetic response to positive manipulation.

Input and *output* energies can be defined as the amount of energy saved by an individual overnight by the warming treatment, and the amount of extra energy expended during the release period by warmed birds above the level of controls, respectively. These values were calculated for adult Great Tits according to the methods in Chapter 2 for swallows. In this study the mean input value was 8.6 ± 0.2 kJ. The mean output value was 15.2 ± 5.8 kJ. Thus there seems to be an energetic overcompensation of warmed birds over the two year period of 1.8 (ratio of output to input). This value is similar to that obtained in swallows treated a similar way (Chapter 2). When this ratio is calculated for each year, this pattern remains at 1.8, even though in 1998 energy expenditures are higher.

5.3.3.2 Index of provisioning efficiency

The highest efficiency ratio was found in the warmed group in 1997 (7.1). This was higher than controls in this year, which exhibited an efficiency of 4.5. In 1998 the pattern is reversed, with controls showing greater efficiency (1.8) than birds in the warmed group (0.7), although this figure lies below that of controls in 1997 (Figure 5.5(b)).

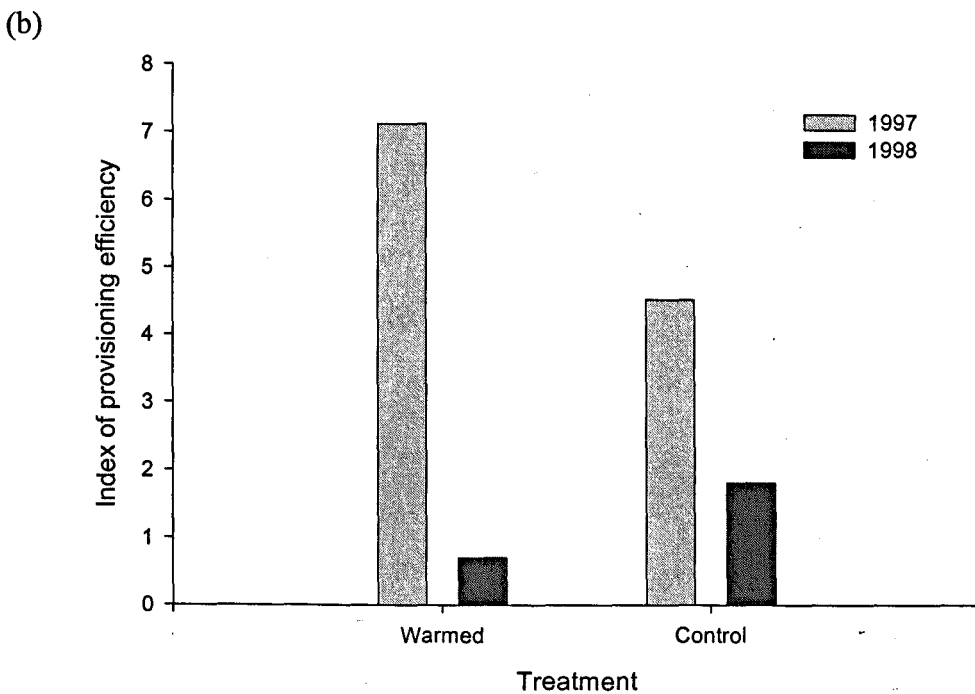
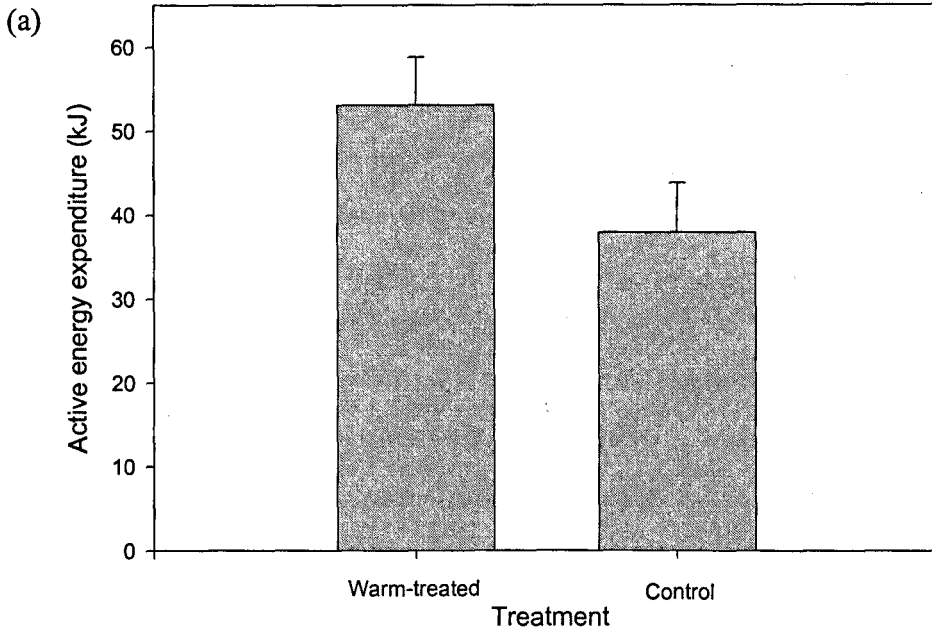


Figure 5.5(a) Active energy expenditure (AEE) during the release period (14 ± 1.2 h) by Great Tits within Control and warmed treatments across two years of study. (b) Index of provisioning efficiency (I_e) of warmed and Control birds in 1997 and 1998.

5.3.3.3 *Parental visiting rate*

Brood size and food abundance had no effects on the nest visitation rates of adult Great Tits in this study. There were no effects of treatment or sex and no significant interaction between the two (Table 5.2(e)). There was a significant effect of year on nest visitation rates, and year also showed a significant interaction with treatment group, revealing an increase in nest visitation by warmed birds in 1997, which exhibited 24 ± 4 visits h^{-1} , above controls of that year, which showed a mean of 10 ± 5 visits h^{-1} ($t_{(20)} = 2.54$, $p = 0.02$). In 1998, a different pattern was seen, where controls showed a slightly higher nest visitation rate (6 ± 3 visits h^{-1}), than the warmed group (3 ± 4 visits h^{-1}) Figure 5.6(a) & (b). Birds in this study also tended to visit their nests more often on warmer days (Table 5.2(e)).

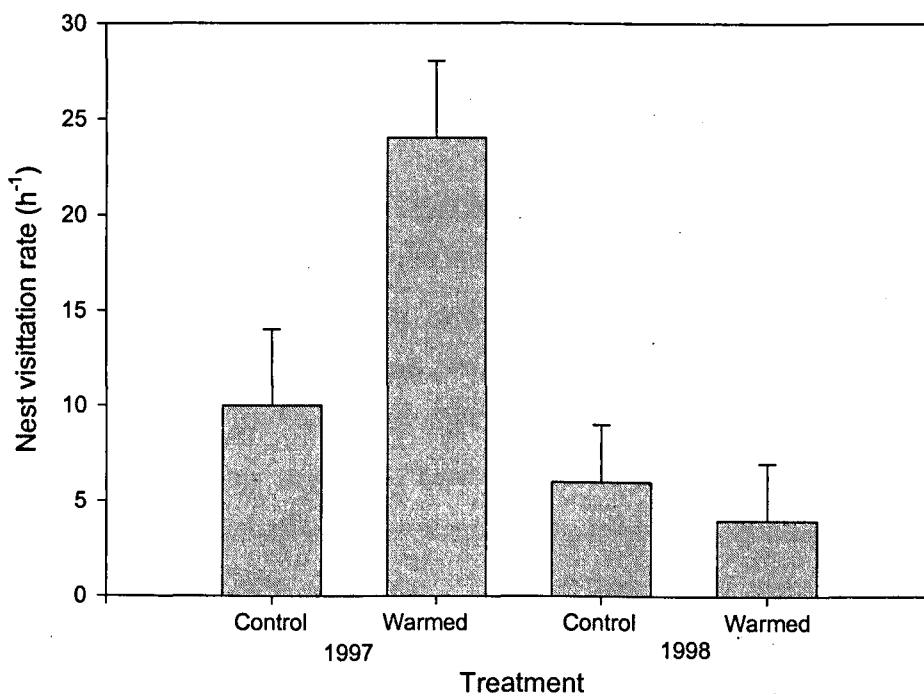


Figure 5.6. Predicted mean nest visitation rates (h^{-1}) \pm standard error, by adult Great Tits allocated to Control and warmed treatment groups in (a) 1997, and (b) 1998 field studies.

5.3.4 Prey quality

There was no effect of treatment on the mean prey item volume delivered to the nest in 1997 ($F_{(1,4)} = 0.11$, $p = 0.759$). Birds allocated to the warmed group delivered larvae with a mean volume of $0.060 \pm 0.014 \text{ cm}^3$, controls delivering a mean volume of $0.067 \pm 0.014 \text{ cm}^3$. Across years there was no difference between warmed groups, although there was a trend for birds in 1998 to deliver larger prey ($0.087 \pm 0.014 \text{ cm}^3$), when compared with 1997, but this was not significant ($F_{(1,4)} = 1.73$, $p = 0.259$).

5.3.5 Nestling growth and mortality rates

There were no effects of treatment, brood size or brood age on mass changes in nestlings (Table 5.3(a)). There was an overall trend for nestlings to lose mass over the trial period, nestlings in 1997 losing, on average, $0.83 \pm 0.35 \text{ g}$, and those in 1998 losing more, $1.46 \pm 0.40 \text{ g}$. This year trend is not significant, however (Table 5.3(a)). The power of this analysis is 32%. Nestlings born in 1998 were significantly more likely to die before fledging age than in 1997 ($F_{(1,16)} = 5.91$, $p = 0.027$), this is confirmed by the overall mortality rate of nestlings ($[\text{total number of nestlings dying} / \text{total number of nestlings hatched}] * 100$) in this study, which was higher in 1998 (32%) than in 1997 (11%).

5.3.6 Food availability and environmental conditions.

1997 showed significantly higher food abundance than 1998 (Table 5.3(b)), with year explaining 36% of the variation seen in the data. There was also a significant change in mass of caterpillar frass over time, peaking in 1997 at week 19 (Figure 5.7). Frass trap replicates within year were not significantly different from each other. In 1997 temperature increased more steadily between February and June than in 1998 (Figure 5.8(a)), with certain weeks showing significantly lower temperatures in 1997 than in 1998 (Table 5.3(c)). There were three 'blocks' of these lower temperatures, in weeks 9-10, 14-15, and 23-25. There was also one block where 1997 temperatures are warmer than those in 1998 (weeks 6-8). There were no year or week effects on precipitation (Table 5.3 (d), Figure 5.8(b)).

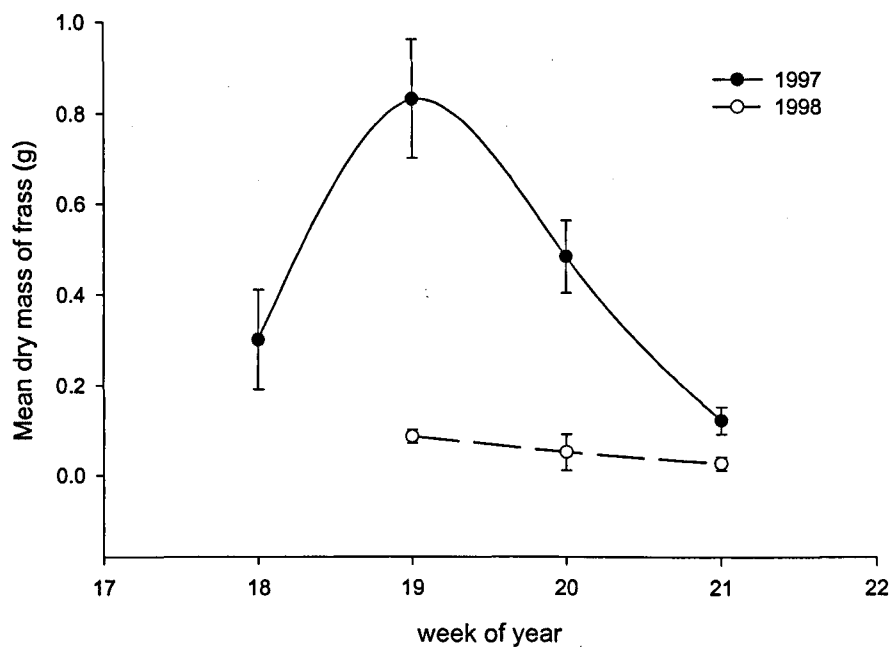


Figure 5.7. Mean dry mass (\pm standard error) of caterpillar frass collected from two 0.5 m^2 traps in mixed woodland in the Stirling area in 1997 (solid line) and 1998, over a four-week period (weeks 18-21). Curves fitted using smoothing.

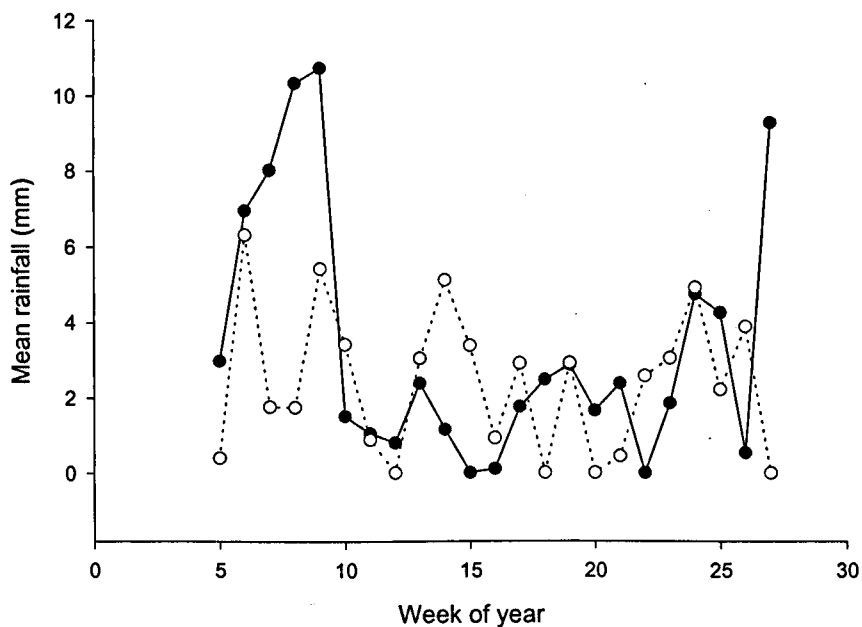
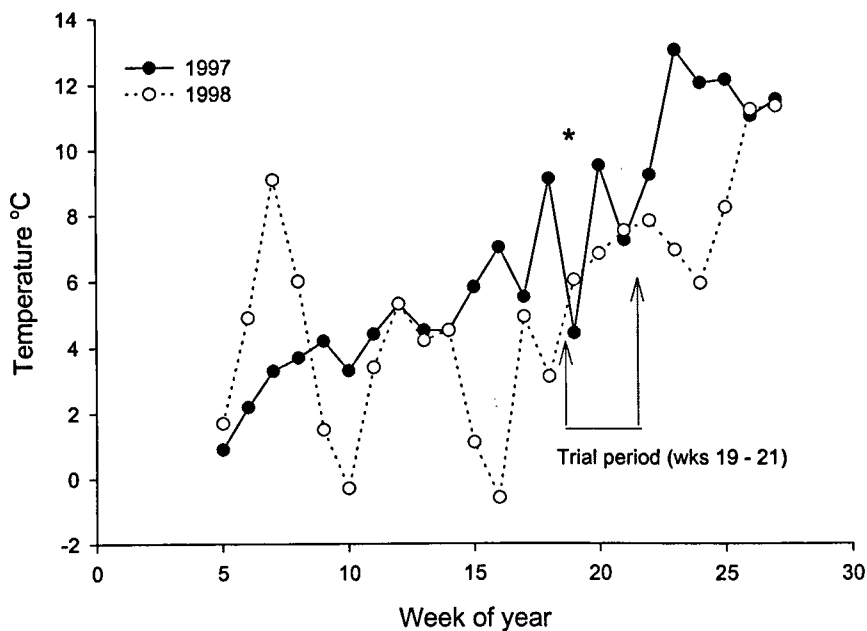


Figure 5.8. (a) Minimum temperatures ($^{\circ}\text{C}$), averaged by week, over time. Solid line denotes 1997, dashed line represents 1998. The period of experimentation is marked with arrows (weeks 19-21). * denotes the time of peak food abundance in 1997. (b) precipitation (mm), averaged by week, over time in 1997 (solid line), and 1998 (dashed line).

Table 5.2. Results of statistical analyses. REML results are presented in terms of the Wald (χ^2) statistic, ANCOVA results in the form of F ratios. d.f.s and p values are quoted for each term. (a) represents adult mass changes overnight (M_{ov}), (b) adult mass changes over trial (M_{rel}), (c) fatscore changes over trial period (FS_{rel}), (d) active energy expenditure (AEE), and (e) adult nest visitation rate (VR).

(a)	Variable (M_{ov})	F ratio	d.f.	p value
	initial mass	7.84	1,20	0.005
	Treatment	0.57	1,20	0.451
	Sex	2.54	1,20	0.111
	treatment*sex	3.80	1,20	0.05
(b)	Variable (M_{rel})	wald statistic	d.f.	p value
	Excluded terms			
	Brood size	0.24	1	0.628
	Nestling age	0.03	1	0.864
	Initial mass	0.80	1	0.372
	Release period	0.66	1	0.416
	Treatment	0.11	1	0.738
	Year	0.50	1	0.518
	Sex	0.18	1	0.671
	Treatment*year	0.06	1	0.812
Treatment*sex	1.17	1	0.279	
	Residual d.f.	24		
(c)	Variable (FS_{rel})	wald statistic	d.f.	p value
	Minimal adequate model			
	Initial fatscore	13.00	1	<0.0001
	Excluded terms			
	Brood size	0.00	1	0.963
	Nestling age	1.14	1	0.285
	Release period	1.78	1	0.182
	Treatment	0.73	1	0.393
	Year	0.10	1	0.757
	Sex	1.36	1	0.243
Treatment*year	0.16	1	0.692	
Treatment*sex	2.14	1	0.143	
	Residual d.f.	23		
(d)	Variable (AEE)	wald statistic	d.f.	p value
	Minimal adequate model			
	Release period	19.43	1	<0.0001
	Treatment	8.99	1	0.003
	Year	4.06	1	0.044
	Excluded terms			
	Maximum temperature	0.98	1	0.323
	Food abundance	0.24	1	0.624
	Brood size	0.27	1	0.591
	Visiting rate	0.00	1	0.953
	Sex	0.25	1	0.618
	Treatment*sex	0.13	1	0.722
	Treatment*visiting rate	0.07	1	0.795
	Year*treatment	0.00	1	0.994
		Residual d.f.	15	

Cont.....

(e)	Variable (VR)	wald statistic	d.f.	p value
	Minimal adequate model			
	Year*treatment	5.07	1	0.024
	Maximum temperature	4.42	1	0.035
	Treatment	1.21	1	0.272
	Year	5.03	1	0.025
	Excluded terms			
	Brood size	0.07	1	0.786
	Food abundance	1.86	1	0.173
	Sex	1.83	1	0.177
	Treatment*sex	0.04	1	0.838
	Residual d.f.		20	

Table 5.3. Results of statistical analyses. REML results are presented in terms of the wald (χ^2) statistic, ANCOVA results in the form of F ratios. d.f.s and p values are quoted for each term. (a) nestling mass changes (N_{growth}), (b) caterpillar frass data (F_{larvae}), (c) minimum temperature °C (T_{min}), and (d) precipitation mm (P_{mm}). Significant terms ($p < 0.05$) are shown in **bold**.

(a)	Variable N_{growth}	wald statistic	d.f.	p value
	Nestling age	0.26	1	0.609
	Brood size	0.51	1	0.475
	Year	1.41	1	0.235
	Treatment	0.06	1	0.810
	Year*treatment	0.24	1	0.624

(b)	Variable F_{larvae}	F statistic	d.f.	p value
	Year	18.05	1,8	<0.002
	Week	5.05	1,8	0.025
	Trap number	0.44	1,7	0.526

(c)	Variable T_{min}			
	Year	1.22	1,41	0.277
	Week	61.70	1,41	<0.0001
	Year * week	4.54	1,41	0.039

(d)	Variable P_{mm}			
	Year	1.50	1,42	0.227
	Week	1.79	1,42	0.187
	Year * week	0.60	1,41	0.442

5.4 Discussion

5.4.1 State-dependent trade-offs

The Great Tits in this study were faced with two very different years in terms of food availability and weather conditions. In both 'good' and 'poor' food years, adult Great Tits significantly increased their daytime energy expenditure in response to body state manipulations, indicating that body-state does indeed trade-off against reproductive effort in this species, this coupled with the findings of Chapter 2 using swallows, this suggests that body-state is an important parameter influencing the trade-off between reproduction and survival in a range of species with differing foraging ecologies and reproductive strategies.

5.4.2 Overnight maintenance

Verhulst & Tinbergen (1997) found that female brood rearing Great Tits exhibited significantly higher daily energy expenditure (DEE) than males, and attributed this to overnight brooding in the female, a behaviour which the male does not take part in. Although we found no such sex differences in active energy expenditure in either year or treatment, there was a trend towards increased mass loss in Control females during the overnight period. However, this was not coupled with an increased energetic flux during the overnight period. The lack of evidence of an effect of overnight temperature treatment on mass changes has also been seen before in Sand Martins (*Riparia riparia*) and canaries (*Serinus canarius*). Jones (1985) found no significant mass changes in these birds roosting at temperatures between 5°C and 30°C, thus since our manipulation temperatures were within this range, we would expect the same result. Overnight mass loss is due to mass lost via defecation and evaporative water loss (EWL). As ambient temperature increases EWL tends to increase, however defecation rate decreases, as there is less need for energy from fat stores, especially within the thermoneutral zone (Jones 1985). Thus, a similar level of mass loss is seen in the birds within this study. Verhulst & Tinbergen (1997) also describe sex differences regarding the relationship between DEE and nest provisioning rate. This was not seen in this study where both remained unrelated to sex.

5.4.3 Food availability

Data were collected from 2 frass traps, this covered the period within which trials were performed and would have also covered a significant part of the brood rearing period for most Great Tits in the area. Seki & Takano (1998) used a similar system to estimate biomass and abundance of similar prey, and although our collections were

not as extensive as this our frass trap data does show that significantly less frass was produced in 1998 than in 1997. This is probably related to the two periods of cold temperatures in 1998, especially in weeks 14-15, which could have affected adult lepidopteran survival and reproductive output. Thus in 1998 there was no 'caterpillar burst' for foraging tits to capitalise on, and food was scarce. Indeed, adult Great Tits were seen provisioning their nests with bread in one case (personal observation), which provides little useful nutrition.

5.4.4 Adult behavioural mechanisms

In 1997 when food was relatively abundant, birds exhibited lower energy expenditures in both Control and warmed groups, when compared to 1998. There was also a significant trend for birds allocated to the warmed group to show higher visiting rates in response to the manipulation. This implies that birds in this year place all the 'extra' energy gifted to them by overnight warming into reproductive effort, in fact expending more energy than is 'given' to them. This bias in the allocation of energy towards reproduction has been seen before in brood rearing swallows (Chapter 2). Warmed birds also showed a higher provisioning efficiency than controls in 1997. This evidence suggests that birds in 1997 are operating under condition 1 described earlier (Figure 5.1(b)).

In 1998 parent birds behaved differently, showing increased energy expenditure in both warmed and Control groups, suggesting a higher work rate but with lower efficiency, the pattern of 1997 being reversed and warmed birds showing reduced provisioning efficiency. There was still an increase in energy expenditure, above controls, with the warming manipulation, however, a corresponding increase in visiting rate was not seen. This may suggest a bias of energy allocation towards self investment, however, an increase in nest provisioning may not be expected, as search times are likely to be longer in years of low food abundance (Naef-Daenzer & Keller 1999). This would force lower provisioning rates even with an increased parental effort. With food availability so much lower in 1998, it is possible that although parent birds attempted to compensate for the reduced food available, they were unable to do so simply because food was too limiting in this year. Thus, the nest visitation rate changes are inconclusive in determining the strategy operating among birds in 1998, however, under condition 2, described earlier, there are several ways to tease apart the effort strategies of parent birds in this study.

In both years birds increased energy expenditure, as predicted by both conditions. Since nest visitation rate is not useful alone, without any estimates of foraging performance, the absence of an increased response in 1998 cannot rule out regime 1 in this case. Also there were no year or treatment effects on parental mass or fat score changes, perhaps suggesting an optimal mass for provisioning Great Tits, but also suggesting that although food was less abundant, parents invested enough to maintain their own fat and mass levels. This finding complies with regime 2.

5.4.5 Nestling growth and mortality

Warming a parent bird does not seem to confer any advantage upon its brood, regardless of food availability, and even though that brood may be provisioned at a higher rate. A reduction in load size may account for this, as predicted by optimal foraging theory, as provisioning rate and load size tend to balance each other out. However, since parent birds were taken overnight and some female Great Tits will still brood their nest overnight when chicks are aged 10-12 days ((Tinbergen & Dietz 1994), then this may be partially an effect of increased nestling overnight costs. An alternative explanation is that after the 10 days nestling Great Tits are losing mass to obtain their optimal fledging mass. This gradual mass loss may confound any effects of changing parental provisioning, as even though birds in warmed nests receive more food, they use this to increase growth and protein stores and not fat deposition. There were no treatment effects on brood mass changes, only a year trend, with broods in the 'low' food year showing increased mass loss over the trial period. This coupled with broods in 1998 suffering a higher mortality rate, suggests either that parent birds were switching strategy in a bad year towards their own survival (regime 2), or that they could not compensate for the low food availability with increased parental effort. Maintenance of adult fat and mass levels supports the conclusion that the former is true. If parent birds had been working harder to no avail, we would have expected to see some cost exposed and exhibited in parental condition. These results point to a potential difference in strategy by adult Great Tits in 1997 and 1998.

5.5 Conclusion

We argue that in times of low food availability parent birds will shift their energy allocation strategy to favour their own survival over that of their chicks and hence, future reproduction. The relationship between body state and reproductive effort is therefore plastic, with birds in good years biasing energy allocation towards

reproduction in order to maximise fitness (Figure 5.1(b)). When their own survival, as well as that of their broods is compromised in a bad year, however, this relationship shifts to a bias in energy allocation towards somatic investment (Figure 1(c)). Each of these is likely to be a fitness maximising strategy, which comes into play depending upon the food availability within the environment.

This study provides evidence that reproductive effort and energetic allocation strategies are linked to environmental conditions in the Great Tit, such as food availability. Naef-Daenzer & Keller (1999) suggested that parents in low food years even though they attempt to increase parental effort by increasing search times, are unable to compensate for the lack of food, and thus high costs are incurred. This study suggests that although in years of slight food reduction, birds may attempt to increase parental effort, there is a point at which survival and thus fitness is jeopardised and the trade-off function is shifted to give an advantage to the parent.

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6 General discussion

6.1 Summary of results of experimental work

My aim was to investigate the individual changes in energy expenditure and behaviour of state-manipulated birds to identify any general rules which may be applicable to life history theory. The studies presented here have generated such a rule, and suggest a novel model to describe the relationship between reproduction and survival (somatic investment). In this study, an increased state (positive) is analogous to the effects of more favourable weather or food conditions than usual, while a decreased state is similar to less favourable conditions. Under these differing conditions the shape of the trade-off function could be variable. The results presented in here suggest that when there are more favourable conditions which have a positive effect on body state, breeding birds will invest more heavily in reproduction, and when conditions are poor, the reverse is true, and somatic investment is maintained at the expense of reproduction. This thesis also indicates that energy reserves at the start of foraging could be important throughout the reproductive cycle of an individual.

This study does not however consider nestling state changes as a component of the state as a family as a whole, under differing conditions. Instead I have assumed that all nestlings were in comparable state independent of manipulation group. This assumption is valid as all broods experienced comparable natural ambient temperatures overnight, and therefore, were likely to emerge in similar states.

The data presented here have provided some of the few studies which have successfully manipulated individual state, in an efficient way and subsequently detected an energetic and behavioural response. The magnitude of the response was of a size easily picked up by the doubly labelled water and standard behavioural techniques. This suggests that state is a vital element in this trade-off, but leaves the way open for more extensive investigation of the role of state on other components of reproductive effort.

This thesis has shown that birds in a positive state will increase energy expenditure and nest visitation rates. The increase in energy expenditure was more than the amount of energy saved by the bird by the overnight temperature manipulation. Sustained high levels of energy expenditure have been seen to detrimentally affect parental survival (Daan *et al.* 1996; Lemon 1993), however it is expected that birds will resume a 'control'

level of expenditure after 24h, due to the short-term nature of the manipulations employed in this thesis

6.2 State-dependent Life History Theory

Traditional views of life history theory place age at the centre of each life history model (Hutchings 1993; Smith 1995; Tatar *et al.* 1996; Wiebe & Martin 1998). State-dependent models do not necessarily negate age as an important state variable, but are simply an attempt to define life history strategies in more detail, by discovering which variables are important in determining an individual's resource allocation strategy. With the aid of stochastic dynamic programming this can then be interpreted at the population level and give a useful insight into life history evolution (Houston & McNamara 1992; McNamara & Houston 1992; McNamara & Houston 1996).

Empirical studies of the type reported in Table 6.1., and those presented in this thesis, are based at the individual level and therefore can give insight into the state variables to be considered when modelling at the population level. They also provide support for the state-based approach to life history theory, given that they have been identified during a relatively brief period of research and are not an example of publication bias emerging over a long period of time. The examples shown in Table 6.1. have been selected under certain criteria: 1. They have manipulated or measured a change in the state variable tested, and 2. They have observed a behavioural or physiological response as a result of that change in state.

Table 6.1. Examples of empirical studies of state-dependent behaviour, showing the year of publication, species studied, state variable identified by study and the various methods used to quantify changes in the differing activities observed in these studies. In the Methods column C and E represent correlative or experimental study respectively.

Year	Species	Class	State variable tested	Methods	State-mediated activity	Author(s)
1990	<i>Turdus merula</i>	Bird	Nutrition	E	Dawn chorus	Cuthill & MacDonald
1992	<i>Aquila adalberti</i>	Bird	Body condition	C	Natal dispersal	Ferrer
1993	<i>Ground squirrels</i>	Mammal	Body condition	C	Risk taking/ foraging	Bachman
1993	<i>Larus fuscus</i>	Bird	Flight muscle density	E	Egg laying	Bolton <i>et al.</i>
1994	<i>Uroleucon jaceae L.</i>	Insect	Nutritional quality/ condition	E	Predator avoidance	Stadler <i>et al.</i>
1994	<i>Sturnus vulgaris</i>	Bird	Body mass	E	Foraging / predation risk	Witter <i>et al.</i>
1995	<i>Capreolus capreolus</i>	Mammal	Body condition	C	Natal dispersal	Wahlstrom & Liberg
1995	<i>Uca beebei</i>	Crustacean	Food availability/body condition	E	Mate signalling	Blackwell <i>et al</i>
1995	<i>Tachycineta bicolor</i>	Bird	Body condition	E	Egg laying	Winkler & Allen
1995	<i>Hylobates pelagica</i>	Bird	Nestling energy reserves	E	Brood rearing	Bolton
1995	<i>Halobaena caerulea</i>	Bird	Body mass	C	Incubation	Chastel <i>et al.</i>
1996	<i>Arctic fox</i>	Mammal	Body condition	C	Natal dispersal	Tannerfeldt & Angerbjorn
1996	<i>Vireo olivaceus</i>	Bird	Fat reserves	E	Migration	Sandberg & Moore
1996	<i>Hylobates pelagicus</i>	Bird	Body mass	C	Foraging/incubation	Bolton
1996	<i>Buthus occitanus</i>	Crustacean	Mass / body size ratio	C	Risk taking / foraging	Skutelsky
1997	<i>Hirundo rustica</i>	Bird	Body cond./testosterone levels	C	Mate signalling	Galeotti <i>et al</i>
1997	<i>King penguin</i>	Bird	Body condition	C	Incubation	Olsson
1997	<i>King Penguin</i>	Bird	Body condition	C	Incubation	Olsson & Brodin

Table 6.1. continued. Examples of empirical studies of state-dependent behaviour. Table shows the year of publication, species studied, state variable identified by study and the various methods used to quantify changes in the differing activities observed in these studies. In the Methods column C and E represent correlative or experimental study respectively.

Year	Species	Phylum	State variable	Methods	State-mediated activity	Author(s)
1997	<i>Charr</i>	Fish	Body condition	E	Risk taking / foraging	Damsgard <i>et al</i>
1997	<i>Lepomis macrochirus</i>	Fish	Body size	C	Overwinter survival	Carnigelli
1997	<i>Venturia canescens</i>	Insect (para)	Energy reserves	E	Egg laying	Sirot
1998	<i>Otus asio</i>	Bird	Fat reserves	C	Fledging	Beltoff & Duffy
1998	<i>Fratercula arctica</i>	Bird	Nestling energy reserves	E	Brood rearing	Wernham & Bryant
1998	<i>Salmo salar</i>	Fish	Body mass	E	Diurnal foraging	Metcalfe <i>et al</i>
1998	<i>Turdus merula</i>	Bird	Body mass	C	Foraging	Creswell
1998	<i>Thalassoica antarctica</i>	Bird	Parent and nestling body condition	C/E	Brood rearing	Tveraa
1999	<i>Gryllus lineaticeps</i>	Insect	Nutritional status	E	Mate signalling	Wagner & Hoback
1999	<i>Erithacus rubecula</i>	Bird	Fat reserves	E	Daily singing	Thomas
1999	<i>Oceanodroma leucorhoa</i>	Bird	Nestling energy reserves	E	Brood rearing	Takahashi <i>et al</i>
1999	<i>Ovis canadensis</i>	Mammal	Body mass	C	LRS	Berube <i>et al</i>
1999	<i>Onchorhynchus kistutch</i>	Fish	Body size	E	Risk taking / foraging	Reinhardt & Healey
2000	<i>Shearwaters</i>	Bird	Nestling energy reserves	E	Brood rearing	Granadeiro <i>et al</i>
2000	<i>Erithacus rubecula</i>	Bird	Dawn energy reserves	E	Winter foraging	Godfrey & Bryant

6.3 Patterns within empirical studies of body state

6.3.1 Predation risk and foraging activity

All individuals need to forage for resources in order to maintain themselves and any current activity, such as reproduction. During a reproductive event parents will be foraging for their offspring as well as themselves, but during non-breeding months their effort will be allocated to survival to the next or first reproductive event. When individuals forage they have to balance the benefits of gaining food against the potential costs of their increased activity alerting predators. Reinhardt & Healey (1999) reared juvenile Coho salmon (*Oncorhynchus kistutch*) of two size groups with varying food rations and studied the risk-taking behaviour of these fish. Smaller fish took more risks than larger ones and lack of food caused more risk taking in smaller fish, but not larger ones. This study suggests that Coho salmon use their own body size as cues for long-term, state-dependent feeding behaviour. Cargnelli & Gross (1997) also found similar results in bluegills (*Lepomis macrochirus*). Although these two studies provide good evidence for body size being a significant state variable, an improvement would have been a manipulation of body size via selection experiments, rather than arbitrary size classes. State-dependent shifts in diurnal activity were found in a study undertaken by Metcalfe *et al.* (1998) on salmon, where behaviour was mediated by an individual's mass. Similar results were found in Arctic Charr, where starvation risk mediated risk-taking behaviour (Damsgard *et al.* 1997).

Work in this area is not exclusive to fish, however (Bachman 1993; Cresswell 1998; Godfrey & Bryant 2000; Skutelsky 1996; Stadler *et al.* 1994; Witter *et al.* 1994). Godfrey & Bryant (2000) used similar methods to those presented in this thesis, manipulating energy expenditure in the European Robin (*Erithacus rubecula*) via overnight temperature during winter months. Birds which had undergone a negative manipulation (chilled) were less likely to vocalise, but showed increased energy expenditure due to increased foraging. Those, which had been warmed, however, showed foraging strategies similar to Control birds, but engaged more in vocal behaviours. This is one of the clearest examples of a direct manipulation on energy reserves affecting behaviour. Another experimental study used additional artificial mass loads to increase body mass, and food restriction to decrease body mass, in the European starling (*Sturnus vulgaris*) (Witter *et al.* 1994). Birds with additional mass showed changes in flight takeoff parameters, which ultimately lead to changes in

predator avoidance strategies. Those with higher mass left cover late and spent more time under cover, conversely, those with lowered mass spent more time foraging.

It is apparent from the examples cited in this section that physiological state variables, such as energy reserves or body size, are key factors in the trade-off between the need to forage to sustain somatic investment and other components of fitness, such as reducing predation risk, seeking mates or defending a territory.

6.3.2 Natal dispersal and body condition

Belthoff & Dufty (1998) presented a model of natal dispersal in juvenile screech owls (*Otus asio*). This model predicted that owls with sufficient fat reserves would disperse when corticosterone reached appropriate levels in the blood plasma, but those with inferior fat levels would be unable to disperse following this cue. Dispersal reduces sibling competition and thus would allow the lower quality males to improve body condition and eventually disperse, although those which dispersed first would no doubt gain a significant advantage. The predictions of this model were confirmed in field observations, where better quality juveniles dispersed first. In this case the 'state variable' of interest is body condition, or fat reserves, although birds may also take account of other variables not measured here, before choosing to disperse, such as territory quality or weather conditions, or perhaps even the quality of its sibling(s). Although the model created in this study seems intuitive, a much better empirical test could have been performed by manipulating body condition and corticosterone levels of juvenile owls.

It has also been suggested in another raptor, the Spanish Imperial Eagle (*Aquila adalberti*), that dispersal tendency is due to individual state variables rather than being genetically determined (Ferrer 1992). State-dependent behaviour has also been used to describe dispersal patterns in mammals such as the Arctic fox (Tannerfeldt & Angerbjorn 1996). Dispersal of Roe deer (*Capreolus capreolus*) is related to population density, but (Wahlstrom & Liberg 1995) have proposed that dispersal is also due to an interaction of body condition with different population densities, as heavier individuals tended to disperse from the population. It would seem that the most important state variable in dispersal decisions is that of body condition and that these decisions are made to maximise survival and other fitness components.

6.3.3 State-dependent signalling

Signalling of male quality to attract a mate can be energetically expensive and thus is normally thought to be honest in nature (Vehrencamp *et al.* 1989; Backwell *et al.* 1995; Mappes *et al.* 1996; Veiga & Puerta 1996). However, the intensity of signalling may be limited by resources and a trade-off exists between this and somatic investment. If an individual is given extra food resources, however, then we would expect signalling to increase in intensity if it is honest. An experimental manipulation of food availability was performed on male fiddler crabs (*Uca beebei*) (Backwell *et al.* 1995), which build small mud pillars close to their nest to attract females. After food supplementation the number of pillars increased two fold, but the proportion of males within the population building pillars did not change. This suggests a trade-off, but it also shows that pillar building can be attributed to individual state. It would be an interesting study to introduce a negative manipulation of some kind into this system. One very interesting experimental study is that of Wagner & Hoback (1999). Female variable field crickets (*Gryllus lineaticeps*) prefer males with a high chirp rate and long chirp duration. These higher chirp rates are energetically costly, and thus, Wagner & Hoback (1999) tested the chirp rate and duration of male cricket signalling in relation to nutritional status, by manipulating the nutrition available to two groups of crickets. Males on a high-nutrition diet called at significantly higher chirp rates. Thus males invest any surplus power into chirping which will attract a mate, as males showed no differences in mass. This suggests a state-mediated system. The direct manipulation of the nutritional value of food has its problems, but it is preferable to simply increasing food supplies, and is an attempt to manipulate a potential state variable, similar to the approach taken in this thesis, rather than confounding state and food availability. Thomas (1999) used food supplementation to increase short-term foraging success in the European Robin (*Erithacus rubecula*). Birds increased song output following supplementation, however, ambient temperature also had a significant effect on song output. This again suggests that body reserves are important in evaluating the expression of a signal.

6.3.4 Optimal allocation of resources to reproduction

Few studies of 'state' have been focused on reproduction and to date most are correlative in their nature. Olsson (1997) and Olsson & Brodin (1997) have provided some of the best correlative evidence for state-dependent decisions during reproduction, suggesting that body condition and food availability are the main determinants of

reproductive investment in King Penguins. Olsson (1997) also showed that male incubating penguins base the decision to abandon their egg purely on their own energy reserves. Berube *et al.* (1999) provides evidence for long-term state-dependent behaviour in Bighorn sheep (*Ovis canadensis*). The longest lived ewes in this study had the highest body mass when young adults and this a high reproductive success throughout their lifetime, suggesting body size to be a viable state variable upon which to base reproductive decisions in this species. Several recent studies have manipulated offspring body reserves in an attempt to determine reproductive costs and the regulation of food provisioning and parental body condition (Bolton 1995; Granadeiro *et al.* 1998; Takahashi *et al.* 1999; Tveraa 1998; Wernham & Bryant 1998). Wernham & Bryant (1998) experimentally decreased energy demand in nestling puffins (*Fratercula arctica*) by supplementary feeding. This led to a decrease in parental provisioning rates, as parents made the decision not to feed nestlings in a positive state, whilst maintaining their own body condition. Takahashi *et al.* (1999) also used supplementary feeding of nestlings in the Storm Petrel to increase body reserves, and observed similar results as Wernham & Bryant (1998). However they also decreased the initial amount of food delivered to the nestlings, and thus diminished body reserves, by removing one provisioning parent. Following this manipulation the remaining parent increased feeding rates but did not fully compensate for its partner, again body condition was maintained. In the above examples parent birds maintained their own body condition whilst changing their nestling provisioning rates. This suggests that there is a threshold level of condition which below which an individual would experience an unacceptable reduction in the probability of survival. The results presented in this thesis concur with this.

Although mate removal will ultimately lead to lower nestling body reserves, it may also have another conflicting effect upon the behaviour of the remaining individual. A much neater manipulation here would have been to remove food when it was delivered, or to have directly manipulated nestling state via temperature manipulations. The above studies, however, do show that the physiological state of offspring can in fact be a state variable, which parents will use to determine resource allocation. The lack of good experimental studies in the area of reproduction is likely to change, as the discussion of the part state has to play in life history theory develops.

Table 6.2. Summary of studies shown in Table 6.1. Table shows the number of studies with stated methods, state variables and activities monitored. A taxonomic breakdown of these studies is also shown.

Classification	Bird	Mammal	Fish	Invertebrate	
	19	4	5	4	
Activity	Pre-brood rearing	Brood rearing	Post-brood rearing	Non-reproductive	Other
	9	5	4	13	1
State variable	Body size/mass	Body condition	Energy reserves	Offspring state	Other
	8	16	2	4	1
Methods	Experimental	Correlative			
	17	15			

6.4 Summary of evidence

The majority of empirical work described in the above section is based on vertebrates (84%). This is possibly because vertebrates are easy to manipulate or observe in their natural environments and offspring can be easily monitored as most perform intensive parental care and conspicuous foraging. From all the studies quoted here approximately half are observational in nature (Table 6.2). Although purely observational and correlative data can provide some useful insights, it is those studies which have manipulated a trait in order to gain a behavioural response which give the clearest quantitative results and can be best used to determine key state variables. There are several examples of manipulative studies on birds during reproduction, however, they chose to manipulate nestling state and thus had only the potential to affect parental state, converse to those studies in this thesis. Those studies which do manipulate state variables are using either indirect manipulations, such as nestling state, or are manipulating individuals via food supplementation or restriction, i.e. via their extended phenotype. This method of manipulating body condition is quite common, however it does pose problems, including that of confounding factors, which the studies shown in this thesis have attempted to overcome by using direct temperature manipulations of energy reserves. More specifically, these problems include:

Firstly when providing extra food within the environment, it is hard to ensure an even distribution of resources to all manipulated individuals, increasing error within the resulting variation. Since there is already a wide range of variation across individuals in terms of quantifiable behaviour, it is obviously best to choose the most appropriate and efficient manipulation. The acceptability of food supplementation as a state manipulation is not clear. An increased exposure to food, for example, may alter individual state variables, but it may also be interpreted by the subject as a cue for increased food availability in the long-term. Any subsequent behavioural changes may then be due to individual perceptions of future success rather than being a response to the current state.

If food supplementation is used during the rearing of offspring, it is also hard to determine the flow of resources. Individuals with increased food resources may choose to allocate the extra food to their offspring in addition to themselves, therefore changing foraging behaviour. The causes of any subsequent behavioural changes would then be hard to tease apart from each other. It is better practice to only manipulate one variable.

Only one other study shown here has used temperature manipulation as a direct manipulation of body reserves.

Other manipulations, which could have been used to directly affect parental provisioning in this thesis such as brood size changes or hormones, were not used. This was because it was my intention to only manipulate parental energy reserves and behaviour. Both decreased and increased brood size would affect the thermoregulatory effects of huddling, thus affecting brood behaviour. The effects of hormones whilst increasing or decreasing metabolism would have been hard to quantify, and may also have had further side-effects, again adding to error. Denardo & Sinervo (1994) found that side-blotched lizards (*Uta stansburiana*), when implanted with high doses of corticosterone showed reduced competitive advantage and settled for smaller home ranges. Thus, corticosterone may have been a useful manipulation method, however, behavioural side-effects may confound any response seen. Other naturally occurring hormones, which may have been used in this context and the action they have upon metabolism, are summarised in Table 6.3. It is clear that each potential hormone affecting metabolism and behaviour carries with it a potentially confounding effect. Thus, it was decided since individuals undergo changes in ambient temperature within a normal day, overnight temperature changes would provide a model more applicable to a natural situation and would be less liable to confounds. However the temperature manipulations used in this thesis may still carry perceptual confounds.

Table 6.3. Summary of hormones and their actions which could have been used instead of temperature manipulations in this thesis. Potential side-effects are also presented.

Hormone	Specific action	Side-effects
Testosterone	Increases aggression. Increase in muscle mass.	Not affecting energy as such, merely decreasing parental behaviour.
Corticosterone	Increases metabolism of fats and protein.	Causes confound as initially gives extra energy, but decreases reserves. Response would be hard to interpret.
Insulin	Promotes fat storage	Increases reserves, but on coarse level, may increase mass and thus flight costs.
Glucagon	Promotes the breakdown of fats	Similar to corticosterone and may induce mass-dependent flight costs.
Melatonin	Regulates sleep patterns	Hard to quantify changes in sleep patterns and keep constant within groups.
Adrenalin	Increases metabolic rate	Changes in behaviour associated with 'flight or fight' mechanism.
Thyroxine (or TSH)	Increases metabolic rate	Potential changes in behaviour from increased metabolic rate.

6.5 Stochastic Dynamic Programming.

6.5.1 State-dependent life history equations.

Houston & McNamara (1999) have produced an equation, which encompasses state-dependent life histories, and defines the expected number of descendants left in a particular state (y) after one reproductive cycle (i.e. fitness), by an individual in state x with a chosen reproductive action (u):

$$a_{xy}(u) = S_{\text{mat}}(x;u) P_{xy}(u) + N_{\text{off}}(x;u) b_{xy}(u)$$

Where S_{mat} is the probability that an individual taking action u in state x survives to the next reproductive event; P_{xy} is the probability that an organism in state x at time t is in state y at t + 1; N_{off} represents the number of offspring produced between t and t+1 which survive until t+1; and b_{xy} is the probability that an offspring which survives until t+1 is in state y at this time.

This study can provide discussion for the terms S_{mat} and $P_{xy}(u)$ in this equation, as this study did not attempt to monitor nestlings in great detail (i.e. mass at dawn; growth) and did not manipulate nestling condition. There is also the potential confound of nestling growth in the latter stages of nestling development.

If u is equated to reproductive effort, for example, and measured by changes in energy expenditure and nest visitation as in this study, then reproductive effort depends upon an individual's state. We would then expect to see a survival function (S_{mat}) decreasing for u and fixed for x. This relationship we have seen in the data provided in these chapters. Reproductive effort was state-dependent, however, it was only enhanced when birds were left with extra energy at dawn. So, birds in a positive state are more likely to invest in reproduction, whilst survival in this study was held constant, in terms of mass and fat score, although there may be additional deleterious or advantageous effects on survival we did not or could not measure them.

When considering $P_{xy}(u)$, we would expect with increasing u (u = reproductive effort), a decreasing probability of high states and an increasing probability of low states at t+1. This is assuming that the state variable is body condition, which can be measured in a

variety of ways, including mass and fat score, and that increased reproductive effort will depress condition. In this study an increase in effort was only brought about by an 'energetic cushion' and thus body condition was not sacrificed over the time period of our trial. In terms of energy reserves the birds which were given extra energy and those which had an energy deficit will all probably have similar energy reserves the next morning. This study has only performed short-term energy manipulations in order to examine the role of energy status in mediating reproductive behaviour. However, birds will naturally differ in state, due to past weather conditions, brood size, and individual quality, and so the process of using internal state to aid in resource allocation decisions will occur day after day throughout an individual's life. Thus, although our results show that energy reserves at dawn are an important state variable it is not the only one, and any discrepancies between our empirical data and theory are likely to be due to our simplified definition of state.

6.6 *Modelling the effects of overnight expenditure on foraging behaviour.*

Rands (2000) has produced a stochastic dynamic model, which encompasses the effects of changes in overnight temperature upon the trade-off between self feeding and provisioning nestlings. This model was based upon a starling-sized bird, but since an energetic and behavioural response to temperature manipulations were seen in both study species used in this thesis, then the potential for a general rule follows.

The outcome of Rands' modelling of diurnal patterns shows most individuals foraging for nestling at the start of the day. As the day continues the number feeding their offspring declines and provisioning is replaced by self feeding, followed, in turn, by a sharp decrease in provisioning whilst the majority of the population rest or brood young. During the mid-afternoon nestling provisioning will increase once more and continue until nightfall. This description of events is also intuitively correct, and consistent with the widely-held belief in a mid-day lull in activity.

When modelling the effects of overnight temperature upon state, and the subsequent allocation strategies employed, the same state variable is used as in this thesis, i.e. energy reserves at dawn. Figure 6.1 shows the optimal policy for one day generated from the Rands model. When parental reserves are high the parent should rest, only initiating offspring provisioning when nestling states fall below a certain threshold (Figure 6.1). The inconsistency between Rands (2000) model and my results are due to

the model's linkage of parental and nestling state. Because this model is based upon natural changes in overnight temperature and not the manipulations undertaken in this thesis, parental state has to be linked to nestling state. Thus when parents are in high states, the nestlings are too. This poses a conflict and makes the model hard to interpret in terms of my experiments. Since all nestlings in my study were assumed to be in comparatively similar states at the end of the overnight period, then parental and offspring states are not linked in these experiments. Thus warmed parents may have 'expected' their nestlings to be in similarly high states, would have discovered upon returning to the nest after release that this was not the case. Since nestling begging is thought to be honest in nature, parents responded to this by increasing provisioning and using all of their extra reserves in reproductive effort. Low parental reserves mean that the parent should feed itself at the expense of nestling provisioning (Figure 6.1.). This is consistent with the results of Chapter 2 in this thesis. However, it is difficult to calculate the region of Figure 6.2, which includes the manipulations described in this thesis, due to the units of scale of the x and y-axis. This model provides a good framework from which to draw conclusions about parents feeding birds in natural circumstances. The experiments described in this thesis provide evidence for parental behaviour in birds being mediated by physiological state. The differing predictions emerging from Rand's model (Rands 2000) complement the empirical patterns observed here, in that they provide theoretical support for a close linkage between body state, behaviour and reproductive effort.

6.7 Summary

This study has provided evidence for state-dependent behaviour in passerine birds during brood rearing, the period in the annual cycle when most parent birds are 'working' hardest. It is more likely that a trade-off will be exposed at a time of high energy expenditure and parental effort. In assuming survival and fecundity are solely related to age, an assumption typical of many life history models, we assume age is the only state variable, which is obviously not the case, as has been demonstrated here. Houston & McNamara (1999) in their recent book state that in order to construct a state-dependent life history model, several pieces of information are needed. This has been the major flaw in many empirical studies to date, which have not manipulated the potential state variable. This study provides some of the first evidence for a state variable, which should be applicable across species: energy reserves at dawn.

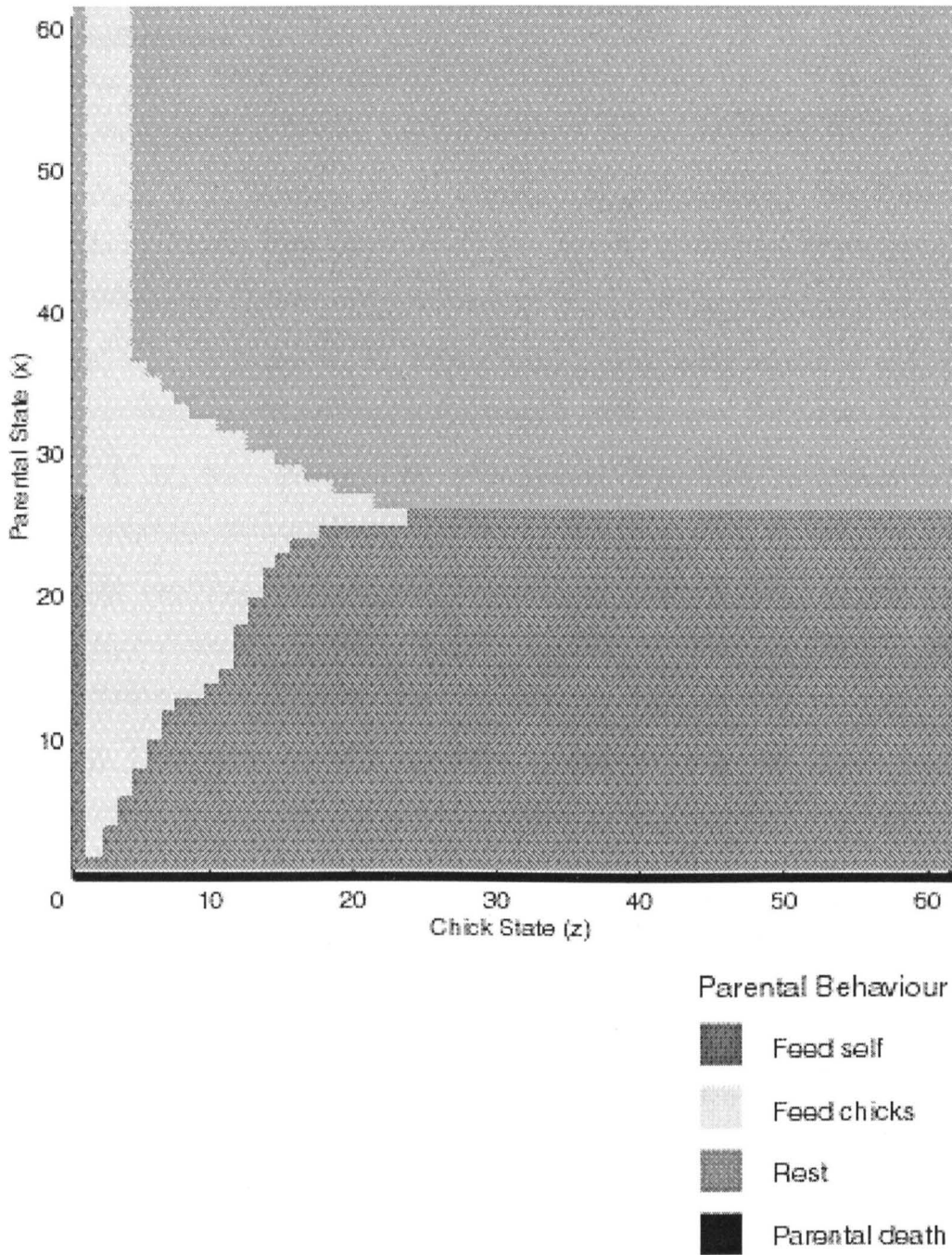


Figure 6.1. Optimal policy generated from Rands (2000) model. Parental behaviour is split into four groups: feed self; feed chicks; rest and death. Death occurs when parental state = 0. Both parental and nestling state are measured in dynamic programming units. With kind permission from Sean Rands.

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