Resource Allocation During Avian Incubation

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Declaration

I declare that the work recorded in this thesis is entirely my own and that it is of my own composition, except where stated below. No part of this thesis has been submitted for any other degree.

Chapter three was written jointly by myself, Pat Monaghan and Ruedi Nager. I was first author of the manuscript.

Pat Monaghan and Graeme Ruxton commented on earlier drafts of chapters four to nine.

Jane Reid

January 2001

For Su and George,

with love and heartfelt thanks for all those 3am Sunday lifts up the road.

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Abstract

The ways in which birds allocate resources during the incubation phase of reproduction were investigated using empirical data gathered from populations of starlings (*Sturnus vulgaris*) breeding in Shetland and Spain, and modeling. The consequences of the allocations made to incubation for the resources allocated to other phases of life are discussed.

Experimentally reducing the energetic demand of incubation by reducing the rate of heat loss from within a nest increased the proportion of offspring that fledged during the same breeding attempt, and the proportion of clutches that hatched completely during the subsequent attempt. Thus the energetic demand of incubation was shown to be sufficient to limit parental fitness, and was suggested to influence the way in which parents allocated resources to other reproductive phases, both within and between breeding attempts.

Starlings nesting in poorly insulated cavities built larger nests and reduced the rate of heat loss from within the cavity to a greater extent than starlings nesting in well-insulated cavities. However, the rate of heat loss from within a completed nest was still related to the insulative quality of the original cavity. As experimentally reducing heat loss rate increased breeding success, the acquisition of a well insulated nest site was suggested to be an important phase of a starling's breeding attempt.

Experimentally reducing the rate of heat loss from a nest also increased mean incubation-bout duration and thus the proportion of the day that female starlings spent incubating. This change is consistent with the hypothesis that parents terminate incubation bouts in response to their own condition rather than to egg temperature. The contradictory results of previous studies may be explained if, given energetic limitation during incubation, parents leave the nest when the costs of doing so are minimised.

As a consequence of the time that incubating females allocated to activities away from the nest, eggs experienced mean temperatures that were below the predicted optimum for embryonic development. However, female nest attentiveness and mean egg temperature increased as the incubation period progressed, a change that may have been due to increased allocation to incubation rather than to changes in the demands of incubation or to improved foraging conditions.

Experimentally enlarging a clutch for the duration of the incubation period reduced the proportion of the original clutch that hatched, and the proportion of offspring that fledged successfully. This is likely to have been because the addition of extra eggs directly affected the physical conditions experienced by the embryos, and affected a parent's ability to incubate the entire clutch equally. Clutch enlargement may also energetically constrain a parent's incubation ability. However, modeling suggested that the energetic debt accrued by an incubating parent does not necessarily increase with increasing clutch size, with the exact relationship depending on mean incubation temperature and the thermal properties of the clutch. Thus the consequences of incubation demands for optimal clutch size in birds are not necessarily clear.

Male assistance with incubation was suggested to increase the proportion of offspring that hatched and fledged successfully and reduce the time that females spent incubating, and therefore to increase female fitness. However, male assistance was associated with monogamy. As male fitness may generally be maximised by polygyny, sexual conflict over male incubation was predicted. Males were suggested to incubate when they were unlikely to attract multiple females. However, primary females may have increased the chance that a male would incubate by destroying secondary females' clutches.

In conclusion, incubating a clutch of eggs can require substantial allocations of parental time and energy, affecting the resources available for and required by other life phases. Thus incubation can be costly, although costs may be state-dependent, and act through parents and/or their current offspring. Incubation demands may therefore be sufficient to influence overall resource allocation patterns and life-history strategies in birds.

Chapter one

General Introduction

A huge variety of life-history strategies is observed within the natural world. Traits such as an organism's lifespan, its age at first breeding, the number of reproductive attempts made and the number of offspring produced during each attempt can all vary greatly, both within and between species.

An observed life-history strategy arises from the way in which an organism allocates available resources between the different phases of its lifetime. During any phase an individual must 'decide' how much to invest in growth and the maintenance of its own body, and in reproduction (Roff 1992; Stearns 1992). Over evolutionary time the ways in which resources are allocated have consequences for, and are further influenced by, major biological phenomena, such as the organism's morphology and physiology, and the social structures of communities (Horn & Rubenstein 1978; Clutton-Brock 1991). The factors that shape resource allocation patterns and consequent life-history strategies are therefore of considerable academic interest. Further, in the context of our increasing need to manage wild communities, the ability to predict the likely responses of life-history traits to environmental change is increasingly becoming of applied value (Crick *et al.* 1997; Aviles *et al.* 2000; Dahlgren & Sobel 2000; Reindorf *et al.* 2000; Saether & Bakke 2000; Siriwardena *et al.* 2000). Thus, gaining an understanding of the ways in which organisms allocate resources between different activities has become a major goal of behavioural ecology, attracting considerable theoretical and empirical study (Newton 1989; Roff 1992; Stearns 1992; McNamara & Houston 1996; Daan & Tinbergen 1997).

As discussed in more detail in ***chapter two*** of this thesis, life-history theory has been developed as a framework within which observed life-history traits can be interpreted in terms of patterns of resource allocation. Such interpretation requires an understanding of the ways in which the resources allocated to any individual life phase can affect the resources available for others, and hence the fitness costs and benefits associated with the resource allocation made to any particular phase. An important means of gaining an understanding of such costs and allocation patterns is the experimental manipulation of natural allocations and the observation of the animal's consequent responses, both within and between reproductive events (Partridge 1992; Roff 1992; see Box 2.1 on page 26 for further explanation and discussion).

For several reasons, birds are good model species on which to carry out such experiments. Basic aspects of bird biology and physiology are relatively well understood, and the natural histories of many species have been recorded in detail, providing a solid base of knowledge on which to build. Many birds are iteroparous breeders, allowing investigation of the ways in which resources are allocated between different reproductive attempts. Further, individual breeding attempts can generally be divided into the relatively discrete periods of courtship and nest building, egg production, incubation and chick rearing, and the resource requirements of different phases can be manipulated independently of each other. Thus birds provide useful systems in which the consequences and determinants of within-attempt allocation patterns can be investigated (Lessells 1991; Monaghan & Nager 1997).

However historically, equal importance has not been attached to the demands and fitness costs of each phase of avian reproduction. Instead, the demand of chick-rearing has long been assumed to impose the greatest constraint upon parents' reproductive rates, and thus to be the major influence on avian resource allocation patterns and life history traits. For example, David Lack (1947) proposed that the optimal number of eggs for a bird to lay should be determined by the maximum number of offspring that parents are able to raise successfully. The majority of the experimental tests of this hypothesis have manipulated the number of chicks that a parent must provision (Roff 1992), making the assumption that chick-rearing demands limit breeding productivity. Further, experimental studies investigating issues such as the consequences of mate removal for breeding success, the existence of reproductive costs, and patterns of division of parental care have been carried out predominantly during the chick-rearing period (*eg*, Wright & Cuthill 1989; Johnson *et al.* 1992; Riedstra *et al.* 1998; Moreno *et al.* 1999; Murphy *et al.* 2000). In comparison, the possible evolutionary importance of the resources allocated to earlier reproductive stages has been largely disregarded (Monaghan & Nager 1997). However, there has been an increasing realisation that such tight focussing on the chick-rearing phase may limit our understanding of overall resource allocation patterns. In particular, experiments have repeatedly shown that contrary to the prediction of Lack's brood size hypothesis, parents are often able to successfully rear experimentally enlarged broods (Linden & Møller 1989; Ydenberg & Bertram 1989; Dijkstra *et al.* 1990). A number of possible explanations for this discrepancy have been suggested whilst still focussing on chick-rearing demands (Lessells 1991). Optimal brood size may be lower than expected if caring for a large brood reduces a parent's residual reproductive value (Charnov & Krebs 1974; Nur 1984), if brood parasitism is likely (Rothstein 1990), or if environmental variation precludes individual optimisation of traits (Dhondt *et al.* 1990). However, optimal clutch size may equally be limited by constraints imposed during earlier reproductive phases, such as the demands of building a large enough nest to hold the clutch, or of producing or incubating a large number of eggs (Slagsvold 1989; Monaghan & Nager 1997; Thomson *et al.* 1998).

The realisation that the demands of early reproductive stages may play an important role in the evolution of avian life history strategies has lead to a series of recent studies on the demands and costs of egg production. Such experiments have shown that producing extra eggs can affect egg and offspring quality (Monaghan *et al.* 1995; Nager *et al.* 2000), and also the provisioning ability and subsequent fitness of the parents (Heaney & Monaghan 1995; Monaghan *et al.* 1998; Nager *et al.* in press). Hence egg production can be sufficiently demanding to influence major life history traits. However, the extent and nature of the fitness costs associated with incubation, the process by which birds modify the physical environment of their eggs (Beer 1964), have still received relatively little attention. This is despite the fact that the temperature, gaseous environment and degree of physical disturbance that embryos experience whilst within the eggs greatly influences their development and survival (Lundy 1969; Drent 1975; Carey 1980; Webb 1987), and that the provision of optimal conditions for offspring during the incubation period can impose substantial time and energy demands on incubating parents (Yom-Tov & Hilborn 1981; Drent *et al.* 1985; Williams 1996; see ***chapter two*** for further discussion).

Using field studies on starlings (*Sturnus vulgaris*) breeding in Shetland and Spain and theoretical modeling, this thesis investigates the demands, fitness costs and patterns of resource allocation associated with the incubation phase of avian reproduction. The ways in which parents allocate resources in order to meet demands, the consequences of these allocations, and the means by which parents may be able to minimise incubation demands are discussed.

Chapter two is a review chapter written for the forthcoming Oxford University Press book *Avian Incubation*. It discusses in more detail the need for an understanding of the fitness costs associated with incubation, and presents a review of the existing evidence that such costs exist. ***Chapter two*** also discusses the ways in which fitness costs of incubation arise, the circumstances under which they occur, and the ways in which costs may be distributed between parents and offspring. ***Chapter three*** reports an experimental demonstration of a fitness cost of incubation in starlings breeding in a cool climate. ***Chapters four*** and ***five*** consider the consequences of the idea, introduced in ***chapter two***, that a trade-off exists between the time that an incubating parent spends foraging, and the time spent incubating the clutch. These chapters discuss the ways in which parents allocate time to incubation both from moment to moment when deciding when to terminate the current incubation bout (***chapter four***), and in terms of the total time allocated to incubation per day (***chapter five***). ***Chapter five*** also considers the consequences for the offspring of the parent's time allocation to incubation. ***Chapter six*** presents a model of the relationship between a parent's own energy level and the temperature at which it maintains its clutch. The model clarifies the consequences of the time allocated to incubation for the condition of the parent and the temperatures experienced by the developing offspring, and discusses the reasons for the occurrence of energetic limitation during the incubation period. Further, ***chapter six*** assesses the possible energetic consequences for a parent of incubating clutches of different sizes. ***Chapter seven*** describes the consequences of experimentally enlarging the clutch size of starlings, investigating the physical and energetic consequences for incubating parents and for the embryos themselves. Thus ***chapters six*** and ***seven*** investigate the role that incubation demands may play in influencing optimal clutch size in birds.

Given the existence of fitness costs of incubation, birds would be expected to evolve strategies to minimise those costs. ***Chapter eight*** investigates the consequences of biparental rather than uniparental incubation for the developmental conditions experienced by the embryos and the success of the breeding attempt. The circumstances under which males assist females with incubation in a facultatively polygynous starling population are discussed. ***Chapter nine*** discusses the role of nest construction and nest site selection in reducing the rate of heat loss from the clutch and thus in reducing the energetic demand of incubation.

The final discussion (***chapter ten***) briefly reviews the knowledge of the resource requirements and fitness consequences of incubation that has been gained from studying the egg-laying reptiles and mammals, and highlights some of the key areas towards which future studies of incubation might profitably be directed.

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Chapter two

Incubation and the costs of reproduction

J.M.Reid, P.Monaghan & R.G.Nager

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Abstract

Life-history theory invokes the concepts of resource limitation and consequent fitness costs of resource allocations to provide explanations for the ways in which animals allocate resources between different life phases. We investigate the correlative, theoretical and experimental evidence that the resource requirements of incubation can be sufficient to limit parents' ability to invest resources elsewhere, and that fitness costs of incubation consequently arise.

We present the idea that despite adaptations to minimise incubation demands, incubating a clutch is likely to require considerable parental investment of time and energy. We discuss the possibility that an incubating parent's allocation of time to activities other than incubation affects the quality of the developmental conditions provided for the offspring, and is therefore costly in terms of offspring fitness. Further, we investigate whether parental allocation of time to incubation rather than other activities can also result in fitness costs. Specifically, we investigate the limitations that incubating a clutch imposes on the time available for parents to forage, and to sire or care for other offspring. Hence we consider the evidence that fitness costs of incubation arise due to energetic constraints upon the parents, and to lost parenting opportunities. Given resource limitation during incubation, we consider the ways in which incubating parents resolve trade-offs between the resources allocated to different activities, and thus the ways in which fitness costs are manifested in parents and in their current offspring. Finally we discuss the conditions under which incubation costs are manifested, and their state-dependent action in individuals.

Introduction: resource allocation trade-offs during reproduction

Life-history theory is concerned with explaining the diversity of life cycles observed in nature. It provides a framework within which we can interpret variability in how organisms allocate resources between growth, self-maintenance and reproduction, both within and between species.

A central tenet of life-history theory is that resources are finite, and thus that allocations made to one aspect of life will reduce the resources available for investment in others (Roff 1992; Stearns 1992). The consequent competition for resources between different life-history traits will constrain their evolution, with the allocation made to any particular trait reflecting a compromise between conflicting optima. In terms of allocation of resources to reproduction, such constraints and compromises translate into costs of reproduction, defined as the extent to which investment in one reproductive phase reduces a parent's capacity to invest in subsequent phases of the same breeding attempt, or in other attempts. Over evolutionary time, trade-offs between the resources allocated to different phases will be resolved by natural selection so as to minimise overall reproductive costs, maximising an individual's lifetime fitness. Thus, in order for overall resource allocation patterns and consequent life-history strategies to be interpreted, an understanding of the resource limitations and fitness costs associated with each component of reproduction is required.

A high proportion of studies on resource allocation trade-offs and reproductive costs has been carried out on birds. Birds are generally iteroparous breeders, and each breeding event is divided into the relatively discrete stages of courtship and mating, egg production, incubation and chick rearing. Coupled with the relative ease with which avian breeding behaviour can be studied, this means that birds are suitable organisms for investigating resource trade-offs, both between different reproductive attempts and between different phases of the same attempt (Lessells 1991; Heaney & Monaghan 1995, 1996; Monaghan & Nager 1997). However, until recently, such studies have focussed almost exclusively on trade-offs involving the demands of rearing chicks (Lindén & Møller 1989; Dijkstra *et al.* 1990), the assumption being that the resource requirements of early reproductive stages are relatively trivial (Monaghan & Nager 1997). In this chapter, we evaluate the evidence that the time and energy demands of the incubation phase of avian reproduction can be substantial, and can represent an important component of reproductive costs in birds.

Why might incubation be costly?

The way in which avian embryos develop and hence the success of a breeding event is greatly influenced by the physical environment that embryos experience whilst inside the egg. Specific temperatures, humidities and degrees of mechanical disturbance are required to ensure that embryos hatch successfully and in good condition (Lundy 1969; Carey 1980; Webb 1987). However, given fluctuating external conditions and the relative inability of embryos to modify their own environment, parents must generally regulate the developmental environment experienced by their offspring. Brood parasites such as cuckoos achieve this regulation by exploiting environments created by other parents (Davies 2000). White-rumped swiflet (*Aerodramus spodiopygius*) eggs are warmed by the body heat of older chicks still present in the nest (Tarburton & Minot 1987), and megapodes exploit natural heat sources or enclose their eggs within purpose-built mounds of decomposing vegetation (Jones & Birks 1992). However in the majority of species, parents regulate developmental conditions by directly incubating their eggs.

Early models of incubation dynamics suggested that, due to deployment of basal metabolic heat to warm the clutch and the relative lack of physical activity involved in sitting on a nest, incubation may be a relatively undemanding phase of avian reproduction in terms of energy expenditure (Walsberg & King 1978). However, recent studies have shown that maintaining a gradient between the physical conditions within a nest and the surrounding environment can impose considerable energetic demands upon parents (reviewed in Williams 1996). The demand of rewarming cold eggs may be particularly high (Vleck 1981; Biebach 1986), and overall demands may approach those experienced whilst rearing chicks (Moreno *et al.* 1991; Williams 1996; Ward 1996). Further, regulating the embryos' developmental environment requires parents to spend considerable time sitting on the nest, restricting the time available for other activities such as foraging or attracting further mates.

Parents may be able to minimise the resource requirement of incubation to some extent. Nests may be constructed to minimise the rate of heat loss from the clutch (Schaefer 1980; Møller 1984, 1987; Nager & von Noordwijk 1992; *chapter 9*), and nests and nest sites may be selected for their thermal quality (Inouye *et al.* 1981; Walsberg 1981; Hoi *et al.* 1994). Brood patches may have evolved to facilitate efficient transfer of heat to eggs (Bailey 1952), and eggs could be shaped to facilitate efficient packing under the brood patch (Barta & Székely 1997). Division of incubation duties between partners or other helpers at the nest may reduce the time and energy demands imposed upon any one individual (*chapter 8*). Variation in the effectiveness of these measures, and in the discrepancy between external conditions and the optimal developmental conditions for the embryos, means that the resource requirements of incubation will vary within and between species. However in general, the provision of a high quality developmental environment for offspring may require deployment of parental resources, in terms of time and energy, to incubation.

We investigate the correlative, theoretical and experimental evidence that the time and energy requirements of incubation can limit the resources available for investment elsewhere, and thus that resource allocation trade-offs and fitness costs of incubation can arise. We discuss the circumstances under which costs are observed, and investigate the ways in which they are manifested in terms of effects on parents and on their current offspring.

Costs of spending time away from the nest

Particularly for parents nesting in hot, cold or arid environments, allocating time to activities away from the nest and leaving clutches of eggs unattended may allow the conditions experienced by embryos to diverge rapidly from the developmental optimum. Allowing divergence may adversely affect offspring and hence parental fitness in multiple ways. There will be a direct and immediate fitness cost to spending time off the nest if the conditions to which eggs are consequently exposed are severe enough to kill the embryos outright, an occurrence that is most likely in extreme climates. However, as embryos are relatively resistant to short periods of exposure to suboptimal conditions

(Drent 1975; Webb 1987; Sockman & Schwabl 1998), sublethal consequences of divergence may be more common than embryo mortality. Relatively little is known about how the conditions experienced during development influence future phenotype and fecundity in birds. However, poor incubation conditions may impair an individual's future performance, reducing the reproductive value of the offspring (Lindstrom 1999; Metcalfe & Monaghan 2001). The commonest consequence of leaving a clutch unattended is the slowing of embryonic development and hence the elongation of the incubation period (Webb 1987). Indeed, intraspecific variation in the duration of incubation has frequently been related to variation in parental attentiveness (Lifjeld & Slagsvold 1986; Lifjeld *et al.* 1987; Nilsson & Smith 1988; Aldrich & Raveling 1990), and the conditions experienced within the nest can have a greater effect on development rates than intrinsic egg quality (Ricklefs & Smeraski 1983; *Chapter 7*). A prolonged incubation period can adversely affect offspring in several ways. Embryos may expend more energy prior to hatching (Vleck & Hoyt 1980) resulting in greater depletion of resources and poorer hatchling condition, and the time for which a clutch is vulnerable to predation is increased (Perrins 1977; Bosque & Bosque 1995; Tombre & Erikstad 1996). Delayed hatching may itself have a fitness cost if late-fledging offspring are disadvantaged when competing for food or territories, or suffer a reduced chance of accumulating sufficient resources for over-wintering, moult or migration (Arcese & Smith 1985; Pettifor *et al.* 1988; Verboven & Visser 1998; Visser & Verboven 1999). Hence, via detrimental effects on their offspring, incubating parents may accrue considerable fitness costs by allocating too much time to activities away from the nest.

Costs of spending time incubating

Whilst spending time away from a nest may affect parental fitness via their current offspring, failing to allocate time to activities other than incubation may affect parental fitness directly, by affecting their ability to complete the current breeding event, or to breed again either simultaneously or subsequently.

Evidence for fitness costs of incubation arising from energetic limitation

Incubating parents must meet the energetic demand of regulating the nest environment either by foraging or by depleting stored resources. As a parent's body condition can influence both that parent's ability to provision dependent offspring and its chance of surviving to breed again (Bolton 1991; Jones 1992; Golet *et al.* 1998; Wendeln & Becker 1999), allowing body condition to deteriorate during incubation may be costly for a parent, reducing the fitness benefits accrued from both current and future broods. However, foraging and incubation are generally mutually exclusive activities and, unless provisioned on the nest by partners or helpers, incubating parents must leave the clutch unattended in order to find food. A fitness cost due to energetic limitation during incubation would arise if the time and energy demands imposed were substantial enough to prevent parents from maintaining both the nest environment and their own body condition at optimal levels, reducing the survival or fecundity of either themselves or their offspring.

Analysis of time-energy models suggests that incubation may indeed be a marked period of energetic limitation during reproduction (Yom-Tov & Hilborn 1981; Moreno & Hillstrom 1992). This may be because incubation restricts foraging time rather than because the absolute energetic requirement of regulating clutch temperature is prohibitively high (Moreno & Hillstrom 1992; *Chapter 6*). Although these models have been analysed using species-specific parameter values, their conclusions may apply more generally, at least to passerines in which only one parent incubates (Yom-Tov & Hilborn 1981). Thus, especially because incubation periods may often fall before seasonal peaks in food availability, incubation may commonly be a period of time and energy limitation in birds.

Given time and energy limitation, a trade-off between the time that parents spend incubating and the time spent foraging is predicted. Indeed, there is considerable correlative evidence that the way in which incubating birds allocate time between incubation and other activities depends on the balance between endogenous and exogenous resources and hence on energetic state (sensu McNamara & Houston 1996). The time spent incubating can increase with food availability (Drent *et al.* 1985; Rauter & Reyer 1997) and with the occurrence of incubation feeding by a male (Lifjeld *et al.*

1987; Nilsson & Smith 1988; Halupka 1994; Hatchwell *et al.* 1999). In their cross-species analysis, Martin & Ghalambor (1999) found a positive relationship between the level of incubation feeding and nest attentiveness, although Conway & Martin (2000) attach less importance to this trend. Further, individuals that commence breeding in better body condition spend more time on the nest (Lifjeld & Slagsvold 1986; Afton & Paulus 1990; Aldrich & Raveling 1990; Hegyi & Sasvari 1998), suggesting that parents' incubation strategies may often be energy-limited. As changes in attentiveness can affect the duration of the incubation period (see earlier), such energy limitation during incubation may have fitness consequences for offspring and parents. However, conclusive evidence for the existence of a trade-off between incubation and foraging and a consequent fitness cost of incubation must be provided experimentally, by manipulating either the energetic demand of incubation or the ability of a parent to meet that demand, and observing resultant phenotypic changes. Box 2.1 summarises the rationale for such experiments, and outlines the manipulations and fitness measures that could be used to demonstrate costs of incubation. The results of the experiments that have been undertaken are discussed in the main chapter text.

Box 2.1. Demonstration of costs of reproduction.

A fitness cost of any reproductive phase arises when the resource requirement of that phase is sufficient to significantly constrain the resources available for investment in other phases (Roff 1992; Stearns 1992). Such resource limitation will result in trade-offs between the allocations made to different stages, within or between reproductive events (Stearns 1992). Individuals, however, differ in their capacity to allocate resources. Thus the individuals investing most in one activity may also invest most in another, resulting in positive rather than the expected negative correlations between observed allocations. To eliminate such correlations, conclusive evidence for the existence of resource trade-offs and consequent fitness costs can only be provided by experiment. Quantitative genetic experiments can be used to demonstrate genetic correlations between life-history components, and phenotypic consequences of experimentally manipulated resource allocation patterns can demonstrate changes in individual fitness (Reznick et al. 1986; Partridge 1992). Such experiments must be confined to the reproductive phase during which evidence of a trade-off is sought. Although both genetic methods and phenotypic manipulations have limitations (Reznick 1992), only phenotypic methods have as yet been used to estimate fitness costs of avian incubation.

Phenotypic consequences of manipulating resource allocation patterns may be manifested in parents or offspring during current or subsequent reproductive phases. Whilst the inclusive fitness cost of a resource allocation is the quantity that selection will act to minimise, this cost is determined by the sum of all individual phenotypic consequences, and measurement is empirically difficult. Thus in practice, fitness costs of reproduction are usually estimated by examining a small number of phenotypic parameters.

In the context of demonstrating incubation costs, the possible means of manipulating resource trade-offs and measures of subsequent reproductive performance are listed below, together with single examples of studies that have been undertaken. Details and outcomes of all studies are discussed in the main chapter text. Whilst the consequences of manipulating incubation demands for incubation parameters are reasonably well documented (reviewed in Thomson et al. 1998), their impact on the subsequent reproductive phases that may more accurately reflect overall fitness consequences remain relatively unexplored.

Box 2.1 *continued.*

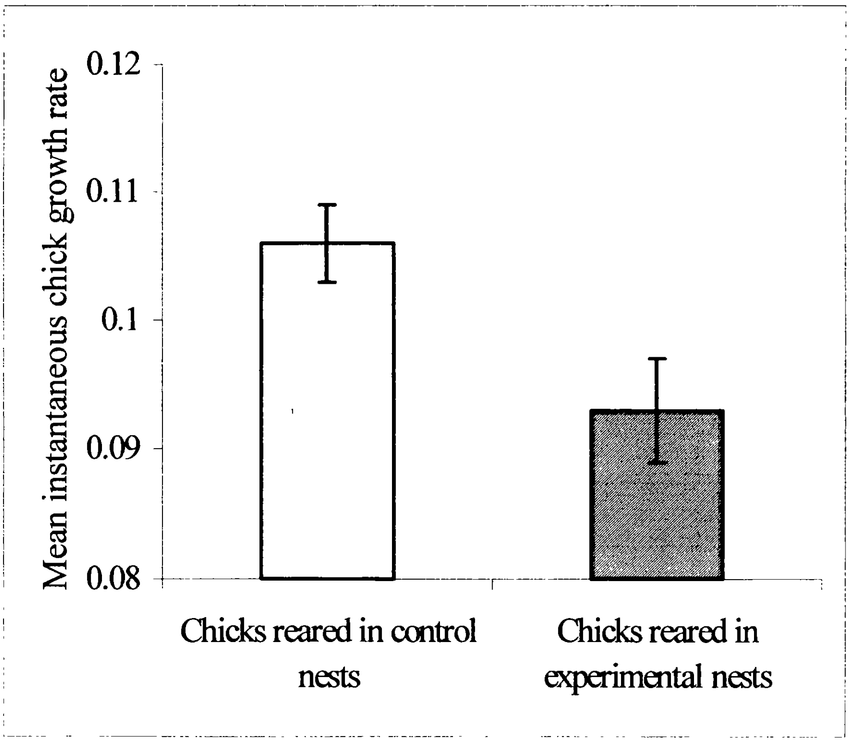
Factor manipulated	Consequences observed during incubation	Future consequences
• Incubated clutch size (*Chapter 7*) • Duration of incubation period (*Tombre & Erikstad 1996*) • Nest microclimate (*Chapter 3*) • Availability of food to incubating parent (*Nilsson & Smith 1988*) • Initial condition of incubating parent	• Duration of incubation period (*Nilsson & Smith 1988*) • Degree of hatching asynchrony (*Chapter 7*) • Proportion of eggs hatching (*Chapter 7*) • Chick condition at hatching (*Chapter 7*) • Adult condition during incubation (*Tombre & Erikstad 1996*)	• Proportion of current brood fledging (*Chapter 3*) • Fledging condition of chicks (*Heaney & Monaghan 1996*) • Post-fledging condition of offspring • Recruitment of current offspring • Future fecundity and survival of current offspring • Chick-rearing ability of adults (*Heaney & Monaghan 1996*) • Post-breeding condition of adults • Future adult survival • Time until the next breeding attempt (*Brugger & Taborsky 1994*) • Future reproductive success (*Chapter 3*)

Parents' incubation effort has frequently been manipulated by adding or removing eggs from their clutch, the underlying assumption being that incubation demands increase with increasing clutch size. Whilst this has been experimentally confirmed in terms of both the energy required for steady-state incubation (Biebach 1981, 1984; Haftorn & Reinertsen 1985) and the total daily energy expenditure of an incubating bird (Coleman & Whittall 1988; Moreno *et al.* 1991), energetic demands do not change with all clutch size changes, and the extra energy required to incubate a single additional egg may be relatively small (Moreno *et al.* 1991; Moreno & Sanz 1994). Further, the number of eggs in a clutch influences the clutch's intrinsic thermal properties, with large clutches cooling down more slowly than small clutches when left unattended (Frost & Siegfried 1977; *Chapter 7*). This reduction in cooling rate may be sufficient to enable parents to forage for the extra time required to meet a higher energetic demand of incubation without mean clutch temperature falling (*Chapter 6*). Thus, as experimentally altering clutch size may alter both the energetic demand of incubation and the ability of parents to meet that demand whilst maintaining clutch temperature, clutch size manipulations may not be the most rigorous way to investigate resource trade-offs and costs of incubation. Whilst positive evidence would still be convincing, an apparent absence of costs can not necessarily be accepted as evidence that such costs do not exist.

Nevertheless, several studies have examined the consequences of enlarging a clutch for incubation performance (reviewed in Thomson *et al.* 1998). Clutch enlargement frequently prolongs the incubation period (Coleman & Whittall 1988; Moreno & Carlson 1989; Smith 1989; Székely *et al.* 1994; Siikamäki 1995; Sandercock 1997; Wiebe & Martin 2000; *Chapter 7*), increases hatching asynchrony (Moreno & Carlson 1989; *Chapter 7*) and reduces hatching success (Andersson 1976; Moreno *et al.* 1991; Siikamäki 1995; *Chapter 7*). Such changes may reduce offspring and hence parental fitness, and have been interpreted as evidence of fitness costs arising from increased incubation demands (Moreno & Carlson 1989; Thomson *et al.* 1998). However, parents may be physically unable to incubate all eggs within enlarged clutches equally, and thus clutch enlargement may affect incubation performance by constraining a parent's incubation ability physically rather than energetically. Peripheral eggs within enlarged clutches may be incubated inefficiently, leading to within-clutch temperature differences that could prolong incubation, increase hatching asynchrony and reduce hatching success in the absence of increased incubation demands (Sandercock 1997; *Chapter 7*). Indeed, many clutch enlargements have failed to demonstrate the changes in either adult time budget or adult mass that would be expected had adult energy balance been affected (Jones 1987; Moreno *et al.* 1991; Székely *et al.* 1994; Siikamäki 1995; Sandercock 1997; Cichon 2000). Further, observed increases in adult mass loss may be due to elongated incubation periods arising from physical constraints on efficient incubation rather than to increases in the energetic demand imposed per unit time (*eg*, Moreno & Carlson 1989). Hence in the majority of clutch enlargement experiments, it is difficult to entirely exclude the possibility that physical rather than energetic constraints were responsible for observed changes in incubation performance.

Few studies have assessed the consequences of clutch enlargement during incubation for measures of post-hatching breeding performance. Experimental clutch enlargements have frequently not been reversed at hatching, and fitness costs of incubating enlarged clutches have thus been confounded with costs of rearing the resultant enlarged broods (Monaghan & Nager 1997). However, three studies that have examined consequences of increased clutch size during incubation only have suggested energetic consequences of clutch enlargement for parents rather than solely incubation effects on offspring. Common tern (*Sterna hirundo*) chicks belonging to parents that had incubated experimentally enlarged clutches but reared their original brood size showed reduced growth rates compared to chicks belonging to control parents (Heaney & Monaghan 1996, Fig. 2.1). This effect was attributed to the energetic consequences of incubating an enlarged clutch for parents' provisioning ability. Similarly in starlings (*Sturnus vulgaris*) and collared flycatchers (*Ficedula albicollis*), chicks reared by parents that had incubated enlarged clutches were in poorer condition at fledging than chicks reared by parents that had incubated their natural clutch size (Cichon 2000; *Chapter 7*). Poor nestling growth may negatively affect post-fledging survival (Nur 1984; Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Magrath 1991). Thus clutch size manipulations have provided some evidence that costs of incubation may arise due to energetic limitation. However, these experiments do not completely exclude the possibility that poor fledgling condition resulted from poor incubation conditions rather than reduced parental provisioning ability. Clearer demonstration of energetic costs of incubation may be achieved by directly manipulating either the energy obtained or the energy expended by incubating parents.

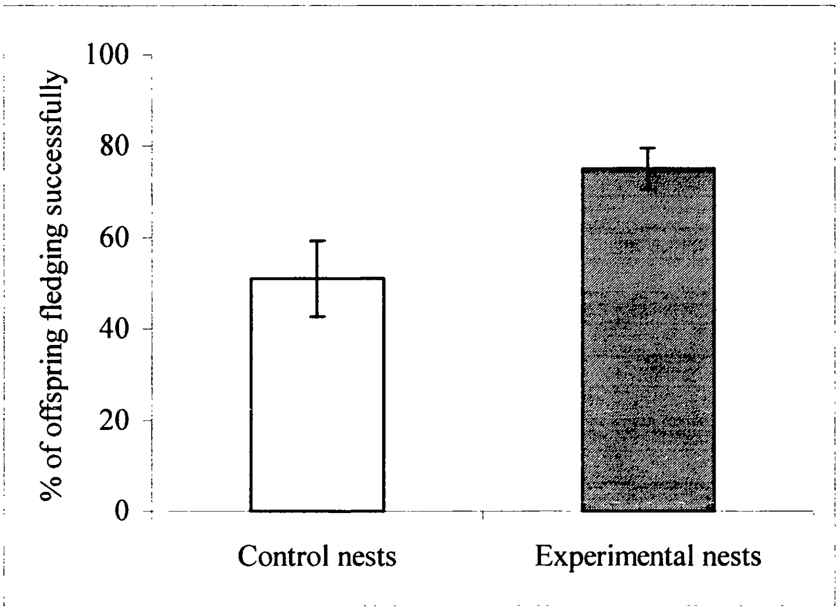
Figure 2.1. Common tern (*Sterna hirundo*) chick growth rates were significantly higher in control nests where parents laid, incubated and reared a clutch of two eggs than in experimental nests where parents had incubated an extra egg ($t_{24} = 2.53$, $P = 0.02$, after Heaney & Monaghan 1996). In this study, experimental pairs laid two eggs compared to the more typical clutch size of three, and may therefore have been of relatively poor quality. Clutches were experimentally enlarged from two to three eggs, constituting an increase of 50% whilst remaining within the natural range of variation. The combination of low quality birds and a relatively large clutch size manipulation may have increased the chance of detecting a cost of incubation.



Several studies have manipulated rates of parental energy expenditure or energy intake during incubation, and observed consequent changes in the division of time between foraging and incubation. Reducing the demand of incubation by providing heat to nests affected parental nest attentiveness in pied flycatchers (*Ficedula hypoleuca*), great tits (*Parus major*) and starlings (von Haartman 1956; Bryan & Bryant 1999; *Chapter 4*), as did manipulating the rate of heat loss from storm petrel (*Hydrobates pelagicus*) nest cavities (Bolton, unpublished). Attentiveness was increased by providing supplementary food to incubating female wheatears (*Oenanthe oenanthe*, Moreno 1989a) and decreased by removing male snow buntings (*Plectrophenax nivalis*) and thus depriving incubating females of being fed on the nest (Lyon & Montgomerie 1985). Hence there is experimental evidence that an energetic trade-off between incubation and foraging exists across a range of species, and thus that incubation can be a period of resource limitation.

Fewer studies have provided clear evidence that manipulating adult energy balance actually has fitness consequences. However, providing heat to starling nests during incubation increased fledging success in the same brood and hatching success in subsequent unmanipulated second clutches (*Chapter 3*, Fig. 2.2). Increasing overall incubation demands by experimentally prolonging incubation periods affected hatching success and female condition in barnacle geese (*Branta leucopsis*, Tombre & Erikstad 1996), hatching success and laying date in the subsequent season in storm petrels (Minguez 1998) and the time until the next breeding attempt in black swans (*Cygnus atratus*, Brugger & Taborsky 1994). Removing provisioning males reduced hatching success in snow buntings (Lyon & Montgomerie 1985) whereas provision of supplementary food increased hatching success in blue tits (*Parus caeruleus*, Nilsson & Smith 1988), although neither of these two studies found a change in fledging success, and supplementary feeding did not affect wheatear breeding performance (Moreno 1989a). Thus there is experimental evidence that fitness costs due to energetic limitation can arise during incubation, but may not always do so (see page 38).

Figure 2.2. A greater proportion of offspring fledged successfully in starling (*Sturnus vulgaris*) nests where the rate of heat loss from within a nest (and thus parental energy expenditure) was experimentally reduced for the duration of the incubation period, than in unmanipulated control nests ($U_{33} = 72.0$, $P = 0.02$, after *Chapter 3*).

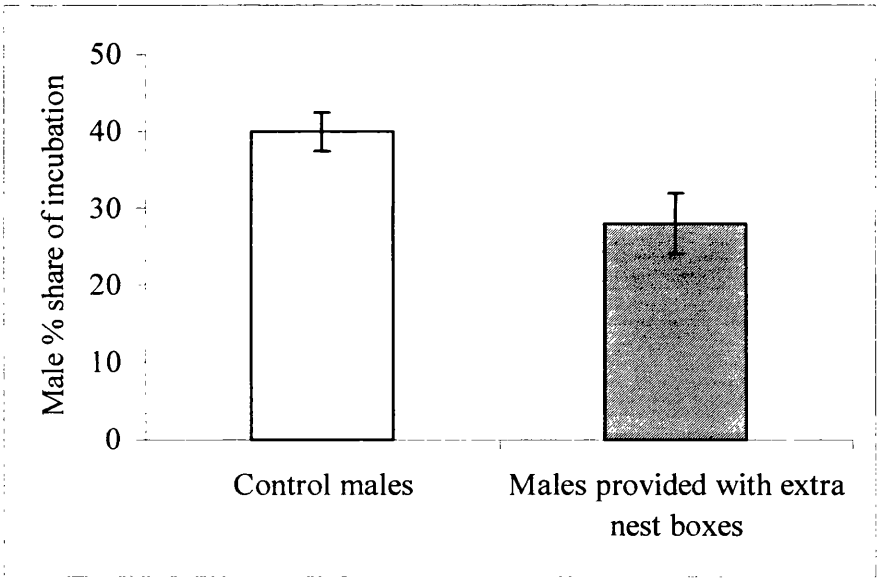


Evidence for fitness costs of incubation arising from limitations on mating opportunities.

If the time allocated to incubating one clutch of offspring significantly reduces a parent's chance of obtaining further mating opportunities and thus the number of progeny sired, there will be non-energetic fitness costs of incubation. As male reproductive rate may often be limited by the number of mates acquired (Clutton-Brock 1991; Andersson 1994), such costs may apply particularly to males.

Incubation may preclude activities such as song and display that function in mate attraction (Whitfield & Brade 1991; Albrecht & Oring 1995; Catchpole & Leisler 1996), and thus reduce a male's ability to attract additional mates. Hormone implants have not as yet been used to manipulate male investment in mate attraction and conclusively demonstrate a trade-off with paternal care during incubation as has been done during chick-rearing (Hunt *et al.* 1999; Moreno *et al.* 1999). However, experimentally increasing male starlings' chances of attracting secondary females by providing some males with additional nest boxes caused those males to incubate less and display more (Smith 1995, Fig. 2.3), suggesting a trade-off between mate attraction and incubation.

Figure 2.3. Male starlings (*Sturnus vulgaris*) contributed significantly more time to incubation when a single nesting opportunity was available than when experimentally provided with a second nest-box and thus a second opportunity to attract a mate ($F_{1,28}$ = 7.01, $P = 0.01$, after Smith 1995).



Incubating one clutch may reduce a polygamous parent's ability to care for other simultaneous broods. Correlative evidence from facultatively polygynous species suggests that parents with multiple clutches contribute less time to incubating each one, decreasing the total time for which each clutch is attended (Pinxten *et al.* 1993; Smith *et al.* 1995; Fitzpatrick 1996; *Chapter 8*). Reduced care for one brood due to the allocation of resources to incubating another will be costly if the reduction significantly reduces a brood's survival or reproductive value. This has been suggested to be the case. Lack of male help can prolong incubation periods (Smith *et al.* 1995; *Chapter 8*) and reduce hatching and fledging success (*Chapter 8*). Further, in their review of male removal experiments, Bart & Tornes (1989) concluded that the loss of male help may have particularly severe fitness consequences if it occurs during the incubation period. However, other studies have not shown such effects. A lack of male incubation did not affect breeding success in starlings (Pinxten *et al.* 1993) or reed warblers (*Acrocephalus scirpaceus*, Duckworth 1992). However, these studies did not examine the consequences of reduced male help for female condition. As male assistance with incubation increases the foraging time available to females (Kleindorfer *et al.* 1995; *Chapter 8*), fitness costs of reduced male incubation effort may be met by females rather than offspring. Further studies on the role of male assistance during incubation and the ability of females to compensate for its absence are required.

Finally, time spent incubating may reduce a male's opportunity to obtain extra-pair copulations. Cross-species analysis suggests that extra-pair paternity rates are generally low in species where males contribute extensively to incubation (Schwagmeyer *et al.* 1999). Further, male fairy martins (*Hirundo ariel*) adjust the time allocated to incubation in response to the availability of fertile females, suggesting the existence of a trade-off between incubation and attempting extra-pair copulations. The consequent low levels of male attendance prolonged incubation periods, although no reduction in hatching success was found (Magrath & Elgar 1997). Equally, incubating the first-laid eggs in a clutch may reduce a male's mate-guarding ability, involving a potential cost in terms of lost paternity. Whilst this hypothesis has not been rigorously tested, it may explain why, in species where males assist females with incubation, males often do not incubate until after the clutch has been completed whilst females commence incubation on the penultimate egg (Power *et al.* 1981).

In summary, there may be substantial fitness costs of incubation in terms of lost reproductive opportunities arising from the time spent on the nest. Whilst in general these may apply predominantly to males, females may be similarly affected in species where incubation roles are reversed.

Ecological fitness costs of incubation

Parents may experience costs to remaining on nests for long periods during incubation, such as increased vulnerability to predation or infection by nest parasites. Indeed, the risk of predation on the nest may be a major evolutionary influence on incubation behaviour (Conway & Martin 2000). Further the requirement to return to a nest may constrain a parent's ability to track mobile and unpredictable food supplies. However, such costs are largely unquanitified.

Discussion: occurrence and distribution of incubation costs

Experimentally manipulating the resource requirements of incubation can alter the ways in which parents allocate resources between activities, both within and between reproductive phases. This evidence, and that from correlative studies, suggests the existence of resource trade-offs and hence resource limitation during incubation. Further, experimentally induced changes in allocation patterns have affected measures of both current and future reproductive success. Thus there is evidence that the resources required for incubation can be sufficient to limit parental fitness, and hence that incubation can be a costly stage of avian reproduction.

Who pays the costs of incubation?

The way in which costs are distributed between parents and current offspring depends on how incubating parents resolve trade-offs between investment in current and future reproduction, and hence on their allocation of time between incubation and alternative activities. Largely due to links with mating and social systems, the determinants of breeding parents' time allocations to mating activities have attracted considerable attention. Investment patterns are likely to depend on multiple ecological factors that vary between individuals and species (reviewed in Clutton-Brock 1991). Patterns of time allocation between foraging and incubation also vary greatly between species. In relatively large and long-lived species with precocial young, parents often remain on the nest for long periods during incubation, meeting energetic requirements predominantly from stored endogenous resources (Aldrich & Raveling 1983; Afton & Paulus 1990; Hepp *et al.* 1990; Erikstad & Tveraa 1995). As it is likely to minimise the incubation period and the frequency of energetically demanding clutch rewarming, continuous incubation may be the most efficient incubation strategy. In such species, time is predominantly allocated to incubation rather than to foraging, and costs of incubation may therefore operate via parents to a large degree. Indeed, whilst experimentally manipulating incubation demands in such species can affect measures of offspring fitness (*eg*, hatching success: Tombre & Erikstad 1996; Minguez 1998), increased costs are often borne substantially by incubating adults (Heaney & Monaghan 1996; Tombre & Erikstad 1996; Minguez 1998).

In contrast, continuous incubation is unlikely to be physiologically possible for small-bodied passerines, as the resources required to sustain long incubation bouts equate to large proportions of normal body mass (Moreno 1989b). In small-bodied species, parents generally incubate intermittently, resolving the trade-off between foraging and incubation so as to spend considerable time away from the nest. When only one parent incubates, this resolution frequently results in clutches being left unattended, and costs of incubation may often affect current offspring directly. Indeed, mean passerine egg temperatures are typically well below the optimum for embryonic development (Haftorn 1983, 1988; Webb 1987; Williams 1996; *Chapter 5*). In such species, experimental manipulations have provided little clear evidence that increased energetic costs of incubation are borne by parents. This is partly because few studies have rigorously investigated the consequences of manipulated incubation demands for estimators of adult fitness other than body mass. In particular, there is a lack of studies that have measured adult survival or future reproductive performance, or more rigorous indicators of physiological condition (although see Cichon 2000; *Chapter 3*). However, there is experimental evidence that parents may preferentially preserve their own condition at the expense of their current offspring. Patterns of parental mass loss are difficult to interpret directly as indicators of resource limitation during incubation, as mass loss may reflect the post-laying atrophy of reproductive organs (Ricklefs & Hussell 1984) or be an adaptation to reduce flight costs during chick-rearing (Moreno 1989b; Merilä & Wiggins 1997) rather than reflecting physiological stress. However, in experiments designed to test these alternatives, the provision of supplementary food to incubating parents did not alter mass trajectories (Hillström 1995; Merkle & Barclay 1996; Slagsvold & Johansen 1998). This suggests that parents allocate resources during incubation so as to optimise their own condition, passing supplementary resources on to offspring when they become available. Indeed, the only study that has assessed the consequences of supplementary feeding for both adult mass and incubation strategy found increases in nest attentiveness but not in adult mass (Slagsvold & Johansen 1998).

Hence energetic trade-offs during incubation can be resolved so that costs are manifested in both parents and current offspring to some degree. However, although more experiments are clearly needed across a wider range of species, incubation costs may be manifested extensively in current offspring in small intermittently incubating species, and by parents to a greater degree in larger species that incubate continuously. The suggestion that intermittently incubating passerines invest preferentially in their own condition during incubation whereas larger species invest more in current offspring is perhaps contrary to expectation (Stearns 1992), and to the conclusions of studies carried out during the chick-rearing period (Sæther *et al.* 1993; Mauck & Grubb 1995; Weimerskirch *et al.* 1995). However, such allocation patterns make more sense in the context of within-brood and within-season trade-offs involving incubation effort, as passerines with altricial offspring may have to invest in their own condition during incubation in order to successfully rear the current brood and breed again within the same season (Moreno 1989b).

Condition-dependence of costs

The majority of the studies that have demonstrated clear energetic fitness costs to incubation have been carried out in relatively cold environments (Lyon & Montgomerie 1985; Nilsson & Smith 1988; Heaney & Monaghan 1996; Tombre & Erikstad 1996; Bolton, unpublished, *Chapter 3*). However, as egg temperature regulation may be less demanding in warm climates, more studies are required to assess whether similar costs apply in other environments. Further, even in cold climates, costs of incubation may only become apparent during particularly hard conditions. Supplementary feeding of female wheatears reduced incubation period only in the coldest of three springs (Moreno 1989a), incubating goldeneyes (*Bucephala clangula*) lost more mass in cold weather (Mallory & Weatherhead 1993), and male assistance with incubation increased hatching success in moustached warblers (*Acrocephalus melanopogon*) during April but not during May (Kleindorfer *et al.* 1995).

Even when costs of incubation are evident on average, their impact may vary with parent and offspring condition, not affecting all parents, or all offspring within a brood. Costs of incubation due to energetic limitation may only affect parents in poor condition (Moreno & Sanz 1994; Heaney & Monaghan 1996; Minguez 1998; Fig. 2.1). Investing in incubation rather than in attracting mates or seeking extra-pair copulations may entail little cost for poor quality individuals that would anyway have achieved little additional mating success (discussed in *Chapter 8*). Embryos within well-provisioned eggs may be able to withstand chilling or prolonged incubation periods with no adverse consequences for their subsequent development or reproductive value. Hence egg quality may influence incubation costs, and the possibility that the resources that parents are able to invest in egg-production may influence those required for incubation as yet remains unexplored. Further, little is known about how embryo sex may affect incubation demands, and sensitivity to varying conditions. Thus, whilst there is now clear evidence that incubation can be a costly activity, there is a clear need for further research into state-dependent action and interactions with other reproductive stages before the role of incubation in the evolution of avian life history strategies can be fully understood.

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Chapter three

Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation

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Abstract

Changes in the resources allocated to particular stages of reproduction are expected to influence allocation to, and performance in, subsequent reproductive stages. Experimental manipulation of individual investment patterns provides important evidence that such physiological trade-offs occur, and can highlight the key environmental variables that influence reproductive costs. By temporarily altering the thermal properties of starling nests, we reduced the energetic demand of first-clutch incubation, and examined the effect of this manipulation on performance during the same and the subsequent reproductive attempts. Compared with controls, starlings investing less in incubation were more successful in fledging young, and were more likely to hatch all their eggs if a subsequent reproductive attempt was made. Our results show that incubation demands can limit reproductive success, and that resources saved during incubation can be reallocated to later stages of the same reproductive attempt and to future reproductive attempts. This study also shows that small changes in thermal environment can affect breeding success by altering the energetic demands imposed on incubating parents, independently of the effect of temperature on other environmental variables such as food supply.

Introduction

Life history theory posits that resource allocation in reproducing individuals is shaped by physiological trade-offs; increased investment of limiting resources in one activity must be offset by decreased investment in competing activities during the same or subsequent reproductive attempts (Stearns 1992). However, the expected negative relationships between investment in competing activities can be difficult to demonstrate in practice. Confounding variables such as individual quality, and hence the amount of resources available for investment, can even result in positive rather than negative associations being observed (Reznick *et al.* 1986; Partridge 1992). Experimental manipulation of investment is therefore an important tool in the study of physiological trade-offs, as it allows resource investment to be considered independently of resource availability (Roff 1992; Stearns 1992). Hence, manipulation of the demands of specific reproductive phases is central to our understanding of resource allocation during reproduction. Furthermore, such studies can provide useful insights into which reproductive phases are sufficiently demanding to limit reproductive performance.

Birds are iteroparous breeders, with each reproductive attempt being divided into the distinct stages of egg-laying, incubation and chick-rearing. The demand of each reproductive stage can be manipulated independently, and the consequences for other stages within both current and future reproductive attempts can be measured (Partridge 1989; Lessells 1991; Monaghan & Nager 1997). Birds are therefore good model species in which to investigate the influence of physiological trade-offs on resource allocation. However, most previous experimental studies of trade-offs in birds have manipulated the demands of chick-rearing, the implicit assumption being that the earlier stages of reproduction are much less demanding and are unlikely to limit later investment (Stearns 1992; Monaghan & Nager 1997). There is increasing evidence that this is not correct with respect to egg formation (*eg*, Bolton *et al.* 1992; Nager & van Noordwijk 1992; Monaghan *et al.* 1998), but few studies have examined the fitness consequences of altering incubation demands in isolation from the other reproductive stages (Monaghan & Nager 1997). These few studies have generally increased rather than decreased incubation demands, either by prolonging the incubation period (Tombre & Erikstad 1996) or by increasing clutch size during incubation only (Moreno *et al.* 1991; Heaney &

Monaghan 1996). Although potentially demonstrating the existence of physiological trade-offs, increasing the demand of incubation cannot clarify the extent to which resources saved during incubation can be re-allocated to other stages of reproduction. This can only be investigated by experimentally reducing incubation demands.

The energy required to maintain clutch temperature depends on the rate at which heat is lost from the clutch and nest, and is therefore influenced by environmental temperature. Variation in environmental temperature has previously been linked to variation in breeding success (Jarvinen 1993; Sheaffer & Malecki 1996; Skinner *et al.* 1998). However, the extent to which relatively small changes in thermal conditions can be sufficient to alter reproductive performance as a consequence of direct effects on the energy expenditure of incubating birds, independently of more general effects on food availability and foraging costs, has rarely been investigated. By experimentally manipulating the rate of heat loss from nests, the potentially crucial role of the thermal environment in determining the outcome of a breeding attempt can be examined.

In this study we experimentally altered the thermal environment of incubating birds, thereby reducing the energetic demand of incubation, and studied the consequences of this manipulation for the success of their current and subsequent reproductive attempts. In doing so we tested the hypothesis that reduced investment during one reproductive stage can translate into improved performance in future stages, and investigated the extent to which the thermal conditions experienced during incubation can directly affect reproductive performance.

Methods

A substantial proportion of the energetic demand of incubation is thought to occur whilst rewarming a clutch that has been allowed to cool down (Williams 1996). Cooling occurs most frequently in species where only one parent incubates, as the clutch is left unattended whilst that parent forages. Hence incubation is likely to be most demanding for uniparental incubators nesting in cold environments. Accordingly, we studied an individually marked population of cavity nesting starlings (*Sturnus vulgaris*) on Fair Isle, Shetland (59°N, 2°W), between mid-April and mid-July 1998. Air temperatures on Fair

Isle for these months were well below the optimal incubation temperature of approximately 36-39°C (Lundy 1969; Webb 1987); the maximum air temperature recorded during the incubation period was only 12.7°C. Observation showed that female starlings were almost solely responsible for incubation and hence clutches were regularly left unattended and cooled down rapidly whilst females foraged.

Fifty-seven first brood nests were discovered, of which a randomly selected thirty-four were studied intensively. Seventeen of these were experimentally manipulated to reduce the energetic demand of incubation, and 17 served as unmanipulated control nests. Laying date, egg biometrics, and hatching and fledging success and dates were recorded in these 34 intensively studied nests. Chicks were weighed at three days old and again at ten days, when maximum wing and maximum tarsus measurements were also taken. There were no significant differences between the control and experimental nests in terms of clutch size (control mean 4.7 ± 0.1, experimental mean 4.5 ± 0.2, Mann-Whitney U_{34} = 112.5, $P = 0.21$), mean egg mass (control mean 8.0 ± 0.1g, experimental mean 8.3 ± 0.2g, $t_{31} = -1.79$, $P = 0.09$), overall clutch mass (control mean 38.3 ± 0.9g, experimental mean 37.5 ± 1.0g, $t_{31} = 0.60$, $P = 0.55$) or laying date (control mean 5.1 ± 0.6 days into May, experimental mean 5.2 ± 0.7 days into May, $t_{32} = -0.20$, $P = 0.84$). Hence no correction for these factors was needed when comparing parameters of breeding success between the control and experimental groups. The remaining 23 nests were visited during the chick rearing period to ascertain whether any chicks fledged successfully. Although full details of clutch size, egg mass and laying date could not be collected for all of these nests due to time constraints, there was no evidence to suggest that they differed from either control or experimental groups in any of these parameters.

A heating mat 5cm in diameter (Radio Spares 12V silicone-polymide mat) was inserted under each of the 17 experimental nest cups. Mats were camouflaged with moss, and starlings did not appear to react to their presence. The mats were powered by a constant 4.2V battery supply and produced heat continuously from clutch completion until the first egg hatched, when they were switched off. The impact of the heating mat on the rate of heat loss from each experimental nest was measured by placing a plaster disc warmed to 32°C into a nest and measuring the rate at which it cooled down with and without the heating mat switched on. The measurement was repeated in control nests.

The amount of heat produced by the mats was too small to prevent the disc from cooling, but was sufficient to reduce the rate at which it cooled by 0.22 degrees/minute or 20% (*Chapter 4*). When the mat was switched off there was no difference in the rate of heat loss between control and experimental nests. Thermistors attached to TinyTalk dataloggers (Gemini Dataloggers Ltd, Chichester, U.K) were placed among eggs, and nest temperature was recorded every 72 seconds throughout incubation. Over the whole incubation period, there was no significant difference in mean nest temperature between control and experimental nests (control median 25.3°C, experimental median 24.4°C, Mann Whitney U_{32} = 112, P = 0.56), and thus the manipulation did not affect the actual temperature at which the clutch was incubated, but reduced the investment that females made in incubation.

The occurrence and progress of the second clutches laid in the 57 first brood nests was monitored. The heating mats were removed from the 17 experimental nests before the start of the second laying period, so that neither the 17 previously heated nor the 40 previously unmanipulated nests were heated during the second broods.

Two-tailed statistical tests were used throughout, and non-parametric tests were used when the assumptions of parametric tests were violated by the data distributions. One of the experimental nests was omitted from the analysis as it was accidentally destroyed by humans.

Results

There was no significant difference between the proportion of first clutch eggs that hatched in control and experimental nests (control mean 82.4 ± 8.0%, experimental mean 95.9 ± 2.9%, Mann Whitney U_{33} = 105.5, P = 0.14). However, the proportion of first clutch eggs from which young fledged was significantly higher in experimental nests than control nests (control mean 51.0 ± 8.3%, experimental mean 74.9 ± 4.5%, Mann Whitney U_{33} = 72.0, P = 0.02). Hence breeding performance was enhanced in the nests that were experimentally heated during incubation.

The duration of the incubation period did not differ significantly between experimental and control nests (control mean 12.5 ± 0.2 days, experimental mean 12.1 ±

0.2 days, $t_{29} = 1.61$ $P = 0.12$. Nor was there a significant difference in the duration of the fledging period (control mean 23.2 ± 2.2 days, experimental mean 23.6 ± 1.3 days, $t_{26} = -0.67$, $P = 0.51$), or in the mass of chicks at three days old (control mean 22.5 ± 1.7g, experimental mean 22.9 ± 1.9g, $t_{27} = -0.14$, P = 0.92) between the two groups. As a measure of condition, the ratio of mass to tarsus^3 was calculated for the chicks at 10 days old (Freeman & Jackson 1990). There was no significant difference in mean ratio for chicks in control and experimental nests (control mean 3.23 ± 0.08 g/m^3, experimental mean 3.46 ± 0.08g/m^3, $t_{27} = -1.93$, $P = 0.06$), although there was an obvious trend towards better condition in the experimental chicks.

Six of the 16 experimental pairs that successfully fledged any first brood young laid second clutches. The corresponding figure for the unmanipulated nests was 14 out of 32. These proportions did not differ significantly (Chi^2 Test $\chi^2_1 = 0.01$, $P > 0.5$). There were also no significant differences in terms of second brood laying date (control mean 19.0 ± 3.0 days into June, experimental mean 21.1 ± 0.8 days into June, $t_{18} = -0.95$, $P = 0.36$), clutch size (control mean 3.3 ± 0.4, experimental mean 3.6 ± 0.3, $t_{18} = -0.62$, $P = 0.54$), mean egg mass (control mean 8.06 ± 0.20g, experimental mean 8.17 ± 0.17g, $t_{18} = -0.39$, $P = 0.70$) or clutch mass (control mean 27.02 ± 3.56g, experimental mean 29.63 ± 2.17g, $t_{18} = -0.65$, $P = 0.53$).

Either none or all of the second clutch eggs hatched in 16 out of the 20 second brood nests, the majority of failing nests being deserted during harsh weather. Thus the second clutch hatching success data was heavily skewed to extreme values, precluding valid comparison of mean second clutch hatching success in control and experimental nests. The complete second clutch hatched successfully in significantly more of the nests that had been experimentally heated during the first broods (four out of six nests) than in nests that had not been manipulated (two out of fourteen nests, Fisher Exact Probability Test $P = 0.037$). Hence performance in hatching the second brood was improved in pairs whose first brood incubation demand had been experimentally reduced. Unfortunately 77% of second brood chicks died before fledging during a period of storm force gales, making an analysis of fledging success impossible.

Discussion

The experimental treatment reduced the rate at which a clutch of eggs cooled during a parental absence (*Chapter 4*), decreasing the amount of energetically expensive reheating (Biebach 1986) required when parents returned from foraging bouts. The amount of energy required to maintain clutch temperature and adult body temperature during a spell of incubation may also have been reduced to a small extent on the experimental nests, contributing further to the reduction in incubation demands compared with control nests. Since nests were only heated during the first clutch incubation period and the manipulation did not affect first clutch hatching success, experimentally manipulated parents experienced a reduced energetic demand only during the first clutch incubation period.

The experimental reduction in the energetic demand of incubation was associated with increased fledging success during the same breeding attempt. The manipulation could have improved breeding success by directly improving the conditions for embryonic development in the experimental nests. Low incubation temperatures can lead to developmental abnormalities and a prolonged developmental period (Webb 1987). Alternatively, the reduced adult energy expenditure during incubation may have increased success by allowing parents to invest more in their offspring later in the breeding attempt. The possibility that the manipulation improved the thermal environment of the nest for the embryos is difficult to test directly, as the thermal conditions that are optimal for embryonic development in starlings are not known precisely. However, if the manipulation had improved nest conditions then a higher mean nest temperature, greater hatching success, a reduced duration of incubation and a better chick condition at hatching might have been expected in the experimental nests (Webb 1987). We found no evidence of any of these effects. This suggests that the increased first brood fledging success in experimental nests was due, at least in part, to the reduced energetic demand of incubation allowing increased adult investment during chick-rearing. Although not quite statistically significant, the strong trend towards a greater condition ratio in ten day old experimental chicks may be a reflection of this effect.

Of the nests that successfully fledged any first brood young, second clutches were no more likely to be laid in nests that had been experimentally heated during the first clutches than in control nests that had not. Nor did the two groups of nests differ significantly in mean second brood laying date, egg mass, clutch mass or clutch size. Despite the fact that no nests were heated during second clutch incubation, a significantly greater proportion of experimental nests than of control nests hatched their complete second clutch. This difference could not have been due to a physical impact of the previous manipulation on the nest, as starlings rebuilt their nests between their first and second broods, and must have been due to the impact of the first brood manipulation on the adults themselves. The reduced adult energy expenditure during first clutch incubation allowed adults to invest more in their subsequent breeding attempt, again pointing to an effect on adult resource allocation patterns. Although the main effect was on hatching success, our data suggested that clutch size decreased less between first and second broods in experimental nests than in control nests, a trend that would warrant further investigation using larger sample sizes.

Incubation has previously been considered a time of reduced adult energy expenditure compared to other stages of reproduction (Kendeigh 1963; King 1973; Walsberg & King 1978). More recently however, it has been shown to impose significant energetic demands on parents (Haftorn & Reinertsen 1985; Biebach 1986; Toien *et al.* 1986; Thomson *et al.*1998; Turner 1991); a significant energy expenditure is required to maintain clutch temperature whilst foraging time is severely restricted by the need to remain on the nest (Carey 1980; Williams 1996). Changing the thermal properties of the nest by providing heat has been shown to alter parental time budgets during incubation, apparently due to the reduction in energy required to maintain egg temperature (Bryan & Bryant 1999; *Chapter 4*). However, few previous studies have unambiguously shown that the energetic demand of incubation translates into a fitness cost for parents (Monaghan & Nager 1997). Our results demonstrate this cost, and further suggest that resources saved during reduced-demand incubation can be re-allocated to future stages of reproduction, both within and between breeding attempts. Furthermore, our results demonstrate the critical role of the thermal environment within the nest in determining breeding success. Previous studies have suggested a positive relationship between environmental temperature and breeding performance, including in starlings on Fair Isle (P.G.H.Evans, unpublished data). However, non-experimental studies do not tell us whether greater breeding success in warmer weather is due to a reduced rate of heat loss from nests reducing an incubating adult's energy expenditure, or to other environmental effects such as an increase in availability of insect food (Drent 1973). This study demonstrates an enhanced breeding performance that must result from a change in the incubating parent's thermal environment rather than in its food supply. We show that for birds breeding in relatively cold conditions, a very slight difference in the rate of heat loss from the nest during incubation can significantly affect breeding success, as can heat loss during other reproductive stages (Nager & von Noordwijk 1992; Yom-Tov & Wright 1993). The rate of heat loss is influenced by climate, and also by the parent itself, by means of the nest site selected and the way in which the nest is constructed (White & Kinney 1974; O'Connor 1978; Skowron & Kern 1980; Franklin 1995; *Chapter 9*). Hence there should be selection for an optimal allocation of resources to site selection and nest construction, and the outcome of a breeding attempt may be influenced by the availability of good nest sites and insulating materials. In starlings, males are responsible for the majority of nest-building, with females choosing mates largely on the basis of the completed nest (Cramp & Perrins 1994). In so doing, females may be using nest quality as a sexually selected indicator of male quality (Andersson 1991; Soler *et al.* 1998), but our results suggest that they are also behaving to maximize their direct fitness gains (Moreno *et al.* 1995; Moreno *et al.* 1999).

Physiological trade-offs resulting from the cost of incubation that we demonstrate may have an important bearing on the evolution of a bird's life history strategy, including the determination of parameters such as optimal clutch size (Stearns 1992). Lack (1947) hypothesized that optimal clutch size is determined by the number of chicks that parents can afford to provision, but it has repeatedly been shown that birds can successfully rear experimentally enlarged broods (Linden & Møller 1989; Dijkstra 1990). The fitness cost of incubation demonstrated here, together with that of egg-laying, may provide an explanation for the discrepancy between the empirically optimal clutch size and that predicted by Lack. That laying larger clutches imposes greater fitness costs on parents has been demonstrated (Monaghan *et al.* 1995; Monaghan *et al.* 1998), and there is an increasing body of evidence to suggest that the cost of incubation increases with clutch size (Thomson *et al.* 1998). Optimal clutch size may therefore be determined by the number of eggs that parents can afford to lay and incubate as well as the number of young they can afford to rear.

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Chapter four

The effect of clutch cooling rate on starling (*Sturnus vulgaris*) incubation strategy.

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Abstract

In avian species where only one parent incubates, that parent must divide its time between the mutually exclusive activities of incubation and foraging in such a way as to maintain both body condition and clutch temperature within certain limits.

In a uniparental incubator, the starling, we experimentally reduced the rate at which unattended clutches of eggs cooled down, and monitored the resulting changes in the parent's incubation strategy. Opposite to the predictions of standard models of time allocation during incubation, parents spent a much greater percentage of each 24 hours incubating when the rate of clutch cooling was reduced. Incubation-bouts lasted significantly longer on experimental nests than on control nests, both during the daytime and overnight. Mean foraging-bout duration did not differ between the two groups of nests. These results are consistent with the hypotheses that parental foraging success cues the end of a foraging-bout, and that parental energy level cues the end of an incubation-bout.

However, most previous studies suggest that parents spend less time incubating when the rate of clutch cooling is slow. If parental energy level cues departure, these results can only be explained if the amount of time available for incubation is constrained in these cases by the time a parent must spend foraging in order to maintain body condition. Such parents should take more time away from incubation when the unattended clutch cools slowly, as this is when the cost of being absent is minimised.

Introduction

Parents have finite resources, and therefore must make decisions about how best to divide resources between mutually exclusive activities. The way in which this dilemma is resolved is particularly interesting when the allocation of time and energy to one activity results in a debt building up in the time or energy demands of the excluded activities. A good example of this is avian incubation.

To hatch successfully, avian eggs must be maintained at a temperature that allows embryonic development. The optimal temperature range for development is thought to be between approximately 36°C and 39°C (Lundy 1969; Drent 1975; Webb 1987) and as there are few environments in which ambient temperature remains constantly within this range, incubation by parents is required to prevent embryos from chilling or overheating. In species where only one parent incubates, that parent must divide its time between the mutually exclusive activities of incubating to control clutch temperature, and foraging to meet its own energy requirements (Drent *et al.* 1985; Jones 1989). Hence daytime incubation is frequently intermittent, with each incubation-bout being followed by a foraging-bout during which the clutch is left unattended and begins to equilibrate with ambient temperature. The parent must balance the time spent foraging against the cost of allowing the clutch to depart from the optimal incubation temperature (Webb 1987; Williams 1996), and against the energetic demands of rewarming or cooling the clutch upon its return to the nest (Williams 1996).

An intermittent incubation strategy results from two sets of behavioural decisions made by the parent. Firstly, an incubating parent must decide when to terminate an incubation-bout and depart from the nest, influencing incubation-bout duration. Secondly, a foraging parent must decide when to terminate a foraging-bout and return to the nest, thereby influencing foraging-bout duration. An optimally incubating parent must be able to select the appropriate moments at which to terminate incubation- and foraging-bouts. The optimal division of time is likely to vary with environmental conditions and indeed, incubation- and foraging-bout durations have previously been shown to vary consistently with weather (Yom-Tov *et al.* 1978; Davis *et al.* 1984; Cartar & Montgomerie 1987), stage of incubation (Drent 1975; Weathers & Sullivan 1989) and time of day (Davis *et al.* 1984; Morton & Pereya 1985; Haftorn & Ytreberg 1988). Thus it is likely that when deciding to terminate a bout, the parent is responding to environmentally determined proximate cues.

The cue to terminate a foraging-bout is likely to be linked to adult foraging efficiency. For example, an adult may decide to stop foraging and return to the nest after achieving a certain energetic gain or level of food intake (Drent *et al.* 1985; Jones 1989; Weimerskirch 1994). The nature of the proximate cue to terminate an incubation-bout has been much discussed (White & Kinney 1974; Yom-Tov *et al.* 1978; Carey 1980, Davis *et al.* 1984; Drent *et al.* 1985; Haftorn & Ytreberg 1988; Haftorn & Reinertsen 1990; Chaurand & Weimerskirch 1994), and two main hypotheses have been proposed. Firstly, White & Kinney (1974) proposed that egg temperature cues a parent to depart from the nest (the 'egg-temperature' model). A parent is hypothesised to sense egg temperature via its brood patch, and to terminate its incubation-bout when the clutch reaches a certain threshold temperature. Secondly, Chaurand & Weimerskirch (1994) proposed that a parent's own mass determines when an incubation-bout will end. They found that Blue Petrels terminate incubation-bouts when their body mass falls to a certain threshold. This idea can be developed into a model in which a parent's energy level cues the end of an incubation-bout (the 'parental-energy' model). A parent continues to incubate until its energy level dwindles to a threshold, at which point it leaves to forage.

In this paper, we are concerned with the factors that determine when a parent decides to terminate an incubation-bout. The egg-temperature and parental-energy models make conflicting predictions concerning the change in the duration of incubation bouts expected when clutch cooling rate is reduced. The egg-temperature model predicts that incubation-bout duration will decrease with a slow clutch cooling rate. Eggs will cool down less during a parental absence and hence when the parent returns, it will take less time to reheat the clutch to the threshold level for departure. Conversely, the parental-energy model predicts that incubation-bout duration will increase as the rate of clutch cooling decreases. The rate of adult energy expenditure required to restore and maintain clutch temperature will be reduced when the rate of heat loss from the clutch is slow, and hence a parent can continue to incubate for longer before its energy decreases to the threshold level at which it must forage. Hence by experimentally altering the rate of heat loss from a clutch, it is possible to test the opposing predictions of the egg-temperature and parental-energy models of the termination of the incubation bout. In this study we experimentally reduced the rate at which unattended starling clutches cooled down, and monitored the resulting changes in the duration of the parent's incubation bouts.

Methods

A population of cavity nesting starlings was studied on Fair Isle, Shetland between mid-April and mid-July 1998. The mean air temperature during the first clutch incubation period was 10.5°C, much colder than the temperature required for embryonic development. In starlings, the female is almost exclusively responsible for incubation, and when the female departs to forage the eggs are left unattended and lose heat rapidly. Hence on Fair Isle, there is likely to be strong selection for an optimal division of time between incubating and foraging.

A small amount of heat (0.25 Watts) was supplied to 17 first clutch nests continuously during the incubation period, by inserting a 5cm diameter heating mat (Radio Spares 12V silicone-polymide mat) under each nest cup. The heat produced was just sufficient to reduce the rate at which the unattended clutch cooled down, but was not enough to maintain nest temperature in the absence of the adult. Seventeen control nests were left unmanipulated. To quantify the effect of the heating mats on clutch cooling rate, a plaster disc warmed to 32°C was placed in each control and experimental nest, and in the absence of the parent, the rate at which the disc cooled down relative to ambient temperature was measured. The mean cooling rates for the control and experimental nests did not differ significantly with the heating mats switched off (means of 1.22 ± 0.04 degrees/minute and 1.18 ± 0.06 degrees/minute respectively, $t_{32} = -0.68$, $P = 0.50$). Cooling rates slowed significantly in the experimental nests when the heating mats were switched on (new mean 0.96 ± 0.05 degrees/minute, Paired t test $t_{16} = 2.37$, $P = 0.03$), such that the cooling rate of the heated experimental nests was significantly slower than that of the control nests ($t_{32} = -3.32$, $P = 0.003$). Hence the manipulation successfully reduced the rate at which an object placed in an experimental nest cooled down, a difference of 0.22 degrees/minute or 20%. Given that the rate at which the unattended clutch cooled down was reduced in the experimental nests in this way, after a given parental absence the eggs in the experimental nests will have been at a higher temperature when the parent returned. Thus the energy required to restore clutch temperature was reduced in the experimental nests. As the heating mats remained on continually, the energy expended in maintaining clutch temperature during an incubation-bout will also have been reduced to some extent.

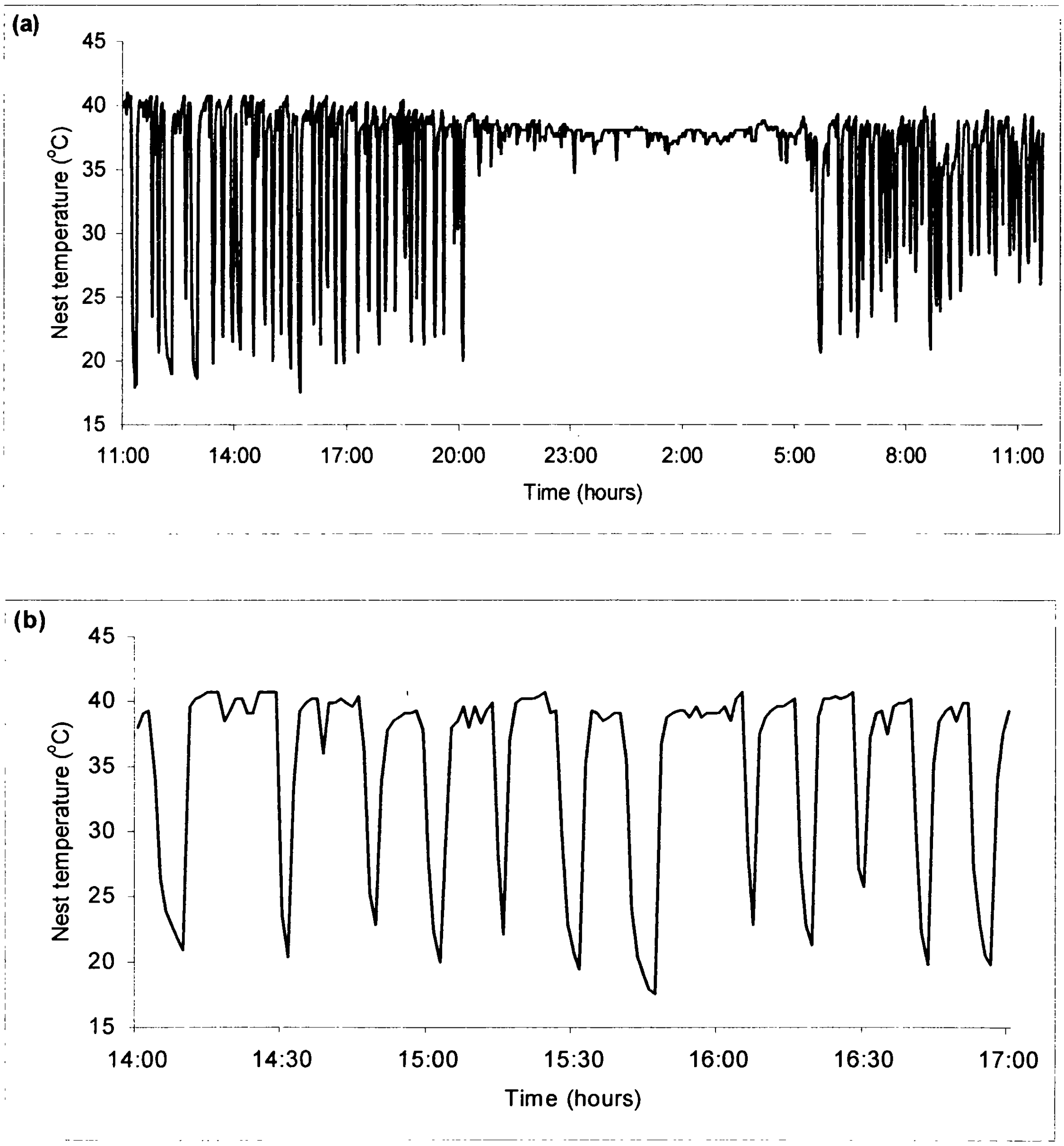
Pairs of experimental and control nests were matched for laying date and, as closely as possible, location. This design helped to ensure that there was no significant difference between the control and experimental groups in terms of clutch size (control mean = 4.76 ± 0.13, experimental mean = 4.53 ± 0.15, Mann-Whitney U-Test $U = 112.5$, $N_1 = N_2 = 17$, $P = 0.213$), mean egg mass (based on nest means, control mean = 7.99 ± 0.11g, experimental mean = 8.32 ± 0.15g, $t_{31} = -1.79$, $P = 0.09$), overall clutch mass (control mean = 38.3 ± 0.9g, experimental mean = 37.5 ± 1.0g, $t_{31} = 0.60$, $P = 0.55$) or laying date (control nest mean = 5.1 ± 0.6 days into May, experimental mean = 5.2 ± 0.7 days into May, $t_{32} = -0.20$, $P = 0.84$).

Thermistors attached to TinyTalk data loggers (Gemini Dataloggers Ltd, Chichester, U.K.) were placed in a pair of control and experimental nests simultaneously for two day periods during incubation. The thermistor was positioned level with the top surface of the eggs, such that it was in contact with the parent's brood patch when the parent was present and the nest air when the parent was absent. The loggers recorded nest temperature every 72 seconds during this time. A 72 second sampling interval (hereafter 72SSI) was the shortest possible interval that could be maintained for 24 hours without overloading the logger's memory capacity. The times when a parent was incubating and was absent from the nest generally showed as clear peaks and troughs on the resulting temperature traces, allowing times of arrival and departure to be deduced (Fig. 4.1). Direct observation by JMR and video tapes of birds at nests showed that these points could generally be accurately identified on the temperature traces. The traces show a clear demarcation between the quiescent 'overnight' incubation period when then parent remained continually on the nest, and the active 'daytime' incubation period when the parent was alternately incubating and foraging (Fig. 4.1).

During the daytime period, identification of the points of arrival and departure allowed the durations of the incubation-bouts and foraging-bouts, and hence the percentage of the daytime spent incubating to be calculated. The duration of the parent's overnight incubation session was also calculated. In addition, loggers in pairs of experimental and control nests were set to a 10 second sampling interval (hereafter 10SSI) for shorter periods of two to four hours during active daytime incubation. These traces allowed more accurate estimation of incubation-bout and foraging-bout duration. To minimize disturbance to the birds, nest visits were kept to a minimum and measurements were made as quickly as possible. Heating mats and thermistors were camouflaged with moss, and dataloggers were positioned at least 3m from the nest so that temperature data could be downloaded without disturbing the incubating parent. The birds showed no visible behavioural reaction to the presence of the heating mats and thermistors, and none of the manipulated nests were deserted during the study. The manipulation did not affect the mean number of chicks hatching in control and experimental nests (4.0 and 4.4 chicks respectively, $t_{30} = -0.79$, $P = 0.43$).

Data were analyzed by considering simultaneously recorded traces from the paired experimental and control nests. As paired tests could then be used, no correction was necessary for the date or time to which the trace corresponded. Two-tailed statistical tests were used throughout, and non-parametric tests were used when the assumptions of parametric tests were violated by the data distributions. Means are quoted in the form 'mean ± one standard error'.

Figure 4.1. Temperature recorded on a single starling nest over (a) a 24 hour period, and (b) an expanded 3 hour section of this trace. The nest temperature is high when the parent is incubating and falls sharply during the daytime foraging bouts when the nest is left unattended. Arrivals and departures of the incubating parent result in sudden clear changes in nest temperature. The overnight incubation session runs from 20:20 until 05:30, and nest temperature is consistently high during this period (a). Parents typically continue to incubate after the nest has reached a constant temperature (b).



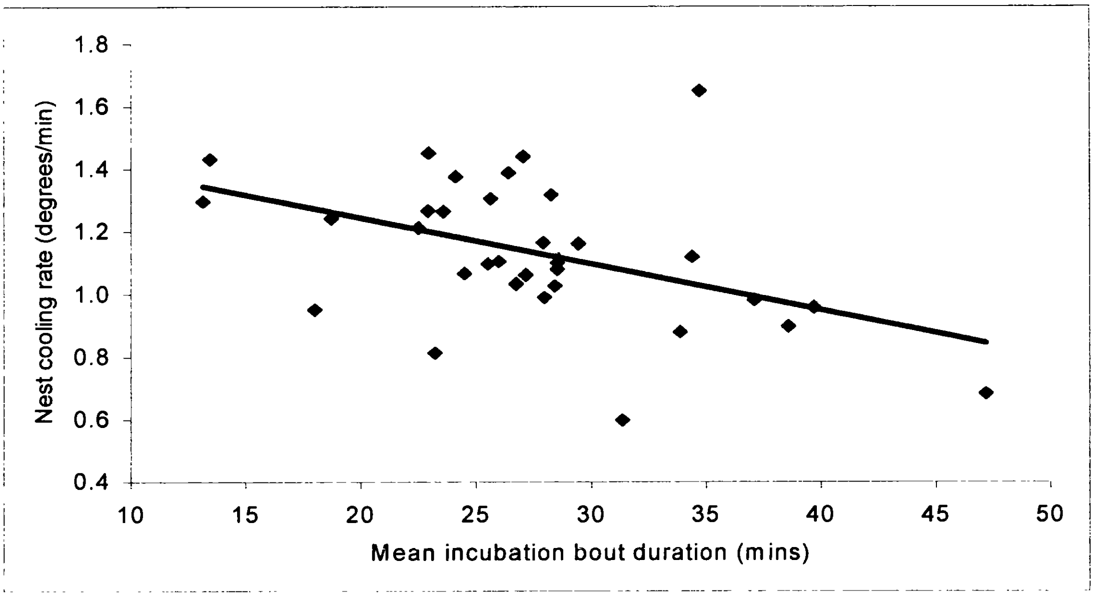
Results

We obtained 82 good quality pairs of 72SSI traces, spread over 16 of the 17 pairs of control and experimental nests (the 17th pairing included a nest that failed for unknown reasons at the start of the incubation period). Mean incubation-bout and foraging-bout durations were calculated from these traces. Forty-one pairs of 72SSI traces allowed unambiguous estimation of the duration of the overnight incubation session.

The mean duration of the continuous overnight incubation session was significantly longer on experimental nests than on control nests (means of 500.4 ± 11.2mins and 464.6 ± 19.3 mins respectively, Paired t test $t_{15} = -2.19$, $P = 0.04$). This was due to overnight incubation finishing significantly later in the morning on experimental nests (mean finish times of 4:37am ± 5.7mins and 5:18am ± 7.3mins on control and experimental nests respectively, Paired t test $t_{15} = -2.99$, $P = 0.009$) rather than starting significantly earlier in the evening (mean start times of 9:15pm ± 9.2mins and 8:49pm ± 6.5mins on control and experimental nests respectively, Paired t test $t_{15} = 1.51$, $P = 0.16$).

During the daytime, incubation was intermittent with relatively short bouts of incubation being interspersed with bouts of foraging. Mean incubation-bout duration was significantly longer on experimental nests than on control nests (means of 30.5 ± 1.7minutes and 24.5 ± 1.6 minutes respectively, Paired t test $t_{15} = -3.10$, $P = 0.007$). Further, across all 33 nests, mean daytime incubation-bout duration was significantly negatively correlated with nest cooling rate as measured using the plaster disc (Fig. 4.2). In contrast, the duration of foraging-bouts did not differ significantly between experimental and control nests (means of 4.3 ± 0.4minutes and 5.0 ± 0.3 minutes respectively, Paired t test $t_{15} = 1.37$, $P = 0.19$).

Figure 4.2. Across the 33 nests studied, mean daytime incubation bout duration was significantly negatively correlated with nest cooling rate. Pearson correlation $r_{32} = -0.455$, $P < 0.02$.



By analyzing one simultaneously recorded pair of 10SSI traces available for 12 of the 17 pairs of nests, we calculated a second estimate of mean daytime incubation-bout and foraging-bout duration. The shorter sampling interval allowed us to estimate the durations of short bouts with greater accuracy. As with the 72SSI data, mean incubation-bout duration was significantly longer on experimental nests than on control nests (medians of 23.1 minutes and 17.5 minutes respectively, Wilcoxon matched pairs test $T = 12$, $N = 12$, $P < 0.05$). Mean foraging-bout duration did not differ significantly between the two groups (experimental median 4.1 minutes, control median 6.1 minutes, Wilcoxon matched pairs test: $T = 16$, $N = 12$, $P > 0.05$), although there was a trend towards shorter foraging-bouts on experimental nests. The mean incubation-bout and foraging-bout durations estimated from the 10SSI traces did not differ significantly from those estimated from the 72SSI traces for either experimental or control nests (Incubation-bout duration; control nests, $t_{22} = -1.34$, $P = 0.19$; experimental nests, $t_{22} = -1.09$, $P = 0.29$.

Foraging-bout duration; control nests, $t_{22} = 1.55$, $P = 0.14$; experimental nests, $t_{22} = -0.19$, $P = 0.85$). Hence the 10SSI estimates of mean incubation-bout and foraging-bout duration reinforce the 72SSI estimates, and there is no evidence that the relatively long 72 second interval introduced any important error into our estimates.

There was no evidence of a relationship between daytime incubation-bout duration and time of day. Out of the 59 temperature traces from which the durations of 15 or more consecutive incubation-bouts could be deduced, only five showed a significant correlation between bout length and time of day. Visual inspection and quadratic regression showed no evidence of non-linearity.

As a consequence of their longer daytime incubation-bouts, females on experimental nests spent a significantly greater proportion of the daytime period incubating than did females on control nests (means of 87.8% and 82.1% respectively, Paired *t* test on arcsin transformed proportional data, $t_{15} = -2.91$, $P = 0.01$). Using the mean overnight incubation session duration and the mean proportion of the daytime incubation period spent on the nest, the mean time spent incubating on experimental and control nests during each 24 hour period was estimated (Total time in minutes T = overnight bout length X + ((24 x 60) - X) x (proportion of active time spent incubating)). A significantly greater percentage of each 24 hours was spent incubating by parents on experimental nests than on control nests (means of 1325.6 minutes or 92.1% of the day and 1263.5 minutes or 87.7% of the day respectively, Paired *t* test, $t_{15} = -3.02$, $P = 0.009$).

Discussion

On average within each 24 hours, parents spent significantly more time incubating on the experimental nests in which the rate of clutch cooling was reduced, than on control nests. This increase was due to significant increases in mean daytime incubation-bout duration and in the duration of the overnight incubation session. On average, the experimental parents showed a 7.7% (35.8 minute) increase in overnight incubation duration over the control parents, and between a 24.5% (6.0 minute, 72SSI data) and 32.0% (5.6 minute, 10SSI data) increase in average daytime incubation-bout duration. The overnight incubation session started no earlier on experimental nests than on control nests, but continued significantly later into the next morning. As there was no relationship between incubation-bout length and time of day, the extension of the overnight incubation session later into the morning cannot have affected the estimate of the mean daytime incubation-bout length of the experimental birds. Such prolonged incubation-bouts in response to a decreased clutch cooling rate are predicted by the parental-energy model of incubation. If a reduced rate of energy expenditure is required to keep a clutch warm, an adult can remain on the nest for longer during each incubation-bout before its energy reaches the threshold level for departure, extending each daytime bout and prolonging the overnight bout later into the morning. The prediction of the egg-temperature model, that incubation-bout duration should decrease with decreased clutch cooling rate, is not upheld, and there is further evidence that this model is not correct. If egg temperature cues an incubating parent to depart from the nest, then the parent should leave as soon as the clutch reaches the threshold temperature rather than continuing to incubate beyond this point. The nest temperature traces recorded on Fair Isle show that parents frequently continue to incubate after the nest has reached a constant temperature (Fig. 4.1).

Mean foraging-bout duration did not differ significantly between control and experimental nests and, as our manipulation should not have affected the parent's foraging ability and parents were randomly allocated to experimental and control groups, this result is consistent with the hypothesis that foraging-bout duration depends on foraging efficiency (Drent *et al.* 1985; Jones 1989; Weimerskirch 1994). However, while the duration of the foraging bouts themselves did not change, the overall time devoted to foraging was less in experimental birds as they took fewer foraging breaks. This was presumably as a consequence of the reduced energy requirement for warming the eggs.

Heat is lost from a clutch of eggs by radiation and convection to the atmosphere, and by conduction through the nest material (Khaskin 1961; Turner 1991). Hence the rate of clutch cooling experienced in a nest depends on the temperature gradients between the eggs, the nest and the surroundings, and on the insulative properties of the nest. Eggs will cool more slowly when nest and ambient temperatures are high, and when the nest provides better insulation. Several previous studies have compared incubation-bout duration with ambient temperature, nest temperature and nest insulation (Table 4.1), and our result that incubation-bout duration increases as clutch cooling rate decreases differs from the results of the majority of these studies. Twenty-one studies (six experimental) on 16 species of intermittent incubators found mean incubation-bout duration to decrease as ambient temperature, nest temperature or nest insulation increased (and hence the presumed rate of clutch cooling decreased), including in starlings in the Waddensea (Drent *et al.* 1985). Seven studies (one experimental) on seven species found no relationship between mean incubation-bout duration and clutch cooling rate whilst only one previous study found that, as in this study, incubation-bout duration increased as clutch cooling rate decreased. Dusky Flycatchers spent more time incubating at higher ambient temperatures (Morton & Pereya 1985). Hence if the parental-energy model of incubation is indeed correct, we must explain why the majority of studies apparently conflict with its prediction that incubation-bout duration should increase with decreased clutch cooling rate.

Table 4.1. Reported relationships between mean incubation bout duration and ambient temperature, nest/egg temperature and nest cooling coefficient.
* signifies an experimental study.

Species	**Source**	**Bout duration correlated with:**	**Correlation**
Magellanic penguin (*Spheniscus magellanicus*)	Stokes & Boersma 1998	Ambient temperature	Negative
Goldeneye (*Bucephala clangula*)	Mallory & Weatherhead 1993	Ambient temperature	Negative
African jacana (*Actophilornis africana*)	Tarboton 1993	Ambient temperature	Negative
White-rumped sandpiper (*Calidris fuscicollis*)	Cartar & Montgomerie 1987	Ambient temperature	Negative
Tree swallow (*Tachycineta bicolor*)	Lombardo *et al.* 1995	Ambient temperature	Negative
Bank swallow (*Riparia riparia*)	Ellis 1982	Ambient temperature	None
Pied wagtail (*Motacilla alba*)	Fitzpatrick 1996	Ambient temperature	None
Water pipit (*Anthus spinoletta*)	Rauter & Reyer 1996	Ambient temperature	None
Meadow pipit (*Anthus pratensis*)	Halupka 1994	Ambient temperature	None
Skylark (*Alauda arvensis*)	In Drent 1970	Ambient temperature	Negative
Wren (*Troglodytes troglodytes*)	In Drent 1970	Ambient temperature	Negative
Pied flycatcher (*Ficedula hypoleuca*)	Haftorn & Ytreberg 1988	Ambient temperature	Negative
Dusky flycatcher (*Empidonax oberholseri*)	Morton & Pereyra 1985	Ambient temperature	Positive
Great tit (*Parus major*)	Haftorn 1981	Ambient temperature	Negative
Willow tit (*Parus montanus*)	Haftorn 1979	Ambient temperature	Negative
Starling (*Sturnus vulgaris*)	Drent *et al.* 1985	Ambient temperature	None
Savannah sparrow (*Passerculus sandwichensis*)	Davis *et al.* 1984	Ambient temperature	Negative
Harris's sparrow (*Zonotrichia querula*)	Norment 1995	Ambient temperature	Negative
White-crowned sparrow (*Zonotrichia leucophrys*)	Norment 1995	Ambient temperature	Negative
Village weaver (*Ploceus cucullatus*)	White & Kinney 1974	Ambient temperature	Negative
Red bishop (*Euplectes orix*)	Slotow *et al.* 1995	Ambient temperature	None

Table 4.1 *continued.*

Ringed turtle dove (*Streptopelia risoria*)	In Davis *et al.* 1984	Nest/egg temperature	Negative*
Barn swallow (*Hirundo rustica*)	Smith & Montgomerie 1992	Nest/egg temperature	Negative
Pied flycatcher (*Ficedula hypoleuca*)	In Drent 1970	Nest/egg temperature	Negative*
Pied flycatcher (*Ficedula hypoleuca*)	Haftorn & Reinertsen 1990	Nest/egg temperature	Negative*
Starling (*Sturnus vulgaris*)	Drent *et al.* 1985	Nest/egg temperature	Negative*
Savannah sparrow (*Passerculus sandwichensis*)	Davis *et al.* 1984	Nest/egg temperature	Negative*
Barn swallow (*Hirundo rustica*)	Møller 1991	Nest cooling coefficient	Negative*
Tree swallow (*Tachycineta bicolor*)	Lombardo *et al.* 1995	Nest cooling coefficient	None*

The fact that starling incubation-bout duration has been shown both to decrease and increase with decreased clutch cooling rate in different studies (Drent *et al.* 1985, this study) suggests that the factors determining incubation strategy are in fact more complex than described by the basic parental-energy model. The model assumes that the parent can forage with a high enough efficiency to maintain both clutch temperature and adult body condition at optimal levels. Where food is scarce or can only be gathered slowly this may not be the case, and resolution of the conflicting demands of incubation and foraging must involve either the time spent incubating falling below that required to maintain clutch temperature, or the time spent foraging falling below that required to maintain adult body condition. Where such constraints operate, a parent that is responding to its own energy level should maintain its body condition at the expense of time spent incubating, therefore risking clutch cooling. These parents should spend the extra time away from the nest when the costs of doing so are minimized, and this is likely to be when the rate of clutch cooling is slow. At these times, the eggs will cool less during the parent's enforced absence and the risk of chilling will be reduced. Thus when the parent's foraging requirement limits its incubation behaviour, an optimally incubating parent might be predicted to spend less time incubating when the clutch cools slowly, as observed in the majority of studies. Hence both the observed increase and decrease in starling incubation-bout duration with decreasing clutch cooling rate can be explained by the parental-energy model of incubation, if starling incubation strategy is sometimes constrained by foraging efficiency. This hypothesis suggests that Fair Isle is an area of food superabundance for starlings but that starling incubation is constrained by foraging in the Waddensea. There is some evidence that this may be the case. Drent *et al.* (1985) concluded that the incubation strategy of the Waddensea starlings was driven by foraging requirements. They also suggested that foraging-bout duration was determined by the time taken to fill the stomach. Mean starling foraging-bout durations were twenty minutes on the Waddensea but only four to five minutes (see results) on Fair Isle. Fair Isle starlings could often feed successfully immediately outside their nest cavities, reducing the time and energy needed to travel to foraging areas. The ground on Fair Isle remains permanently damp enough to allow easy probing for invertebrates, and as there is little diurnal variation in ambient temperature, there is unlikely to be a period of the day when their invertebrate prey is difficult to obtain. Due to its relatively high latitude, during the spring there are more daylight hours available for foraging on Fair Isle than in the Waddensea. Further, despite the fact that Fair Isle is cold, starlings here can anomalously rear two broods within a single season, something that is achieved nowhere else north of southern Scotland (Feare 1984; Cramp & Perrins 1994; P.G.H.Evans pers. comm.).

We conclude that the energy level of an optimally incubating parent may act as the proximate cue that prompts it to terminate an incubation-bout and depart from the nest. Hence the parent behaves in response to its own body condition rather than directly to the condition of the embryo. This is analogous to the strategy that parents follow whilst feeding chicks (Weimerskirch 1998). However, we suggest that incubation strategy is commonly constrained by the parent's foraging requirements, forcing parents to reduce their nest attendance when the costs of doing so are low. It would be interesting to investigate how the condition of the parent at the start of incubation influences its incubation strategy, and how condition and strategy vary over the incubation period.

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Chapter five

Regulation of egg temperature in starlings (*Sturnus vulgaris*)

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Abstract

Incubating birds must maintain their eggs within a narrow range of temperatures if the embryos are to develop successfully. However, to maintain their own body condition, parents must also spend time foraging. Since incubation and foraging are often mutually exclusive activities, the way in which parents divide time between the two has important consequences for the thermal environment experienced by the offspring.

In a wild population of starlings, mean egg temperature was several degrees cooler than the predicted optimum for embryonic development. This was because parents frequently left clutches unattended rather than because they were physically unable to heat eggs to optimal temperatures. However, parents divided up the time allocated to foraging such that eggs rarely cooled below the temperature at which embryonic development ceases. Thus parents apparently optimised the conditions provided for offspring given the constraint that their own foraging requirements imposed upon their incubation behaviour.

Mean starling egg temperatures increased significantly during incubation periods. This was suggested to be due to continued brood patch development and to an increase in the time that parents allocated to incubation, rather than to increasing ambient temperatures, improved nest insulation or the physiological development of embryos. As egg temperatures increased as an incubation period progressed independent of date, our data suggest that an increased time allocation to incubating older embryos may reflect a change in the parent's optimal pattern of resource allocation rather than a temporal improvement in foraging conditions.

Introduction

Animals must often divide limited time and resources between competing activities (Roff 1992; Stearns 1992). Thus, the ability of an individual to invest optimally in any single activity may be constrained by its own requirement to invest simultaneously elsewhere. Such constraints on optimal behaviour may be particularly pronounced during reproduction, when parents must trade-off investment in activities that maximise their own lifetime fitness against investment in activities that maximise the fitness of the current brood of offspring. Although animals have often been suggested to time breeding attempts so that periods of peak demand coincide with periods of maximum resource availability (Poulin *et al.* 1992; Bancroft *et al.* 2000), the extent to which parents are able to simultaneously meet the demands of competing activities may still be limited. In such cases, parents must decide how best to allocate limited resources, a decision that is likely to affect the quality of the care that is provided for offspring.

The thermal conditions that avian embryos experience during the incubation period greatly influence their development and thus their survival chances (Lundy 1969; White & Kinney 1974; Drent 1975; Webb 1987). The egg temperatures that are optimal in terms of maximizing hatching success and minimizing the time until hatching have been well characterised in laboratory studies across several species (*eg*, Lundy 1969; Stubblefield & Toll 1993; Strausberger 1998). Maximum success is generally achieved if eggs are incubated between 36°C and 39°C (Webb 1987), although the exact optimum varies between species. Although embryonic development can continue at temperatures between approximately 26°C and 41°C (Lundy 1969; White & Kinney 1974; Drent 1975), departure from the optimal range can result in slow or abnormal development (Zhang & Whittow 1992), reducing hatching success (Webb 1987; Evans 1989; Ancel *et al.* 1994; Strausberger 1998) and prolonging the incubation period (Haftorn 1981, 1983; Strausberger 1998). The magnitude of these effects depends on the extremes of temperature to which embryos are exposed, the duration of exposure and the embryo's stage of development at exposure (Drent 1975; Webb 1987). Thus the temperatures that embryos experience during the incubation period must be closely controlled in order for breeding success to be maximised.

In the face of fluctuating environmental temperatures and the inability of embryos to regulate their own temperature (Sotherland *et al.* 1987), avian egg temperatures are generally controlled by incubating parents (Drent 1975; Carey 1980). However, incubation can be energetically demanding (reviewed in Williams 1996). Some species meet incubation demands almost entirely from stored reserves (*eg*, Hepp *et al.* 1990; Erikstad & Tveraa 1995), and others are provisioned on the nest by mates (*eg*, Nilsson & Smith 1988; Hatchwell *et al.* 1999). However, parents of other species must meet incubation demands by spending time foraging. Foraging and incubation are often mutually exclusive activities (White & Kinney 1974; Drent *et al.* 1985), and thus incubating parents have to depart from the nest in order to find food. Leaving eggs unattended and allowing embryos to depart from the optimal temperature range can reduce offspring fitness. However, as poor body condition can reduce chick-rearing ability (Bolton 1991; Wendeln & Becker 1999) and also a parent's chance of surviving to breed again (Jones 1992; Golet *et al.* 1998), allowing their own body condition to deteriorate may also be costly for parents. Thus during the incubation period, parents are likely to have to resolve an important trade-off between the time spent foraging and the time spent incubating (Drent 1975; Vleck 1981; Jones 1989; Hainsworth *et al.* 1998). The existence of a trade-off between energy intake and the time spent on the nest has been experimentally demonstrated (Lyon & Montgomerie 1985; Moreno 1989), and inferred from correlative studies across a range of species, including starlings (Drent *et al.* 1985; Chaurand & Weimerskirch 1994; Halupka 1994; Rauter & Reyer 1997; see *Chapter 2* for further discussion).

Using a population of starlings (*Sturnus vulgaris*), we investigated patterns of parental time allocation to incubation, and the ways in which allocations changed over the course of the incubation period. We discuss the consequences of these allocations for egg temperatures, and thus for the developmental conditions that are likely to have been experienced by offspring.

Methods

A population of roof nesting starlings was studied in the Ebro Delta, Spain (2°E, 41°N), between March and June 1999. In this population, the majority of females incubated alone with no assistance from males, and hence clutches were left unattended and cooled down during females' breaks from incubation.

In order to measure the temperatures at which eggs were incubated, single model eggs containing thermistors were added to clutches the day after laying was completed. At this time, a single real egg was fostered from each study nest to a neighbouring host nest, so that all study nests retained their natural clutch size throughout the incubation period. Eggs were returned to their natural nests and model eggs were removed the day before clutches were due to hatch. Eighteen such nests were studied, with laying dates spread over a six-week period between 30th March and 15th May.

Model eggs were made from Fimo modeling clay (EberhardFaber, Neumarkt, Germany), and closely matched real starling eggs in shape and colour, being immediately accepted by adult starlings in all cases. A thermistor mounted in silicone-based heat transfer compound (Electrolube, Berkshire, UK) was positioned in the centre of each model egg, with a lead running out of the blunt pole and through the side of the nest to a TinyTalk data logger (Gemini dataloggers Ltd, Chichester, UK). The logger recorded the temperature of the model egg every 72 seconds, and was positioned outside the nest cavity so that data could be downloaded without disturbing incubating birds. Model eggs were initially positioned randomly within clutches but as leads were slack and very flexible they were free to move around within a nest, usually changing position between nest visits. In each nest, the temperature of the model egg was recorded over a minimum of six days during the course of the 12 day starling incubation period, and mean, maximum and minimum egg temperatures were calculated for each nest on each day. Ambient temperature was simultaneously recorded using further thermistors and loggers that were positioned adjacent to nest cavities.

In the laboratory, the thermal properties of the model eggs were compared with those of freshly laid starling eggs taken from unstudied nests. When subjected to identical thermal conditions, model eggs lost and gained heat slightly faster than real eggs, although these differences equated to less than 10% of the real egg warming and cooling rates ($n = 10$ for each group, mean exponential cooling coefficients: 0.72 ± 0.05

and 0.65 ± 0.05 for model and real eggs respectively; mean exponential warming coefficients: 0.53 ± 0.03 and 0.48 ± 0.06 respectively). However, after multiple consecutive cycles of 25 minutes of artificial incubation at 40°C followed by 8 minutes of cooling towards an ambient temperature of 18°C, approximately mimicking the pattern of incubation observed in the field, the mean temperature recorded at the centres of real and model eggs did not differ (Paired *t* test, $t_9 = 0.77$, $P = 0.46$). Hence the mean temperature recorded in model eggs can be taken as a realistic estimate of the mean temperature that real eggs experienced. Further, as the heat capacity of model eggs was slightly lower than that of real eggs, model eggs in nests are likely to have equilibrated rapidly with the real clutch, reducing the difference in warming and cooling rates and accurately reflecting real clutch temperature.

In nests, the maximum temperatures reached by model eggs were generally achieved after long periods of continuous incubation. Despite their slightly reduced warming rates, the real eggs are also likely to have reached their maximum temperatures during this time, and thus maximum model egg temperature is likely to be a reasonable estimate of maximum real egg temperature. The minimum temperatures to which model eggs fell may have been slightly lower than those reached by real eggs, but due to the short cooling periods involved in the field, the error is likely to have been less than 0.5°C.

The mass of the model eggs and the rate at which they cooled when moved from a 40°C incubator to an 18°C incubator did not change between the beginning and end of the field season (n = 10, mean initial mass 8.2 ± 0.1g, mean final mass 8.2 ± 0.1g, paired *t* test, $t_9 = -0.60$, $P = 0.74$; initial exponential cooling coefficient 0.72 ± 0.05, final exponential cooling coefficient 0.75 ± 0.09, paired *t* test, $t_9 = -0.39$, $P = 0.83$). Thus there was no evidence that the physical properties of the model eggs changed during the course of the fieldwork, for example due to water loss or gain. Hence any changes in model egg temperature over the course of any incubation period must have arisen from changes in nest temperature rather than changes in the thermal properties of the model eggs themselves.

To investigate whether egg temperatures changed as incubation periods progressed, within each nest, a general linear model was used to relate the mean, maximum and minimum egg temperatures recorded on each day to the number of days since the start of incubation and the mean ambient temperature for that day, with non-significant factors being eliminated stepwise. To investigate whether temperature changes occurred independently of any concurrent seasonal changes in environmental conditions, a cross-nest analysis was also carried out. The mean egg temperatures recorded in all the nests that contained clutches on a specific calendar day were examined in relation to the number of days since the start of incubation in each nest. This analysis was completed for each of the 17 days (spread between 4th April and 6th May) on which data from five or more nests were available.

In each study nest, a 'free' thermistor that was not enclosed in a model egg was used to record whether an adult was present on the nest, a technique that we have used successfully in other studies and validated using video recordings of nests (*Chapter 4*). Thermistors were positioned level with the top surface of the clutch, touching the parent's brood patch when the parent was present and the nest air when the parent was absent. In each nest, temperature was logged every 72 seconds for single 24 hour periods during both the first half and the second half of the incubation period. The early and late sampling periods for each nest were separated by at least 4 days, and by 5.9 days on average. Points of parental arrival and departure showed as clear peaks and troughs on the temperature traces, allowing the durations of incubation bouts and foraging bouts and hence the percentage of each daytime that parents spent incubating to be calculated. Manual watches from hides confirmed that times of arrival and departure could be correctly identified on the temperature traces, and data were discarded on the rare occasions when thermistors were observed to have been dislodged from position.

The temperature regime experienced by embryos is likely to be influenced by the insulative quality of the nest. As a measure of insulative quality, the rate of heat loss from each nest was measured by placing a plaster disc warmed to 35°C in the nest, and measuring the rate at which it cooled down (*Chapter 4*). This measurement was made after the first egg was laid in each nest and again when the first chick hatched, with clutches being placed in insulated containers whilst readings were taken. Newton's cooling equation (Disc Temperature = Ambient Temperature +($\mathrm{Bexp}^{(-\mathrm{C} \times \mathrm{time})}$), where B and C are fitted positive constants) was fitted to each cooling curve recorded. The value of the exponential coefficient C reflects the rate of heat loss, and the values of C calculated for each nest at laying and at hatching were compared.

Parametric statistical tests were used unless the data distributions violated the appropriate assumptions, when equivalent non-parametric tests were used. All tests were two-tailed, and means are presented ± one standard error.

Results

Overall, the mean model egg temperature recorded over the whole study period was 32.6 ± 0.4°C (n = 18), but egg temperatures ranged between 10.4°C and 40.2°C.

Ambient temperature averaged 17.5°C over the study period, but increased as the season progressed, from 14.5°C during the first fieldwork week to 19.8°C during the last week. However, the weather was sufficiently variable such that ambient temperature did not increase significantly with the number of days since the start of incubation over any of the individual incubation periods studied (Spearman correlation, $P > 0.05$ for all 18 nests). Both mean egg temperature and minimum egg temperature increased significantly as incubation progressed in 15 out of 18 nests, significantly more often than expected by chance (Binomial probability, $P < 0.001$). There were non-significant increases in temperature in two of the remaining three cases. Mean and minimum temperatures also increased significantly during incubation when averaged across all nests (Fig. 5.1), increasing from 31.4 ± 0.5°C to 34.9 ± 0.4°C and from 22.5 ± 0.9°C to 29.2 ± 0.5°C respectively. Ambient temperature was a significant predictor of mean and minimum egg temperatures in only four and three of the 18 study nests respectively.

There was no significant linear relationship between maximum egg temperature and either the number of days into incubation or ambient temperature in 16 out of the 18 nests. However, the daily maximum egg temperatures recorded in each nest increased significantly between the first day and the third day of the incubation period (first day, 35.0 ± 0.5°C; third day, 36.4 ± 0.5°C, paired t test, $t_{17} = 3.60$, $P = 0.002$), but did not increase further between the third and final days of incubation ($r_s = 0.38$, $N = 8$, $P = 0.35$, Fig. 5.1). In consequence, as the incubation period progressed, eggs spent more time within the optimal temperature range (>36°C) and less time at temperatures below which embryonic development could not continue (<26°C) or would have been greatly slowed (<30°C, Fig. 5.2).

Figure 5.1. Mean (± 1 SE) mean (a), minimum (b) and maximum (c) egg temperatures on each day during the incubation period (n = 18 nests). Average mean and minimum temperatures increased significantly with stage of incubation ($r_s = 0.99$, $N = 11$, $P < 0.001$ and $r_s = 0.96$, $N = 11$, $P < 0.001$ respectively). Mean maximum temperature did not increase significantly across all days ($r_s = 0.56$, $N = 11$, $P = 0.1$). The dotted line signifies the 36°C threshold for optimal embryonic development.

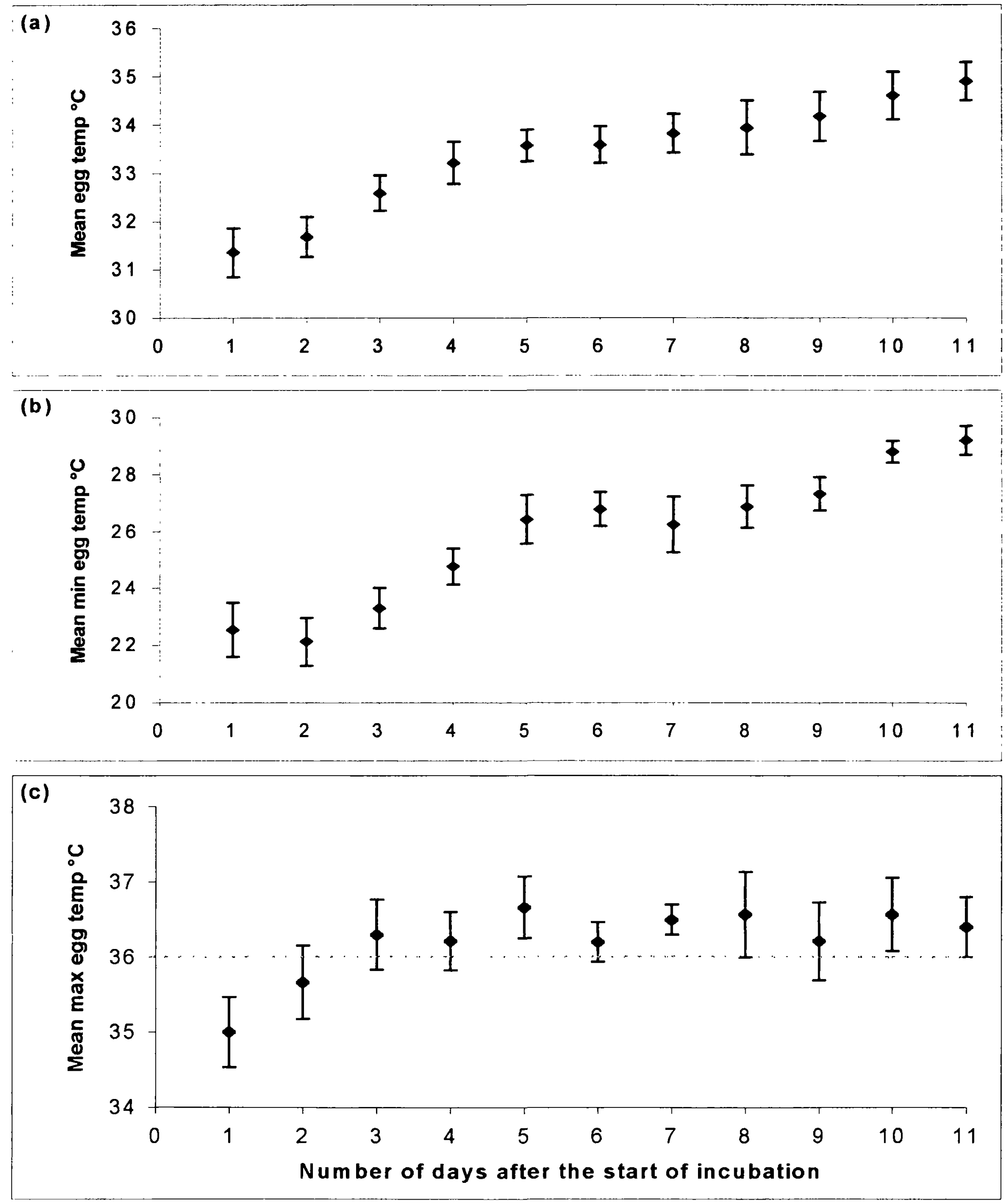
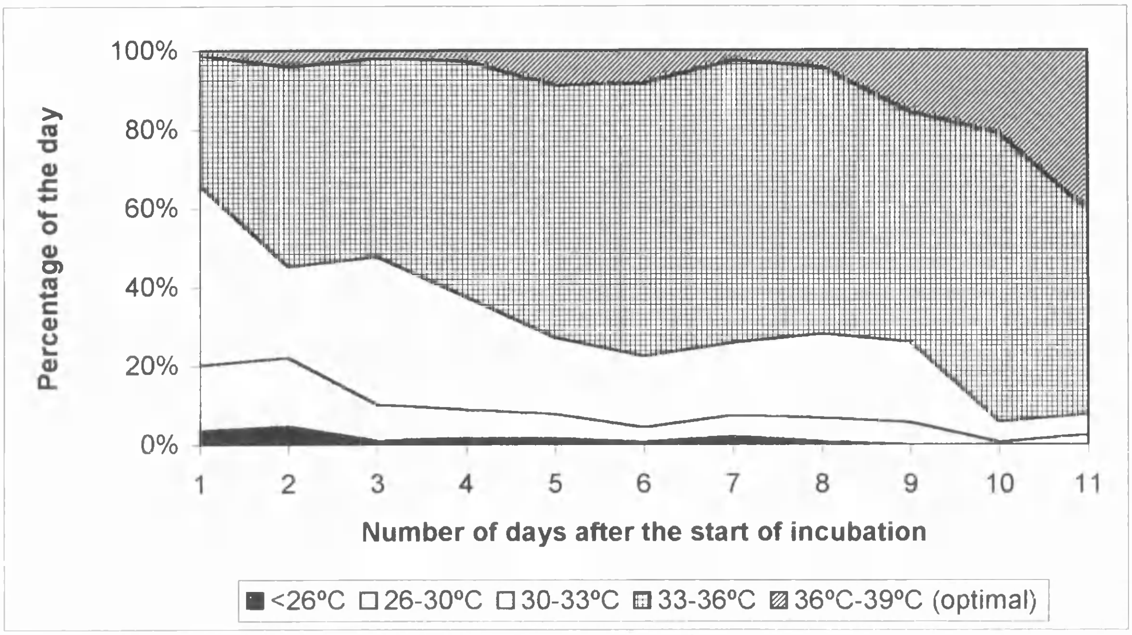


Figure 5.2. Average proportion of time that eggs spent at different temperatures on each day during the incubation period (n = 18 nests).



Across all the nests from which data were collected on any one calendar day, mean egg temperature was significantly correlated with the number of days since the start of incubation in each nest on 12 out of 17 occasions, significantly more often than expected by chance (Binomial probability, $P < 0.001$). Thus mean egg temperature tended to increase as incubation periods progressed independent of any temporal changes in prevailing environmental conditions.

Daytime incubation bouts lasted significantly longer during the second half of the incubation period than during the first half (first half mean 20.8 ± 1.9 minutes, second half mean 27.0 ± 1.4 minutes, paired *t* test, $t_{11} = -3.05$, $P = 0.01$), and foraging bouts were significantly shorter (first half mean 8.8 ± 1.2 minutes, second half mean 6.9 ± 0.7 minutes, paired *t* test, $t_{11} = 2.21$, $P = 0.04$). Hence overall, parents spent a greater proportion of the daytime on the nest during the second half of the incubation period (first half mean 70.2 ± 2.7%, second half mean 78.7 ± 2.0%, paired *t* test on arcsin transformed data, $t_{11} = -4.27$, $P = 0.001$). Thus, given that parents spent a constant average of approximately 9 hours on the nests overnight throughout the incubation period, clutches were incubated for an average of 76.5 minutes extra per daytime during the second half of the incubation period.

The rate at which heat was lost from nests did not change significantly between laying and hatching (mean C values of 0.89 ± 0.05 and 0.84 ± 0.05 respectively, paired *t* test, $t_{16} = -1.75$, $P = 0.15$).

Discussion

Data from model eggs suggest that naturally incubated starling eggs experienced a mean temperature of approximately 32.6°C during the incubation period. This is similar to the mean egg temperature of 32.2°C recorded across a range of wild-nesting passerines (Webb 1987), and is well within the ranges reported in other studies (*eg*, Weathers & Sullivan 1989; Williams 1996).

Mean egg temperatures were several degrees lower than the 36°C to 39°C temperature range at which the hatching success of artificially incubated eggs is maximised. Thus wild starlings apparently failed to maintain their eggs at the temperatures that laboratory studies suggest are optimal for embryonic development. However, on the majority of days during the incubation period, starling eggs approached or were within the optimal temperature range whilst clutches were actually being incubated by parents. Thus mean egg temperatures were not lower than expected because parents were physiologically unable to heat eggs to 36°C or above. Instead, mean temperatures were low because parents were regularly absent from their nests, leaving their clutches unattended and allowing them to cool towards ambient temperature. Hence incubating parents' allocations of time to activities away from the nest resulted in eggs spending substantial amounts of time below the optimal temperature range. As eggs frequently fell to temperatures at which embryonic development is likely to have slowed, and sometimes reached temperatures at which it may have ceased altogether, this pattern of time allocation may have had developmental and fitness consequences for embryos.

Starlings are iteroparous breeders, and selection may favour parents that invest in their own condition, increasing their chance of reproducing again in the future, as well as investing in current offspring. Thus, parental allocation of time to activities such as foraging away from the nest is perhaps expected. However, as this allocation affected egg temperatures, parents and offspring may conflict over the extent of the parent's allocation to foraging. There may be evolutionary pressure for the embryo's optimal thermal regime to converge with that provided by their parents and indeed, embryos are generally resistant to short periods of cooling such as those experienced during parents' foraging breaks (Drent 1975; Zerba & Morton 1983; Morton & Pereyra 1985; Webb 1987; Sockman & Schwabl 1998). However, parents may be able to minimise the extent to which conflict arises by optimising their pattern of nest attentiveness within the constraint imposed by the time allocated to foraging. The total time that a parent opts to spend away from a nest could be divided between many short or a few long foraging breaks, with different strategies resulting in the creation of different thermal environments within a nest. In this study, as eggs rarely fell below the 26°C threshold at which embryonic development ceases, the majority of trips made by adult starlings were shorter than the time taken for eggs to cool to this temperature. Indeed, egg temperatures below 26°C were never recorded during the last three days of the incubation period. Hence, as reported previously (Haftorn 1988; Weathers & Sullivan 1989), parents organised their nest attentiveness pattern such that, given their allocation of time to foraging, the time that offspring spent at temperatures at which development could continue was maximised.

Mean starling egg temperatures increased significantly as incubation periods progressed; older embryos spent more time within the optimal temperature range and less time at temperatures at which development would have been greatly slowed. As ambient temperature did not increase significantly during any of the individual incubation periods studied and the mean rate of heat loss from nests did not decrease significantly over the course of incubation, the observed increases in egg temperature cannot have been due to changes in either of these two factors. Further, laboratory experiments have shown that despite the higher metabolic rates of older embryos, older eggs tend to lose heat more rapidly than younger eggs. This may be because increasing embryonic circulation increases the rate at which heat is dissipated, or because of changing egg composition

(Turner 1987; Hilton *et al.* in prep.). Hence observed increases in egg temperature are unlikely to have been due to the physiological development of the embryos.

The extent to which a parent's brood patch has developed may affect the maximum temperature reached by a clutch after a period of continuous incubation, and maximum egg temperature increased during the first three days of incubation but not subsequently. Zerba & Morton (1983) recorded a similar temporal increase in the maximum temperatures reached by the eggs of white-crowned sparrows (*Zonotrichia leucophrys*). This suggests that parents' brood patches may have been incompletely developed when incubation started, and that development was completed during the early stages of the incubation period. Similar patterns of brood patch development have been suggested in multiple previous studies (Jones 1971; Drent 1975; Afton 1979; Haftorn 1983; Zerba & Morton 1983; Morton & Pereyra 1985). Hence continued physiological development of parents' incubation ability may have contributed to the increase in mean egg temperature during the first few days of incubation. However, further brood patch development is unlikely to account for the continued increase in egg temperature over the whole incubation period. Instead, this increase most probably occurred because parents spent more time on nests as incubation periods progressed. Clutches were left unattended less often and for shorter periods during the second half of the incubation period, reducing the time for which eggs were allowed to cool, thus raising the minimum and mean temperatures experienced. Hence the developmental conditions experienced by embryos apparently improved as incubation periods progressed, probably as a result of an increase in the amount of time that parents allocated to incubation.

Adult nest attentiveness and hence the temperatures experienced by offspring have frequently been reported to increase markedly over the course of egg-laying (Caldwell & Cornwall 1975; Drent 1975; Haftorn 1979; Morton & Pereyra 1985; Wilson & Verbeek 1995). However, after clutch completion and the onset of full incubation, attentiveness and egg temperatures have been suggested to remain rather constant (Lundy 1969). Indeed, many studies have found no evidence that mean egg temperatures change over the course of incubation (Haftorn 1979, 1983, 1988; Morton & Pereyra 1985; Zerba & Morton 1983; Weathers & Sullivan 1989). Studies that have reported increases have often failed to control for the position of the temperature probe with respect to the developing embryo (*eg*, Caldwell & Cornwall 1975; Afton 1979), or for the possible influence of increasing ambient temperature (*eg*, Wilson & Verbeek 1995). Similarly, parental nest attentiveness often remains constant throughout the period of full incubation (*eg*, Caldwell & Cornwall 1975; Haftorn 1979), or may even decrease as hatching is approached (Thompson & Raveling 1987; Mallory & Weatherhead 1993). However, Drent (1970,1975) reports a clear increase in both nest attentiveness and egg temperature in herring gulls (*Larus argentatus*), and female yellow-eyed juncos (*Junco phaeonotus*) made shorter foraging trips as incubation periods progressed, increasing the minimum temperatures that eggs reached. However, as the frequency of foraging trips also increased with time in this species, mean egg temperatures remained unchanged (Weathers & Sullivan 1989). Hence overall, remarkably few studies have rigorously investigated how egg temperatures change over the course of incubation (Webb 1987). This study reports such an increase in a passerine for the first time, and further studies are required to clarify how common this phenomenon might be.

As exposing embryos to poor developmental conditions may reduce their chance of survival, our results raise the question of why parents did not provide warmer conditions for embryos earlier during the incubation period, either by completing brood patch development earlier, or by spending more time on the nest. Forming a brood patch is likely to be costly for parents, as energy must be expended to compensate for the increased rate of heat loss from the defeathered area (Buchholz 1996; Wilson *et al.*1998), and to grow replacement feathers (Schieltz & Murphy 1995). Hence there may be selection for parents not to form a full brood patch until a clutch has successfully been laid. As brood patches take several days to develop (Drent 1975), completion may not be possible until after incubation has started.

Nest attentiveness may have increased as incubation periods progressed as a result of a simultaneous seasonal improvement in foraging conditions (Moreno 1989). However, the study nests were widely scattered throughout a 15km^2 area of paddyfields, with fields adjacent to different nests being flooded and drained independently on different days. Thus adult starlings are likely to have experienced large changes in local foraging conditions that were unrelated to season. As the incubation periods that were studied were spread over seven weeks, it is unlikely that food availability can have increased consistently within each of the individual 12-day incubation periods. Further, as mean egg temperatures increased significantly with embryo age across all the nests that contained clutches on any individual calendar day, the evidence suggests that parents increased the time that they allocated to incubation as incubation periods progressed independent of environmental conditions. Thus we suggest that as incubation periods progressed parents allocated more time to incubation, increasing their attentiveness at a cost of reduced energy intake, and thus at a potential cost in terms of their own condition.

As increasing current investment in reproduction reduces the resources available for future investment (Stearns 1992), at any moment parents should increase their investment if the fitness benefit of doing so exceeds the consequent reduction in the fitness benefits received in the future. This might apply if the fitness benefit gained per unit of current investment increases, or if the relative contribution of the current breeding attempt to the parent's lifetime fitness increases. As chilling has been suggested to have more severe fitness consequences for older embryos than for younger embryos (Romanoff & Romanoff 1972; Drent 1975; Webb 1987), the fitness benefit of investing in incubation and preventing chilling might increase as embryos age. Further, the contribution of the current brood to the parent's lifetime fitness may increase as an incubation period progresses, as the opportunity to breed again before the next season decreases (Montgomerie & Weatherhead 1988; Rytkönen *et al.* 1995). Thus an increasing level of investment in incubation and hence increasing egg temperatures over an incubation period may reflect an adaptive pattern of allocation of parental resources, despite the potential developmental consequences for young offspring.

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Chapter six

The energetic consequences of clutch temperature and clutch size for a uniparental intermittent incubator

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Abstract

In uniparental intermittent incubators, incubating parents must simultaneously regulate both the temperature of the clutch and their own energy level. To examine the energetic consequences for parents of providing different thermal environments for clutches of different sizes, a dynamic model of incubation was constructed, in which the energy level of an incubating adult and the temperature of its clutch were simultaneously described.

Adult energy balance after a day of incubation decreased as mean clutch temperature increased, such that the debt accrued whilst maintaining a clutch within the optimal temperature range of 36 to 39°C was predicted to be prohibitively high. This was despite the fact that the mean metabolic rate required to maintain such temperatures did not exceed 2BMR. Thus the model can explain the observation that eggs of uniparental intermittent incubators nesting in the wild are incubated at temperatures below the developmental optimum.

Consistent with empirical studies, the metabolic demand of incubation was predicted to increase with clutch size. This increase was predicted to affect adult energy balance and hence the cost of incubation when clutches were incubated at optimal temperatures, but not at the lower temperatures actually observed in the wild. Hence the energetic demand of incubation may be unlikely to influence optimal clutch size in starlings. However, the exact relationship between clutch size and adult energy debt depended greatly on the nature of the relationship between clutch size and clutch thermal properties. Thus the consequences of clutch size for the cost of incubation are not clearly predictable, and caution may be required when using experimental clutch enlargements during incubation to manipulate costs of reproduction.

Introduction

As successful hatching of avian embryos is dependent upon eggs being exposed to the correct temperatures during development, tight regulation of clutch temperature by incubating parents is essential (Lundy 1969; Webb 1987). Recent empirical studies have suggested that, at least when environmental temperatures are below the thermoneutral range, incubation is energetically demanding for the parent, requiring an increase in metabolic rate to a level approaching that experienced during chick rearing (reviewed in Gloutney *et al.* 1996; Williams 1996; Thomson *et al.*1998). This energetic demand will have fitness consequences if parents cannot compensate for it, resulting in an energy debt being accrued, or if in compensating, parents fail to provide the optimal developmental conditions for their offspring. A number of studies have suggested that such fitness effects occur (see *chapter 2*). Experimentally altering the demand of incubation (*Chapter 3*) or the ability of parents to meet this demand (Lyon & Montgomerie 1985; Nilsson & Smith 1988) can affect breeding performance. Such effects are likely to be most acute in uniparental intermittent incubators in which only one parent incubates and that parent's incubation bouts are interspersed with foraging bouts (White & Kinney 1974; Williams 1996). Allowing eggs to cool can reduce offspring fitness (Webb 1987), and hence the energetic demand of incubation must be met whilst the time available for the parent to forage is limited by its need to remain on the nest (Drent *et al.* 1985; Moreno & Hillstrom 1992). However, little is known about exactly how a parents' energy balance varies with the temperature at which it maintains its clutch, and hence whether uniparental intermittent incubators nesting in the wild are likely to be energetically capable of providing the optimal developmental conditions for their offspring.

Further, there has been debate about whether the demand of incubation varies significantly with clutch size (Thomson *et al.* 1998). If larger clutches are more demanding and more costly to incubate, then incubation may play a role in limiting optimal clutch size in birds (Monaghan & Nager 1997). Several studies have shown that, below the thermoneutral temperature range, the metabolic demand of maintaining a clutch at a constant temperature increases with clutch size (Biebach 1981, 1984; Haftorn

& Reinertsen 1985). Consequently, the overall energetic demand of incubation can also increase with clutch size (Coleman & Whittall 1988; Moreno *et al.* 1991) although this has not always been found to be the case (Moreno & Carlson 1989; Gloutney *et al.* 1996), and increases are not always linear (Moreno & Sanz 1994). However, larger clutches cool more slowly than smaller clutches when left unattended (Frost & Siegfried 1976; *Chapter 7*) and hence may retain higher mean temperatures given the same pattern of parental attendance (*Chapter 7*). Hence it is not clear how the ability of parents to meet the energetic demand of incubation whilst maintaining a specific incubation temperature might vary with clutch size. Indeed, experimental clutch enlargement has not always affected measures such as adult mass, hatching success or the duration of incubation as might have been predicted assuming that enlargement caused a costly increase in incubation demands (reviewed in Thomson *et al.* 1998; Cichon 2000). There is a clear need for further study (Haftorn & Reinertsen 1985; Moreno & Sanz 1994; Thomson *et al.* 1998), and the consequences of clutch size for the relationship between mean clutch temperature and adult energy balance have not previously been explicitly investigated.

We simulated the energy balance of a uniparental intermittent incubator and the corresponding temperature of its clutch over a daytime during incubation. Hence we investigated the relationship between adult energy balance and mean clutch temperature, and examined how this is influenced by the number of eggs in the clutch. Based on this modeling, we discuss the mean temperature at which parents should maintain their eggs, and consider whether the energetic consequences of incubation might influence optimal clutch size in uniparental intermittent incubators.

Methods

During each simulation, a parent was assumed to incubate for a set period and then forage for a set period, with the same pattern of incubation and foraging bouts being repeated for a set number of hours equating to one daytime. During incubation bouts parents expended energy and warmed up their clutches, and during foraging bouts they gained energy whilst their clutches cooled down.

Unattended clutches cooled according to Newton's Law of Cooling,

$$dT/dt = -\alpha_c(T-A) \qquad (1),$$

where T(t) describes clutch temperature at time t, A is ambient temperature and α_c is the exponential cooling coefficient of the clutch. Similarly, when a parent was present on the nest, the clutch warmed up according to the equation

$$dT/dt = -\alpha_H(T-B) \qquad (2),$$

where α_H is the exponential heating coefficient of the clutch and B is the effective temperature of the parent's brood patch.

Foraging parents were assumed to expend energy ($E(t)$) at a constant rate during a fixed flight time to and from their foraging grounds ($dE/dt = -\beta_1$), and to accrue energy at a constant rate whilst at their foraging grounds ($dE/dt = \beta_2$). Although these relationships are likely to give simplistic estimates of the patterns of energy expenditure and intake during foraging breaks (Hilton *et al.* 2000), overall predictions are likely to be sufficiently accurate for the purposes of this model.

Incubating parents expended energy at a rate that was described by the equation

$$dE/dt = -(\gamma + \delta(B-T)/(B-T_{min})) \qquad (3),$$

where T_{min} is the temperature of the clutch at the end of the preceding unattended period, γ is the energy required to maintain a constant clutch temperature per unit time and δ is a constant. The quantity $\delta(B-T)/(B-T_{min})$ describes the increment of energy required to rewarm a cool clutch. The magnitude of this increment depends on current and initial egg temperature and thus on the duration of the previous inattentive period and the time since the current incubation bout began (Vleck 1981; Biebach 1984, 1986; Drent *et al.* 1985), decreasing to zero as clutch temperature approaches brood patch temperature.

Forward difference approximations (Smith 1978) to these equations were used to simulate the changes in energy and temperature after small time intervals using Delphi Pascal (Borland version 4.0), and the mean temperature experienced by the clutch was recorded at the end of each simulated day. Parents were assumed to remain continuously on the nest overnight, and to expend energy at a constant rate $dE/dt = -\gamma$ whilst they did so. The final energy balance of the adult after each 24 hours was recorded, and the mean energy expended per minute over the whole period was calculated as a measure of mean metabolic rate. The values of the exponential clutch cooling and heating coefficients α_c and α_H and the constants γ and δ were all allowed to vary with clutch size, and hence the consequences of clutch size for adult energy expenditure, metabolic rate and clutch temperature were investigated.

In order to parameterize the model, a wild population of starlings (*Sturnus vulgaris*) was studied in the Ebro Delta, Spain (2°E, 41°N). Female starlings are often solely responsible for incubation and as this species has previously been well studied, many of the relevant energetic parameters have been measured and are available in the literature. Model temperature-sensing eggs were temporarily inserted into wild clutches of between two and seven eggs, replacing one of the real eggs (see *Chapters 5 & 7* for details), and temperature was recorded every 72 seconds throughout the incubation period. Estimates for α_c and α_H were obtained by fitting equations (1) and (2) to the cooling and warming curves recorded as clutches were alternately incubated and left unattended (*Chapter* 7, Table 6.1). Model egg temperature traces were also used to estimate the duration of the active daytime (mean of 750 minutes) and effective brood patch temperature (B). This was taken to be the maximum temperature that eggs reached after long periods of continuous incubation, and was found to be 36.8°C. This is lower than reported brood patch skin temperatures (Drent 1975), presumably reflecting inefficiencies in heat transfer between brood patch and clutch. Values of γ were estimated from Biebach (1984) and δ was calculated from empirical measurements made in our laboratory (G. Hilton unpublished data, Table 6.1). To examine the robustness of the model to variation in these parameter values, simulations were repeated using values that described large clutches to be maximally and minimally demanding compared to small clutches (Table 6.1). The extreme values chosen approximate to the extreme values in the empirical data.

Table 6.1. Values of the parameters α_c, α_H, γ and δ used during three simulations: (1) mean values of empirical data, giving the best estimate of parameter values, (2) parameter values set to make large clutches maximally demanding to incubate, (3) parameter values set to make large clutches minimally demanding to incubate.

Clutch Size	**2**	**3**	**4**	**5**	**6**	**7**
α_C **(1)**	0.060	0.058	0.050	0.040	0.035	0.033
(2)	0.060	0.058	0.055	0.052	0.048	0.045
(3)	0.060	0.053	0.046	0.039	0.032	0.025
α_H **(1)**	0.130	0.120	0.100	0.095	0.090	0.085
(2)	0.130	0.120	0.100	0.090	0.080	0.070
(3)	0.130	0.125	0.120	0.115	0.100	0.095
γ **(1)**	63	66	69	72	75	78
(2)	63	67	71	75	79	83
(3)	63	65	67	69	71	73
δ **(1)**	30	32	32	32	32	32
(2)	30	31	32	32	33	33
(3)	31	32	32	32	32	32

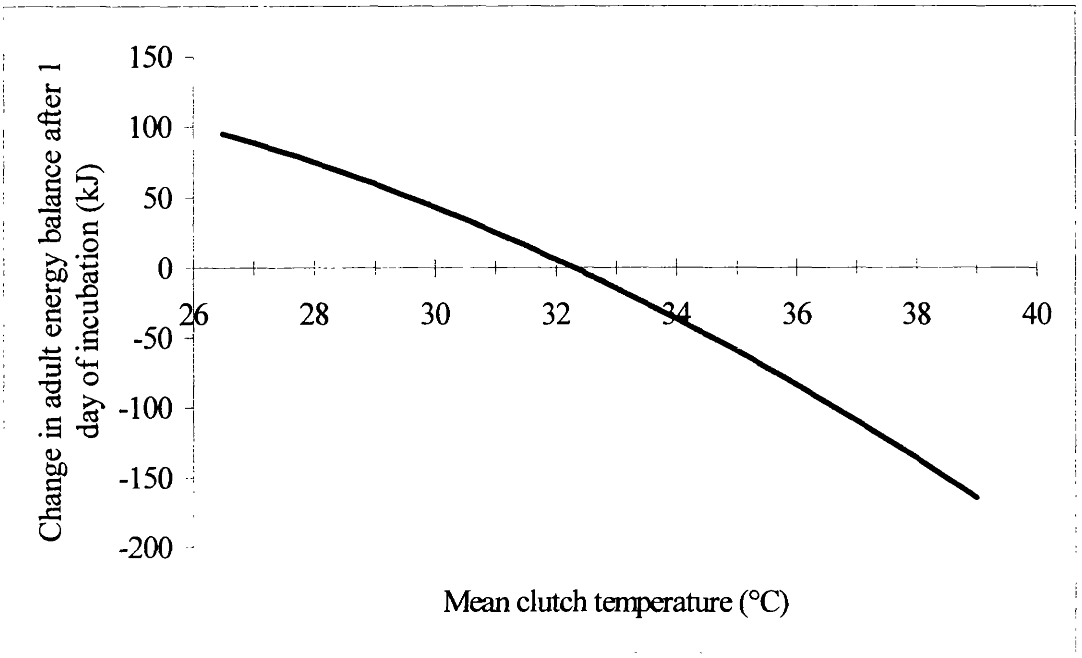
Values for starling basal metabolic rate (BMR = 50J/minute), flight costs (8.5BMR) and rate of energy intake whilst foraging (530J/minute) were estimated from Williams (1996), Biebach (1986) and Drent *et al.* (1985) respectively. The metabolic demand of foraging was assumed to be 4BMR (Bautista *et al.* 1998). Ambient temperature (A) was set at 17°C; this is approximately the mean air temperature recorded at the Spanish field site and is below the estimated thermoneutral temperature range at which incubation is likely to become demanding (White & Kinney 1974; Williams 1996). Observations of the times of parental arrivals at and departures from nests showed that 95% of foraging bouts lasted between 2 and 20 minutes, and 95% of incubation bouts lasted between 5 and 50 minutes. Typical flights to foraging grounds lasted approximately 20 seconds.

For each clutch size between two and seven, simulations were repeated for 100 combinations of incubation and foraging bout durations, with foraging bouts lasting between 2 and 20 minutes in steps of two, and incubation bouts lasting between 5 and 50 minutes in steps of five. Outcomes were ranked with respect to the mean clutch temperature achieved, and the strategy by which parents could achieve each mean temperature whilst finishing with the most positive energy balance was defined as the optimal strategy to obtain that clutch temperature. Regression lines were fitted through the set of optimal strategies to ascertain the optimal relationship between adult energy balance, metabolic rate, and mean incubation temperature for each clutch size.

Results and Discussion

The model predicts that a parent's final energy balance after a day of incubation will decrease as the mean temperature at which that parent incubates its clutch increases (Fig. 6.1), a relationship that arises because parents cannot simultaneously forage and incubate their clutch. Spending more time incubating raises mean clutch temperature to the detriment of energy balance, whereas spending more time foraging improves energy balance whilst reducing mean clutch temperature.

Figure 6.1. The energy debt that a parent accrues after a single day of incubation increases as the mean temperature at which it maintains its clutch increases. Parents are predicted to be able to maintain a clutch at a maximum temperature of approximately 32.5°C without going into energy debt, and maintenance at 36°C is predicted to result in a debt of approximately 80kJ per day.



Any mean clutch temperature above approximately 32.5°C is predicted to result in the parent making a net energy loss (Fig. 6.1), a temperature that is well below the range of 36 to 39°C that is thought to be optimal in terms of maximising the rate of embryonic development and hatching success (White & Kinney 1974; Webb 1987). Indeed, the model predicts that maintaining a clutch at a mean temperature of 36°C will be prohibitively demanding for a single parent. A starling maintaining this temperature will make a net energy loss of approximately 80kJ per day (Fig. 6.1) or 960 kJ over the 12 day starling incubation period (Cramp & Perrins 1994). As 1g of body fat provides approximately 39kJ of energy (Pennycuick 1989), an adult would have to burn almost 25g of fat in order to meet this demand, representing up to a third of a female starling's body mass (Cramp & Perrins 1994). Such drastic mass losses during the incubation period are unlikely to be possible, and are not observed in the field (Ricklefs & Hussell 1984).

Increasing the rate at which foraging parents gain energy alters the position of the clutch temperature versus adult energy balance relationship relative to the energy axis, reducing the energy debt that a parent accrues whilst maintaining its clutch at a certain temperature. Thus by increasing their foraging efficiency, parents could increase the temperature at which they are able to maintain their clutch without building an energy debt. However, the model predicts that in order to maintain a clutch at 36°C without going into debt, a foraging parent would have to increase its energy intake rate by 80% above a rate that is already set as high as that observed during chick-rearing (Drent *et al.* 1985), a rate that is unlikely to be possible. Thus the model predicts that female starlings incubating alone should be energetically unable to maintain their clutch within the optimal incubation temperature range.

Mean egg temperatures of wild passerines have indeed been found to be well below the optimal range. We recorded a mean daytime starling egg temperature of 32.2°C, and similar figures have been recorded for other passerines (reviewed in Webb 1987; Williams 1996). Further, given Drent *et al.*'s (1985) estimate of starling energy intake rate, the mean egg temperature observed in the field closely matches the maximum temperature that the model predicts adult starlings to be able to maintain whilst also maintaining a constant energy balance (Fig. 6.1). Thus the model suggests that parents allocate time and energy to incubation such as to maintain their own body condition rather than to provide the optimal temperature regime for the embryos. Indeed, incubating passerines have been recorded to lose little or no mass during the incubation period (Moreno & Carlson 1989; Moreno 1989; Moreno *et al.* 1991), and observed mass losses have sometimes been attributed to post-laying atrophy of the sexual organs rather than loss of somatic tissue (Ricklefs & Hussell 1984). Thus the model provides a quantitative explanation for the mean incubation temperature at which wild starlings maintain their clutches, an explanation that seems likely to be broadly transferable to other uniparental intermittent incubators.

The conclusion that parents cannot maintain clutches at 36°C arises despite the model's prediction that maintaining this temperature requires a mean metabolic rate of less than 2BMR (Fig. 6.2), a rate that is well within the range that is physiologically possible (Drent & Daan 1980; Ricklefs & Williams 1984). Thus the model supports the view that incubation represents an energetic bottleneck during reproduction (Yom-Tov & Hilborn 1981) not because the energetic demand of maintaining clutch temperature is in itself too high, but because the ability of parents to meet this demand is limited by their limited opportunity for foraging (Drent *et al.*1985; Moreno & Hillstrom 1992).

In agreement with the majority of empirical studies, the model predicts that the metabolic demand experienced by an incubating parent increases with clutch size (Fig. 6.2). An increase in metabolic rate of approximately 4% per extra egg is predicted, a result that agrees closely with Biebach's (1984) empirical data, and that holds true independently of the mean temperature at which a clutch is held. Further, the model suggests that at mean clutch temperatures within the optimal range of 36°C or above, the increased metabolic demand of incubating a larger clutch will translate into an increased energy debt for parents (Fig. 6.3). At 36°C, the debt is approximately 20% greater for a clutch of seven eggs than for a clutch of two eggs, requiring an adult starling to burn an extra 4.5g of fat over the incubation period. Thus, at or above 36°C, incubating a larger clutch is predicted to affect adult energy balance and hence fitness, suggesting that at these temperatures, the energetic consequences of incubating clutches of different sizes may influence the optimal number of eggs that a female should lay.

However, the same is not true at the 32 to 33°C temperature range within which wild passerines usually maintain their clutches (Webb 1987). At these temperatures, parents are predicted to be able to meet the increased metabolic demand of incubating a larger clutch without accruing a larger energy debt (Fig. 6.3). As large clutches cool down more slowly than small clutches, parents with large clutches can increase their foraging time enough to compensate for the increased energetic demand of incubation without affecting the mean temperature of their clutch. Thus the model suggests that although incubation is an energetically demanding stage of reproduction, a small increase in demand due to the presence of an extra egg does not necessarily translate into a corresponding increase in cost in terms of adult energy balance. This result sheds new light on the results of some empirical studies, as the observation that experimental clutch enlargement does not always affect hatching success, the duration of incubation or adult body condition has previously been unexplained (Jones 1987; Moreno *et al.* 1991; Thomson *et al.* 1998). Indeed, given the mean temperature at which wild starlings maintain their clutches, these results suggest that the energetic demand of incubation is unlikely to influence optimal clutch size in starlings.

Figure 6.2. The mean metabolic rate of an incubating parent over a day during the incubation period increases with clutch size. Maintenance of any clutch at 36°C is predicted to require a metabolic rate of less than 2BMR.

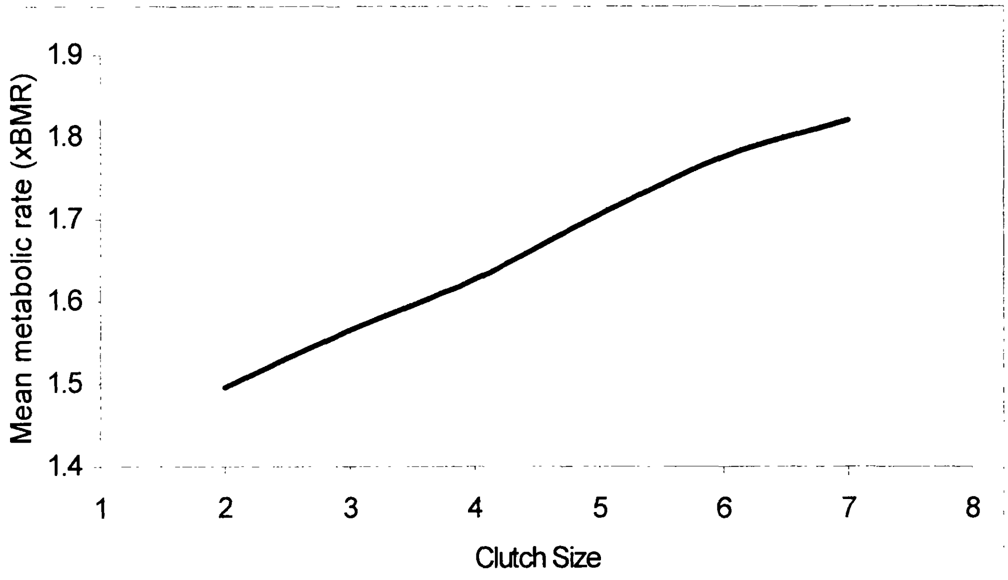
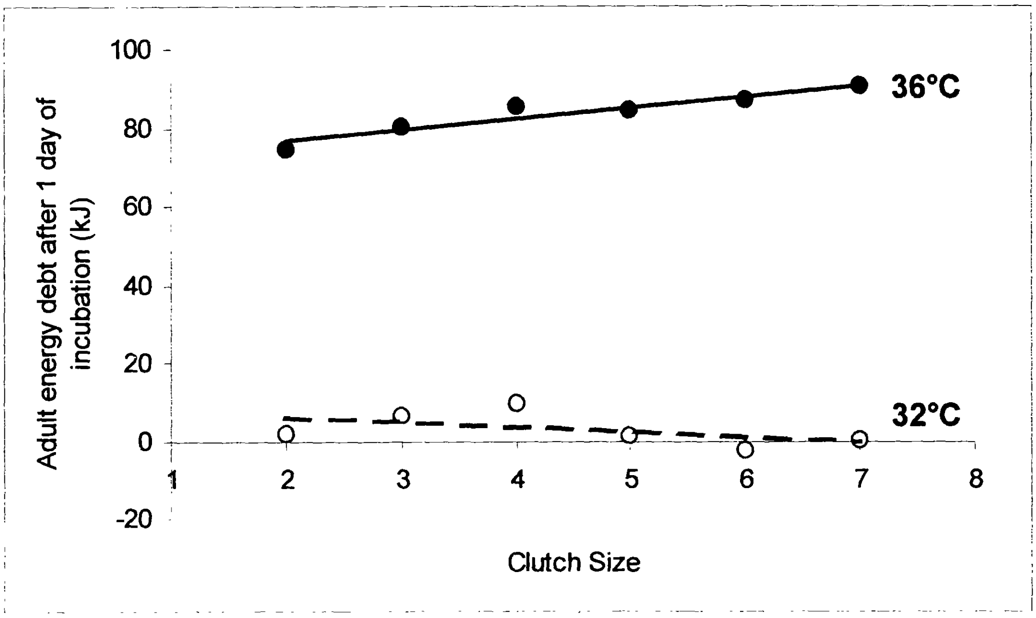
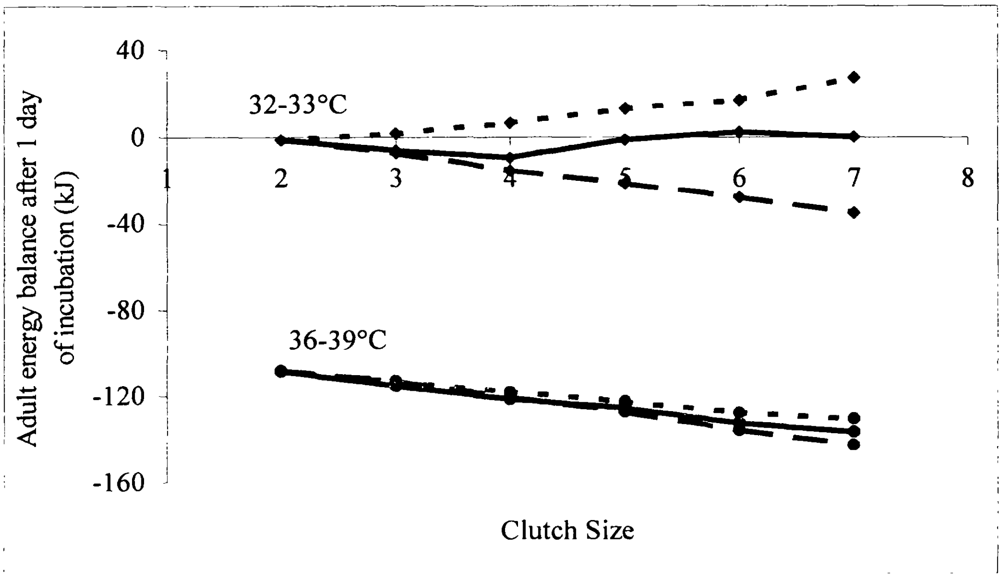


Figure 6.3. The energy debt that an incubating parent accrues after a single day of incubation increases significantly with clutch size if the clutch is maintained at 36°C (solid line and filled circles, $y = 2.87x + 70.79$, $P = 0.03$), but does not vary significantly with clutch size if the clutch is maintained at 32°C (dashed line and open circles, $y = -1.18x + 8.16$, $P = 0.31$).



However, the quantitative predictions of the model are dependent on exactly how the values of the parameters α_c, α_H, γ and δ vary with clutch size. Altering the values of these parameters such as to make large clutches either maximally or minimally demanding to incubate compared to small clutches affects the relative final energy balances of adults incubating clutches of different sizes. Maintaining a large clutch above 36°C resulted in a greater energy debt than maintaining a small clutch at the same temperature under all conditions (Fig. 6.4). However, at the lower mean temperatures that wild clutches usually experience, the greatest parental energy debt can arise when incubating either a large or a small clutch depending on the parameter values used (Fig. 6.4).

Figure 6.4. For a parent maintaining its clutch at a mean temperature of 36-39°C, the energy debt accrued increases with clutch size for all three sets of values of α_c, α_H, γ and δ reported in table 6.1 (best estimate parameter values ((1) in table 6.1), solid line; large clutches maximally demanding ((2) in table 6.1), dashed line; large clutches minimally demanding ((3) in table 6.1), dotted line). However, for parents maintaining clutches at 32-33°C the consequences of clutch size for energy debt vary greatly with parameter values, with either large or small clutches resulting in the greatest debt.



Thus the relationship between clutch size and the energy debt accrued by the incubating adult is likely to vary, depending on variation in the thermodynamic properties of clutches of different sizes. Hence the importance of the energetic demand of incubation in determining optimal clutch size and the clutch size that is predicted to be optimal is unlikely to be constant. This finding can explain the observation that different studies have yielded conflicting results as to whether hatching success and adult condition are affected as a result of clutch enlargement (*eg*, Moreno & Carlson 1989; Siikamäki 1995). Although experimental clutch enlargement has previously been successfully used to manipulate the cost of incubation (*eg*, Heaney & Monaghan 1996), this study suggests that caution is needed when planning such experiments in passerines, as incubation costs may not be simply linearly related to clutch size.

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Chapter seven

The consequences of clutch size for incubation conditions and hatching success in starlings (*Sturnus vulgaris*)

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Abstract

We manipulated starling (*Sturnus vulgaris*) clutches so that sibling eggs were incubated within either natural-sized clutches, or clutches that had been experimentally enlarged but were still within the natural range of variation. Thus we investigated the consequences of incubated clutch size for hatching and fledging success.

Eggs incubated within enlarged clutches hatched less successfully than eggs incubated within natural-sized clutches, suggesting that clutch size affects the conditions experienced by embryos during incubation. Eggs in enlarged clutches may have hatched poorly because clutch enlargement altered nest microclimate, increasing mean egg temperature and causing eggs to lose more water during the incubation period. There was no evidence that clutch enlargement altered nest microclimate by energetically constraining parents from incubating effectively. Instead, intrinsic physical properties of enlarged clutches may have affected clutch temperature directly.

Parents that had incubated experimentally enlarged clutches subsequently fledged fewer chicks than control parents, suggesting that constraints imposed during incubation may influence the optimal number of eggs that parents should lay. However, future studies should investigate whether parents laying naturally large clutches can minimize the costs of incubating many eggs by adaptively tailoring the shape and composition of their eggs to their expected clutch size.

Introduction

In order to develop and hatch successfully, avian embryos must be exposed to the correct physical conditions during incubation (Drent 1975; Deeming *et al.* 1987; Webb 1987). Nest microclimate is particularly important, with exposure of eggs to inappropriate temperatures or water vapour pressures leading to developmental abnormalities or mortality (Lundy 1969; Webb 1987). As natural environments rarely provide exactly the correct conditions for the embryos, parents must regulate nest microclimate if the offspring are to hatch and fledge successfully. This is usually done by incubating the clutch. However, experimentally enlarging the size of the clutch for the duration of the incubation period has been shown to reduce the success of the breeding attempt (Moreno *et al.* 1991; Heaney & Monaghan 1995; Monaghan & Nager 1997), imposing a fitness cost on parents. Thus optimal clutch size may be influenced by constraints imposed during incubation (Monaghan & Nager 1997).

An understanding of the mechanisms by which enlarging a clutch can reduce breeding success is an important step in enabling us to predict how parents laying naturally large clutches might minimize the costs involved, hence maximizing their lifetime fitness. Enlarging a clutch could influence breeding success by affecting the parents and their subsequent brood-rearing capacity, or by affecting embryos directly. However, previous studies have concentrated on investigating the consequences of clutch enlargement for parents, and comparatively little is known about the direct consequences for embryos. Incubation has been shown to impose an energetic demand on parents (Haftorn & Reinertsen 1985; Weathers 1985; Toien *et al.* 1986), a demand that can increase with clutch size (Biebach 1981; Biebach 1984; Haftorn & Reinertsen 1985), with females incubating enlarged clutches having a higher daily energy expenditure (Moreno *et al.* 1991), consuming more food (Coleman & Whittall 1988) and losing more mass (Moreno & Carlson 1989). Thus, clutch enlargement might reduce breeding success by energetically constraining the parent's incubation ability, or by affecting the parent's allocation of energy reserves between incubation and the subsequent chick-rearing period (Heaney & Monaghan 1996; Cichon 2000). However, as eggs retain fixed shapes throughout the incubation period, clutches of different sizes have intrinsically different physical structures. Larger clutches take up more space, and the proportion of an egg's surface that is in contact with other eggs, with air trapped between the eggs and with air circulating around the clutch will also vary with clutch size. The idea that these intrinsic structural properties of clutches of different sizes might directly influence the conditions that embryos experience during incubation and hence embryo survival, has been given little previous consideration.

In this study we manipulated clutches during incubation so that sibling eggs were incubated within clutches of different sizes, before being restored to their original brood. Hence, whilst controlling for inherited egg quality, we investigated whether clutch size has direct consequences for hatching success. By monitoring incubation temperature and chick condition we investigated the consequences of incubated clutch size for the physical conditions experienced by embryos and chicks and thus attempted to clarify the mechanisms by which the size of the incubated clutch might affect the success of the breeding attempt.

Methods

Fieldwork was carried out on a roof-nesting population of starlings (*Sturnus vulgaris*) in the Ebro Delta, Spain (2°E, 41°N), between March and June 1999. Pairs of first clutch nests on the same or adjacent roofs in which egg-laying began within 36 hours of each other were randomly allocated to control and experimental groups. The day after laying was completed, a randomly chosen egg was transferred from each control nest to its paired experimental nest and a model egg was added to each. Hence control nests retained their natural clutch size throughout incubation but experimental nests contained a clutch that had been enlarged by two, both including a model egg. All control clutches contained four or five eggs, and hence all enlarged clutches contained six or seven eggs. As 12% of natural nests contained six or seven eggs, the enlarged clutches were not outwith the natural range of variation, and in all cases the extra eggs were easily accommodated within the experimental nest cups. The transferred eggs were returned to their natal nests and the model eggs were removed the day before the clutches were due to hatch. Thus the transferred eggs were incubated within larger clutches than their siblings, but the resulting chicks were reared alongside their siblings by their natural parents. During the egg transfer process, the entire control clutch was carried between the control and experimental nests so that any reduction in viability of the transferred egg compared to its siblings could not have been due solely to the transfer procedure.

Nineteen pairs of control and experimental nests were studied. There were no significant differences between control and experimental nests in natural clutch size (means of 4.3 ± 0.1 and 4.2 ± 0.1 respectively, paired t-test $t_{18} = 0.90$, $P = 0.38$), date of first laying (means of 42.1 ± 2.3 and 41.3 ± 2.8 days after the beginning of March respectively, paired t-test $t_{18} = 0.75$, $P = 0.46$), mean egg mass (means of 7.4 ± 0.1g and 7.3 ± 0.1g respectively, paired t-test $t_{18} = 0.76$, $P = 0.46$) or clutch mass (means of 32.2 ± 1.3g and 30.4 ± 0.9g respectively, paired t-test $t_{18} = 1.14$, $P = 0.26$). Two nests were predated and hence the transferred eggs were successfully returned to their natal nests in 17 cases.

Model eggs were made from Fimo modelling clay (EberhartFaber, Neumarkt, Germany), and matched real starling eggs as closely as possible in shape and colour. They were immediately accepted by adult starlings in all cases. A thermistor mounted in silicone-based heat transfer compound (Electrolube, Berkshire, UK) was positioned in the centre of each model egg, with a lead running out of the blunt pole and through the side of the nest to a TinyTalk datalogger (Gemini dataloggers Ltd, Chichester, UK). The logger recorded the temperature at the centre of the model egg every 72 seconds throughout the incubation period. Loggers were positioned outside nest cavities, allowing data to be downloaded without disturbing incubating birds. Model eggs were initially positioned randomly within the clutch, and as the connecting leads were slack and very flexible the eggs were fairly free to be moved around, their position usually having changed between nest visits.

Clutches typically cooled down when incubating parents left the nest, and were rewarmed when parents returned. To compare the cooling and rewarming rates of eggs in natural-sized and enlarged clutches, single periods of cooling and heating were randomly selected from the egg temperature traces recorded in each nest, with periods from paired control and experimental nests being matched as closely as possible in time. Exponential equations were fitted to these temperature traces (Cooling curve equation: Egg Temperature = Ambient Temperature + ($\mathrm{Bexp}^{(-\mathrm{Cxtime})}$); heating curve equation: Egg

Temperature = (B-Ambient Temperature)(1-$\exp^{(-C\times time)}$) + Ambient Temperature, where B and C are fitted positive constants). The value of C describes the rate of egg cooling or warming, and the values for eggs in natural-sized and enlarged clutches were compared.

Laboratory experiments showed that model eggs cooled down and rewarmed slightly faster than real starling eggs when subjected to identical thermal conditions. However, these rates differed by less than 10% and hence the rate of temperature change recorded in the model eggs provides a useful estimate of the rate at which real eggs lost and gained heat. Further, the mean temperature recorded in the centre of a model egg did not differ significantly from that recorded in the centre of a real egg after three hours of alternate warming and cooling simulating intermittent incubation (paired t-test, $t_9 = 0.77$, $P = 0.46$). Hence the mean temperature recorded in model eggs is a good measure of the mean temperature at which real eggs were incubated (see *Chapter 5*).

To investigate the magnitude of the temperature variation within a clutch, two model eggs containing thermistors were placed within clutches that were not otherwise being studied, allowing two temperature traces to be simultaneously recorded from the same nest. Two of the nest's real eggs were fostered out to neighbouring nests for 24 hour periods during this time so that the difference between the two temperature traces could be compared when the model eggs were within a natural-sized clutch and when they were within a clutch that had been enlarged by two.

All eggs were weighed on the day of laying and again the day before hatching was due. In order to estimate the typical durations of parents' foraging and incubation bouts for use in simulations, a minimum of two hours was spent observing the times of parental arrival and departure from each pair of nests during the incubation period. These observations also allowed the percentage of the day that parents spent incubating on control and experimental nests to be estimated. As paired control and experimental nests were watched simultaneously, no correction for environmental conditions or the time of day at which observations were carried out was required when comparing the two groups.

The transferred eggs were returned to their natal nests before they hatched, thus restoring the original clutches. The number of chicks hatching and fledging from each nest and the date on which they did so was recorded. Chicks were weighed within 24 hours of hatching and again at 16 days old, when tarsus length was measured. Mass and tarsus length had already peaked by this age. As a measure of pre-fledging condition, the mass:tarsus^3 ratio was calculated for chicks at 16 days old (Freeman & Jackson 1990).

Parametric tests were used unless the data distributions violated the assumptions, when equivalent non-parametric tests were used. All tests were two-tailed, and means ± one standard error are presented in the results.

Results

The hatching success of the transferred eggs that were incubated within enlarged clutches was similar to that of the other eggs incubated within the enlarged clutches, but was significantly lower than that of their siblings that were incubated within natural sized clutches (Fig. 7.1). However, hatching success in enlarged clutches was no worse than that recorded in natural starling populations breeding at similar latitudes (Cramp & Perrins 1994). The fate of nine of the chicks hatching from transferred eggs could be determined with certainty. These chicks were no less likely to survive to fledge than their siblings or than the chicks from the eggs with which they were incubated (Fig. 7.1), suggesting that being incubated within an enlarged clutch had no effect on post-hatching chick mortality. Overall, parents that had incubated natural-sized clutches fledged significantly more of their offspring than parents that had incubated enlarged clutches (Fig. 7.2).

When left unattended, eggs in enlarged clutches cooled significantly more slowly than eggs in natural-sized clutches (mean C values of 4.3 ± 0.3 and 5.5 ± 0.4 respectively, $t_{18} = 2.61$, $P = 0.02$), which would tend to increase their mean temperature. However when parents returned, enlarged clutches were rewarmed significantly more slowly than natural-sized clutches (mean C values of 9.7 ± 0.6 and 13.8 ± 1.5 respectively, $t_{18} = 2.61$, $P = 0.02$), which would tend to decrease their mean temperature. To investigate whether these opposing effects might have a predictable overall impact on the mean temperature of eggs in enlarged clutches, we used the empirically determined warming and cooling coefficients to simulate egg temperature over a single period of cooling followed by a single period of warming in both natural-sized and enlarged clutches. Although the mean model egg temperature recorded in enlarged clutches was significantly higher than that recorded in natural-sized clutches (means of 33.6 ± 0.3 and 32.6 ± 0.3 respectively, $t_{18} = -2.41$, $P = 0.02$) the direct consequences of clutch size for egg temperature could not be deduced as there was also a strong trend towards parents spending a greater proportion of each day incubating enlarged clutches than natural-sized clutches (means of 79.5 ± 1.8% and 75.1 ± 1.4% respectively, $t_{29} = -2.0$, $P = 0.055$).

Figure 7.1. Hatching success (percentage of eggs that hatched) and fledging success (percentage of hatched chicks that fledged) from control clutches, transferred eggs and enlarged clutches. Transferred eggs hatched as successfully as the other eggs from enlarged clutches (means of 58.8% and 66.7 ± 10.0% respectively, $\chi^2_1 = 0.18$, $P > 0.2$). Eggs incubated within natural sized control clutches hatched significantly more successfully than either group (mean of 90.5 ± 6.0%, $\chi^2_1 = 16.3$, $P < 0.01$; Wilcoxon signed ranks test $Z_{19} = -2.1$, $P = 0.03$). Fledging success from transferred eggs was no different from that from control clutches (means of 44.4% and 50.9 ± 8.5% respectively, $\chi^2_1 < 0.01$, $P > 0.5$) or from enlarged clutches (mean of 41.3 ± 10.0%, $\chi^2_1 < 0.01$, $P > 0.5$), nor was there a significant difference between these two groups of nests (Wilcoxon signed ranks test $Z_9 = -1.2$, $P = 0.2$).

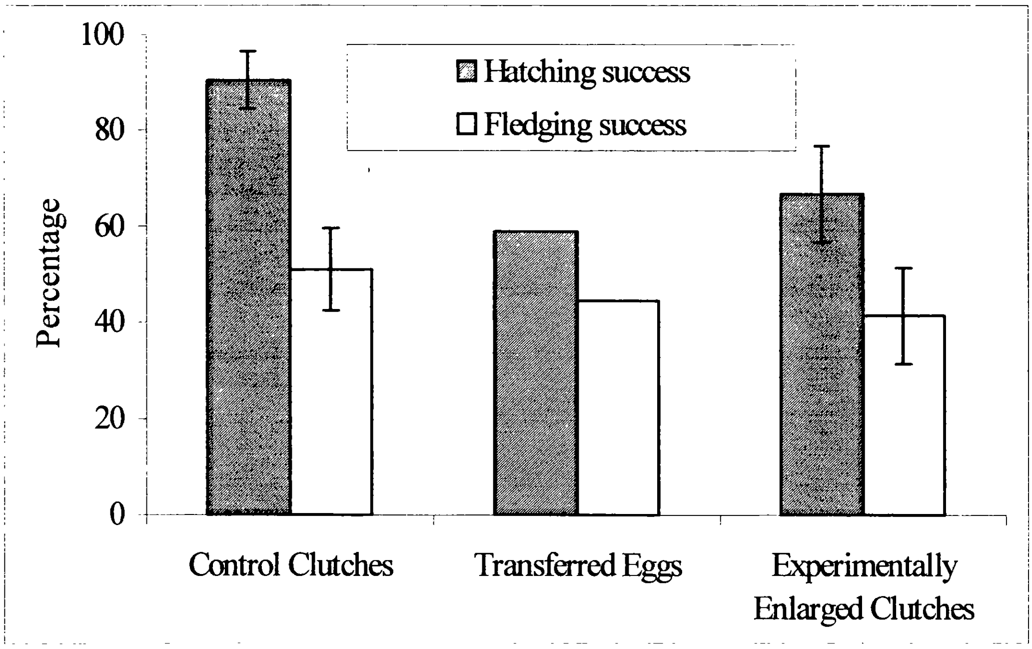
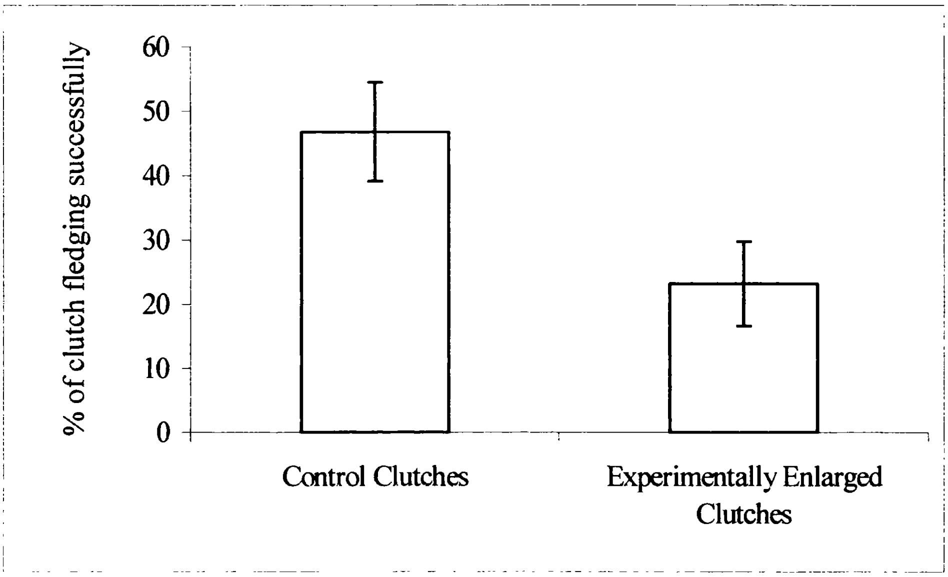


Figure 7.2. Breeding success in control and experimental nests. Control parents fledged significantly more of their original clutch of offspring than experimental parents that had incubated enlarged clutches (means of 46.8 ± 7.7% and 23.2 ± 6.6% respectively, Wilcoxon matched pairs test $Z_{18} = -2.86$, $P < 0.01$).



Overall, 99% of observed parental foraging bouts lasted between 1 and 26 minutes, and 99% of incubation bouts lasted between 1 and 60 minutes. Simulated warming and cooling periods were allowed to last any whole number of minutes between these limits, and the simulation was repeated for all possible combinations of these two values, with mean egg temperature being calculated after each simulation. For each of the 1560 combinations of cooling and warming periods simulated, the predicted mean egg temperature was warmer in enlarged clutches than in natural-sized clutches, by an average of 0.34°C across all combinations of periods.

The temperature difference between two eggs within the same nest was significantly greater (means of 1.4 ± 0.2°C and 1.1 ± 0.2°C respectively, $t_{14} = -2.62$, $P = 0.01$) and significantly more variable (mean standard deviations of 1.4 ± 0.3 and 0.9 ± 0.1

respectively, $t_{14} = -2.35$, $P = 0.02$) when the two eggs were within enlarged clutches than when they were within natural-sized clutches.

The transferred eggs that were incubated within enlarged clutches lost a significantly greater proportion of their initial mass during incubation than their siblings (means of 16.8 ± 3.0% and 10.0 ± 0.6% respectively, $t_{15} = -2.52$, $P = 0.02$), but not significantly more than the mass lost by the eggs with which they were incubated (mean of 12.1 ± 0.9%, $t_{11} = -1.29$, $P = 0.23$). The mean mass of chicks at hatching did not depend on whether they had been incubated within a natural-sized or an enlarged clutch (means of 7.4 ± 0.3g and 7.2 ± 0.3g respectively, general linear model, $F_{1,31} = 0.50$, $P = 0.48$). However, allowing for the number of surviving chicks in the brood, chicks reared by parents that had incubated a natural-sized clutch were in a significantly better condition at 16 days old than chicks reared by parents that had incubated an enlarged clutch (means of 1.9 ± 0.05kg/m^3 and 1.8 ± 0.05kg/m^3 respectively, GLM, $F_{1,19} = 5.04$, $P = 0.04$).

Discussion

On average, the transferred eggs that were incubated within enlarged clutches hatched significantly less successfully than their siblings that were incubated within natural-sized clutches. As eggs to be transferred were randomly selected from their natal clutches, their poor hatching success compared to that of their siblings cannot have been due to differences in egg quality. Instead, they must have experienced poorer conditions during incubation. The mean hatching success of the transferred eggs was similar to that of the other eggs incubated within the enlarged clutches, further supporting the conclusions that hatching success was determined largely by incubation conditions rather than inherited egg quality, and that these conditions varied with clutch size. Hence the size of the clutch within which an egg was incubated had direct consequences for embryo fitness.

Transferred eggs lost a greater proportion of their initial mass during incubation than did their siblings, but a similar proportion to the eggs with which they were incubated. As egg mass loss reflects water loss to a large degree (Rahn & Ar 1974) and maintenance of the correct egg water balance is essential for embryos to develop and hatch successfully (Meir & Ar 1991; Packard & Packard 1993; Deeming 1995), we suggest that eggs incubated within enlarged clutches were less likely to hatch because they lost too much water during incubation. The rate at which eggs lose water depends on shell structure (Packard & Packard 1993) and nest microclimate (Walsberg & Schmidt 1992; Vick *et al.* 1993; Ancel *et al.* 1994), with high egg temperatures and low nest water vapour pressures both increasing rates of water loss. The size of the clutch within which an egg is incubated is unlikely to affect shell structure, and thus the poorer hatching success of eggs in enlarged clutches is likely to have been because they experienced different nest microclimates during incubation. In agreement with this suggestion, mean egg temperature was higher in enlarged clutches than in natural-sized clutches.

Incubating parents must divide their time between the mutually exclusive activities of incubating to regulate nest microclimate and foraging to maintain their own energy balance (Carey 1980; Williams 1996; *Chapters 2, 5 & 6*). Parents that spend more time foraging leave the microclimate of their nest unregulated for longer, allowing eggs to equilibrate with ambient conditions. As the energetic demand of incubation can increase with clutch size, parents incubating enlarged clutches may have been forced to forage more in order to maintain their energy balance. Hence clutch enlargement might have altered nest microclimate by energetically constraining the parent's incubation ability. However, as parents incubating enlarged clutches tended to spend more time on the nest than parents incubating natural-sized clutches, there is no evidence that this was the case. Instead, the intrinsic physical properties of enlarged clutches may have affected parents' ability to successfully regulate clutch microclimate, irrespective of their energetic investment in incubation. As larger clutches occupy more space than smaller clutches, parents may have experienced more difficulty in incubating all the eggs within an enlarged clutch simultaneously, even though enlarged clutch sizes were within the range of natural clutch sizes. Consistent with this hypothesis, the temperature difference between eggs within the same clutch was on average greater and more variable within enlarged clutches than within natural-sized clutches. In the warm and arid Spanish environment, peripheral eggs may have lost water to the surroundings fairly rapidly. Further, clutches of different sizes had different thermal properties, directly affecting the temperatures experienced by eggs during incubation. Our simulation suggests that whatever the pattern of heating and cooling, mean incubation temperature will be higher in enlarged clutches. Thus intrinsic properties of clutch size can explain the higher mean incubation temperatures recorded in enlarged clutches. It has also been shown that nest water vapour pressure can be lower in nests containing larger clutches (Kern & Cowie 1995). Hence physical properties of enlarged clutches mean that their component eggs are inherently likely to lose water rapidly, a loss that might be particularly costly for starlings nesting in arid climates.

Chicks hatching from transferred eggs did not suffer greater mortality during the rearing period than their siblings, suggesting that post-hatching survival was influenced more strongly by the conditions experienced during rearing than by any effects carried forward from incubation. However, chicks reared by parents that had incubated enlarged clutches were in a significantly worse pre-fledging condition than chicks reared by parents that had incubated natural-sized clutches. As both groups of chicks had similar masses at hatching, this suggests that chicks from enlarged clutches experienced poorer rearing conditions. Parents that had incubated enlarged clutches thus may have been less able to care for their chicks. Instead of foraging more during incubation, parents incubating enlarged clutches may have compensated for the increased energetic demands of incubation by reducing their allocation of resources to chick-rearing. Such within-reproductive attempt trade-offs to compensate for the demands of incubation have previously been reported (Heaney & Monaghan 1996; Thomson *et al.* 1998; Cichon 2000).

Although chick mortality was no higher in experimental nests than in control nests, the poor hatching success of eggs from enlarged clutches resulted in a reduced fledging success in experimental nests. Hence we provide further evidence that incubating an enlarged clutch imposes a fitness cost on parents. Further, as poor fledging condition has been correlated with poor offspring survival (Magrath 1991; Ringsby *et al.* 1998) and future reproductive success (Both *et al.* 1999), clutch enlargement may have further reduced the lifetime fitness of offspring and parents. Thus in line with other studies we suggest that by reducing parents' chick-rearing ability, the energetic demand of incubating an enlarged clutch may limit optimal brood size in birds (Monaghan & Nager 1997). However, as shown here, the physical properties of enlarged clutches can also reduce hatching success irrespective of parental energy expenditure. Thus the intrinsic physical properties of clutches of different sizes may further influence the number of eggs that a parent should lay. Parents' physical inability to incubate many eggs simultaneously might impose an upper limit on optimal clutch size but as large clutches maintain intrinsically warmer incubation temperatures, parents nesting in cold climates may even be selected to lay large clutches in order to minimise costly egg chilling.

However, parents laying naturally large clutches may be able to minimize the cost of incubation by adapting the design of their eggs to their expected clutch size. The egg shape that maximizes the efficiency with which a clutch can be packed under the brood patch may vary with clutch size (Barta & Székely 1997). Hence parents could maximise their ability to incubate many eggs simultaneously by laying eggs of the optimal shape given their clutch size. Further, parents could alter the shell structure or composition of their eggs to compensate for the rates of water loss that eggs within clutches of different sizes are inherently likely to experience. Future studies should investigate such effects within wild bird populations. If eggs are tailor-made for a specific clutch size, then the cost of incubating an experimentally enlarged clutch may be greater than the cost of incubating a natural clutch of the same size, as experimental clutch enlargement places the eggs in a physical environment for which they are not designed.

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Chapter eight

Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*)

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Abstract

The extent to which male parental care improves the success of a breeding attempt is recognised as an important factor in shaping avian breeding systems. However, the consequences of male assistance with incubation and the circumstances under which males incubate are poorly understood.

We studied a population of starlings in which male participation in incubation was variable. Incubation periods were shorter and hatching success, hatchling mass and fledging success were greater in nests where males assisted females with incubation. These effects did not appear to arise because males incubated only on high quality nests or when mated to high-quality females, or because of differences in male chick-rearing effort. Instead, male incubation may have improved breeding performance directly, by improving the developmental conditions experienced by embryos. Although females spent less time incubating when males assisted, the male's contribution meant that total nest attendance increased. Incubating males maintained clutches at marginally lower equilibrium temperatures than females but rewarmed cool clutches more rapidly. Hence overall, clutches spent more time at warmer temperatures when males assisted with incubation.

Male incubation was associated with effective monogamy. However, most males mated polygynously and did not incubate. Males that incubated had nests that insulated poorly and were initiated relatively late within a colony, and so may have been less likely to attract further females. The occurrence of male incubation may therefore be determined by a male's ability to attract multiple females. However, primary females may have increased the chance that a male would incubate by destroying secondary females' clutches.

Introduction

The extent to which parents care for their offspring has evolutionary consequences for animal morphology and physiology, and for the social structures of animal communities (Ketterson & Nolan 1994; Reynolds & Székely 1997; Kokko 1998; Webb *et al.* 1999). Identification of the selection pressures that shape patterns of parental care is therefore a major goal of behavioural ecology (*eg*, Clutton-Brock 1991). Individual parents are expected to allocate resources amongst reproductive activities so as to maximise their own lifetime fitness (Roff 1992; Stearns 1992). Thus, in order to interpret observed allocations to parental care, it is important to understand the fitness costs and benefits for each parent of caring for or deserting their offspring (Székely & Cuthill 1999; Székely *et al.* 1999; Gubernick & Teferi 2000).

In birds, parental care is generally required during both incubation and chick-rearing if the brood is to fledge successfully. Females are generally involved in both these activities (although see Clutton-Brock 1991; Andersson 1995; Eens & Pinxten 2000), but the role of the male is more variable. Recent theoretical and empirical studies suggest that the ability of female birds to breed successfully in the absence of male help may influence breeding system evolution, affecting frequencies of extra-pair copulations and mate desertion (Székely & Cuthill 1999, 2000; Møller 2000), and the stability of social monogamy (Lack 1968; Kokko 1999). Assessment of the value of male care is therefore important, and the consequences of male assistance with chick-rearing, and the circumstances under which males assist, have been relatively well studied in a range of passerine species. Paternal provisioning can increase fledging success (Johnson *et al.* 1992; Smith *et al.* 1994; Moreno *et al.* 1999), chick growth rate (Bjornstad & Lifjeld 1996; Markman *et al.* 1996) and fledgling condition (Johnson *et al.* 1992), and thus increase female fitness. However, time spent provisioning one brood of offspring can constrain a male's ability to attract further mates or provision other broods (Sandell *et al.* 1996; Hunt *et al.* 1999; Moreno *et al.* 1999) and hence be costly for males. Consequent intersexual conflict over the extent of male provisioning can drive the evolution of passerine mating systems and multiple related aspects of breeding behaviour (Davies 1985, 1992; Davies & Hatchwell 1992; Houston *et al.* 1997; Smith & Sandell 1998; Alonzo & Warner 2000).

Considerably less is known about the occurrence and consequences of male assistance with incubation. Males can improve incubation performance indirectly by provisioning incubating females on the nest (Lyon & Montgomerie 1985; Nilsson & Smith 1988). However, as male passerines often lack well developed brood patches (Bailey 1952), their ability to regulate clutch temperature and thus contribute directly to incubation remains relatively unclear. Although the extent to which a male incubates has been linked to his mating status (Pinxten *et al.* 1993; Smith *et al.* 1995; Smith & Sandell 1998), the possibility that intersexual conflict over male incubation arises and influences mating systems has rarely been investigated.

We studied a facultatively polygynous population of European Starlings (*Sturnus vulgaris*) in which some males assisted females with incubation whilst others did not. We investigated the ability of males to incubate effectively, the circumstances under which they did so, and the consequences of their help for female time budgets and breeding success. Based on these findings, we discuss the possible role of male incubation in influencing mating systems in starlings.

Methods

A population of cavity nesting starlings was studied in the Ebro Delta, Spain (2°E, 41°N) between March and June 1999. Nests were situated in holes in roofs of widely scattered agricultural buildings. Each roof contained between two and ten nests.

To determine whether females were incubating alone or whether males were assisting, each nest was observed for a minimum of three two-hour spells during the incubation period. Two hours was sufficient to observe multiple change-overs, and the times of male and female arrivals and departures were recorded. Males either contributed substantially to incubation or were not observed to incubate at all. Non-incubating males were easily recognised as they frequently stood outside nest cavities. All males assisted with provisioning all their chicks.

To determine how many nests were attended by each male, colonies were observed on at least eight further occasions during the breeding attempt (as Smith *et al.* 1994). Possibly as a result of occasional hybridisation with spotless starlings (*Sturnus unicolor*), the study population exhibited considerable plumage variation. A maximum of six males bred within a single colony (mode of three). Thus, within each colony, males could generally be distinguished using individual plumage characteristics. Four different observers independently attributed the same mating status to males during both simultaneous and consecutive observation periods, and hence male identifications were repeatable. As colonies were separated by up to 2km and males remained within sight of their known colony almost continuously during observation periods, it is very unlikely that the same male bred simultaneously in different colonies. Data from two colonies containing males whose mating status remained uncertain were excluded from the analyses. Nests belonging to polygynous males were defined as primary and secondary in the order in which laying began.

To investigate the incubation ability of males and females, model eggs containing thermistors were placed in 38 nests the day after full incubation commenced, and were removed the day before the clutch was due to hatch (see *Chapters 5 & 7* for details). In 19 nests the addition of the model egg enlarged the natural clutch size. In the remaining 19 nests it replaced a real egg that was removed as part of another experiment (see *Chapter 7*). As the occurrence of male incubation had been determined before model eggs were deployed, we ensured that the enlarged clutches were evenly distributed between nests where males did and did not incubate. In no case did the addition of a model egg alter whether or not a male incubated. Model eggs had similar thermal properties to real eggs (*Chapters 5 & 7*). Thermistors were positioned in the centres of model eggs, and TinyTalk data loggers (Gemini Dataloggers Ltd, Chichester, UK) were used to record egg temperature every 72 seconds throughout the incubation period.

The nest observation periods were used to link model egg temperatures to the presence of either the male or the female on the nest, and to estimate the proportion of each day for which each sex incubated. The equilibrium temperatures at which males and females maintained clutches and the frequencies with which they rewarmed cool clutches through at least 3°C were compared. To estimate the rate at which males and females rewarmed clutches, the equation (Egg Temperature = (B-Ambient Temperature)(1-exp$^{(-K*time)}$) + Ambient Temperature, where B and K are fitted positive constants) was fitted to warming curves taken from egg temperature traces. The exponential coefficient K represents the rate of clutch rewarming. Temperature probes that were not enclosed within model eggs were used to continuously record whether any parent was present on the nest, a technique that we have used previously and validated using video playback (*Chapter 4*).

To investigate whether the occurrence of male incubation was related to nest quality, we measured the insulative quality of nests. The rate of heat loss from within each nest was measured by inserting a plaster disc warmed to 35°C, and measuring the rate at which it cooled down (see *Chapter 4* for methodology). The equation (Disc Temperature = Ambient Temperature +(Bexp$^{(-C*time)}$), where B and C are fitted positive constants) was fitted to the cooling curve recorded. The exponential coefficient C reflects the rate of heat loss.

Egg laying dates were recorded in each nest, and eggs were weighed on the day of laying and again the day before hatching was due. The number of chicks hatching and fledging and the dates on which they did so were recorded in each nest. Chicks were weighed within 24 hours of hatching and again at 16 days old, when maximum tarsus length was also measured. The ratio of mass to tarsus^3 was calculated as a measure of pre-fledging chick condition (Freeman & Jackson 1990).

Proportional data were arcsin transformed and parametric statistical tests were used unless data distributions violated the assumptions, when equivalent non-parametric tests were substituted. All tests were two-tailed, and means are presented ± one standard error.

Results

Twelve of the 35 males whose mating status was confidently ascertained were monogamous, attending only one nest. All twelve assisted with incubation on that nest, being responsible for 42.3 ± 1.8% of the time for which the clutch was incubated on average. The other 23 males were polygynous, each initially attending two active nests. However, eleven (47.8%) of the 23 secondary clutches were destroyed during egg-laying or early during the incubation period. Other starlings were thought to have been responsible, as eggs punctured by bill holes were found within nest cavities, and destruction by female starlings was twice observed. Destruction was distinct from nest predation, in which the whole clutch was typically consumed. Secondary clutches that were destroyed were more closely synchronised with the same male's primary clutch than secondary clutches that were not destroyed (mean inter-clutch intervals of 2.8 ± 0.6 and 10.0 ± 2.0 days respectively, $U_{22} = 16.5$, $P = 0.002$). No primary polygynous clutches or clutches belonging to monogamous males were destroyed, and thus secondary clutches were destroyed significantly more often than any other category ($\chi^2_2 = 20.7$, $P < 0.001$). The twelve polygynous males whose secondary clutches were not destroyed did not incubate on either of their two nests. Four of the eleven polygynous males that lost their secondary clutches assisted their primary female with incubation. None of these obtained replacement secondary clutches. The remaining seven males whose secondary clutches were destroyed did not incubate on their primary nests, and five obtained replacement secondary clutches. Thus 16 males had one active nest (including four failed polygynists) and participated in incubation, 17 males had more than one nest and did not incubate, and two males did not incubate on their one remaining nest. Thus the occurrence of male incubation was associated with the possession of a single active nest (and thus effective monogamy) more often than expected by chance ($\chi^2_1 = 24.4$, $P < 0.001$).

The 12 secondary clutches that were not destroyed did not differ significantly from the 19 primary clutches on which males did not incubate in any measured parameters other than (by definition) laying date (table 8.1). Hence data from these nests were pooled, and breeding performance was compared between the 16 nests on which males assisted females with incubation and the 31 primary polygynous and surviving secondary nests on which females incubated alone. As producing a replacement clutch can affect a female's subsequent reproductive performance (Monaghan *et al.* 1998), data from the five replacement secondary clutches were not included in these analyses.

Table 8.1. Comparison of reproductive parameters of polygynous males' primary and secondary nests (* indicates a significant difference between primary and secondary nests at the 95% confidence level after Bonferroni correction).

	Primary polygynous nests			**Secondary polygynous nests**			**t-test / Mann-Whitney Utest**	
	Mean	**SE**	**n**	**Mean**	**SE**	**n**	**t / U**	**P**
Lay date (in April)	**8.3**	2.5	19	**20.2**	2.2	12	-3.30	**0.002***
Clutch size	**4.3**	0.1	19	**4.0**	0.3	12	0.91	**0.37**
Egg mass (g)	**7.3**	0.1	17	**7.4**	0.1	9	-0.52	**0.61**
Clutch mass (g)	**31.9**	1.6	17	**29.6**	3.3	9	0.71	**0.49**
Nest cooling coefficient	**0.85**	0.04	17	**0.86**	0.04	9	-0.10	**0.92**
Incubation period (days)	**12.7**	0.1	18	**12.9**	0.3	11	-0.92	**0.37**
Egg mass loss (%)	**10.7**	0.7	16	**11.9**	1.0	7	-0.96	**0.35**
Hatchling mass (g)	**6.8**	0.2	15	**6.4**	0.3	5	0.76	**0.46**
% of eggs hatching	**73.9**	5.7	19	**75.7**	9.4	12	102.5	**0.63**
% of hatchlings fledging	**50.9**	9.3	18	**51.2**	10.2	11	94.0	**0.82**
Fledgling condition	**1.93**	0.1	8	**1.92**	0.1	4	15.5	**0.93**
% of offspring fledging	**36.6**	6.7	19	**34.4**	7.4	12	106.0	**0.74**

Clutches laid by females that were and were not assisted by incubating males did not differ with respect to mean laying date, clutch size, egg mass or clutch mass (table 8.2). However, nests where males incubated were of poorer insulative quality than nests where males did not incubate (Mean C values of 1.02 ± 0.06 and 0.86 ± 0.03 respectively, t_{40} = 2.82, P = 0.007). Although laying dates were spread over a seven week period overall, laying was fairly synchronous within each colony. On average, nests where males incubated were initiated significantly later within a colony than nests where they did not (mean ranked positions from the end of laying in each colony of 1.8 ± 0.4 and 3.0 ± 0.3 nests respectively, U_{66} = 197.0, P = 0.007).

Hatching success was higher, newly hatched chicks were heavier, incubation periods were shorter and eggs lost less mass independent of the duration of incubation in nests where males assisted with incubation than in nests where they did not. However, the proportion of hatchlings that survived to fledge did not differ significantly between the two groups of nests, and chicks in nests where males incubated were no longer in better condition at 16 days old. Overall, more offspring fledged successfully in nests where males assisted with incubation than in nests where females incubated alone (see table 8.3 for all data).

Table 8.2. Comparison of clutch parameters in polygynous nests (where males did not incubate) and monogamous nests (where males assisted females with incubation).

	All polygynous nests			**Monogamous nests**			**t-test / Mann Whitney Utest**	
	Mean	**SE**	**n**	**Mean**	**SE**	**n**	**t / U**	**P**
Lay date (in April)	**12.9**	2.0	31	**10.1**	2.2	16	-0.87	**0.39**
Clutch size	**4.2**	0.1	31	**4.1**	0.1	16	-0.16	**0.87**
Egg mass (g)	**7.3**	0.1	26	**7.4**	0.1	16	0.67	**0.51**
Clutch mass (g)	**31.2**	1.5	26	**30.6**	1.1	16	-0.25	**0.80**

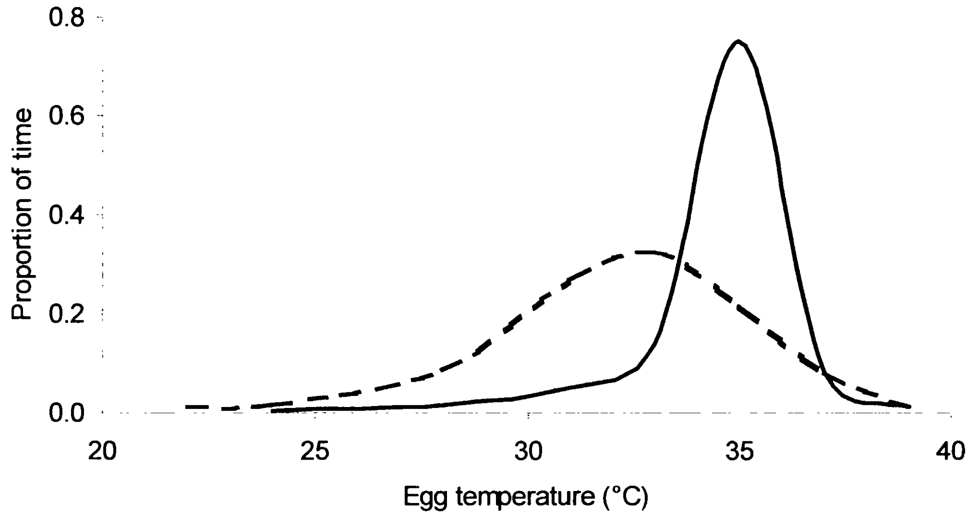
Table 8.3. Comparison of (a) incubation performance, (b) chick-rearing performance and (c) overall breeding success in polygynous nests (where males did not incubate) and monogamous nests (where males assisted females with incubation). * indicates a significant difference between polygynous and monogamous nests at the 95% confidence level after within-section Bonferroni correction.

		All polygynous nests			**Monogamous nests**			**t-test / Mann Whitney Utest**	
		Mean	**SE**	**n**	**Mean**	**SE**	**n**	**t / U**	**P**
(a)	Incubation period (days)	**12.8**	0.1	29	**11.9**	0.2	16	-3.71	**0.001***
	Egg mass loss (%)	**11.1**	0.5	23	**8.5**	0.7	13	-2.85	**0.007***
	Hatchling mass (g)	**6.7**	0.2	20	**7.7**	0.3	12	3.17	**0.003***
	% of eggs hatching	**74.6**	4.9	31	**96.9**	3.1	16	108.5	**0.001***
(b)	% of hatchlings fledging	**51.0**	6.9	29	**59.7**	7.5	16	184.5	**0.41**
	Fledgling condition	**1.9**	0.1	12	**1.8**	0.1	7	26.5	**0.19**
(c)	% of offspring fledging	**35.8**	4.9	31	**56.3**	6.9	16	141.5	**0.025***

Females spent substantially less time incubating when assisted by males than when incubating alone (means of 46.3 ± 1.1% and 74.0 ± 1.1% of the daytime respectively, $t_{30} = 15.92$, $P < 0.001$), a reduction of approximately 3.5 hours during an average daytime of 12.5 hours. Incubating males were responsible for a smaller proportion of the total incubation time than females (means of 42.3 ± 1.8% and 57.7 ± 1.8% respectively, paired t-test $t_{13} = 4.32$, $P = 0.001$). However overall, clutches were attended for more time each day when males assisted than when females incubated alone (means and ranges of 81.9 ± 1.4% (75.2 - 94.1%) and 74.0 ± 1.1% (66.5 - 79.4%) of the daytime respectively, $t_{30} = -4.28$, $P < 0.001$), an increase of approximately one hour per day on average.

Males maintained clutches at lower equilibrium temperatures than females incubating the same clutch (means of 35.8 ± 0.4°C and 36.3 ± 0.3°C respectively, paired t-test t_{12} = 5.71, $P < 0.001$), although the mean difference was only 0.5°C. Males rewarmed cool clutches more rapidly than females (mean K values of 0.16 ± 0.03 and 0.13 ± 0.02 respectively, paired t-test t_{10} = -2.53, P = 0.03), but did so less frequently (means of 0.28 ± 0.05 and 0.98 ± 0.1 times per hour respectively, paired t-test t_{12} = 9.3, $P < 0.001$). Overall, eggs experienced higher minimum temperatures (means of 29.3 ± 0.3°C and 25.1 ± 0.4°C respectively, t_{36} = -7.81, $P < 0.001$) and spent more time at temperatures at which embryonic development is likely to have been more rapid (Figure 8.1) when males assisted females with incubation.

Figure 8.1. Proportion of the daytime that clutches spent at different temperatures when males assisted females with incubation (solid line) and when females incubated alone (dashed line). Male assistance with incubation altered the distribution of temperatures that eggs experienced (Two-sample Kolmogorov-Smirnov test, $D_{6,7}$ = 29.4, $P < 0.05$), increasing the proportion of time that eggs spent at higher temperatures. This change is likely to have increased the overall rate of embryonic development (Webb 1987).



Discussion

A greater proportion of eggs hatched successfully and newly hatched chicks were heavier when males assisted with incubation than when females incubated alone. Incubation periods were shorter when males assisted, reducing the time for which clutches were likely to have been vulnerable to predation (Erikstad & Tveraa 1995; Bjornstad & Lifjeld 1996). Thus male incubation was associated with improved overall incubation performance.

Incubation performance might improve as a direct result of male assistance. However, a non-causal relationship between male incubation and incubation performance might also arise, for example, if males were more likely to incubate on high quality nests, or when mated to high-quality females that could hatch chicks rapidly and in good condition independent of male help. A causal link can only be conclusively demonstrated by experimentally preventing males from incubating (*eg*, Bart & Tornes 1989). However, several lines of evidence suggest that here, incubation performance improved as a consequence of male help rather than of attributes of the nest or female. Clutch size, egg mass, clutch mass and laying date can reflect female quality (Tinbergen & Daan 1990; Goodburn 1991; Verhulst *et al.* 1995; Rooneem & Robertsen 1997; Phillips & Furness 1998), and nests on which males did and did not incubate did not differ with respect to any of these parameters. Further, we have shown experimentally that a small reduction in the rate of heat loss from within a nest during incubation can increase breeding success independent of female quality (*Chapter 3*). As males incubated on nests that insulated poorly, other things being equal, breeding success in these nests would have been expected to be low. The high success actually observed suggests that the male's contribution was important. Finally, the mechanisms by which male help may have improved incubation performance are relatively clear. Although females spent considerably less time incubating per day when males assisted than when incubating alone, the male's contribution meant that overall, clutches were attended for an extra hour per day on average. As incubation may be costly for females largely because the time spent incubating constrains the time available for foraging (Drent *et al.* 1985; Moreno & Hillstrom 1992), it is unlikely that any female would have been able to compensate completely for this difference. Indeed, the mean time for which a nest was attended when both parents incubated exceeded the maximum attentiveness recorded for a female incubating alone. As male starlings maintained clutches at only marginally lower equilibrium temperatures than females and rewarmed cool clutches more rapidly, the increased total nest attentiveness when males incubated meant that clutches spent more time at higher temperatures. Further, as reflected by the reduced rate of egg mass loss when males assisted (Rahn & Ar 1974), increased adult attendance may also have reduced the rate at which eggs lost water. Such temperature and water loss changes can improve hatching success and shorten incubation periods (Ricklefs & Smeraski 1983; Webb 1987; Walsberg & Schmidt 1992; Packard & Packard 1993; Vick *et al.* 1993). Hence male assistance with incubation may have significantly improved the developmental conditions experienced by embryos, increasing hatching success and shortening incubation periods independent of female or nest quality.

A greater proportion of offspring fledged successfully in nests where males assisted with incubation than in nests where females incubated alone. This was due to improved hatching success rather than to a subsequent improvement in hatchling survival. As secondary clutches laid soon after the same male's primary clutch were frequently destroyed, overlap between polygynous males' primary and secondary chick-rearing periods was minimal, and males were likely to have been able to contribute significantly to provisioning all offspring. Indeed, despite being lighter at hatching, polygynous males' chicks were no longer in poorer condition at 16 days old. Thus the increased breeding success in nests where males incubated was predominantly due to the male's contribution to incubation, not to subsequent differences in chick-rearing effort.

Even though male starlings have poorly developed brood patches (Cramp & Perrins 1994) they were effectively as capable as females at regulating clutch temperature. Similar incubation ability has been reported in male Swallows and Zebra Finches (Ball 1983; Zann & Rossetto 1991). Thus the functional role of the brood patch is unclear, especially as defeathering and vasodilation are likely to be energetically demanding, requiring considerable physiological changes (Bailey 1952) and increasing the rate of body heat loss (Buchholz 1996; Wilson *et al.* 1998). As male passerines are often slightly larger than females they may be more able to transfer heat to eggs in the absence of a specialised structure. However, the hypotheses that the female's bare skin area may play an important role in regulating nest humidity as well as temperature, or may significantly reduce the energetic demand of maintaining high clutch temperatures would be worthy of investigation.

Despite the apparent fitness benefit of incubation in terms of increased immediate reproductive success, less than half of males incubated. However, incubation may be costly for males in terms of lost mating opportunities. Trade-offs between incubation and seeking further matings have been demonstrated (Smith 1995; Magrath & Elgar 1997) and male incubation was effectively associated with monogamy in this study. As extra pair paternity rates in starlings may not vary significantly with mating status (Smith & von Schantz 1993) and apparent success reflects genetic success (Smith & Sandell 1998), overall, male fitness may generally be maximised by polygyny rather than by monogamy and incubation (Pinxten & Eens 1990). In contrast, female fitness is likely to be maximised by male incubation. As well as increasing the number of offspring fledged, male assistance may reduce the cost of incubation for females. Assisted females spent less time incubating and met the high energetic demand of rewarming a cool clutch (Vleck 1981) less often. Thus male assistance is likely to have reduced the energetic demand experienced by incubating females and simultaneously increased the foraging time available for females to meet that demand. Hence, intersexual conflict over the male's contribution to incubation, and thus mating system, might be predicted.

As 60% of females incubated alone, many males achieved their absolute optimal mating system. However, for males that cannot attract multiple females, or for whom failing to incubate is particularly costly, incubation may be the optimal strategy. As the nests where males assisted with incubation insulated poorly, offspring left unattended in these nests may have been particularly likely to experience detrimental developmental conditions. Further, as male starlings are largely responsible for nest construction and completed nests function in mate attraction (Cramp & Perrins 1994), the males that incubated may have been less able to attract females. Males also incubated more often when their primary female laid late within a colony, when further nest sites and females were likely to have been locally scarce. Thus patterns of monogamy and male incubation are consistent with the hypothesis that starling mating system and level of paternal care was determined by a male's ability to provide high quality nests and obtain multiple females.

These results raise interesting questions about how incubating females might increase their chance of receiving male help. If males are more likely to incubate later clutches, then females could delay breeding relative to the rest of their colony. However as delays reduce the time available for rearing second broods, delaying may be a costly strategy. Alternatively, primary females may increase the likelihood of male incubation by preventing secondary breeding attempts. Clutch destruction may take place for reasons other than sexual conflict, such as competition for nest sites. However, the high rate of secondary clutch destruction is consistent with the hypothesis that primary females destroy secondary clutches in order to gain male help. Primary females were responsible for destruction on both observed occasions, and female-female aggression and nest destruction have previously been observed in several facultatively polygynous populations (Davies 1985; Breiehagen & Slagsvold 1988; Pinxten & Eens 1990; Veiga 1990; Smith & Sandell 1998). Secondary nest destruction resulted in males incubating primary clutches in only four (36%) of eleven cases. However, when males did not incubate and secondary clutches were replaced, destruction desynchronised the primary and secondary breeding attempts. As males may increase their relative level of investment in provisioning primary broods when primary and secondary attempts are well separated (Smith *et al.* 1994, 1995; Smith & Sandell 1998), destroying secondary clutches may benefit primary females irrespective of whether or not the male subsequently incubates.

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Chapter nine

The thermal consequences of nest construction in starlings (*Sturnus vulgaris*)

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Submitted manuscript.

Abstract

We investigated the relative influence of the insulative quality of the nest site and of the nest itself on the rate at which heat was lost from within a nest, and hence on the thermal environment that starlings (*Sturnus vulgaris*) provided for developing offspring.

Starlings breeding in poorly insulated nest cavities built larger nests that reduced the rate of heat loss from within the cavity to a greater extent than starlings breeding in well insulated cavities. However, starlings did not compensate completely for the rate of heat loss from the original nest site and overall, heat was lost more rapidly from within a completed nest when the insulative quality of the original site was poor. We suggest that a failure to compensate for a rapid rate of heat loss from a poorly insulated nest site may have fitness consequences, and thus that the acquisition of a well insulated site may be an important component of a starling's reproductive strategy.

Nests also play a role in mate attraction in starlings. However, as nest size was a poor predictor of the rate of heat loss experienced from within a nest and did not signal the ability of a male to acquire a well insulated site, nest characteristics other than size may have been more likely to influence mate choice in this population.

Introduction

In order for offspring to survive to independence and hence for a breeding attempt to be successful, parents must generally provide a regulated and secure environment in which young can develop safely. The use of a specialised nest structure to help provide such an environment is observed within many taxa and is especially common in birds, where the majority of species build a nest of some description (Collias & Collias 1984; Brooke & Birkhead 1991). Even in groups such as ground and cavity-nesting birds where nests are not essential for the structural support of the brood, the construction of a nest may still increase the chance of breeding successfully. Nests may protect eggs and chicks from climatic extremes (Moreno *et al.* 1995) and from predators (Collias & Collias 1984), and a high quality nest may also increase a male's chance of attracting a mate (Johnson & Searcy 1993; Hoi *et al.* 1994; Grubbauer & Hoi 1996). More subtlely, recent experimental studies in birds have demonstrated that the insulative quality of the nest environment can affect the success of a breeding attempt (Lombardo *et al.* 1995; *Chapter 3*). This relationship may arise because the rate of heat loss from a nest directly affects the quality of the developmental conditions experienced by offspring. Alternatively, by increasing the demand of thermoregulation, poor insulation may affect the ability of parents to incubate, or their subsequent ability to rear chicks. Hence nest-building parents must create a high quality thermal environment for their developing offspring. Indeed, consistent with the hypothesis that thermal considerations should influence nest design, birds have been suggested to tailor the insulative quality of their nests to local thermal conditions (Kern 1984; Møller 1987; Franklin 1995). However, the thermal environment experienced within a nest is likely to arise as a function of the insulative quality of the nest site as well as of the nest itself, and little is known about the relative importance of the two. If, by constructing a nest, parents are able to compensate for the thermal quality of the original site, then thermal considerations may not exert a major influence on nest site selection. If, however, the thermal conditions provided for developing offspring depend to a large extent on the intrinsic thermal properties of the nest site itself, then the acquisition of a well insulated site may be a crucial stage of a breeding event.

Using a wild population of starlings (*Sturnus vulgaris*) nesting in natural cavities, we measured the rate at which heat was lost from nest cavities both prior to nest construction and after nests had been completed. Thus we compared the relative influence of the nest and of the nest site on the overall rate at which heat would have been lost from the brood, and hence assess the importance of obtaining a well insulated site for the developmental conditions provided for dependent offspring.

Methods

Fieldwork was carried out in the Ebro Delta, Spain (2°E, 41°N) between March and June 1999, where starlings built their nests in cavities under loose tiles on the roofs of agricultural buildings. Nests were constructed from grass and straw and were rebuilt at the start of each breeding season, with little nest material remaining in cavities between years.

Starling colonies were visited regularly during the month before laying began, and cavities that were being actively defended by particular males were identified. By observing colonies from a distance, this was achieved without disturbing the birds. In this way, the cavities in which nests were likely to be built were located before nest-building began. Colonies were subsequently revisited so that the progress of nest-building and egg-laying within in each cavity could be followed.

As a measure of the insulative quality of a nest site, the rate at which heat was lost from a standard object placed within the site was measured. A plaster disc with a thermocouple embedded in the centre was warmed to 35°C and placed in a nest cavity. Using a TC-08 thermocouple data logger (Pico Technology Ltd, Cambridge, UK), the temperature of the disc was recorded every 10 seconds as it cooled towards an ambient temperature that was recorded simultaneously. Newton's cooling equation (Egg Temperature = Ambient Temperature + ($B\exp^{(-C*\mathrm{time})}$), where B and C are positive fitted constants) was fitted to the cooling curve recorded, a model that provided an excellent fit to the data (mean R^2 of 0.995, range of 0.985 to 0.999). The best-fit value of the exponential cooling coefficient C reflects the rate at which the disc cooled down relative to ambient temperature and thus represents the rate at which heat was lost from within the nest site. This process was repeated and the value of the cooling coefficient was estimated for each nest cavity both before nest building began and again when the first egg was laid, 22.6 days later on average. The egg was removed from the nest and stored safely in an insulated box whilst the post-laying measurement was made.

In order to verify that cooling coefficient estimates were not influenced by any seasonal environmental effects, rates of heat loss from within ten roof cavities that were not being used by breeding starlings were also estimated. These cavities were situated adjacent to active nest cavities, and cooling coefficients were measured early during the season and again when laying commenced in the adjacent active cavities (24.3 days later on average). Estimated rates of heat loss from unused cavities did not change during this period (mean initial and final cooling coefficient values of 1.05 ± 0.05 and 1.03 ± 0.05 respectively, paired t test, $t_9 = -1.0$, $P = 0.34$). Thus any change in the estimated rate at which heat was lost in an active starling nest cavity between the initial measurement and measurement at laying was due to the construction of the nest.

As the roofs in which nests were built were sloping, starlings initially blocked the lower end of the nest cavity with a 'bung' of nest material, providing a solid base above which a nest cup was constructed. The length of the bung and the diameter of the nest cup were measured when the first egg was laid. The quantity of material covering the cup floor was scored on a scale of 0 to 3, with 0 representing an absence of floor covering, 1 representing partial covering, 2 representing a complete covering less than 1cm deep, and 3 representing a complete covering more than 1cm deep. The bung, diameter and floor covering measurements for each nest were correlated with each other and, using factor analysis (SPSS Version 8.0), they were combined into a single variable describing nest size that encompassed 59.9% of the original variation in the three individual measures.

In starlings, males are responsible for the majority of nest construction and in the partially polygynous population studied here, approximately a quarter of males defended more than one nest cavity and constructed more than one nest. In order to ensure independence of data, when two nests belonging to the same male were studied, the mean values of the nest dimensions and cooling coefficients measured in that male's nests were used in the analyses. Thus individual males rather than individual nests formed the unit of analysis. In practice, the dimensions and cooling coefficients of the nests belonging to the same male tended to be very similar, and the qualitative results of the analyses did not differ when data were pooled in this way, and when all nests were considered independently. Parametric statistical tests were used throughout the analysis, as in no case did the data distributions violate the appropriate assumptions. All tests were two-tailed, and means are presented ± one standard error.

Results

The initial rate of heat loss was measured in 43 cavities (belonging to 33 different males) in which nests were subsequently built and eggs laid. The initial cooling coefficient values recorded in empty cavities varied between 0.82 and 1.74 $°C^{-1}$ with a mean of 1.10 $\pm$ 0.04 $°C^{-1}$. Thus the insulative quality of empty cavities varied greatly, with heat being lost more than twice as rapidly in some cavities as in others. At laying, mean cooling coefficient value was 0.91 $\pm$ 0.03 $°C^{-1}$ (range of 0.66 to 1.32), and thus the construction of a nest significantly reduced the rate at which heat was lost from the test object (Paired t test, $t_{32} = 8.4$, $P < 0.001$), a mean reduction in cooling coefficient of 0.19 or approximately 17% of the original value.

The magnitude of the reduction in the rate of heat loss following the construction of the nest was positively correlated with the rate at which heat was lost in the empty nest cavity (Fig. 9.1). Hence during nest construction, starlings reduced the rate of heat loss from within a cavity to a greater extent when the insulative quality of the original site had been poor. However, the rate of heat loss in a nest at laying was still strongly correlated with the rate of heat loss in the empty site (Fig. 9.2). Thus despite reducing the rate of loss to a greater extent, the nests built by starlings with poorly insulated nest sites did not fully compensate for the relatively rapid rate at which heat was lost from the unmodified cavity.

Figure 9.1. The relationship between the change in the rate of heat loss from within a starling nest cavity following construction of a nest, and the rate at which heat was lost from within the empty cavity. The change in heat loss rate was correlated with the original rate of heat loss ($r_{31} = 0.56$, $N = 33$, $P = 0.001$).

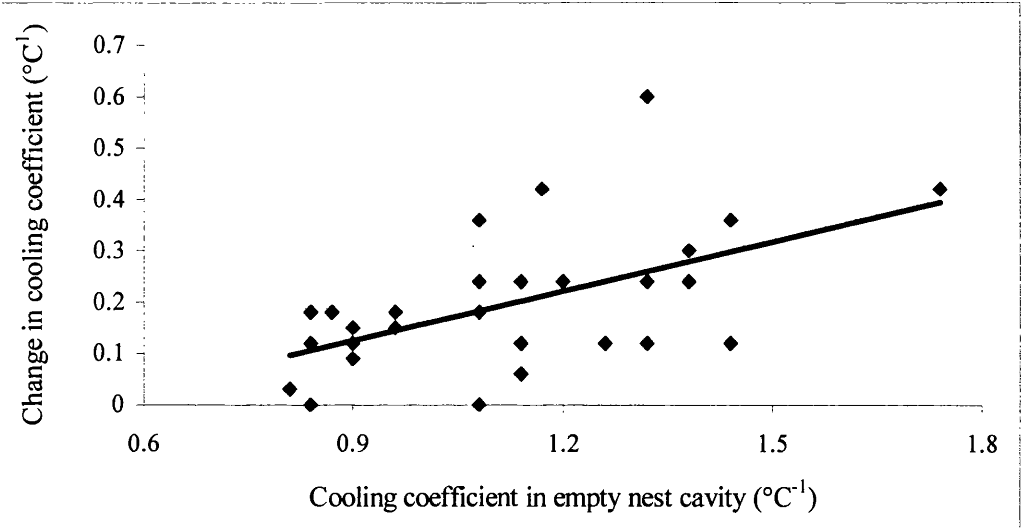
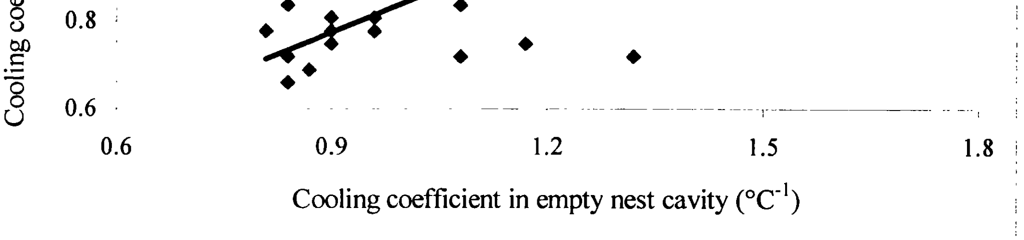
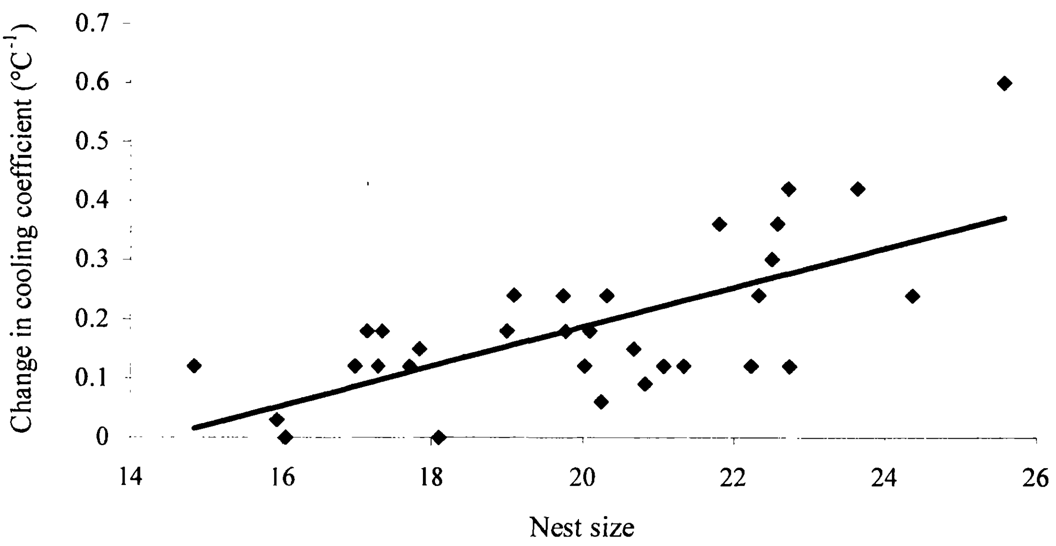


Figure 9.2. The relationship between the rate at which heat was lost from within a completed starling nest and the rate of heat loss from within the empty cavity. The rate of heat loss from within a nest was correlated with the insulative quality of the original cavity ($r_{31} = 0.82$, $N = 33$, $P < 0.001$).



The magnitude of the reduction in the rate of heat loss from within a cavity following the construction of the nest was correlated with the overall size of the nest (Fig. 9.3). Thus the larger the nest that was constructed, the greater the reduction in the rate of heat loss from within the site. As expected given the relationship between the insulative quality of the original cavity and the magnitude of the reduction in heat loss during nest construction, nest size was also correlated with the initial rate of heat loss from the cavity ($r_{31} = 0.40$, $N = 33$, $P = 0.02$). Thus starlings breeding in poorer nest sites built larger nests. However, there was no relationship between nest size and the rate at which heat was lost from within a nest at laying ($r_{31} = 0.03$, $N = 33$, $P = 0.87$), so actual nest size was a poor predictor of the quality of the thermal environment that would have been experienced by offspring.

Figure 9.3. The relationship between the change in the rate of heat loss from within a starling nest cavity following nest construction, and the size of the nest that was constructed. The change in the rate of heat loss was correlated with the size of the constructed nest ($r_{31} = 0.67$, $N = 33$, $P < 0.001$).



Discussion

The construction of a nest within a cavity nest site significantly reduced the rate at which heat was lost from a standard object placed within the cavity. Such reductions in rates of conductive and convective heat loss are likely to affect other objects similarly. Hence constructing a nest is likely to reduce the rate at which heat is lost from unattended clutches of eggs during incubation, and from chicks during the subsequent rearing period. A reduction in the rate of heat loss from within a nest may also increase the proportion of time that a parent can spend incubating (Bryan & Bryant 1999; *Chapter 4*), further improving the developmental conditions provided for offspring. Although the average reduction in cooling coefficient was only 0.19 or 17%, this reduction in heat loss rate is similar in magnitude to that which, when experimentally induced during the incubation stage of a starling's breeding attempt, significantly increased the proportion of offspring that fledged successfully (*Chapter 3*). Thus the construction of a nest has thermodynamic consequences that may be sufficient to improve breeding success, and nest construction can be viewed at least partly as an adaptation to improve the thermal conditions experienced by parents and developing offspring.

Starlings that built nests in cavities within which the rate of heat loss was initially rapid reduced the rate of heat loss to a greater extent than starlings breeding in cavities that were initially well insulated. Since across the range of nest sizes constructed the thermal quality of the actual nest was correlated with nest size, a relationship that has been reported previously (Schaefer 1980; Skowron & Kern 1980; Hoi *et al.* 1994; Grubbauer & Hoi 1996), this is likely to have been because starlings nesting in poorer sites built larger nests. However, the overall rate of heat loss from completed nests was still greater in sites where the original rate of loss had been rapid. Thus nest-building starlings did not compensate completely for the original insulative quality of their cavity. This suggests that the thermal environment that parents provide for developing offspring depends on the insulative quality of the nest site that they acquire. These results are consistent with those of a study on Pouched Mice, in which the thermal quality of the nest site had a greater impact on the conditions experienced by young than the thermal quality of the nest itself (Ellison 1995). Nest-building starlings may have failed to compensate completely for a rapid rate of heat loss from a nest site because the cost of building a larger nest and reducing heat loss further was greater than the cost of continued heat loss. Alternatively, the addition of more nest material may have had little further impact on the rate at which heat was lost from the site. Experimental manipulation of the amount of material within an individual nest site would be required in order to examine the full relationship between nest size and insulative quality, and thus to test the latter hypothesis.

The consequence of the rate of heat loss experienced within a nest for the breeding success achieved in that nest could not be investigated directly in this study. The number of offspring reared during a breeding attempt depends greatly on the amount of care provided by the attending parents, and in the facultatively polygynous starling population studied here, the extent to which males contributed to parental care varied markedly between nests, greatly influencing breeding success (*Chapter 8*). Thus in this study, the consequences of nest quality for breeding success were confounded by the variable occurrence of paternal care. Further, as parents that provide poor nests may also perform poorly in other aspects of parental care, a correlative study cannot prove a deterministic link between nest quality and breeding success. However, although the range of heat loss rates from standard objects placed within completed nests was narrower than the range of rates in empty cavities, there was still a twofold variation between nests. The magnitude of this range is greater than the mean reduction in heat loss that was due to the construction of a nest, and also than the magnitude of the experimental reduction in heat loss that improved breeding success during a study on another population of starlings (*Chapter 3*). Thus failure to compensate for the rate of heat loss from a poor nest site is likely to have fitness consequences for parents. Further, as starlings nesting in poorly insulated cavities built larger nests and constructing a large nest may itself be costly, requiring considerable time and energy (Gauthier & Thomas 1993; Lens *et al.* 1994; Nores & Nores 1994; Cavitt *et al.* 1999), the overall fitness cost associated with breeding in a poorly insulated cavity may be high.

Multiple factors are likely to influence where a parent decides to situate a nest. For example, nest location may be influenced by the presence of nests of the same (Ramsay *et al.* 1999) or other species (Bogliani *et al.* 1999), and may influence the chance that a nest will be predated (Hatchwell *et al.* 1996, 1999) or parasitised (Larison *et al.* 1998; Moskat & Honza 2000). However, as nest-building starlings did not compensate fully for selecting a poorly insulated nest site, a failure that may be costly, the acquisition of a well insulated nest site is likely to be an important stage of a breeding attempt. Previous studies have suggested that birds may indeed select nest sites at least partly on the basis of their thermal characteristics (Inouye *et al.* 1981; Walsberg 1981). In cavity nesting species, the availability of potential nest sites may limit breeding opportunities (Newton 1994) and competition over high quality sites may be intense. The outcome of such competition and hence an individual's ability to compete may have a substantial bearing on an individual's subsequent reproductive performance (Ingold 1998; Ramos *et al.* 1997). Studies of the allocation of resources during avian reproduction have traditionally commenced with egg-laying, but this study suggests that it may also be important to consider the investment that an individual is able to make during earlier stages of a breeding attempt.

In species such as starlings where males are responsible for the majority of nest construction, it has often been suggested that females choose mates at least partly on the basis of the constructed nest or nests (Collias & Victoria 1978; Collias & Collias 1984; Evans & Burn 1996). Nest size has frequently been considered to be a principal parameter on which selection might act (Hoi *et al.* 1994, 1996; Palomino *et al.* 1998; Soler *et al.* 1998). Females choosing large nests may gain direct benefits if larger nests are of better thermal quality (Hoi *et al.* 1994, 1996), or 'good genes' if nest size is a sexually selected indicator of male quality. However, in this study, although nest size was related to the insulative quality of the actual nest, size was a poor predictor of the overall thermal environment that offspring and parents would experience. Further, as the males that built large nests had generally acquired nest sites that were thermally poor, there was no clear evidence that nest size signaled male quality. Thus in starlings, nest characteristics other than size may function in mate attraction.

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Chapter ten

General Discussion

The problem of protecting offspring and regulating developmental conditions is, in viviparous and ovoviviparous organisms, solved by retaining offspring internally until after considerable development has taken place. However, the evolution of oviparity, especially coupled with the late development of endothermy, requires the corresponding evolution of post-laying parental care for eggs (Clutton-Brock 1991). In many species, this takes the form of incubation. Whilst incubation is perhaps most widespread in birds, it is also observed in other vertebrate taxa. A wide range of reptiles and a small number of mammals also lay eggs that require environmental conditions to be regulated in order for the embryos to develop and hatch successfully (Matthews 1969; Bellairs 1970). In order to elucidate overall principles of the resource requirements and life-history consequences of incubation, it is likely to be valuable to draw together our knowledge of incubation in terrestrial vertebrates in general.

The processes of egg-production and incubation in oviparous mammals are relatively poorly known. Indeed, the egg-laying behaviour of the spiny anteater was observed for the first time within the last decade (Rismiller & Seymour 1991), and our knowledge of platypus embryology is based on a small number of museum specimens of *Ornithorhynchus anatinus* (Hughes & Hall 1998). Hence at present, our knowledge of mammalian biology adds little to the understanding of the resource allocation patterns associated with incubation.

In contrast, a considerable amount is known about reptile embryology and incubation. In many ways, the incubation conditions required by reptilian and avian embryos are similar. In particular, both require tightly regulated thermal environments (Lundy 1969; Ferguson 1985). The incubation temperatures that maximise hatching success are typically slightly lower in reptiles than in birds (*eg*, 28°C in broad-shelled turtles (*Chelodina expansa*, Booth 2000) and 30°C in the lizards *Lampropholic guichenoti* and *Bassiana duperreyi*, Booth *et al.* 2000). However, bird and reptile eggs incubated in natural situations may experience similar degrees of temperature fluctuation

(Webb 1987; Booth 1998a; Elphick & Shine 1999; *chapter 5*), and hence the problems faced whilst incubating a clutch may to some extent be similar for avian and reptilian parents. However, as well as similarities, there are also marked differences in the optimal developmental conditions for birds and reptiles. In particular, the frequent egg-turning required to maximise hatching success in birds (Lundy 1969; Deeming *et al.* 1987; Wilson & Wilmering 1988) is not required and can even be harmful in reptiles (Ferguson 1985; Chan 1989). Despite the acknowledgement that gaseous conditions may greatly affect embryonic development in both birds and reptiles, the extent to which gaseous environments vary in the field, and the role of parental incubation in regulating gaseous exchange, are poorly understood. These are gaps in our knowledge that could very valuably be addressed.

Deviations from optimal developmental conditions can affect reptilian embryos in similar ways to birds. As in birds, slight increases in mean incubation temperature can shorten the incubation period (Marco & Perez-Mellado 1989; Booth 1998b; Downes & Shine 1999; Angilletta *et al.* 2000; Booth *et al.* 2000). Embryos are able to survive short periods of exposure to suboptimal temperatures (Angilletta *et al.* 2000), but are unable to actively compensate for changes in thermal conditions (Booth 1998c). The consequences of deviations from optimal conditions depend on the magnitude and duration of the deviation, and the embryo's age at exposure (Downes & Shine 1999). However, considerably more is known about the physiological and fitness consequences of small fluctuations in developmental conditions in reptiles than in birds. Small temperature changes can influence rates of embryonic oxygen consumption (Booth 1998b; Booth 2000) and metabolism (Steyermark & Spotila 2000), and the development of major body functions (*eg* heart rate, Birchard & Reiber 1996). Post-hatching phenotypic consequences of incubation conditions have also been demonstrated on a number of occasions. Most particularly, developmental temperature can affect sex determination in a range of reptiles, including turtles, crocodilians, lizards and sphenodons (Harlow & Shine 1999; Rhen & Lang 1999; Shine 1999a; Bragg *et al.* 2000; Broderick *et al.* 2000). Sex determination is likely to occur due to the temperature-dependent activity or expression of genes such as Dmrt1 (Kettlewell *et al.* 2000). Despite reports in the popular press, temperature-dependent sex determination has not been conclusively demonstrated in birds, and may be less likely as, unlike reptiles, all birds show chromosomal sex determination (Tagaki *et al.* 1972; Ansari *et al.* 1988). However, as the gene Dmrt1 is thought to play a role in avian (and mammalian) sexual development (Kettlewell *et al.* 2000), it would be interesting to investigate the possibility that temperature-dependent expression might also occur and affect developmental patterns in avian embryos.

Once sex has been determined, developmental conditions can further influence reptile hatchling morphology and physiology. For example, incubation temperature can affect snout and rail lengths and head widths in lizards and turtles (Booth 1998b; Madsen & Shine 1999; Booth 2000; Booth *et al.* 2000; Brana & Ji 2000), locomotor performance and chemosensory ability in lizards (Downes & Shine 1999), and post-hatching behaviour in Pine Snakes (*Pituophis melanoleucus*, Burger 1998a, 1998b). Such changes may have considerable consequences for offspring fitness. Specifically, incubation regime has been shown to influence an individual's future ability to detect and escape from predators (Burger 1998a, 1998b; Downes & Shine 1999). Such clear links between developmental conditions and post-hatching phenotype and fitness have rarely been made in birds, although artificial curtailment of the incubation period can affect hatchling morphology and locomotory ability in mallards (*Anas platyrhynchos*) and pheasants (*Phasianus colchicus*, Persson 2000). The possibility that the conditions experienced during early development may have important and permanent consequences for an individual's future fitness and life history is attracting increasing attention (*eg*, Metcalfe & Monaghan 2001). Some studies have now considered the consequences of incubation conditions for chick survival in birds (*eg*, *chapter 7*). However, carefully controlled studies of the consequences of incubation conditions for an avian embryo's subsequent behaviour, growth and reproduction would prove extremely interesting, and would fill an important gap in our current knowledge.

Although more is known about the links between incubation conditions and embryo development and phenotype in reptiles than in birds, much less is known about parental incubation behaviour, or about the demands and costs that incubation may impose upon parents. This line of investigation could profitably be pursued by herpetologists. However, one major study on tropical pythons (*Liasis fuscus*) suggests that the thermal quality of the nest site and thus the energetic demand of incubation can greatly affect a female's future life-history. Females laying in cold sites incubated for longer, suffered higher mortality due to starvation and predation, and took longer to breed again than females laying in warm sites (Madsen & Shine 1999). Thus, as in starlings (*chapters 3 & 9*), acquisition of a well insulated nest site may play an important role in determining a female's current and future reproductive success. Indeed, there is evidence that the skink *Bassiana duperreyi* may actively select warm nest sites, allowing it to breed successfully in relatively cold climates (Shine 1999b). However, other lizards (eg, *Nannoscincus maccoyi*) may have evolved to tolerate cold conditions rather than to avoid them. Embryos of this species actually developed faster when exposed to relatively low temperatures (Shine 1999b), although the consequences of low temperatures for embryo energy expenditure or hatchling morphology and physiology were not reported. Similar developmental tolerance to cold has been suggested in birds that inhabit particularly extreme environments (*eg*, penguins, Webb 1987), but has not yet been rigorously demonstrated.

Although environmental effects on the development of reptilian embryos have been clearly demonstrated, individual phenotypes can be further influenced by interactions with parental and genetic factors. Both maternal and paternal effects on incubation have been demonstrated. Embryo sex determination has been linked to the concentration of maternally-produced hormones present in the yolk as well as to temperature (Bowden *et al.* 2000), and paternal genotype can influence the duration of incubation, and offspring morphology (specifically snout size) and early growth rates (Olsson *et al.* 1996). Finally, once the sex of a reptile embryo has been determined, its future development may be influenced by gender-dependent environmental interactions. Elphick and Shine (1999) observed sex-specific phenotypic responses to exposure to fluctuating incubation conditions. Although the duration of the incubation period has been reported to differ between male and female embryos in black guillemots (*Cepphus grylle*, Cook *et al.* submitted), nothing is known about the specific responses of male and female embryos to different environmental conditions in birds. The intriguing possibilities that incubation requirements might differ between the sexes, and that parents might therefore adjust their incubation effort in response to the sex of their offspring remain to be investigated. Indeed, given the recent interest in investigating offspring sex-specific patterns of parental investment during chick-rearing (Leonard *et al.* 1994; Nishiumi *et al.* 1996; Lessells *et al.* 1998; Radford & Blakey 2000) and egg-production (Anderson *et al.* 1997; Cordero *et al.* 2000), it is surprising that patterns of parental effort during incubation have received such scant attention.

Traditionally, investigation of avian life-history strategies has focussed largely on the resource allocations made during chick-rearing (see *chapter 1*). Although there is still much work to be done, some headway has now been made in addressing this bias with respect to egg-production and incubation. However, there is evidence from both birds and reptiles that nest site quality can have substantial life history consequences for both parents and current offspring. Investment in nest-site acquisition and nest-building must therefore be viewed as a major life-history phase, the demands and consequences of which desperately require experimental investigation. In birds, the majority of experimental studies on passerine resource allocation have been carried out in nest-box populations. Such study systems obviously confer huge advantages in terms of nest accessibility, and thus in the ease of high-quality data collection. However, as nest-box provision may result in the availability of many nest sites of relatively similar thermal quality, the use of nest-boxes may remove a major determinant of patterns of reproductive investment. It would therefore be extremely valuable to pursue the investigation of resource allocation and life-history strategies to a greater extent in naturally-nesting populations.

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