

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

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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.

Keywords: breeding success; nest structure; egg temperature; energy expenditure; starling, *Sturnus vulgaris*

1. 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 three 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 (e.g. Bolton *et al.* 1992; Nager & Van Noordwijk 1992; Monaghan *et al.* 1998). It is now clear that maintaining eggs at the appropriate temperature for development usually involves additional energy expenditure (Thomson *et al.* 1998; Bryan & Bryant 1999). Few studies have examined the fitness consequences of altering the amount of energy required to incubate eggs 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), and examining the effect on reproductive performance. 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 reallocated 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,

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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.

2. METHODS

A substantial proportion of the energetic demand of incubation is thought to occur while 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 while 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, UK (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 36–38°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 while females foraged.

Fifty-seven first-brood nests were discovered, of which a randomly selected 34 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 old, 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 (all means \pm s.e.; control mean 4.76 ± 0.14 , experimental mean 4.53 ± 0.15 , Mann–Whitney $U_{34} = 112.5$, $p = 0.213$), mean egg mass (control mean 7.99 ± 0.11 g, experimental mean 8.32 ± 0.15 g, $t_{31} = -1.786$, $p = 0.089$), overall clutch mass (control mean 38.3 ± 0.9 g, experimental mean 37.5 ± 1.0 g, $t_{31} = 0.599$, $p = 0.553$) or laying date (control mean 5.1 ± 0.6 days into May, experimental mean 5.2 ± 0.7 days into May, $t_{32} = -0.198$, $p = 0.844$). 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 5 cm in diameter (Radio Spares 12 V silicone–polyamide mat, Glasgow, UK) 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 4.2 V 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 $0.22^\circ\text{C min}^{-1}$ or 20% (Reid *et al.* 2000). 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® data loggers (Gemini Dataloggers Ltd, Chichester, UK) were placed among eggs, and nest temperature was recorded every 72 s 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 $U_{32} = 112$, $p = 0.564$), 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.

3. RESULTS

There was no significant difference between the proportion of first-clutch eggs that hatched in control and experimental nests (control mean $82.4 \pm 8.0\%$, experimental mean $95.9 \pm 2.9\%$, Mann–Whitney $U_{33} = 105.5$, $p = 0.144$). However, the proportion of first-clutch eggs from which young fledged was significantly higher in experimental nests than control nests (control mean $51.0 \pm 8.3\%$, experimental mean $74.9 \pm 4.5\%$, Mann–Whitney $U_{33} = 72.0$, $p = 0.021$). 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, $t_{29} = 1.605$, $p = 0.119$). 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, $t_{26} = -0.674$, $p = 0.506$) or in the mass of chicks at three days old (control mean 22.5 ± 1.7 g, experimental mean 22.9 ± 1.9 g, $t_{27} = -0.14$, $p = 0.92$) between the two groups. As a measure of condition, the ratio of mass to tarsus cubed was calculated for the chicks at ten days old (Freeman & Jackson 1990). There

was no significant difference in mean ratio for chicks in experimental and control nests (control mean $3.23 \pm 0.08 \text{ g m}^{-3}$, experimental mean $3.46 \pm 0.08 \text{ g m}^{-3}$, $t_{27} = -1.933$, $p = 0.064$), although there was an obvious trend towards better condition in the experimental chicks.

Six out 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 ($\chi^2_1 = 0.01$, $p > 0.5$). 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, $t_{18} = -0.946$, $p = 0.357$), clutch size (control mean 3.3 ± 0.4 , experimental mean 3.6 ± 0.3 , $t_{18} = -0.625$, $p = 0.540$), mean egg mass (control mean 8.06 ± 0.20 g, experimental mean 8.17 ± 0.17 g, $t_{18} = -0.387$, $p = 0.703$) or clutch mass (control mean 27.0 ± 23.56 g, experimental mean 29.6 ± 32.17 g, $t_{18} = -0.645$, $p = 0.527$).

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 were 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 14 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.

4. DISCUSSION

The experimental treatment reduced the rate at which a clutch of eggs cooled during a parental absence (Reid *et al.* 2000), 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 precise thermal conditions that are optimal for embryonic development are poorly understood (Webb 1987). 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 with 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 while 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; Reid *et al.* 2000). 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 show that resources saved during reduced-demand incubation can be reallocated to future stages of reproduction, both within and

between breeding attempts. Furthermore, our results demonstrate the critical role of the thermal environment of 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). 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, 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 & Moller 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, 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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