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Daily changes in body mass of incubating Kentish Plovers

I. Szentirmai, A. Kosztolányi and T. Székely

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We investigated the daily body mass changes in incubating female Kentish Plovers *Charadrius alexandrinus.* We found that the body mass of females decreased over the day. The change in body mass was significant both from morning to midday (median decrease: 3.36%), and from morning to afternoon (8.40%). We suggest two reasons for this decrease: depletion of fat reserves and the evaporation of water from body tissues. These changes may either indicate a physiological cost of incubation, or they may be the result of a strategic body mass regulation.

I. Szentirmai, Department of Ethology, Eötvös University, Pázmány P. sétány 1/c., H-1117 Budapest, Hungary. A. Kosztolányi, Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Egyetem tér 1., H-4010 Debrecen, Hungary. T. Székely, Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK

1. Introduction

One of the key issues in behavioural ecology is how animals allocate time and energy to various activities (Cuthill & Houston 1997). Since resources are often limited, there must be trade-offs between various life-history components. For example, parent birds may enhance their current reproductive value by spending time and energy on incubating their clutch and raising their young, although these behaviours may reduce their residual reproductive value (Roff 1992, Kosztolányi & Székely 2002a). Such trade-offs are often interpreted as acting directly through the depletion of body reserves, i.e. it may indicate a cost of reproduction (Jones 1988, Kacelnik & Cuthill 1990). For example, low body reserves may reduce the chance of initiating a new clutch either in the same breeding season or in future years, or they may reduce the chances of parent's survival until future breeding seasons (Hemborg 1999).

Mass loss during breeding is often interpreted as an indicator of physiological stress. For example, a significant mass loss during incubation has been detected in several Passerines (Moreno 1989, Halpern *et al*. 1997). Furthermore, a positive relationship was observed between mass loss of females and their reproductive effort, whereas the females' ability to allocate energy to self-maintenance decreased with mass loss (Merilä & Wiggins 1997).

Two types of body mass variation have been reported during incubation. Firstly, the mass of the incubating parent decreased in those species in which incubation was carried out by a single parent and/or nest attentiveness was very high (Moreno 1989, Hegyi & Sasvári 1998).

This change may be due to the fact that the incubation metabolic rate (IMR) is often elevated above the metabolic rate of non-incubating birds, e.g. by 19-50% in Passerines (Williams 1996). Secondly, body mass did not show any trend over the course of incubation in those species in which both parents incubated the clutch and/or in which the nest was attended for a low percentage of time (Moreno 1989, Hegyi & Sasvári 1998).

The reproductive stress hypothesis, which argues that the mass loss of breeding birds is due to the increased energetic expenditure, has been frequently criticised. For example, mass loss may simply be due to degeneration of the reproductive organs (Ricklefs & Hussel 1984), or the loss of body mass may be an adaptive adjustment to reduce energetic cost of flight during brood rearing when the demands of the offspring increases (Nornberg 1981). Finally, low body mass reduces wing loading and enhances the take-off ability and flying performance, and thus reduces the risk of predation (Witter & Cuthill 1993).

Although shorebirds *Charadrii* have an immense annual variation in their body mass due to migratory fattening (Piersma 1994), only few body mass changes are documented during the breeding season. Nevertheless, these studies would be particularly important in shorebirds, since it has often been hypothesised that the changes in their body mass (and body condition) should influence their mating and parental behaviours (Ashkenazie & Safriel 1979, Erckmann 1983). Also, many shorebirds breed on the ground, and thus the cost of keeping the eggs within the required temperature range, e.g. on the frozen tundra (Piersma & Morrison 1994) or on desert sand, may have significant consequences on the body mass of incubating parent(s). In line with this argument the body mass of several subarctic shorebirds tended to decrease during reproduction (Soloviev & Tomkovich 1997), possibly due to their elevated metabolism.

The objective of our study was to investigate the daily changes in body mass of female Kentish Plovers *Charadrius alexandrinus*. Kentish Plovers are small ground-nesting shorebirds. Their incubation period is about 25 days and their chicks are precocial. Both the male and the female incubate the clutch (Kosztolányi & Székely 2002b), although shortly after hatching of the eggs one parent commonly deserts the brood (Paton 1995, Székely & Cuthill 2000). Males typically incubate at night, whereas females incubate mostly during the daylight period (Kosztolányi & Székely 2002b).

2. Study area and methods

Field work was carried out in May 1999 in Southern Turkey, near the village of Tuzla (36°42'N 35°03'E). The study site was a salt marsh between Lake Tuzla on the south and arable land on the north. The size of the breeding population of Kentish Plover was about 1000 pairs (Székely *et al*. 1999).

Females were caught on their nest by a funnel-trap, and ringed with a metal ring and an individual combination of colour rings. Each female was captured three times: in the morning (06.00 h-09.00 h, local summer time, i.e. GMT+3 hours), at midday (11.00 h-14.00 h) and in the afternoon (16.00 h-19.00 h). At every capture their body mass was measured (±0.1 g).

Captures of the same female were carried out on different days. We randomised the sequence of captures for each female to eliminate carry-over effect. The interval between first and second captures was 1.11±0.20 days (mean±SE), and between the second and third captures was 2.00±0.53 days. Only nests with three eggs (modal clutch size, Székely *et al.* 1994), and those incubated for more than three days were investigated. Further details of field methods are given elsewhere (Székely *et al.* 1999, Székely & Cuthill 2000, Kosztolányi & Székely 2002b).

The distribution of body mass was not normal, thus we used non-parametric tests such as Friedman two-way ANOVA (factor: time of the day, block: individuals). Comparisons between groups were conducted using Wilcoxon matched-pairs signed-rank tests. In the latter analyses we corrected the significance level for multiple comparisons by sequential Bonferroni adjustment (Chandler 1995). We used SPSS for Windows for statistical analysis. Values are given as median (lower quartile – upper quartile), and we provide the exact two-tailed probabilities. In all analyses the sample size was nine females.

3. Results

Body mass of females decreased during the day from 41.8 g (41.0 g–43.5 g) in the morning to 40.3 g (39.8 g–42.7 g) at midday, and 39.8 g (37.9 g–40.4 g) in the afternoon (Fig. 1.). Thus the body mass of females decreased by 3.36% (2.81%–4.98%) from morning to midday, by 3.72% (2.11%–6.77%) from midday to afternoon, and by 8.40% (1.69%–10.56%)

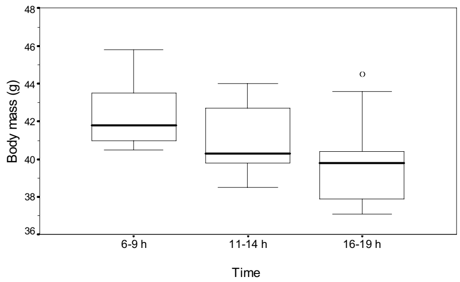

Fig.1. Body mass of incubating female Kentish Plovers over the day (N=9 females in all three periods). The thick horizontal line indicates the median; the bottom and the top of the box are lower (Q1) and upper quartiles (Q3), respectively. The whiskers indicate the lowest and highest observation, within the range defined by Q1-1.5×(Q3-Q1) and Q3+1.5×(Q3-Q1). An outlier is indicated by a circle.

from morning to afternoon. We estimated that females lost about 0.33 g/hour (0.07 g/hour–0.45 g/hour) of their body mass from morning till afternoon.

The mass change between morning, midday and afternoon was highly significant (Friedman test, χ^2=9.314, df=2, P=0.007). The difference in body mass was also significant both between morning and midday (Wilcoxon matched-paired signed-ranks tests, Z=2.549, P=0.008), and morning and afternoon (Z=2.310, P=0.020), whereas the mass change was not significantly different between midday and afternoon (Z=0.980, P=0.383).

4. Discussion

Our results show that incubating female Kentish Plovers lose mass during the day. This result was unexpected, since females often interrupt their incubation by either spending a few minutes in the vicinity of nest and then resuming incubation, or being relieved by their mate for a variable period of time (Kosztolányi & Székely 2002b). In these recess times the females typically forage. Thus the total loss in body mass would have been larger if the females were to incubate constantly during the investigated daytime periods.

We suggest two ways for the observed loss in body mass: depletion of stored body fat and evaporation of water. Depletion of fat stores can be the result of the increased energetic demands of incubation or starvation. For example, it is probably costly to maintain the egg-temperature within the range in which the embryonic development is normal (i.e. between 30 to 40 °C, Purdue 1976). Female Kentish plovers relieve their incubating mate at dawn (Kosztolányi & Székely 2002b), when the ambient temperature is low. At this time of the day an increased metabolic rate may be required to keep the egg temperatures in the optimal range. At midday, when the ambient temperature is high, the parent has to cool the eggs. Thus, at midday the parents often shade the eggs and they may themselves lose a considerable amount of water by evaporation (Hinsley & Ferns 1994). Also, cooling the eggs may elevate the energy expenditure of the parents, for instance an increase of 1.3 BMR was shown in sandgrouse (Hinsley & Ferns 1994). So both cooling and keeping the eggs warm may be costly for the incubating parent, and thus they may result in depletion of fat reserves. The significant decrease in body mass between morning and midday suggests that heating the eggs may be more demanding than cooling in the Kentish Plover.

While the parent is restricted to sitting on its nest, it cannot replenish the lost reserves by feeding. For example, one reason why female Kentish Plovers stop incubating in the evening may be that they have to replenish their body reserves (Purdue 1976, Paton 1995). The other possibility is that nighttime incubation is more demanding than incubation during daytime, and thus if females are exhausted by egg laying (Monaghan *et al*. 1998) then the males are in a better position to carry out nighttime incubation. Future studies, preferably experimental manipulations, are required to identify how the various costs and benefits of incubation vary over the day.

Although we have limited information on the other potential explanations for the observed daily mass loss (such as the degeneration of reproductive organs and strategic body mass regulation), we make the following inferences. Firstly, it is unlikely that the loss of body mass was due to degeneration of reproductive organs (Ricklefs & Hussel 1984), since female body mass changed in a short, i.e. daily basis. Secondly, the strategic adjustment of body mass seems more plausible (Moreno 1989, Witter & Cuthill 1993, Thomas 2000), and we encourage researchers to consider the explanation that reducing body mass may be advantageous for requiring low cost of self-maintenance and/or for reducing the risk of predation. Nevertheless, we do not see any apparent reason why such mass loss would be adaptive only between morning and midday in the Kentish Plover.

In conclusion, our results show that the body mass of female plovers decreases during the day. This decrease may indicate a cost of incubation in terms of depletion of fat reserves and evaporation of water, although we cannot rule out the alternative explanation that body mass regulation is strategic.

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Összefoglalás

Széki lilék napi tömegváltozása a kotlás alatt

Széki lile tojók napi tömegváltozását vizsgáltuk a dél-törökországi Tuzla-tónál 1999 májusában. Az általunk vizsgált kilenc tojó mindegyikét három alkalommal fogtuk be és lemértük a tömegüket: reggel (06.00-09.00 h), délben (11.00-14.00 h) és délután (16.00-19.00 h). Mivel a befogások nem azonos napon történtek, ezek sorrendjét randomizáltuk.

Kimutattuk, hogy a tojó széki lilék tömege szignifikánsan csökken a nap során a kotlási periódus alatt. A madarak tömege 41.8 g (medián) volt reggel, 40.3 g délben és 39.8 g délután. Mind a reggeltõl délig, mind a reggeltõl délutánig történõ tömegcsökkenés szignifikáns volt, míg déltõl délutánig a madarak tömege nem változott szignifikánsan.

A vizsgálatunkban megfigyelt testtömeg csökkenésnek két okát feltételezzük. Az egyik a szülõi zsírtartalékok leépülése, a másik a párologtatás során bekövetkezõ vízvesztés. A zsírtartalékok leépülése feltehetõen a kotlás megnövekedett energetikai igényeinek a következménye, ami különösen nagymértékû lehet a reggeli órákban, amikor a tojásokat melegíteni kell az embriók normális fejlõdéséhez (szignifikáns tömegcsökkenés reggeltõl délig). A tojók vízvesztését a tojások evaporatív hûtése okozhatja a meleg déli órákban. Ráadásul amíg a szülõk kotlanak a fészken csak korlátozott mértékben tudják táplálkozással és ivással pótolni a készleteiket. A tömegcsökkenés tehát utalhat a kotlás költségeire, ugyanakkor nem zárhatjuk ki azt sem, hogy stratégiai szabályzás eredménye. Ennek tisztázására további vizsgálatok szükségesek.

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