Great tits (Parus major) reduce body mass in response to wing area reduction: a field experiment

Joan Carles Senar, Jordi Domènech, and Francesc Uribe
Museu de Ciencies Naturals (Zoologia), P. Picasso s/n, Parc Ciutadella, 08003 Barcelona, Spain

Flight performance is crucial in determining whether a small bird will survive an attack by a predator. Given the importance of body mass in determining flight performance, it has been suggested that birds should strategically regulate body mass as a response to predation risk. However, all experiments up to now have been carried out with captive birds, comparing experimental to control birds. Here we present data from the first experiment in the field using a within-individuals experimental design. The wing area of wild great tits, Parus major, was reduced by reversibly taping primaries five to seven. This allowed for the same individual to alternatively act as control or experimental bird. Great tits reduced body mass (but not pectoral muscle width) during episodes of wing area reduction, lending support to the view that the reduction in body mass experienced by birds during molt is a strategy rather than the result of energetic stress. Theoretical models establishing the different trade-offs that determine optimal body mass should therefore take into account this important life-history episode. Key words: body mass, flight performance, great tits, molt, Parus major, wing area, wing loading. [Behav Ecol 13:725–727 (2002)]

METHODS

We studied body mass variation in great tits in the suburban area of Barcelona (northeastern Spain) in the summer of 1996. Tits were captured with special peanut-baited funnel traps which allowed the birds to be repeatedly trapped (Senar et al., 1997). The traps also worked as permanent feeders, so that highly energetic food (peanuts) were available to the birds ad libitum during the whole experimental period. Captures for each experimental unit (see below) were carried out from dawn to dusk over 2–3 consecutive days. On capture we measured, for each bird, body mass with an electronic balance (precision 0.1 g), tarsus length with a digital calliper (precision 0.1 mm), and wing area with a planimeter (precision 0.1 mm), and pectoral muscle width, as measured by ultrasonound (Carrascal et al., 1998; Newton, 1993). Mass was corrected by regression for body size (tarsus length) and time of capture was not significant (partial correlation \( t = 0.13 \) and time = 0.78 tarsus + 0.12 time \( F_{2,258} = 56.17, p < .001 \)), which explained 30% of the original variance. Analyses were therefore carried out on body mass values statistically corrected for tarsus size and time. Ambient temperature (mean) on the day of capture was not significant (partial correlation \( R = –0.03, p = .63 \)) and was therefore not included in the equation. We carried out our experiments during August–September, at the end of the normal molting period of the species (Gosler, 1993), to avoid the interference of unknown seasonal effects. We only used juvenile birds in the experiments because juveniles do not molt remiges (Jenni and Winkler, 1994).

Wing area was reduced by taping primary remiges five to seven (counted ascendantly) (Figure 1). The taped remiges were separated from the other remiges and positioned such that their rachises lay side by side. This is the normal spatial
relationship of the three feathers when the wing is folded. A rectangular notch was then cut from the feather vanes on each side of the rachises along the feather shaft. Then a strip of tape was attached to the three remiges within the notched area, around the rachises. Control birds also had the notch cut from the feather vanes, but no tape was added. Reduction in wing area, measured on a computer from a digital photograph of an outstretched wing experimentally taped, was of about 8%, which is within the normal range for birds in molt (Hedenström, 1998).

Twenty-six birds were trapped during the third week of August (initial capture: 20–21 August); birds were randomly assigned either to the experimental group, which had remiges taped, or to the control group, which was similarly manipulated but with remiges untapped. Two weeks later, birds were retrapped, remeasured (first recapture: 3–4 September) and had treatments reversed, so that control birds had their remiges taped and previous experimental birds had tape removed. Great tits were retrapped and remeasured again during the second week of September (second recapture: 10–12 September). Eighteen birds were captured at the three trapping periods (9 within each treatment). We analyzed body mass variation using repeated-measures ANOVA. Repeated measures ANOVA, treatment x period interaction: $F_{2,18} = 1.85$, $p = .17$, indicating that variations detected in body mass were not due to variations in muscle width.

**RESULTS**

Average body mass of great tits over the course of the experiment was 16.5 g (SE 0.07, $N = 238$, including all recaptures). Experimental and control birds did not differ in initial standardized body mass (planned comparison: $F_{1,16} = 0.43$, $p = .52$). However, changes in body mass over the course of the experiment differed according to wing area treatment, indicating that birds alternatively increased or decreased their body mass in response to wing area manipulation (repeated-measures ANOVA, treatment x period interaction: $F_{2,32} = 4.13$, $p = .03$, $n = 18$ birds; Figure 2). Overall, birds had a lower body mass when their wing area was experimentally reduced than when they were controls (repeated-measures ANOVA comparing experimental vs. control standardized body mass, 16.26 g, SD = 0.82, vs. 16.82 g, SD = 0.70; $F_{1,17} = 11.89$, $p = .005$). Average percentage of variation in body mass was 3.6% (SE = 0.9%; range 0–11.5%; $n = 18$; comparing second and third experimental periods, see Figure 1). The increase in body mass of control birds during the first 2 weeks of the experiment is probably related to autumn-winter fattening, which is typical for juvenile birds at this time of year (Haftrn, 1976).

Pectoral muscle width did not vary over the course of the experiment according to wing-area treatment manipulation (repeated-measures ANOVA, treatment x period interaction: $F_{2,32} = 1.85$, $p = .17$), indicating that variations detected in body mass were not due to variations in muscle width.

**DISCUSSION**

Although it has long been clear that fat reserves are insurance against reduced or unpredictable food supplies, it has just now been widely recognized that avian fat storage also entails many different costs mainly associated with predation risk (Cuthill and Houston, 1997; Witter and Cuthill, 1993). Body mass is therefore considered to reflect the outcome of this trade-off (Cuthill and Houston, 1997; Houston and McNamara, 1999). Body mass variation according to predation risk (Carrascal and Polo, 1999; Gentle and Gosler, 2001; Gosler et al., 1995; Lilliendahl, 1997; Witter et al., 1994) is thought to operate through the relationship between flight ability and wing loading (body mass/wing area) and is based on the aerodynamic fact that increases in body mass may have an important impact on reducing flight performance (Norberg, 1990; Witter et al., 1994). However, empirical results so far obtained are somewhat contradictory, with some authors finding (Bednekoff, 1996; Kullberg et al., 1996; Lind, 2001; Lind et al., 1999; Metcalfe and Ure, 1995; Norberg, 1995; Swaddle et al., 1996, 1999) and some not finding (Kullberg et al., 1998; Kullberg, 1998; Van der Veen and Lindström, 2000; Veasey et al., 1998) any clear reduction in flight performance because of an increase in body mass or a reduction in wing area. This disagreement is probably related, at least in part, to variations in perceived predation risk by the experimental animals (Carrascal and Polo, 1999; Veasey et al., 1998), so that birds performing routine flights probably adjust their speed to save energy but when under a predator attack sacrifice energetic considerations for maximum speed (Veasey et al., 1998).

This interplay of energetic considerations (Witter and Cuth-
ill, 1993) may explain why coal tits (Parus ater) reduce body mass when under predation risk (Carrascal and Polo, 1999), despite the fact that body mass is not critical to flight performance when escaping from predators (Kullberg, 1998). Our data on great tits agrees with this view and clearly shows how birds reduce body mass as a response to wing area reduction, even though body mass variation may not be critical in enhancing flight performance when escaping from a predator (Kullberg et al., 1998). Hence, the reason for body mass regulation in great tits, as in other species, may be saving energy (Witter and Cuthill, 1993). This reduction in body mass as a strategic way to compensate for increased wing loading may be especially important during molt (Lind and Jakobsson, 2001). Although our results cannot totally rule out the possibility that changes in mass are a by-product of changes in foraging efficiency or in the energy cost of flight (Swaddle and Witter, 1997), the fact that birds were provided with food ad libitum in feeders highly minimizes its eventual effect. Hence, our results are consistent with the view that mass may be strategically adjusted to compensate for changes in wing area. Our study has the enhanced value of having tested for that relationship within individuals and in the field, where many other different selective pressures may be simultaneously operating. This gives a high generality to our results.

It has been suggested that an additional adaptation to reductions in flight efficiency caused by molt could be an increase in pectoral muscle size, and this has been found in molting tree sparrows (Lind and Jakobsson, 2001). We have not found this relationship in great tits, stressing interspecific variability in adaptive strategies (Van der Veen and Lindström, 2000).

Most theoretical frameworks on maintenance of optimal body mass assume that wing area is more or less fixed within individuals (Houston and McNamara, 1999). Given that processes such as molt and feather abrasion periodically reduce wing area and that at least some bird species adjust their body mass accordingly (Lind and Jakobsson, 2001; Swaddle and Witter, 1997; this study), models on the strategic regulation of body mass (Houston and McNamara, 1999) should take into account this important life-history episode.

We thank Lluïsa Arroyo, Luis María Carrascal, Neil Metcalfe, and Vicente Polo for comments on the manuscript and Hermánitas de la Asunción for permission to work on their properties. L. Arroyo also provided field assistance. This study was supported by D.G.I.C.Y.T. research projects PB92-0044-C02-02 and BOS2000-0141 of the Spanish Research Council, Ministerio de Educación y Ciencia, and Ministerio de Ciencia y Tecnología.

REFERENCES


