Body building and concurrent mass loss: flight adaptations in tree sparrows

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Environmental changes are responsible for the evolution of flexible physiology and the extent of phenotypic plasticity in the regulation of birds' organ size has not been appreciated until recently. Rapid reversible physiological changes during different life-history stages are virtually only known from long-distance migrants, and few studies have focused on less extreme aspects of organ flexibility. During moult, birds suffer from increased wing loading due to wing-area reductions, which may impair flight ability. A previous study found that tree sparrows' escape flight (*Passer montanus*) is unaffected during moult, suggesting compensatory aptness. We used non-invasive techniques to study physiological adaptations to increased wing loading in tree sparrows. As wing area was reduced during natural moult the ratio of pectoral-muscle size to body mass increased. When moult was completed this ratio decreased. We show experimentally a novel, strategic, organ-flexibility pattern. Unlike the general pattern, where body mass is positively coupled to pectoral-muscle size, tree sparrows responded within 7 days to reductions in wing area by reducing body mass concurrently with an increase in pectoral-muscle size. This rapid flexibility in a non-migratory species probably reflects the paramount importance and long history of flight in birds.

Keywords: rapid reversible physiology; moult; body mass; pectoral muscle; flight performance; tree sparrow

1. INTRODUCTION

Rapid reversible environmental changes are responsible for the evolution of flexible physiology and rapid physiological responses (Piersma & Lindström 1997). As the majority of birds depend on flight, it is reasonable to assume that natural selection has favoured adaptations that maintain flight ability under varying environmental and physiological conditions. For example, in migrating knots (*Calidris canutus*) organs associated with foraging efficiency increase in size at stopover sites to improve refuelling, but organs improving flight performance are enlarged prior to their departure from stopover sites, thus facilitating long-distance flights of heavy birds (Piersma *et al.* 1999). Moreover, starlings (*Sturnus vulgaris*) have been shown to reduce body mass and pectoral muscle size after extended periods of exercise (Swaddle & Biewener 2000). This implies that the size of organs is adaptively regulated to meet specific demands, for example to improve efficiency during fuelling (Piersma *et al.* 1999) or to enhance flight performance (Piersma *et al.* 1999; Lindström *et al.* 2000; Swaddle & Biewener 2000). Moult, a central life-history stage in birds, is the periodical loss and renewal of flight feathers. This process should affect birds' flight ability, mainly because of the reduction in wing area (Hedenström & Sunada 1999). This in turn increases wing loading, body mass per wing area, which is a critical factor affecting flight ability (Pennycuick 1989). Experimental clipping of feathers to simulate moult gaps has been shown to affect starlings' (Swaddle & Witter 1997) and tree sparrows' (*Passer montanus*) flight ability (Lind 2001). However, when the same starlings were tested two weeks after manipulation, flight ability was back to pre-treatment levels (Swaddle & Witter 1997),

and naturally moulting tree sparrows do not suffer from reduced take-off ability (Lind 2001). Thus, these studies indicate that compensatory flight adaptations exist also during moult. In fact, starlings were found to compensate their experimentally increased wing loading to some extent by reducing their body mass. Yet, despite some preliminary experiments, whether birds can rapidly adjust their physiology to compensate for reduced flight efficiency remains unclear.

To investigate whether tree sparrows compensate for increased wing loading during moult, we studied natural moult and performed a manipulation experiment outside the moult period. We hypothesized that birds adapt to reductions in flight efficiency caused by moult. This generates two predictions: (1) increase of flight muscle and (2) reduction in body mass.

2. METHODS

The study was conducted during 2000, at Tovetorp Zoological Research Station in the southeast of Sweden (58°56′ N, 17°08′ E). The tree sparrow is a small sedentary passerine and member of the group of Old World sparrows (Passeridae) that breeds in most parts of Eurasia (Cramp & Perrins 1994).

(a) *Natural moult*

Nine first-year tree sparrows were caught at the start of moult at the end of August. The birds were kept in an outdoor aviary (7 m × 4 m × 2.7 m) throughout the moulting period, where they were fed hemp and sunflower seeds, oats, a mixture of seeds for pet finches and suet *ad libitum*. Water and a facility for dust-bathing were also supplied continuously and the aviary contained ample protective cover. Tree sparrows complete their primary moult in 70–80 days (Ginn & Melville 1983; J. Lind and S. Jakobsson, personal observations). During this time, all feathers are shed and replaced. At the start, middle and end of

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1915

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moult, the birds were caught in the aviary *ca.* 2 hours after sunrise and taken indoors for measurements of body mass, moult, pectoral muscle size and vertical take-off ability. Therefore, results are presented for primary moult scores 1–10 (start of moult, first two weeks), 21–30 (mid-moult, middle two weeks) and 41–45 (last two weeks of moult).

Body mass was measured using a Precisa 200A electronic balance (Precisa Balances Ltd, Milton Keynes, UK). When analysing body mass and pectoral muscle changes during moult, primary moult score (Ginn & Melville 1983) was used as an indication of time during moult. An old feather scored 0 points, growing feathers scored 1–4 points and a new, fully-developed feather scored 5 points. At primary moult score 0, no primaries are shed and at a score of 45 all primaries are replaced by new, fully-grown feathers. Start of moult is here defined as primary moult score 1–10 and end of moult 41–45, where raggedness is low (less than one missing flight feather per wing). Mid-moult falls in the range 21–30, where raggedness is high (approximately two missing flight feathers per wing). Raggedness, a measurement of gap size in moulting wings (see Lind (2001) for a more detailed explanation and illustration), was estimated by subtracting the score of each growing feather from the score of a fully-grown feather (scored from 0 (a missing feather) to 1 (a fully-grown feather) at steps of 0.1).

Pectoral muscle size was estimated by making impressions of the birds' pectoral region using alginate gel (TopDent, DAB Dental Gruppen, SDI Sweden) (Selman & Houston 1996). After the mould was fixed, it was cut dorsoventrally 10 mm below the impression of the tracheal pit's posterior end, and the cross-sectional area was stamped five times to a paper. A perpendicular line was drawn 5 mm from the apex of the sternum, and the cross-sectional area was digitized and measured using Scion Image software (Scion Corporation, Frederick, MD, USA). A mean was calculated using the five areas from each individual, and this individual mean value was used later in statistical analyses of pectoral muscle size.

Vertical take-off ability was measured using a 160 cm (diameter 40 cm) high semi-transparent tube placed in an outdoor aviary. A cube of mist-net was placed at the top of the tube through which the sky was visible. After the other measurements were taken birds were put, one by one, in a box below the tube. At the sound of a startle noise the top of the box was withdrawn, which stimulated an alarmed take-off. This was repeated three times for each bird; the fastest take-off of these three was used in the statistical analyses since maximum take-off ability was the relevant measurement in this study. Take-off speed was assessed using a digital video camera (Sony DCR-VX1000E: Sony Sweden Office, Spånga, Sweden), which we used to measure the time it took the bird to fly between 50 and 150 cm. All birds were released back into the wild after completion of moult. For dependent samples between the moult stages we used *t*-tests, with Bonferroni-corrected *p*-values (differences are significant at $p < 0.025$; e.g. Rice 1989).

(b) *Experiment*

Twenty-four wild tree sparrows were caught outside the moulting period (February) and individually colour banded. Six birds were placed randomly in each of four similar rooms (2 m × 4 m × 2.8 m). A window on each door enabled us to make observations from outside. The rooms contained two artificial Christmas trees, dead branches and twigs, resembling protective cover. Food and water were placed on a shelf (0.55 × 1.2 m), which extended from the wall. Food (hemp, oats, a mixture of

seeds for pet finches and suet) and water were supplied *ad libitum* and changed daily. Additionally, the birds had access to a bowl containing sand for dust-bathing. Fluorescent daylight tubes were used and the light followed the natural photo regime.

The experiment started with the manipulation of three randomly chosen birds in each room. In order to study the functional aspect of compensatory physiological flexibility to an increased wing loading instead of the physiological changes linked to moult we increased their wing load experimentally by creating moult patterns resembling a natural moult pattern during mid-moult. Since new feathers start to grow if old feathers are pulled out, we cut the feathers to avoid confounding factors due to physiological changes occurring during feather growth. Cut feathers (feathers counted from outside and in towards the body) were: primary 3 (cut close to the base); primary 4 (half was cut (i.e. a reduction of 1.5 primaries per wing)); secondary 1 (half was cut); secondary 2 (cut close to the base (i.e. a reduction 1.5 secondaries per wing)); in addition the second and third outermost pairs of rectrices were cut to one-third and two-thirds, respectively (i.e. a reduction of two rectrices in the tail). Thus, a total of 12 birds were manipulated, leaving the remaining 12 birds as controls, which received identical handling treatment but no feather cutting. After the experiment all cut feathers were pulled out and once feathers were fully-grown, the birds were released.

During the experiment body masses were registered using water bowls placed on electronic balances (Precisa 310c with external displays). When the birds sat on the water bowl, colour bands and body mass were registered simultaneously using video cameras from outside the room. The body masses used in the analyses were the mass on the first morning observed for each individual within 2 hours after the lights were turned on. Pectoral muscle size was registered on the first day (day 1) and on the last day of the experiment (day 7). When pectoral size was measured all birds in a room were caught and alginate impressions were made (see § 2a). All tests are dependent *t*-tests, and the statistical analysis was performed using STASTICA 5.5 (StatSoft Inc., Tulsa, OK, USA).

3. RESULTS

(a) *Natural moult*

Consistent with the prediction that the avian body responds to impaired flight ability caused by moult we found that, during moult, the ratio of pectoral muscle size to body mass tracked changes in raggedness (start of moult, 1.0 ± 0.17 s.e. missing feathers per wing; mid-moult, 1.8 ± 0.13 s.e. missing feathers per wing; mid-moult to end of moult, 0.7 ± 0.2 missing feathers per wing) and thus increased as wing area was reduced, to again decrease as wing area was increased close to completion of moult (start of moult, $2.3 \text{ mm}^2 \text{ g}^{-1} \pm 0.09$ s.e.; mid-moult, $2.8 \text{ mm}^2 \text{ g}^{-1} \pm 0.12$ s.e., $t_8 = -3.68$, $p = 0.006$, significant with Bonferroni correction; mid-moult to end of moult, $2.6 \text{ mm}^2 \text{ g}^{-1} \pm 0.16$ s.e., $t_8 = 3.90$, $p = 0.005$, significant with Bonferroni correction; see figure 1). Body mass, on the other hand, showed a non-significant tendency to increase at the end of moult (start of moult, $21.4 \text{ g} \pm 0.55$ s.e.; mid-moult, $21.9 \text{ g} \pm 0.23$ s.e., $t_8 = -1.1$, $p = 0.30$; mid-moult to end of moult, $22.4 \text{ g} \pm 0.43$ s.e., $t_8 = 2.3$, $p = 0.05$). No decrease in vertical take-off ability was found from the start of moult to mid-moult (start of moult, $0.41 \text{ s} \pm 0.008$ s.e.; mid-moult,
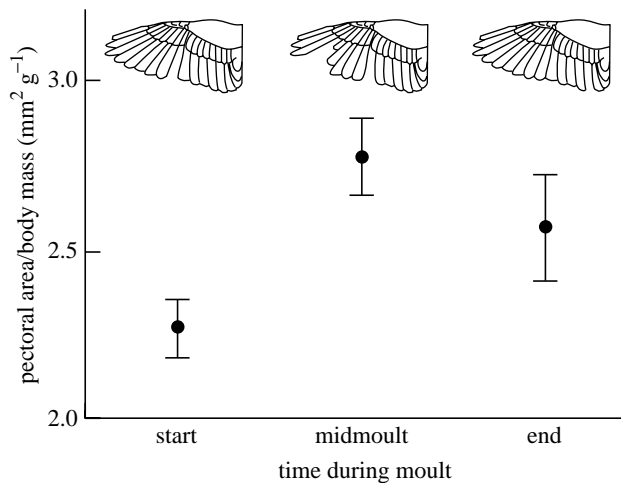
Figure 1. Change of ratio between pectoral muscle size and body mass during natural moult in tree sparrows (mean $\pm$ s.e.). The insets depict representative moult patterns for each investigated moult stage.

Figure 2. Pectoral muscle size change due to experimental reduction of wing area (mean $\pm$ s.e.).

Figure 3. Body mass change due to experimental reduction of wing area (mean $\pm$ s.e.).

0.43 s $\pm$ 0.01 s.e., $t_8 = 1.63$, $p = 0.14$). Nevertheless, take-off ability improved from mid-moult to the end of moult (mid-moult to end of moult, 0.35 s $\pm$ 0.01 s.e., $t_8 = 3.67$, $p = 0.006$, significant with Bonferroni correction).

(b) *Experiment*

After feather manipulation, the pectoral muscle size of the experimental birds increased (day 1, 81.2 mm^2 $\pm$ 2.5 s.e.; day 7, 88.4 mm^2 $\pm$ 2.1 s.e., $t_{11} = -2.51$, $p = 0.03$; see figure 2) and their body mass fell (day 1, 22.6 g $\pm$ 0.33 s.e.; day 7, 21.5 g $\pm$ 0.24 s.e., $t_{11} = 5.30$, $p < 0.001$; see figure 3), whereas the control group was unaffected (pectoral muscle size—day 1, 82.4 mm^2 $\pm$ 3.0 s.e.; day 7, 84.4 mm^2 $\pm$ 1.3 s.e., $t_{11} = -0.71$, $p = 0.49$; body mass—day 1, 22.9 g $\pm$ 0.44 s.e., day 7, 22.5 g $\pm$ 0.40 s.e., $t_{10} = 1.86$, $p = 0.09$). Unequal sample sizes are due to one bird's reluctance to perch on the electronic balance for long enough for a mass to be registered on day 7.

4. DISCUSSION

We believe that the results of our study provide the first empirical and experimental evidence that avian physiology undergoes rapid reversible changes to compensate for limited flight efficiency periodically caused by moult. It reveals that the ratio of pectoral muscle size to body mass is adjusted in concordance with changes in wing area. This ratio increases as wing area is reduced during mid-moult, to again decrease as moult is completed and the wings are fully-grown (figure 1). That tree sparrows adjust body composition in response to wing-load alterations was confirmed in the experiment, which revealed that the birds reduced their body mass concurrently with an increase in pectoral muscle size (figures 2 and 3). The increase in pectoral muscle size may well be an adaptive response to the reduction in wing and tail area, and therefore an underlying reason why tree sparrows have not been found to suffer from impaired escape ability when subjected to simulated predator attacks (Lind 2001).

Due to the rapid body mass adjustments, it is reasonable to believe that body mass reduction is a likely
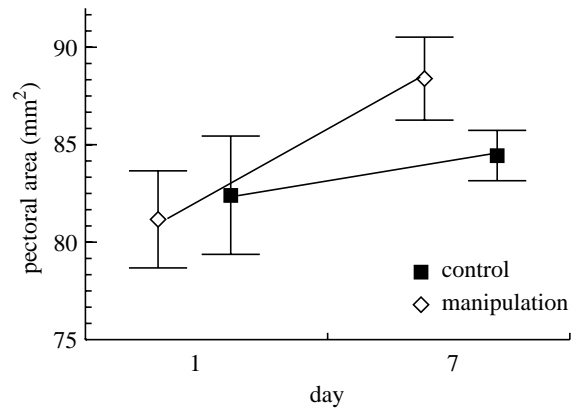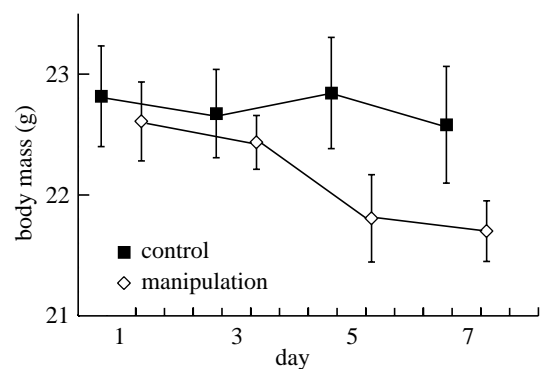
mechanism enabling birds to compensate for the increased wing loading during moult (when shedding flight feathers) as demonstrated in this experiment. However, no consistent pattern emerges since studies report both reductions (Dolnik & Gavrilov 1979; Holmgren *et al.* 1993; Gosler 1994; Meijer *et al.* 1994; Klaassen 1995; Chai 1997; Swaddle & Witter 1997) and increases (Ottosson & Haas 1991; Gosler 1994; Flinks & Kolb 1997; Franklin *et al.* 1999) in body mass during moult. Possible physiological constraints and confounding factors must, however, be acknowledged. As moult commences, birds face an increase in water content in the body (due, for example, to degradation, redistribution and resynthesis of proteins and an increased blood volume perfusing active feather pulps), which results in a slight increase in body mass during the period of moult (Dolnik & Gavrilov 1979); nevertheless, they remain at a low level of body mass compared with other life-history stages (Dolnik & Gavrilov 1979; Lindström *et al.* 1994). Furthermore, since moult (post-nuptial moult) sometimes overlaps with other important life-history stages that affect body mass regulation, namely breeding and migration, reported results are difficult to interpret. Hence, when studying physiological adaptations during moult, it is of utmost importance to separate the moult period from breeding activities and migratory fuelling (however, see Holmgren *et al.* 1993). Nevertheless, conclusions from this study may help elucidate

previously unexplained patterns of body mass regulation during moult. To illustrate, Gosler (1994) found that great tit females (*Parus major*) reduced their body mass during moult, to again increase in mass at completion of moult.

In concordance with an earlier study (Lind 2001), these birds were not impaired in vertical take-off ability from the start of moult to mid-moult, even if take-off ability did improve close to completion of moult. This indicates that the compensations of the body are not perfect and can therefore not keep take-off ability at its optimal level. Yet, an important conclusion is that slow moult most probably does not increase predation risk due to impaired predator evasion. However, moult is an energetically costly period (Murphy & King 1992; Lindström *et al.* 1993), and if moulting birds' foraging rates increase to comply with enlarged physiological demands, they may face an increased risk of predation due to increased exposure (cf. Witter & Cuthill 1993).

An important finding is the fact that pectoral muscle size and body mass changed in opposite directions in the experiment, which demonstrates that these traits are effectively discoupled. This result shows that flight-muscle size is not invariably positively coupled to change in body mass as it appears to be in birds during migration (Biebach 1998; Piersma *et al.* 1999; Lindström *et al.* 2000). Instead, flight-muscle size and body mass can be independently regulated in response to wing loading (see also Piersma 1988). It is interesting to note that both of these adjustments should aid in maintenance of flight performance, and may therefore be seen as an adaptive response to increased wing loading. Maintenance of flight performance is essential from several aspects of bird life history, not only during migration (Biebach 1998; Piersma *et al.* 1999; Lindström *et al.* 2000), but also for foraging (Bautista *et al.* 1998) and for escape from avian predators (Witter & Cuthill 1993).

Even though flight activity was not quantified, it does not seem likely that the effect results from differences in flight activity between the groups. Tree sparrows are social foragers and the most common reason for activity in the holding rooms was flights to the feeding tray and, as a rule, all birds were at the feeding tray simultaneously when birds were observed during weighing. Hence, as with red knots (Dietz *et al.* 1999), the experimental response in pectoral muscle and body mass further suggests that extensive power training is not a prerequisite for this observed change in body composition.

Because no hormonal or neurological manipulations took place, these results also suggest that birds have an ability to assess their own wing loading and can modify organs rapidly in response to workload (Piersma *et al.* 1999). To conclude, this study shows that rapid physiological adaptations that enhance flight are not exclusively found in extreme species in exceptional situations, but may even be found in non-migratory species such as the tree sparrow. This rapid physiological flexibility in a non-migratory species probably reflects the paramount importance and long history of flight in birds.

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