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Compensatory bodily changes during moult in Tree Sparrows *Passer montanus* in Italy

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To cope with fluctuating environments animals have evolved reversible phenotypic flexibility. Some birds demonstrate this phenomenon by changing mass and flight muscle according to changes in wing loading. During moult, birds suffer from reduced wing area because feathers are shed and replaced, resulting in a wing loading increase. Moult is rather well studied in birds, but the perspective of phenotypic flexibility has been neglected. Therefore, we tested predictions generated from experimental studies by collecting information about body mass, flight muscle size and fat stores from an Italian population of Tree Sparrows (*Passer montanus*) to investigate if they compensate physiologically for the wing area reductions they suffer from during moult. Our results did not corroborate predictions based on experimental studies; that is, the Tree Sparrows did not reduce body mass and increase in flight muscle size as a response to wing area reductions during midmoult. Instead, body mass increased throughout moult, flight muscle size did not change, and fat stores decreased as moult progressed. To further investigate compensatory changes, we analysed bodily differences in midmoult between birds differing in moult gap size. Again, contrary to predictions from experimental studies, birds having larger moult gaps were found to have higher body mass. These birds were also found to keep the ratio between flight muscle size and body mass constant over the day whereas birds with small moult gaps reduced this ratio over the day. Birds with large moult gaps were also found to store less fat than birds with small gaps. Physiological constraints may help to explain these results and underlying reasons for the observed variation in bodily regulation in birds are discussed.

1. Introduction

To cope with fluctuating environments animals have evolved reversible phenotypic flexibility patterns (Piersma & Lindström 1997), and birds have been found to change the size of organs rapidly during different stages of their life cycle. In birds, changes in body mass and flight muscle can be induced by changes in wing loading (Piersma *et al.* 1999, Lindström *et al.* 2000, Lind & Jakobsson

2001). Phenotypic flexibility has mainly been studied during migration. For example, birds enlarge organs related to foraging during migratory stopovers as they are accumulating large fuel loads, whereas flight related organs increase in size at the end of the stopover prior to long migratory flights, supposedly to increase flight efficiency (Piersma *et al.* 1999). The underlying reason behind these physiological adaptations is most likely related to flight.

Another critical period in a bird's life, the moulting period, affects birds by reducing wing area and increasing wing loading, which in turn influences a bird's flight performance (Pennycuick 1969, Hedenström 1992). As flight feathers are shed, the moult gaps should affect bird flight negatively due to the resulting wing load increase (Hedenström & Sunada 1999). Experiments have shown that moulting birds suffer from impaired flight ability (Chai 1997, Swaddle & Witter 1997), and it has been suggested that moulting birds should face an increased predation risk due to impaired escape ability (Slagsvold & Dale 1996, Swaddle & Witter 1997). Surprisingly, escape flight in moulting Tree Sparrows (*Passer montanus*) was not impaired when subjected to simulated predator attacks, even though the tree sparrows were missing up to two whole flight feathers per wing (Lind 2001). Surprisingly weak effects of simulated moult were also found in captive pigeons during an experiment of short flights (Bridge 2003). This suggests that birds may be able to compensate, at least partially, for the negative impact moult has on escape flights. Yet, moulting birds may still face an increased predation risk due to increased exposure to predators since they have increased metabolic demands and may be forced to spend more time foraging (Lind 2001).

Even though moult has been studied for long in birds, the perspective of phenotypic flexibility has been neglected. Yet, adaptive physiological changes have recently been found to occur during moult (Lind & Jakobsson 2001). During natural moult, Tree Sparrows increase the ratio between flight muscle size and body mass as wing area is reduced during moult, to again increase the ratio as wing area is restored at the end of moult. Outside the moulting period, tree sparrows were found to respond rapidly to experimental increases in wing loading by concurrently reducing body mass and increasing flight muscle size (Lind & Jakobsson 2001). Similar responses in body mass have been found in Dunlins (*Calidris alpina*), Ruby-throated Hummingbirds (*Archilochus colubris*) and European Starlings (*Sturnus vulgaris*) (Holmgren *et al.* 1993, Chai 1997, Swaddle & Witter 1997). However, since moult is an energetically costly period and is coupled with a high water content in the body (Dolnik & Gavrilov 1979, Murphy & King 1992, Lindström *et al.* 1993) the potential for adaptive phenotypic flexibility may be constrained. Thus, behavioural adaptations during moult may instead be important, as demonstrated by a study on Bullfinches (*Pyrrhula pyrrhula*) which reduce activity levels during moult (Newton 1966).

To compensate for the reduced wing area caused by moult, birds may build more flight muscle and/or reduce body mass thereby increasing the ratio between flight muscle size and body mass (Lind & Jakobsson 2001). Another potential compensation of impaired flight ability is to reduce the amount of fat carried. In this study, we analyze field data from moulting Tree Sparrows to test whether body mass, pectoral muscle size and fat stores vary in response to moulting stages.

2. Methods

Tree Sparrows were trapped with mist-nets from the 27th of July to the 1st of November 2001 in reed beds of Montepulciano Lake Reserve (43° 04' N, 11° 58' E) in Italy. When trapped, body mass was measured on a Pesola spring balance to the nearest 0.1 g. Fat reserves were scored visually according to an 8 point-scale (Kaiser 1993), and pectoral muscle size was estimated visually according to a scale with 4 steps from 0 to 3 (Bairlein 1995).

Both adult and juvenile tree sparrows undergo a complete moult during autumn. Moult was scored separately for each primary and secondary feather according to a scale from 0 to 5 with 6 steps (Ginn & Melville 1983). Old feathers score 0, growing feathers score 1–4 and new fully grown feathers give a moult score of 5. Moult score 1 indicates either a missing feather or a new feather completely in pin. Moult score 2 represents a new feather emerging from sheath up to one third grown. Moult score 3 represents a new feather between 1/3 and 2/3 grown. Moult score 4 represents a feather more than 2/3 grown with sheath at the base. Thus, a bird not yet in moult has a moult score of 0 and a bird that has completed moult has a moult score of 75 (9 primaries and 6 secondaries times 5 points = 75).

Raggedness, the number of missing flight feathers in the wings, which gives a good estimate of the resulting wing area reduction (Lind 2001), was estimated from the moult score of each flight feather. Old feathers (moult score 0) and fully new grown feathers (moult score 5) have a raggedness of 0. A feather with a moult score of 1 has a raggedness of 1 (the new feather is too small to make any contribution to the wing area), moult score 2 = 0.835 ((1 + 0.67) / 2), moult score 3 = 0.5, moult score 4 = 0.165 ((0 + 0.33) / 2).

To study physiological adaptations to increased wing loading during moult we started to analyse when during moult the wing area reductions are most severe. This was done by comparing raggedness of birds during the moult period (start of moult with primary moult score 1–10, midmoult 21–30 and end of moult 41–45). The underlying assumption is that birds in midmoult suffer most from wing area reduction, that is, they have higher raggedness. Then we analysed bodily changes during moult by classifying birds in the same three different moult stages (start, midmoult and end of moult) using primary moult score as a measurement of time and level of wing area reduction (Lind & Jakobsson 2001). We used two categories of time of day (morning: trapped before 9.00, evening: trapped after 18.00). Because there may be physiological differences between young and old birds we analysed them separately, where this was possible, to avoid potential bias due age differences. We also performed analyses during midmoult (from moult score 15–60) comparing birds with high or low raggedness in an attempt to investigate the same question but with an alternative approach (low raggedness = 0.1–1 missing flight feather per wing, high raggedness = 3–4 missing flight feathers per wing). This method also meant that birds with intermediate raggedness were excluded from this analysis.

Moult duration was estimated using recaptures of individuals during moult. To estimate moult duration the difference in moult score between trapping days was divided by the number of days between these capture dates and it is assumed that moult score increases linearly. We used this measurement of moult rate in primary moult score per day, to estimate how long it took to replace all primaries. For comparison, moult duration was also estimated using the same method from captive Swedish Tree Sparrows, which spent the moulting period in outdoor aviaries (same birds as in Lind & Jakobsson 2001) housed at Tovetorp Research Station, south-east Sweden, in the autumn of 2000.

All values given are presented as mean ± SE (if not otherwise stated) and all analyses were performed using SPSS 11.0, ©SPSS Inc.

3. Results

Birds with primary moult score of 1–10 (start of moult) and 41–45 (end of moult) had lower raggedness than birds with a primary moult score of 21–30 (midmoult). Mean raggedness at the start and end of moult was 1.1 missing flight feathers per wing (start, 1.1 ± 0.04, n = 326; end, 1.1 ± 0.09, n = 63) which differed significantly from raggedness during midmoult as revealed by Tukey HSD post-hoc test (2.0 ± 0.05, n = 175, ANOVA with moult stage (start, midmoult and end) as independent factors, $F_{2,561} = 47.5$, $P < 0.001$). This validates the assumption that birds in midmoult suffer most from wing area reduction, that is, they have higher raggedness.

Moult duration may be important for a bird's compensatory aptness during moult. The average moult duration in the population under study was 63.4 days (n = 54 recaptures, 0.71 ± 0.29 SD primary moult score per day). In comparison, the tree sparrows that moulted in aviaries at Tovetorp Research Station, during autumn 2000, moulted their primaries in 76.1 days (0.59 ± 0.17 SD primary moult score per day, n = 16). The difference of 12.7 days in the time required for moult between wild and caged birds was not statistically significant ($t_{68} = 1.54$, $P = 0.13$).

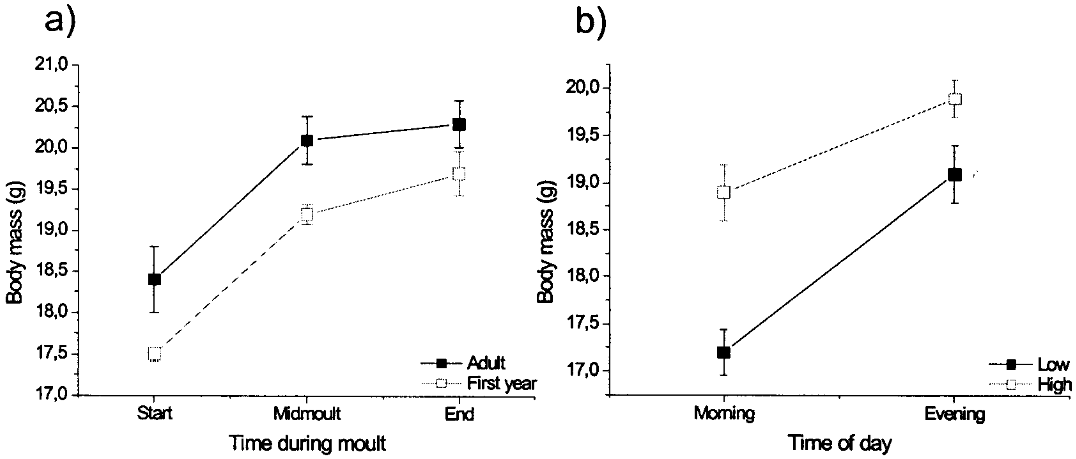

Figure 1. Body mass (mean ± S.E.) during a) three different moult stages for first year birds (open squares) and second calendar year and older birds (filled squares), and b) during midmoult for birds with high (open squares) and low raggedness (filled squares).

3.1. Changes during moult, comparison of birds in different moult stages

In contrast to the prediction that the tree sparrows compensate for the high raggedness in midmoult, body mass increased significantly with increasing primary moult score (ANOVA with moult stage and time of day as independent factors for first year birds: $F_{2,452}$ = 65.1, P < 0.001, start of moult, 17.5 g ± 0.08, n = 289; midmoult, 19.2 g ± 0.12, n = 147; end of moult, 19.7 g ± 0.27, n = 32, adult birds: $F_{2,49}$ = 8.7, P = 0.001, start of moult, 18.4 g ± 0.4, n = 24; midmoult, 20.1 g ± 0.29, n = 12; end of moult, 20.3 g ± 0.28, n = 24, Fig. 1a). Body masses were significantly different between all three stages of moult in first year birds (Tukey HSD post-hoc test, P < 0.01) and in adult birds body mass was lower at start of moult (Tukey HSD post-hoc test, P < 0.05) but there was no significant different between midmoult and end of moult (Tukey HSD post-hoc test, P > 0.05). During this period the overall diurnal body mass increase was 1.2 g for first year birds ($F_{1,452}$ = 80.5, P < 0.001) and 1.9 g for older birds ($F_{1,49}$ = 7.1, P < 0.01). During moult, flight muscle size per body mass was lower during midmoult than at the start of moult in first-year birds ($F_{2,452}$ = 4.1, P = 0.02, start of moult, 0.115 ± 0.002, n = 288; midmoult, 0.105 ± 0.002, n = 140; end of moult, 0.112 ± 0.004, n = 30, Tukey's HSD Post-hoc test between start and midmoult, P = 0.01) whereas no changes were detected in adult birds ($F_{2,49}$ = 0.4, P = 0.96, start of moult, 0.107 ± 0.005, n = 24; midmoult, 0.104 ± 0.008, n = 11; end of moult, 0.107 ± 0.004, n = 20). This ratio did not change with time of day (first year birds: $F_{1'452}$ = 2.1, P = 0.14; adult birds: $F_{1'49}$ = 2.0, P = 0.16).

Because fat score was highly skewed towards zero in the morning, we performed Kruskal-Wallis ANOVAs for morning and evening fat scores separately. Because there were no differences in fat score between first year and adult birds we pooled the data with respect to age (start of moult: Z = 0.9, $n_{\text{first year}}$ = 290, n_{adult} = 25; midmoult: Z = 1.1, $n_{\text{first year}}$ = 150, n_{adult} = 12; end of moult: Z = 1.2, $n_{\text{first year}}$ = 33, n_{adult} = 24). In the morning no differences in fat score were found in the 3 different moult stages (H = 5.0, df = 2, P = 0.08, start, n = 213; midmoult, n = 66; end of moult, n = 30) but evening fat scores were reduced from start to end of moult (H = 17.4, df = 2, P < 0.001, start, n = 112; midmoult, n = 101; end of moult, n = 27, Fig. 2a).

3.2. Changes between birds in midmoult, comparison of birds with different raggedness

For a detailed analysis of potential compensatory changes during moult we used only birds in midmoult, the period when raggedness is generally high and categorised birds according to their

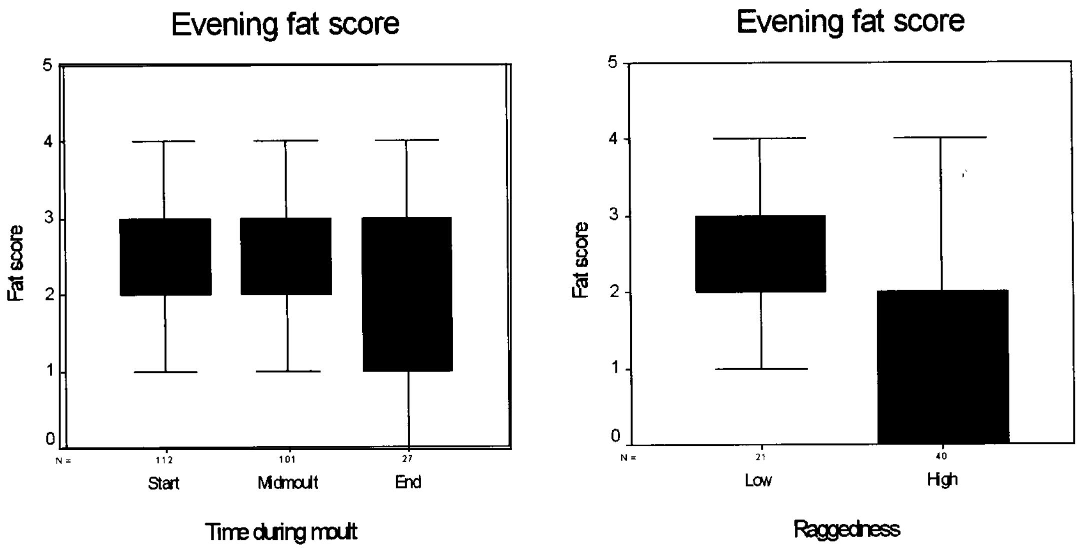

Figure 2. Tree sparrows fat reserves during moult. a) Change in fat score during three stages of moult (median and quartiles). b) evening fat score (median and quartiles) of birds with different levels of wing area reductions (low raggedness=0.1–1 missing flight feather per wing, high raggedness = 3–4 missing flight feathers per wing).

raggedness. Because of the criteria used for this analysis, very few adult birds are incorporated, and consequently there was no possibility to split this analysis in two age classes. Birds varied between 0.165–4 missing flight feathers per wing (mean 2.2 ± 0.8 SD). Birds in high raggedness had a generally higher body mass (ANOVA with time of day, morning and evening, and raggedness, high or low, as independent factors, $F_{1,106} = 22.2$, $P < 0.001$) and during midmoult the overall diurnal increase was 1.4 g ($F_{1,106} = 29.3$, $P < 0.001$). There was a tendency for birds in high raggedness to increase less in body mass over the day (body mass increase, high raggedness = 1.0 g; low raggedness = 1.9 g, Fig. 1b) however, the interaction between raggedness and time of day was not significant ($F_{1,106} = 2.6$, $P = 0.11$). The ratio between flight muscle size and body mass was constant over the day for birds with high raggedness, whereas this ratio was reduced in birds with low raggedness because of decreased mass (interaction between raggedness and time of day, $F_{1,106} = 8.4$, $P = 0.005$, Fig. 3, overall diurnal reduction of flight muscle size/body, $F_{1,106} = 7.2$, $p = 0.08$). Raggedness had no overall effect on this ratio ($F_{1,106} = 0.13$, $P = 0.72$). Birds trapped in the morning did not have different fat scores depending on raggedness (Kruskal Wallis $H = 1.1$, $df = 1$, $P = 0.29$, low raggedness, $n = 32$, high raggedness, $n = 21$). However, birds with different raggedness caught in the evening differed in the amount of fat deposited and birds in high raggedness accumulated less fat than birds in low raggedness ($H = 6.4$, $df = 1$, $P = 0.01$, low raggedness, $n = 21$, high raggedness, $n = 40$, Fig. 2b).

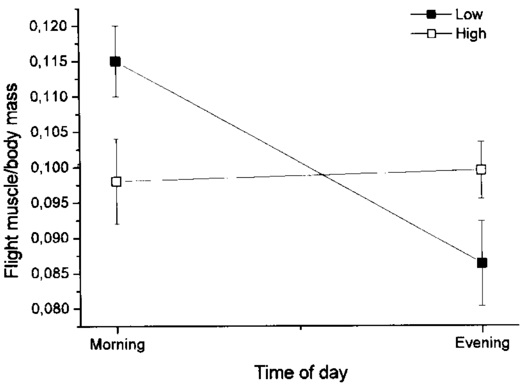

Figure 3. Morning and evening body mass (mean ± SE) of birds with different levels of wing area reduction (low raggedness = 0.1–1 missing flight feather per wing, high raggedness = 3–4 missing flight feathers per wing).

4. Discussion

Patterns of reduced body mass in association with moult observed in experimental studies were not confirmed in this field study. Body mass increased as the season progressed and birds in high raggedness during midmoult were heavier than birds with small gaps in the wings. Although experimental studies (Chai 1997, Swaddle & Witter 1997, Lind & Jakobsson 2001) have shown that birds can respond to wing area reductions by reducing body mass, this does not seem to be a general phenomenon for moulting birds in nature. In order to understand why earlier experimental results could not be corroborated by this field study we compiled information about bodily changes during moult in birds (Table 1). A general pattern emerging is that the predicted body mass reductions are more often found in experimental studies than in field studies. An interesting species is the Stonechat (*Saxicola torquata*) where in naturally moulting individuals of the European subspecies (*S. t. rubicola*) body mass increased during moult (Flinks & Kolb 1997) whereas in an experimental study with individuals of both the European and the African subspecies (*S. t. axillaris*) body mass decreased during moult (Klaassen 1995).

Interestingly, outdoor feeding experiments on moulting birds have shown that birds often seem constrained in their food intake. Both juvenile Whitethroats (*Sylvia communis*) and Bluethroats (*Luscinia svecica*) in moult have drastically increased in body mass when supplied with extra food in the field (Lindström *et al.* 1990, Fransson 1998). Hence, ecological constraints may restrict a birds' physiological response in the wild, which could help explain the discrepancy between field and experimental studies (Table 1). These constraints may include a high water content in the body and an increased blood volume supposedly supplying the pulps of new growing feathers (Myrcha & Pinowski 1970, Dolnik & Gavrilov 1979). Maybe the digestive organs are enlarged to improve the assimilation of nutrients for feather growth. This interpretation is supported by the result that the body mass increase was not related to an increase in fat or flight muscle size.

The birds in the Italian population did not show any pattern which suggest that they increase the ratio between flight muscle size and body mass to compensate for high raggedness in midmoult as Swedish Tree Sparrows have been found to do (Lind & Jakobsson 2001). One reason for this difference is the general increase in body mass observed in the Italian Tree Sparrows since flight muscle size *per se* did not change during moult. One thing that should be mentioned though is that the measurements of flight muscle size differ between the present study and Lind and Jakobsson's study (2001). Because we only had the opportunity to visually assess flight muscle size we may have been unable to detect more fine-tuned patterns of phenotypic flexibility. However, due to the large sample size we still should have fairly strong power in our analyses to detect large changes in muscle size, but we can not be certain that smaller changes did not occur within individuals.

The Tree Sparrows reduced fat stores during moult (Fig. 2) despite the overall increase in body mass, in contrast to the pattern found in migratory species in which pre-migratory fat deposition usually starts at the end of moult (Lindström *et al.* 1994, Jenni-Eiermann & Jenni 1996). Also, birds with large moult gaps stored less fat during midmoult than birds with small moult gaps (Fig. 2).

We suggest three non-mutually-exclusive explanations for this pattern: (1) large fat loads may be avoided to keep energy costs low (Holmgren *et al.* 1993); (2) energy constraints during the later stages of the moult (i.e. later in the season) may restrain the accumulation of fat; (3) birds in late moult and with high raggedness may actively avoid storing large fat deposits to reduce predation risk for example by minimising wing loading (Holmgren *et al.* 1993, Chai 1997, Swaddle & Witter 1997, Lind & Jakobsson 2001). The second reason would contradict the predictions underlying this study since it is assumed that birds should be most constrained during the most intense part of the moult, that is midmoult and not the end of moult. However, as season progresses factors such as increasingly harsher environmental conditions may play a progressively larger role. The third explanation is interesting when considering that the difference between the median fat score of high and low raggedness birds corresponds to an 0.8 g body mass reduction resulting in a 4% lower evening body mass. Regression of body mass for birds trapped in the morning during midmoult with fat

Table 1. Bodily changes during moult in different studies. Table is sorted after whether the study refers to a natural observation or an experiment. Note also that all changes are not statistically verified.

Species	Body mass	Fat	Study	Source
Dunlin	Decrease	–	Natural observation	(Holmgren *et al.* 1993)
Stonechat	Increase (s)	–	Natural observation	(Flinks & Kolb 1997)
Great tit (males) *Parus major*	Increase (s)	–	Natural observation	(Gosler 1994)
Great tit (females)	Decrease	–	Natural observation	(Gosler 1994)
Tree sparrow	Increase	Decrease	Natural observation	This study
Tree sparrow	Increase*	No change*	Natural observation	(Myrcha & Pinowski 1970)
Bullfinch	Increase (s)	–	Natural observation	(Newton 1966)
Brambling *Fringilla montifringilla*	Increase	–	Natural observation	(Ottosson & Haas 1991)
Kestrel	Decrease*	–	Caged	(Dietz *et al.* 1992)
Ruby-throated hummingbird	Decrease	–	Caged	(Chai 1997)
Ruby-throated hummingbird	Decrease	–	Caged	(Chai *et al.* 1999)
Bluethroat	Increase	Increase (s)	Caged	(Lindström *et al.* 1994)
Starling	Decrease*	Decrease	Caged	(Meijer *et al.* 1994)
Starling	Decrease	–	Caged	(Swaddle & Witter 1997)
Starling	Decrease	–	Experimental	(Swaddle & Witter 1997)
Starling	Decrease*	–	Experimental	(Williams & Swaddle 2003)
Tree sparrow	No change**	–	Caged	(Lind & Jakobsson 2001)
Tree sparrow	Decrease	–	Experimental	(Lind & Jakobsson 2001)
White-crowned sparrow	Increase	–	Caged	(Chilgren 1977)
White-crowned sparrow	Decrease*	–	Caged	(Murphy & King 1984)

A seasonal increase from post-breeding to onset of migration/over-wintering is indicated by (s). In the 'study' column, 'natural observation' refers to when birds are trapped in the field and measurements are taken immediately, 'caged' refers to when birds are moulting naturally but in the lab or in an outdoor aviary. 'Experimental' refers to experimental wing area reduction where feathers are cut and not plucked (mostly outside the moulting period), and one asterisk (*) denotes that the effect is not statistically verified and two denote (**) a non-significant trend of an increase throughout the moulting period.

score as independent factor ($P < 0.001, n = 177, r = 0.57$):

eq. 1. $y = 0.79x + 17.7$

However, the magnitude of the resulting body mass reduction does probably not aid in escape flight performance (Kullberg 1998, Lind 2001, but see Krams 2002), but it could instead result in reduced time spent exposed to predators while foraging. This fits with earlier descriptions on moulting birds' behaviour. Bullfinches (Newton 1966), White-crowned Sparrows (*Zonotrichia leucophrys*), Dark-eyed Juncos (*Junco hyemalis*), and European Robins (*Erithacus rubecula*) (Eyster 1954) have all been described to show reduced activity levels during moult and this is likely an important adaptation reducing both energy costs and exposure to predators (see also Haukioja 1971). An interesting behavioural observation is that the Tree Sparrows under study only gather in the reed beds during the moulting period. Since reed beds are not used for insulation during winter this behaviour suggests that they seek protection from predators during moult.

To further understand the variation in how birds regulate their bodies during moult, a trade-off between a slow, safe and relatively cheap (cost per unit time) moult with possibilities of physiological compensation and a fast and potentially dangerous and costly moult with high raggedness may be important (Lind 2001). Interestingly, the Swedish Tree Sparrows appear to moult for almost two weeks longer than the Italian population and the higher moult rate of the Italian Tree Sparrows will result in more feathers growing simultaneously and larger gaps in the wing area. Maximum raggedness was in fact higher than that reported from Swedish Tree Sparrows (Lind 2001, Lind & Jakobsson 2001). Eighty-one out of 444

(18%) Italian birds in midmoult had more than 2.7 missing flight feather per wing (max = 4.25) whereas for Swedish wild Tree Sparrows in midmoult, 2.7 missing flight feathers per wing (of 20 birds) was the maximum gap size found (Lind 2001). And variation in moult speed should affect the extent of physiological constraints birds face during moult. A higher moult speed results in a higher number of simultaneously growing feathers, consequently, body mass is high, for example due to increased blood volume in active feather pulps and a generally higher water content in the body (Myrcha & Pinowski 1970, Dolnik & Gavrilov 1979). And, at least theoretically, many growing feathers lead to greater daily energetic and nutrient requirements (Murphy & King 1992). Therefore, faster moulting birds may be more constrained during moult and, subsequently, physiological flight adaptations may be difficult to detect even if present. Therefore, maybe it is only possible to observe adaptive physiological changes during moult in species and populations with slow moult, for example Swedish Tree Sparrows, (Lind & Jakobsson 2001) and for which flight is imperative as for example in Kestrels (*Falco tinnunculus*) (Dietz *et al.* 1992) and Hummingbirds (Chai 1997), even though experimental tests show that birds have the capability for these physiological changes.

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Kroppsliga förändringar under ruggning hos pilfinkar *Passer montanus*

Djur har utvecklat en förmåga att reversibelt förändra olika organs storlek för att klara av den föränderliga miljön de lever i. Vissa fåglar förändrar sin kroppsvikt och flygmuskulatur beroende på förändringar i vingbelastning. Under ruggning minskar vingarean eftersom fjädrar fälls och byts ut, vilket leder till en ökad vingbelastning. Hur fåglar kan kompensera fysiologiskt för detta under ruggningen är verkligen inte välstuderat.

Därför ville vi testa förutsägelser från experimentella studier genom att samla information om kroppsvikt, flygmuskelstorlek och fettreserver i en italiensk population pilfinkar (*Passer montanus*) och undersöka om de kompenserar fysiologiskt för vingareaförändringar under ruggningen. Våra resultat stämmer inte överens med de experimentella studierna, eftersom vi inte kunde finna mönster som tyder på fysiologisk kompensation. Pilfinkarna minskade inte i kroppsvikt och ökade inte heller storleken på flygmuskulaturen under den period då de har som minst vingarea. Kroppsvikten ökade under hela ruggningen och flygmuskulaturen låg på en jämn nivå.

För att öka möjligheten att finna en eventuell kompensation analyserade vi också kroppsförändringar under mitten av ruggningperioden och jämförde fåglar som hade olika stora ruggningsluckor. Samma mönster påvisades även i dessa analyser. Vi tror att vi inte hittar mönster som tyder på fysiologisk kompensation under ruggningen på grund av fysiologiska begränsningar och därför diskuterar vi bakomliggande faktorer, som möjligtvis kan förklara den variation man finner i studier av detta slag.

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