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MOLT AND MIGRATORY CONDITION IN BLUE TITS: A SEROLOGICAL STUDY[1]

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Abstract. Migration and molt are both energy demanding activities and can be expected to conflict with each other in migratory birds. We studied autumn migrating juvenile Blue Tits (*Parus caeruleus*) and investigated whether molting birds showed signs of diseases or physiological stress to a larger degree than non-molting individuals. There was no evidence that molting birds were more stressed than non-molting individuals, as hematocrit, red blood cell sedimentation rate and the size of subcutaneous fat stores were similar for birds in both groups. However, birds with high levels of subcutaneous fat had low sedimentation rate levels and high hematocrit values, indicating that the level of fat of an individual is associated with its state of health. Birds with large fat stores were more brightly colored than birds with smaller fat stores, suggesting a link between nutritional conditions experienced during molt and the size of fat stores during the subsequent migration. Taken together, our data indicate that fat deposit size in migrating birds might be affected by their current health status, as well as conditions experienced during molt.

Key words: molt; migration; fat stores; blood serology; hematocrit; red blood cell sedimentation rate; Parus caeruleus.

INTRODUCTION

Molt, fat deposition and migration are time- and energy-consuming stages in the life of most migratory birds (Jenni and Winkler 1994). Consequently, these activities are commonly separated in time and generally do not overlap (Payne 1972). That molt is a time-consuming activity is indicated by the fact that late-hatched young in several bird species finish their molt at a later date than early-hatched ones (Bensch and Lindström 1992, Jenni and Winkler 1994). The molting process also is energetically costly due to the production of new feathers (Lindström et al. 1993) and the reduced temperature insulation during renewal of the body feathers (Ginn and Melville 1983). Fat deposition in the face of the coming energetically demanding migration also is a time-consuming activity, and the optimal fat load will be influenced among other factors by predation risk during foraging (Lindström 1990) and the need to migrate as fast as possible in order to quickly reach stopover sites or overwintering grounds (Alerstam and Lindström 1990).

However, many individuals often show a considerable overlap between molt and fat deposition and even between molt and migration. These birds could be late-hatched young which choose to migrate before molt completion despite the disadvantages this might confer in terms of lower insulatory capacity or lowered social status during competition for food or territories (Dhondt 1973, Jenni and Winkler 1994). Whatever the causes of the overlap, it is likely to be costly since some energy has to be spent on thermoregulation or antagonistic activities during intra- or interspecific competition. This energy could otherwise have been allocated towards other body functions such as immunodefense (Baron 1988, Apanius et al. 1994, Gustafsson et al. 1994) or as a fuel during migratory flight (Alerstam and Lindström 1990). One consequence of this could be that birds migrating before molt is completed are more susceptible to diseases or parasitic infections. A possible scenario is that birds compromise between different competing demands. For instance, a bird with low physiological health status or in a low nutritional state could be ex-

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pected to molt into a less brightly colored plumage than healthier individuals (Piersma and Jukema 1993, Hill and Montgomerie 1994).

In this study our aim was to investigate the causes and consequences of individual variation in migratory condition and molt-migration overlap in Blue Tits, *Parus caeruleus*. In particular, we were interested to see whether an individual's stage of molt during migration was related to its current state of nutrition and health. To investigate individual variation in current state of nutrition we measured hematocrit levels, whereas red blood cell sedimentation rate was used as a measure of health state. Hematocrit levels and blood sedimentation rates are serological screening tests widely used in human medicine, but recently have been used by avian ecologists to measure individual state of health and nutrition (Gustafsson et al. 1994). We also investigated whether individual variation in plumage coloration is associated with other aspects of migratory condition (Hill and Montgomerie 1994). Finally, we examined relationships between plumage coloration, blood parameters, fat stores, and molt stage, i. e. whether brightly colored birds have low blood sedimentation rates and high hematocrit levels as compared to less brightly colored birds.

METHODS

STUDY SPECIES

The Blue Tit is a small (about 11 g) passerine which breeds mainly in deciduous forests in Europe (Cramp and Perrins 1993). After fledging, first-year Blue Tits undergo a post-juvenile molt in which they replace their body feathers and wing coverts, but not their flight feathers and only a few or no tail feathers (Cramp and Perrins 1993). Most adults remain on their breeding grounds during winter, whereas many juveniles in northern populations are short-distance daytime migrants (Ulfstrand 1962, Smith and Nilsson 1987). In Sweden the peak migration period is from the second half of September until the first half of October (Ulfstrand 1962).

STUDY AREA AND GENERAL METHODS

We caught migrating Blue Tits between 2 and 12 October 1994 at Hoburgen on the southernmost part of the island of Gotland in the Baltic Sea (56°55′N, 18°08′E). Birds were captured with mist nets as part of a long term standardized ringing program (see Averland and Elfström 1993). Each captured Blue Tit was ringed, sexed and aged according to the criteria given in Svensson (1992). Tarsus length was measured to the nearest 0.1 mm with digital calipers in order to obtain a measure of structural body size and wing length was measured with a ruler to the nearest 1 mm. All birds were scored for the size of their subcutaneous fat stores, using a standardized scale ranging from 0 (no subcutaneous fat) to 6 (maximum amount of subcutaneous fat; see Pettersson and Hasselquist 1985 for a detailed description of this scale). All juvenile Blue Tits also were classified to stage of their post-juvenile molt using the criteria described by Bensch and Lindström (1992). This molt scale runs from 0 (a recently fledged young bird in downy plumage) to 6 (post-juvenile molt completed). Finally, all birds also were scored for plumage color on their yellow underparts using a scale ranging from 1 (low amount of yellow in plumage) to 6 (high amount of yellow in plumage). These classifications were performed by comparing the color of the bird with the color scores from a scale adopted from Kueppers (1982). We only used six scale steps because we found it difficult to separate birds in the higher color classes into further subgroups. All color classifications were done in a separate room under a constant light regime. To check the reliability of our color estimations, 22 birds were classified independently by both of us. The correlation between our scorings was high (Pearson $r = 0.85$, $P < 0.001$), as was the inter-observer repeatability (Repeatability = 77.9%; ANOVA: $F_{1,21} = 8.07$, $P < 0.001$). Hence, we feel confident of the robustness of our plumage classifications.

SEROLOGICAL MEASUREMENTS

To obtain data on blood sedimentation rate and hematocrit, we took blood samples (about 15 μl) from the ulnar vein into 20 μl heparinized capillary tubes. The tubes were immediately sealed with wax at the bottom, and left to stand vertically at 10°C until processed. The subsequent measurements were made by one of us with digital calipers to the nearest 0.05 mm under a magnification glass fitted light source.

Blood sedimentation rate is commonly used in human and veterinary medicine as a diagnostic method for detecting elevated levels of immunoglobulins and fibrinogen (Hokland and Madsen 1989). High SDR is indicative of acute infections and inflammatory diseases (Sharma et al. 1984, Hokland and Madsen 1986). Blood sed-

imentation rate was calculated as the height of the plasma volume (in mm) 5 hours after sampling. To correct for differences in sample volume, the plasma height was divided by the total sample volume (plasma + erythrocytes).

Hematocrit measures the relative amount of red blood cells in the total blood volume (i.e. red blood cell volume/(red blood cell volume + plasma volume)). Hematocrit can be indicative of acute or chronic diseases (e.g., anemia), but also of nutritional deficiencies of certain minerals or proteins which can cause lowered hematocrit (Laurell et al. 1980, Wolkers et al. 1993). Furthermore, both blood and gastrointestinal parasitism as well as bacterial infections could cause lowered hematocrit levels (Harrison and Harrison 1986). Hematocrit was measured after 20 min centrifugation with a microhematocrit centrifuge.

STATISTICAL ANALYSIS

Whenever possible, data were analyzed by using parametric statistics, but when their assumptions were violated (Sokal and Rohlf 1981), non-parametric statistics were employed. Since non-parametric statistics do not generally allow for simultaneous testing of several independent variables, we also used randomization procedures performed with Resampling Stats (Bruce 1991). The rationale behind this method is that the original dependent variable array is randomly shuffled to produce a large sample of new arrays (in our case 1,000). For each permutation, the test statistics are calculated in normal fashion and the number of permutations resulting in test statistics (e.g., regression slope) having higher values than the original test statistics gives the probability of getting this high result by chance alone (Edgington 1981). When using parametric methods, SDR-values were log(ln)-transformed before analysis to achieve normality. Unless otherwise stated, all probability values reported in this paper are from two-tailed tests. Statistical analyses apart from permutation tests were performed with Statview™ SE + Graphics (Abacus Concepts Inc. 1988) and SYSTAT (1992) statistical packages.

RESULTS

MOLT AND FAT STORES

Of the 116 examined individuals, 87 (75%) were still molting when captured at Hoburgen. Sexes were molting in equal frequencies ($\chi^2 = 0.014$, $df = 1$, $P = 0.97$), but females tended to be further in the progress of molt as compared to males (mean score ± SD: males = 4.63 ± 1.00, n = 35; females = 4.97 ± 0.77, $n = 81$; Mann Whitney U-test: $z = 1.80$, $n = 116$, $P = 0.07$).

There was no difference in size of fat stores between molting and non-molting individuals (Mann Whitney U-test: $z = 0.01$, $n = 115$, $P = 0.99$), and size of the fat stores did not correlate with molt stage (Spearman $r_s = -0.013$, $z = 0.14$, $n = 115$, $P = 0.89$). There was no significant difference in fat scores between the sexes, although females tended to have somewhat less fat than males (males = 3.02 ± 1.77, females = 2.49 ± 1.30, Mann-Whitney U-test: $z = 1.67$, $n = 115$, $P = 0.09$).

RELATIONSHIPS BETWEEN MOLT, FAT STORES AND SEROLOGY

Molting individuals had similar red blood cell sedimentation rates as non-molting individuals ($t = 1.01$, $n = 55$, $P = 0.32$), and sedimentation rate was not correlated with the stage of molt (Pearson $r = 0.08$, $n = 57$, $P > 0.10$). Likewise, although hematocrit values tended to decrease with the stage of molt ($r_s = -0.23$, $z = 1.72$, $n = 56$, $P = 0.08$), molting individuals had similar hematocrit values as non-molting individuals (Mann Whitney U-test: $z = 0.62$, $n = 54$, $P = 0.53$). These comparisons are not confounded by sex differences as the sexes did not differ either in sedimentation rate values ($t = 0.81$, $n = 55$, $P = 0.42$) or in hematocrit levels (Mann Whitney U-test: $z = 0.69$, $n = 54$, $P = 0.49$). However, size of fat stores was negatively correlated with sedimentation rates (Fig. 1) and positively correlated with hematocrit values (Fig. 2), indicating a positive relationship between the size of an individual's fat stores and its health and/or nutritional state.

PLUMAGE COLORATION

Male Blue Tits were somewhat more brightly colored than females (mean color scores: males = 3.6, females = 3.5), although this difference was far from significant (Mann-Whitney U-test: $z = 0.001$; $n = 115$, $P = 0.99$). This indicates that, at least among juveniles, sexual dimorphism in the amount of yellow in the plumage is weak or absent in the Blue Tit. We do not have enough data to investigate this among adults, since very few older birds were caught during migration.

There was a significant difference in plumage

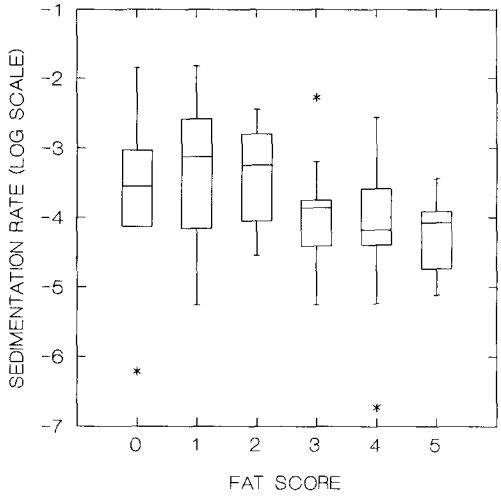

FIGURE 1. Box plot diagram (medians and quartiles) of red blood cell sedimentation rates in relation to fat scores among migrating Blue Tits; Pearson $r = -0.278$, $n = 57$, $P < 0.05$.

scores between molting and non-molting birds (Mann-Whitney U-test: $z = 2.68$; $n = 115$, $P = 0.007$), and plumage scores tended to increase with stage of post-juvenile molt, i.e., birds closer to molt completion were more brightly colored than those in early molt stages ($r_s = 0.18$, $z = 1.92$, $n = 115$, $P = 0.05$). Furthermore, birds with large fat stores were more brightly colored than those with small stores (Fig. 3). Considering the effects of fat and molt score on plumage coloration simultaneously, we found that both had significant effects on plumage coloration (multiple regression; molt: $b = 0.23 \pm 0.11$, $P = 0.02$; fat: $b = 0.17 \pm 0.06$, $P = 0.007$; P determined by randomization).

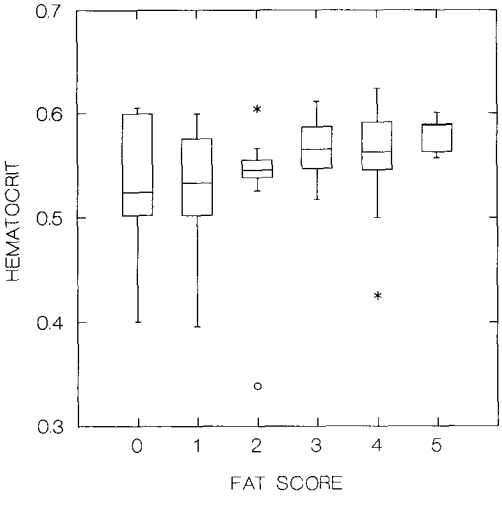

FIGURE 2. Box plot diagram (medians and quartiles) of hematocrit values in relation to fat scores among migrating Blue Tits; Spearman $r_s = 0.360$, $z = 2.63$, $n = 57$, $P < 0.01$.

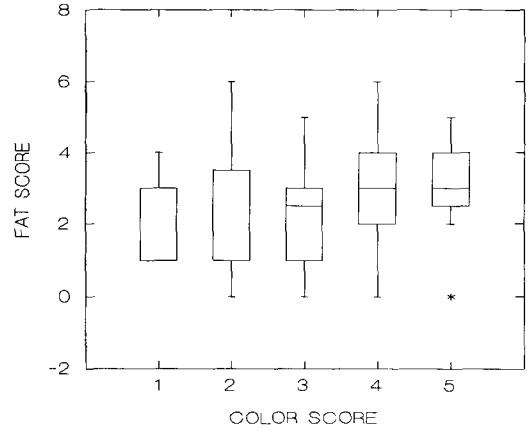

FIGURE 3. Box plot diagram (medians and quartiles) of fat scores in relation to plumage color scores among migrating Blue Tits; Spearman $r_s = 0.226$, $z = 2.82$, $n = 114$, $P < 0.005$.

Finally, we found no significant relationship between sedimentation rate and plumage color score (ANOVA: $F_{1,56} = 0.764$, $P = 0.39$). Similarly, there was no significant association between hematocrit values and color score (Kruskal-Wallis: $H = 2.46$, df = 4, $P = 0.65$).

DISCUSSION

MOLT-MIGRATION OVERLAP AND MIGRATORY CONDITION

As both molt and migration are energy demanding activities, molt-migration overlap can be expected to be energetically stressful (Kjellén 1994). However, we found that the great majority of juvenile Blue Tits captured during migration were still molting, and that molting birds did not show any signs of increased physiological or nutritional stress. More specifically, molting birds had similar fat stores, were in similar nutritional (hematocrit) and health (blood sedimentation rate) state as birds that had completed their post juvenile molt. This suggests that post-juvenile molt is without health consequences even if it overlaps with migration. Post-juvenile molt in the Blue Tit is a process in which mainly body feathers, wing coverts and a few tertials or rectrices are replaced with new feathers. Thus, in contrast to the post-nuptial molt by adult birds, no flight

feathers are replaced during the first year of a Blue Tit's life (Jenni and Winkler 1994).

FAT STORES AND BLOOD PARAMETERS

We found that Blue Tits with small fat stores had higher red blood cell sedimentation rates and lower hematocrit levels compared to birds with larger fat stores. These results are similar to our findings in another small passerine, the Goldcrest *Regulus regulus,* in which migrants with small fat stores also had high sedimentation rates and low hematocrit values (Merilä and Svensson 1995). Taken together, these data suggest that part of the variation in fat stores might be related to health state, i.e., birds with low fat stores might suffer from infections or inflammatory diseases (Harrison and Harrison 1986, Hokland and Madsen 1989). Another possible cause of the low hematocrit values associated with low levels of fat, could be that these individuals suffer from nutritional deficiencies, such as lack of protein (Payne and Payne 1987) or certain minerals (Wolkers et al. 1993).

There are two potential interpretations of these findings. First, migrating with low levels of fat is costly and results in increased susceptibility to diseases because of a reduced nutritional state or because of a decreased infection defense and specific immunoresponse (Baron 1988). Second, birds in low nutritional states or birds suffering from infections could be less efficient in depositing fat than healthier individuals. These two explanations, although not entirely mutually exclusive, differ in their emphasis on cause and effect and future experimental studies are needed in order to differentiate between them. In either case, our results highlight the need to take the health of individual birds into account when analyzing optimal migration patterns and fat deposition strategies. To our knowledge, this has not yet been done despite the increased recent interest in the functional significance of avian fat stores (Alerstam and Lindström 1990, Ekman and Hake 1990, Ekman and Liljendahl 1993, Witter and Cuthill 1993). Actually, physiological health could be a critical state variable connecting current behavioral activities (including reproduction and migration) to future performance (McNamara and Houston 1992, Gustafsson et al. 1994).

PLUMAGE COLORATION

In our study we did not find any significant sex difference in plumage coloration, indicating that plumage dimorphism in the amount of yellow on the body is low among juvenile Blue Tits. Like many other passerine bird species that winter in Europe, the Blue Tit has only one molt period during the year (Jenni and Winkler 1994). Hence, the plumage developed after the post-juvenile molt will be carried by an individual until the end of the breeding season the following year.

We found that birds with small fat stores were less brightly colored than birds with larger fat stores. This suggests that plumage coloration reflects nutritional condition of an individual Blue Tit (see also Hill and Montgomerie 1994). Although the adaptive significance of plumage coloration is unknown in the Blue Tit, there is plenty of evidence from other bird species that brightly colored individuals are at an advantage in antagonistic encounters or in competition for mates (reviewed by Andersson 1994). It also has been suggested recently that plumage coloration could signal migratory capacity and hence serve as a criteria in mate choice in migratory birds (Piersma and Jukema 1993, Fitzpatrick 1994).

The yellow color in the plumage of the Blue Tit and in many other birds is caused by food intake of the carotenoids lutein and zeaxanthin (Partali et al. 1987). Since such carotenoid pigments cannot be synthesized *de novo* by birds, they are ingested and transported in the blood to the growing feather follicles (Hill et al. 1994). Hence, plumage coloration could signal the foraging capacity of an individual, since only birds with a good ability to find the critical food particles could develop a bright plumage during molt (Hill 1992, Piersma and Jukema 1993). Partali et al. (1987) have shown that the carotenoids in the plumage of tits reach the birds through a food chain from tree leaves via foliage-eating lepidopteran larvae, which constitute a major food source for tits during summer (Perrins 1979, Slagsvold and Lifjeld 1985). Most likely, the ability to find the critical food containing these carotenoids will covary with the general foraging ability of the bird. Thus, a bird in good long-term energy balance will be able both to deposit large amounts of fat and to molt into a bright plumage, as indicated in this study.

CONCLUDING REMARKS

Our results suggest a potential for several physiological trade-offs prior to and during migration in the Blue Tit. There are links between health state and fat stores and between fat stores and

plumage coloration, although the directions of the causal relationships remain to be investigated. We encourage future workers to take the above factors into account in order to obtain a more complete understanding of the many aspects influencing individual variation in migratory condition.

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