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SOCIAL DOMINANCE AND ENERGY RESERVES IN WINTERING WOODLAND BIRDS¹

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Abstract. To understand animals' tactics for surviving the winter season, we need to know how they manage their energy reserves. Fat reserves in small birds in winter generally increase with starvation risk. Studies have documented higher fat reserves in response to various sources of variability in energy intake or expenditure. Using three woodland species, Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*), we tested the prediction that the more predictable food supply of socially dominant animals enables them to maintain lower energetic reserves than subordinate conspecifics. We inferred dominance from age and sex categories. The hypothesis was fully supported. In all three species, dominants carried relatively lower fat reserves than subordinates.

Key words: *Carolina Chickadee, dominance, energy reserves, fatness, fat reserves, Tufted Titmouse, White-breasted Nuthatch.*

During the nonbreeding season, temperate-zone birds must survive harsh conditions marked by low ambient temperatures, long nights, and unpredictable foraging success. During that period, energy reserves are required to survive both long nights and reductions in foraging success resulting from unpredictable food supplies and inclement weather. Full understanding of birds' tactics for surviving the winter season requires knowledge of how they manage their energy reserves. Because free-ranging birds carry less fat than the maximum possible (Witter and Cuthill 1993), there appears

to be some fitness cost to carrying extra fat, and predation risk has been hypothesized to be one component of such a fitness cost (Lima 1986, McNamara and Houston 1990).

Heavier birds appear to be less maneuverable when escaping a predator's attack and they also need to forage more intensively at the expense of vigilance to maintain higher fat reserves, so heavier birds should be more vulnerable to predators (Witter and Cuthill 1993). Thus, avian body mass has been proposed to represent a trade-off between risk of starvation and risk of predation (McNamara and Houston 1990), where risk of starvation selects for larger energy reserves, while risk of predation selects for lower mass and, therefore, lower energy reserves. Many experimental studies have demonstrated that an increase in variance in any variable that contributes to risk of starvation (e.g., food intake rate, day length, air temperature, etc.) causes birds to increase their fat reserves (Ekman and Hake 1990, Bednekoff and Krebs 1995, Pravosudov and Grubb 1997).

The advantages of reducing predation risk should cause birds to lower their body mass whenever it is possible to do so without increasing the risk of starvation. This shift can be seen under conditions where food becomes more predictable and available, such as in a laboratory setting with food ad libitum (Ekman and Hake 1990). We can therefore predict that birds with relatively low mass (low energy reserves) may be living under either good nutritional circumstances where they maintain low reserves by preference, or under poor nutritional circumstances where their energy reserves are low by necessity.

During the winter, many birds form social groups marked by a linear dominance hierarchy (Hogstad 1987, Koivula and Orell 1988, Ekman and Lillendahl 1993). In parids, linear dominance follows the order in which adult males are the most dominant individuals followed by juvenile males, and then by adult females

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and juvenile females (Gosler 1996, Lahti et al. 1998). In such groups, dominants enjoy higher survivorship and priority of access to food compared to subordinates (Koivula and Orell 1988, Ekman and Lilliendahl 1993). Because dominants always have priority of access to food, their food supply appears to be more "predictable" than that of subordinates. Thus, in the face of predation risk, dominants should be able to lower their energy reserves without increasing their risk of starvation, whereas subordinates would need to maintain high energy reserves to cope with higher risk of starvation (Clark and Ekman 1995). Such a prediction has been supported experimentally for several passerine species (Ekman and Lilliendahl 1993, Witter and Swaddle 1995, Hake 1996) and nonexperimentally for one species (Gosler 1996). By contrast, two studies found that dominant Willow Tits (*Parus montanus*) were heavier than subordinates, even when structural body size was controlled analytically (Koivula et al. 1995, Verhulst and Hogstad 1996). Verhulst and Hogstad (1996) proposed that the relative importance of predation risk and starvation risk in different situations could result in dominants either carrying larger or smaller fat reserves than subordinates, a hypothesis that could explain different results but which has not been experimentally tested.

Despite the contradictory results, the prediction that subordinates should carry more energy reserves than dominants seems to be the most common in the literature (Witter and Cuthill 1993, Clark and Ekman 1995). We used naturally-occurring body masses of three woodland species, Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*) to test the prediction that socially dominant conspecifics as indicated by age and sex should have relatively lower energy reserves than subordinates.

METHODS

We used records from birds of known age and sex caught alive in central and northeastern Ohio during November–March 1988–1997. Ninety percent of the birds were trapped during the months of December and January. We measured wing-chord to the nearest mm and body mass to the nearest 0.1 g with a spring Pesola balance. Birds previously banded as nestlings and all new birds appearing in continually-monitored trapping locations were classified as juveniles (T. Grubb and P. Doherty, unpubl. data). All birds caught during more than one winter were classified as adults for the second and subsequent years. In Tufted Titmice and Carolina Chickadees, males are generally larger than females, but sex cannot be determined on wing length alone for medium sized individuals. In this study, we labeled individuals larger than the largest known female as males and smaller than the smallest known male as females (T. Grubb, pers. observ.). Some birds in the overlapping zone of wing length that could not be sexed by this measure were sexed by their behavior or by presence or absence of a brood patch during the breeding season. Sex of White-breasted Nuthatches was determined by plumage. For Carolina Chickadee and Tufted Titmouse, we assumed the following intra-specific dominance structure, adult males > juvenile

males > adult females > juvenile females, which has been documented for most parids living in social groups (Gosler 1996, Lahti et al. 1998). White-breasted Nuthatches live in pairs in which males always socially dominate females (Waite 1987), so we used males and females as two categories of dominance.

To index birds' energy reserves, we computed a fatness index by dividing body mass by wing length raised to the third power, a measure of relative fatness that has been used frequently in previous studies (Ekman and Hake 1990, Hake 1996). Such an index also could be affected by variation in muscle mass and mass of food in the gut. Nevertheless, changes in body mass during the winter season are known to be associated mostly with changes in fat reserves (Blem 1990). There has been some controversy regarding the use of ratios, especially when a relationship between a ratio and a component of a ratio are considered (Atchley et al. 1976). Most criticism of statistical use of ratios concerns ratios with no correlation between the numerator and the denominator (Atchley et al. 1976, Knops et al. 1997). In our case, one would expect a strong correlation between wing length and body mass. Therefore, these criticisms do not seem to directly apply to a mass/wing³ ratio. Our own statistical simulations on fatness index ratio also did not show any statistical biases (Pravosudov, unpubl. data). Finally, field studies using both mass and fatness index demonstrated that both parameters show the same patterns and change similarly, suggesting that a fatness index is a good indicator of relative body mass and it does not seem to be statistically biased (Ekman and Lilliendahl 1993, Hake 1996). Therefore, we think that using a mass/wing length³ ratio is justified and this ratio reflects true patterns in birds' energy reserves.

Although energy reserves are sometimes indexed by fat score, i.e., the quantity of interfurcular fat visible through the skin, we could not use fat score because the technique for obtaining this measure had not been standardized across observers and because we do not have this measure for all of our data points.

STATISTICAL ANALYSIS

Our primary interest was to determine whether dominance status, as indexed by age and sex categories, had any relationship with energy reserves. Because birds can increase their mass over the course of the day by as much as 10% (Haftorn 1992), we included in the analyses the time of day associated with each capture. We also included mean daily temperature on the day of capture because temperature is an important determinant of avian energy reserves (Pravosudov and Grubb 1997). Although we pooled data across years to achieve sufficient sample sizes, we used records from only one capture of each bird. If the same bird had been captured more than once, we randomly selected records from one capture for the analysis.

To investigate variation in birds' energy reserves, we employed an ANCOVA in which fatness index was the dependent variable, dominance status as a factor, and mean daily temperature and time of day as covariates. All assumptions for ANCOVA were tested and validated. We employed Spearman correlation analysis on averages for each of the four dominance groups to

TABLE 1. The results of ANCOVA with fatness index as dependent variable, dominance status as a factor, and time of day and mean daily temperature as covariates.

Species	Dominance			Mean daily temperature			Time of Day		
	<i>F</i>	df	<i>P</i>	Slope	<i>t</i>	<i>P</i>	Slope	<i>t</i>	<i>P</i>
Carolina Chickadee	16.1	3,64	<0.001	-0.02	-0.05	0.58	0.06	0.29	0.77
Tufted Titmouse	155.5	3,29	<0.001	-0.02	-0.95	0.35	0.34	3.11	<0.01
White-breasted Nuthatch	17.9	1,27	<0.001	-0.01	-0.09	0.92	0.20	2.70	<0.01

test for the predicted direction of the dominance effect as an ordered alternative to nondirectional heterogeneity ANOVA (Rice and Gaines 1994).

RESULTS

Fatness index was positively and significantly related to time of day in Tufted Titmice and White-breasted Nuthatches, but not in Carolina Chickadees (Table 1). However, when records for all Carolina Chickadees captured, including those for birds of unknown sex and age, were used in a simple regression model, the relationship between time of day and fatness index was positive and statistically significant ($F_{1,543} = 10.34$, $P = 0.001$). Mean daily temperature was not significantly related to fatness index in any of the three species (Table 1). We found significant positive relationships

between fatness index and relative dominance status as expressed by age and sex (adult males > juvenile males > adult females > juvenile females) in Carolina Chickadees and Tufted Titmice ($r_s = 1.0$, $P < 0.01$ for all species, Table 1, Fig. 1), and by sex in White-breasted Nuthatches (Table 1, Fig. 1). None of the interactions between dominance status and the covariates was statistically significant ($P > 0.4$).

Because in Carolina Chickadees and Tufted Titmice we inferred sex mostly from wing length, it is possible that the data might have a gap in the middle range of wing length potentially affecting our results. Although such a gap existed in Tufted Titmice, it did not exist in Carolina Chickadees because many individuals of that species had been sexed by their behavior during the breeding season. To examine whether eliminating middle-sized individuals from the analysis had an effect on our results, we used all individuals including birds with unknown sex and age. Because males are generally larger than females and larger individuals are generally dominant over smaller individuals, we predicted that larger individuals should carry relatively smaller fat reserves. Our data supported that prediction, whether we used all birds including individuals of unknown age and sex or just individuals of known age and sex (Fig. 2). In fact, the relationship between fatness index and wing length was almost identical for the full data set on all the birds and for the subset excluding middle-sized birds that could not be sexed. The analysis of fatness index using all birds provided further evidence that dominant (larger) birds carry less fat reserves than subordinate (smaller) birds (Fig. 2). The subset for Carolina Chickadees had no gap for middle-sized birds, so our sample for this species included males and females of all sizes (Fig. 2). The subset for Tufted Titmice had a gap for middle-sized birds indicating that we only sampled the largest males and the smallest females. However, the largest males are always socially dominant over the smallest females, so the results based on this subset do represent a test of the prediction that dominant birds should carry less fat reserves than subordinate birds. Because White-breasted Nuthatches were sexed by plumage, there was no gap for middle-sized birds.

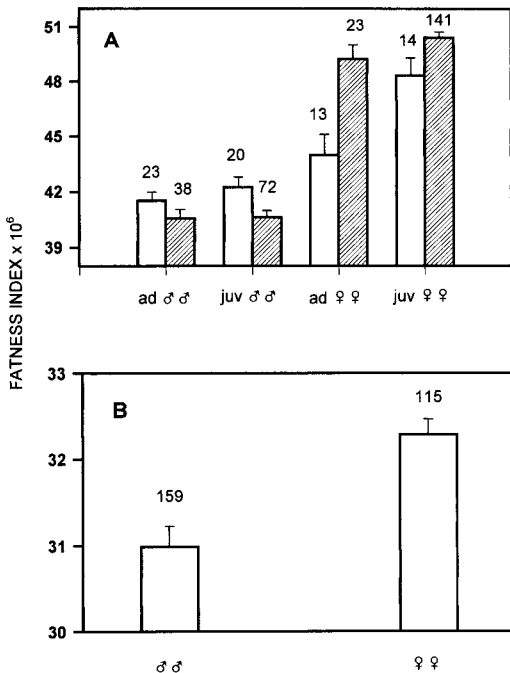


FIGURE 1. The relationship between mean fatness index (\pm SE) and dominance status cross four age/sex categories in Carolina Chickadee (open bars, A) and Tufted Titmouse (hatched bars, A) and across two sex categories in White-breasted Nuthatch (B). Numbers above bars are sample sizes.

DISCUSSION

Our study supports the hypothesis that dominant birds carry lower energy reserves. In all three species examined, dominants apparently reduce their relative body mass because they have priority of access to food, higher predictability of foraging success, and, as a result, lower starvation risk. Therefore, dominants

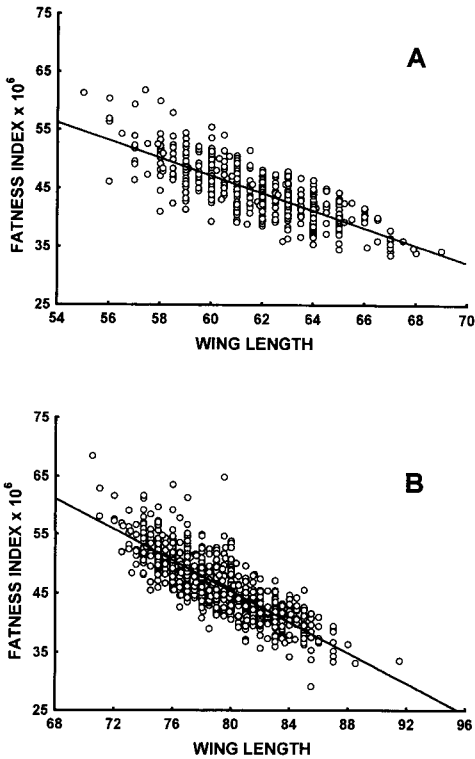


FIGURE 2. The relationship between fatness index and wing length in all available Carolina Chickadees (A) and in all available Tufted Titmice (B).

can reduce their energy reserves to reduce their mass-dependent risk of predation without increasing their risk of starvation.

Lacking a direct measure of dominance status of individual birds, we inferred social dominance from age and sex classes. By including individuals of unknown age and sex, we also demonstrated that larger birds (most likely dominants) tend to carry less fat reserves than smaller birds (most likely subordinates). Such results could potentially suggest that the differences found were not due to the dominance status but were fixed effects of age, sex, or size. However, we think that our findings refer to social dominance and not to just age, sex, or size per se. First, larger Carolina Chickadees appear to dominate smaller conspecifics irrespective of sex (Pravosudov and Grubb 1999), suggesting that the negative correlation between relative fatness and body size is due to different dominance statuses of different-sized birds. Second, several manipulative studies have strongly suggested that changes in fat reserves are caused by the dominance status of an individual independent of sex and age (Ekman and Lilliendahl 1993, Witter and Swaddle 1995, Hake 1996). All of this evidence suggests that dominance directly affects fat reserves, whereas sex, age, and size are most likely related to fat reserves secondarily through their effects on dominance.

An alternative explanation to the negative relationship between body size and fatness index concerns energetic consequences of body size (Calder 1974). When ambient temperature decreases, metabolism in smaller individuals increases proportionally more compared to larger individuals, suggesting that risk of starvation is higher for smaller birds (Calder 1974). This means that larger birds need relatively less energy for existence and, therefore, larger birds may need relatively less fat reserves to decrease risk of starvation compared to smaller birds (Calder 1974). Thus, larger birds may be able to afford to carry less fat reserves than smaller birds irrespective of their dominance status.

It is not clear why we did not detect an effect of temperature on fatness index, because such a relationship would be expected (Pravosudov and Grubb 1997). One possible explanation is that most of the birds used in the analyses were captured during the two mid-winter months of December and January, when variation in temperature was not sufficient. Also, during mid-winter, the body mass of passerines wintering in the Temperate Zone is at the highest level during the year (Bednekoff and Houston 1994), so any short-term effect of temperature may be difficult to detect. It also is possible that birds did not respond to immediate day-to-day changes in temperature, but rather responded to the average changes in air temperature during the season (Pravosudov and Grubb 1997).

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PLASTIC COLOR BANDS HAVE NO DETECTABLE SHORT-TERM EFFECTS ON WHITE-BREASTED NUTHATCH BEHAVIOR¹

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Abstract. We examined whether plastic leg bands had short-term effects on foraging behavior in White-breasted Nuthatches (*Sitta carolinensis*), a species which, because of their very short legs and unusual habit of hanging upside-down on bark, may be particularly susceptible to deleterious effects of plastic

bands. Ten nuthatches were outfitted with varying numbers of colored plastic bands and observed foraging in an aviary after two days of habituation. Wearing up to five plastic bands caused no detectable change in any of the variables measured: number of flights, body position, choice of foraging substrate, seed caching, seed hammering, and seed retrieval.

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