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INTERACTIONS AMONG ENVIRONMENTAL STRESS, BODY CONDITION, NUTRITIONAL STATUS, AND DOMINANCE IN GREAT TITS

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ABSTRACT.—We studied body condition and feather growth rate in Great Tits (*Parus major*) in relation to dominance in two localities during late autumn and early winter. The two localities differed in elevation, ambient temperature, and arthropod availability. We supplemented the two study areas with food (husked peanuts) throughout the study period. The percentage of time tits spent at feeders was higher at El Ventorrillo (the locality that was colder and had lower natural food availability) and was associated with dominance only at this locality. The number of aggressive displacements per hour experienced by each individual was 150 times higher in the area with lower arthropod availability and lower temperatures. Protein reserves (measured as pectoralis muscle thickness) were higher at El Ventorrillo and were positively and consistently related to dominance at both localities. Growth rate of induced feathers was slower at El Ventorrillo but was not directly related to dominance in either locality. Only dominant adult males at El Ventorrillo compensated for the environmental harshness at this locality by attaining a higher feather growth rate than the other sex/age classes. Feather-mass asymmetry of induced feathers during autumn was not associated with body condition, did not change between localities, and was inversely and consistently related to dominance at both localities. The covariation among variables describing bird size, access to supplemental food, body condition, feather growth rate, and asymmetry was different at the two localities. Larger, dominant Great Tits spent more time foraging at feeders, had a thicker pectoralis muscle (i.e. body condition), and grew induced feathers at a higher rate only at the locality with colder temperatures and lower food availability. *Received 9 September 1997, accepted 2 February 1998.*

SOCIAL DOMINANCE, food availability, and environmental stress (e.g. declining temperatures and/or high snow cover) are thought to influence winter survival of small passerines through their effects on body condition and access to food (Gauthreaux 1978, Lundberg 1985, Piper and Wiley 1990). The role of these variables in food access has been studied extensively (Ekman and Askenmo 1984, Millikan et al. 1985, Theimer 1987, Enoksson 1988, Hogstad 1988, Caraco et al. 1989, Desrochers 1989). Body condition generally has been defined in a very broad sense to indicate the ability of an individual to cope with present and future physiological stress, and therefore, the ability to enhance fitness.

Fat reserves are thought to play an important role as energy stores to overcome periods of food scarcity or increased energetic demands (Blem 1990, Bednekoff et al. 1994, Bednekoff and Houston 1994, Rogers 1995, Gosler 1996, Lilliendahl et al. 1996). However, fat reserves may have costs in terms of winter survival, diminished maneuverability, and increased predation risk (e.g. Lima 1986, Witter and Cuthill 1993, Ekman and Lilliendahl 1993, Witter et al. 1994, Clark and Ekman 1995, Gosler et al. 1995, Metcalfe and Ure 1995). Therefore, fat storing may be subjected to selection pressures not directly related to body condition. The complex interaction between fat reserves and environmental conditions also is complicated by the possible inverse relationship between fat stores and dominance in winter (Ekman and Lilliendahl 1993, Witter and Swaddle 1995, Gosler 1996).

Protein reserves are not viewed as short-term energy stores because they are not as easily mobilized as fat and are not maintained as special depots. Muscle proteins are used for energy

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only after both glycogen and lipid reserves are nearly or completely exhausted (see Blem 1990). Therefore, they are thought to measure long-term body condition (Gosler 1991, Newton 1993). Feather growth is linked with protein reserves that are used to obtain amino acids that can be assembled into feather proteins (Murphy 1996a). The width of feather growth bars is increasingly being used as an indicator of long-term nutritional status in winter populations (e.g. Grubb and Cimprich 1990, White et al. 1991, Hogstad 1992, Nilsson et al. 1993, Grubb 1995, Ekman et al. 1996). Moreover, fluctuating asymmetry on the growth of right and left side feathers has been suggested to be a good measure of long-term body condition due to its sensitivity to environmental stress and response to differences in phenotypic quality (Clarke 1992, 1995, Polak and Trivers 1994). Feathers are regenerated at a faster rate and to a greater total length and mass at higher ambient temperatures (Grubb et al. 1991; but see Grubb 1995), and growth is more rapid in summer than in winter (Grubb et al. 1991). Dominance also seems to have a strong effect on daily growth rates, with dominant individuals growing wider bars than subordinates (Grubb 1989, Grubb and Cimprich 1990, Hogstad 1992, Witter and Swaddle 1995). Habitat differences, probably related to habitat-specific nutritional condition, have also been described as a relevant factor affecting feather growth (Grubb and Yosef 1994).

The knowledge of the degree of interaction between these factors is as important as the individual factors themselves. However, it is still unknown whether and how the effect of environmental harshness on the level of protein reserves and induced feather growth change according to dominance status. Moreover, it is also necessary to know the relative importance of these different factors so that we can partition the total variance into its different components.

The aim of this paper is to study in a multifactorial way the incidence of social dominance and environmental stress (measured as ambient temperature and natural food availability) on food availability, body condition, and nutritional/physiological state of Great Tits (*Parus major*). The Great Tit is widely distributed throughout the Palearctic region, although its winter ecology has been studied most frequently in northern latitudes or areas with very cold climates (e.g. Ekman 1989, Hogstad 1989, Matthysen 1990, Gosler 1993, 1996, Bednekoff and Krebs 1995; but see Herrera 1979, Carrascal and Moreno 1992).

We monitored two Mediterranean populations of Great Tits that inhabit contrasting wintering areas. The two localities differ in mean ambient temperature and food availability, but winter climate is milder in both localities than in northern latitudes where the majority of studies on the winter ecology of small passerines has been undertaken. Our main goals were to understand the relationships among dominance, food access, body condition, and induced feather growth in Great Tits in an environment that is less stressful than that at northern latitudes. We predicted that the interaction among these components should be more intense under more stressful conditions, especially the expected positive relationship between protein reserves and feather growth (Blem 1990, Jenni-Eiermann and Jenni 1996). We also predicted that in the colder area with lower food availability, Great Tits should rely more intensely on supplemental food, intraspecific competition (intensity of hostile interactions) for food access should be higher, and body condition should be better. A less marked effect of environmental stress on the growth rate of induced feathers of dominant birds could be predicted in localities with higher environmental harshness. We also predicted that dominant individuals should have higher levels of indices that measure long-term nutritional status (e.g. protein reserves and induced feather growth) owing to their better competitive abilities when interacting for access to food.

Additionally, we tested whether fluctuating asymmetry in tail feathers is linked with developmental stability due to differences in environmental stress or intraspecific competitive pressure. Asymmetry should be higher in colder areas with lower food availability, in less dominant individuals, and in individuals with lower body condition (Swaddle and Witter 1994).

STUDY AREAS AND METHODS

Study areas.—Field work was carried out from November 1994 to January 1995 at two field sites, El Ventorrillo and Desert de Sarriá (hereafter Sarriá).

The El Ventorrillo area was a 6-ha mixed-montane coniferous forest (*Pinus sylvestris, Castanea sativa,* and *Acer* spp.) of continental cold Mediterranean climate (1,500 m elevation) at Sierra de Guadarrama, central Spain (40°45′N, 04°01′W). The area at Sarriá occupied 3 ha of orchards and mixed coniferous forest (*Pinus halepensis* and *Cedrus* sp.) of coastal mild Mediterranean climate (100 m elevation) near Barcelona, northeastern Spain (41°25′N, 02°10′W). Mean daily minimum temperatures and mean daily temperatures during the study period were, respectively, 1.2 and 4.6°C at El Ventorrillo, and 9.9 and 11.7°C in Sarriá (data obtained from weather stations less than 5 km from each plot).

Arthropod availability.—During the sampling period, Great Tits fed mainly on arthropods and seeds taken on the ground or from the outer parts of tree canopies (Herrera 1979, Carrascal and Tellería 1985, Obeso 1987). The relative abundance of arthropods was evaluated at both localities by carefully searching and counting invertebrates larger than 1 mm during 2-min periods in pine foliage (twigs and needles) and on the ground (see Cooper and Whitmore 1990). We also classified the size of each arthropod into one of the following length categories: 1 to 2 mm, 3 to 5 mm, and 6 to 10 mm. Samples were obtained by random sampling in the pine foliage and on the ground in both study areas. The most common taxa (i.e. those most likely consumed by Great Tits) were Arachnida, Diptera, and Hemiptera in the ground samples and Diptera, Arachnida, and Coleoptera in the foliage.

Feeders and bird trapping.—Supplemental food (husked peanuts) was available throughout the study period (i.e. feeders were never empty). Feeders were wooden boxes with one side (20 × 11 cm) covered by a 4.8-mm mesh plastic net that allowed birds access to food. Feeders were suspended from pine branches approximately 50 cm below the canopy and 2 to 4 m above ground. To gather food, birds clung to the netting to obtain small pieces of peanuts. The average time per foraging bout at feeders was approximately 100 s (Moreno and Carrascal 1991). We established an equal number of feeders per ha at the two sites (four feeders at El Ventorrillo and two at Sarriá) so that the amount of food provided was equal between sites.

During the first two weeks of November we used specially designed funnel traps to capture 20 Great Tits at Sarriá (three adult males, three adult females, seven juvenile males, seven juvenile females) and 18 at El Ventorrillo (six adult males, three adult females, four juvenile males, five juvenile females). The distribution of the four sex/age categories did not differ significantly between the localities ($\chi^2 = 1.29$, df = 3, $P = 0.731$). Birds were banded for individual recognition with ICONA (Spanish Ministry of Agriculture) aluminum bands and color bands. Each bird was aged and sexed according to Svensson (1992). Adult Great Tits undergo a complete prebasic molt from June to September. Nearly all juveniles also molt their rectrices during this period (Gosler 1993, Jenni and Winkler 1994, J. C. Senar pers. obs.). Therefore, all of the birds had completed the prebasic molt during the sampling period. We determined body mass (±0.01 g) with an electronic balance. Tarsus length (±0.01 mm) was measured with a digital caliper, and tail length and wing chord (±1 mm) were measured with a ruler.

Ptilochronology.—Before releasing each bird at the capture site, we plucked the right and left fifth rectrix. Birds were recaptured 45 to 60 days later, at which time the induced feathers were plucked. This time is longer than the time taken to grow a feather to final length (Grubb 1989). Nevertheless, we also verified that the induced rectrices had stopped growing by observing the absence of feather sheaths (Ginn and Melville 1983) and the absence of blood in the part of the shaft within the follicle. We examined the original and induced feathers for length, mass, and width of growth bars. The average width of growth bars was calculated for the first 10 growth bars clearly visible from the distal part of each feather (usually beginning 3 to 4 mm from the tip of the feather). Rectrices were fixed to a piece of polyspan by inserting two entomological pins through the feather barbs to mark the distal and the proximal ends of 10 growth bars. The distance between the two marks was then measured with a caliper (±0.01 mm). Total feather length was also measured. Each feather was measured twice and the average of the two measurements was used (the second measurement was done after the completion of the first measurement for all feathers). This value was divided by 10 to estimate the mean rate of feather growth per day.

Daily growth rate of induced feathers was estimated as the average of left and right feathers expressed in mm/day. Daily growth bar width of the original (summer) feathers did not differ significantly between Sarriá and El Ventorrillo ($F = 0.05$, df = 1 and 36, $P = 0.830$) and was not related to autumn-winter induced feather growth at either Sarriá ($r = 0.104$, $n = 20$, $P = 0.662$) or El Ventorrillo ($r = 0.300$, $n = 18$, $P = 0.226$). In order to control for intraspecific differences prior to the experimental removal of feathers (e.g. differences in food intake rate, body condition, health status, etc. during the summer period of feather growth), we also calculated an index by dividing the daily growth bar width of the induced feather (DGI) by that of the original feather (DGO; Grubb 1989, Hogstad 1992, Nilsson et al. 1993). Because results of induced feather growth rates (mm/day) and the DGI/DGO index were highly consistent in ANCOVA tests, for clarity we show results only as mm/day (see Ekman et al. 1996).

Fluctuating asymmetry of induced feathers.—Differences between the two repeated measurements of total feather length and growth bar width in the same feathers were higher than asymmetry estimates (differences between left and right feathers), and asymmetry estimates were not significantly repeatable (using tests proposed by Swaddle et al. 1994 and Merilä and Björklund 1995). Thus, measures of asymmetry using growth bar width or feather length are not repeatable, and we cannot distinguish true asymmetry from measurement error (violation of point 2 in Swaddle et al. 1994).

To overcome this problem, we used the masses of left and right feathers to obtain measurements of fluctuating asymmetry in fully grown feathers. Masses of induced and original feathers were determined to the nearest 0.1 mg with a high precision electronic balance. Each feather was weighed twice (the second measure was done after completion of the first measure of all feathers). Repeatability (r_I; see Lessells and Boag 1987) of the masses of left ($r_I = 0.98$) and right ($r_I = 0.99$) feathers of 38 birds were very high. Estimated asymmetry was also very repeatable and was significantly higher than expected from the estimated measurement error ($F = 3.45$, df $= 37$ and 74, $P < 0.001$; mixed-model ANOVA proposed by Swaddle et al. 1994). The asymmetry of feathers (difference in masses of left and right feathers) approached a normal distribution as shown by a normal probability plot and the Shapiro-Wilk's test ($W = 0.985$, $P = 0.924$) and was not directional because it was centered around zero (t-test for deviation from the null hypothesis of average asymmetry equal to zero: $t = -0.027$, $n = 38$ birds, $P = 0.979$). We obtained a percent asymmetry index by dividing the absolute difference in mass between left (L) and right (R) feathers by their mean:

$$\frac{|L - R|}{(L + R)/2} \times 100 \qquad (1)$$

Feather mass was highly correlated with total feather length ($r = 0.774$, $P < 0.001$, using averages of right and left feathers of 38 birds) and growth bar width ($r = 0.637$, $P < 0.001$). Therefore, feather mass is a proper indicator of induced feather growth, with the advantage that it avoids the problems related to the accuracy of fluctuating asymmetry estimates observed with feather length and growth bar width.

Body condition.—We used ultrasound (with a portable Krautkrämer device) to estimate pectoral muscle mass following the protocol of Newton (1993). The thickness of the pectoral muscle was measured in arbitrary units considering the reflection of the wave on the sternum. Every day of sampling muscular thickness, the Krautkrämer device was calibrated in both localities using two pieces of identical thickness cut from the same metacrilate slab. In a pilot study with a collection of dead individuals preserved frozen, the ultrasound measurement of the pectoralis muscle of unfrozen Great Tits was highly correlated with the thickness of the muscle (measured with an entomological needle and a digital caliper; $r = 0.87$, $n = 6$, $P = 0.024$; L. M. Carrascal unpubl. data). Great Tits were captured multiple times (3 to 35) throughout the study period using funnel traps; ultrasound measurements and body masses were obtained each time. All estimates obtained for each individual bird on different days were averaged for subsequent analyses.

Repeatability of the index of pectoral muscle thickness was high ($r_I = 0.66$; $F = 13.17$, df $= 37$ and 206, $P < 0.001$, $n = 38$ birds). This estimate of pectoral muscle thickness is not significantly associated with an index of the amount of subcutaneous fat in the furcular depression in Great Tits at El Ventorrillo during autumn and winter ($R^2 = 0.04$, $n = 63$, $P = 0.100$; L. M. Carrascal unpubl. data). Therefore, our estimate of muscular thickness provides an index of body condition not related to fat reserves. This index can be considered a relatively stable estimate of body condition within the sampling period, and it probably is associated with muscular strength and possibly with regeneration of induced feathers by providing amino acids that are assembled into feather proteins (Gosler 1991).

Use of supplemental food and intensity of aggressions.—Estimates of differential competitive aggressiveness in Great Tits and intensity of use of supplemental food between the two localities were obtained by videotaping the feeders and recording total time spent feeding and the number of aggressive displacements experienced by individuals. Tripod-mounted zoom videocameras were located 2 to 4 m from the feeders. Color bands were clearly visible, so it was possible to identify individual birds. As a general measure of competitive intensity, we estimated the number of aggressions received per individual. We videotaped a total of 45 h per locality, spread evenly throughout the course of the day (eight different days throughout the study period within each locality).

We obtained a gross measure of intake rate by pooling data for all individuals. We noted the approximate size and the number of small pieces of peanuts Great Tits extracted from feeders (comparing on the TV screen the size of peanut pieces relative to beak length). Average food intake rate was 0.03 g of peanut per minute.

A dominance-linear factor was defined combining sex and age of individuals (see Gosler 1996). Male Great Tits dominate same-aged and younger females (Saitou 1979, Drent 1983, Pöysä 1988, Gosler 1993), and adults usually dominate juveniles of the same sex (Saitou 1979, Sandell and Smith 1991). These observations are supported by observations at El Ventorrillo, where Great Tit dominance hierarchy was established as adult male > juvenile male > adult female > juvenile female (179 total dyadic interactions). Individual dominance scores could be calculated only for the El Ventorrillo population (10 levels for 18 birds). Interaction rates were too low to pro-

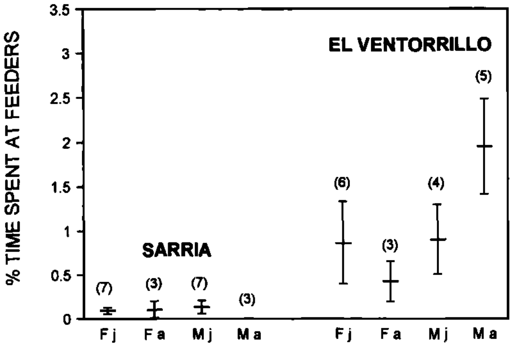

FIG. 1. The effect of locality and sex/age (dominance factor) on the proportion of time Great Tits spend at feeders. Values are $\bar{x}$ ± SE, with sample sizes in parentheses. Fj, juvenile females; Fa, adult females; Mj, juvenile males; Ma, adult males.

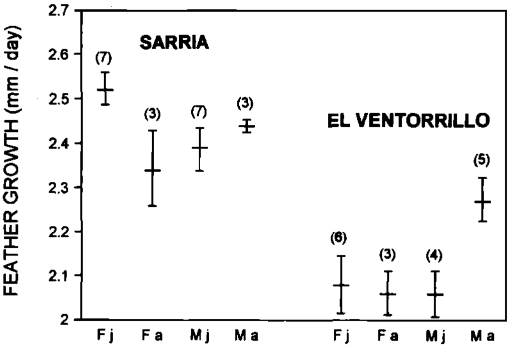

FIG. 3. The effect of locality and sex/age (dominance factor) on growth rate of induced feathers in Great Tits. Values are adjusted means (±SE) controlling for the effect of pectoralis muscle thickness, with samples sizes in parentheses. Fj, juvenile females; Fa, adult females; Mj, juvenile males; Ma, adult males.

vide adequate data for Sarriá population. The lack of information on dominance hierarchy in Sarriá precluded the analysis of the effect of dominance scores on feeders use, body condition, feather growth, and fluctuating asymmetry of induced feathers in the same ANCOVA models. Nevertheless, the dominance-linear factor combining sex and age of individuals clearly defined a dominance hierarchy, because the ordination of sex and age classes explained 91.2% of the variance in dominance scores at El Ventorrillo ($F = 166.69$, df = 1 and 16, $P < 0.001$).

Statistical analyses.—Biometrical differences between the two populations were examined using t-tests. The effects of locality and dominance were analyzed with two-way ANCOVA, using a linear contrast for the dominance factor. Although Figures 1 to 4 show original nontransformed data, ANCOVAs were performed with variables transformed (arcsine for percentages and Box-Cox transformation for feather mass asymmetry) to attain homoscedasticity and normality. A two-parameter Box-Cox transformation of the form $(X + \lambda_2)^{\lambda_1}$ was used with $\lambda_1 = 0.3$ and $\lambda_2 = 1.14$ (λ_2 is the smallest nonzero asymmetry value; Swaddle et al. 1994). Due to the lack of normality and homoscedasticity in the number of aggressive displacements suffered by individuals, the difference between localities in this variable was analyzed by means of a nonparametric Mann-Whitney U-test. The same nonparametric test was used with data on arthropod availability.

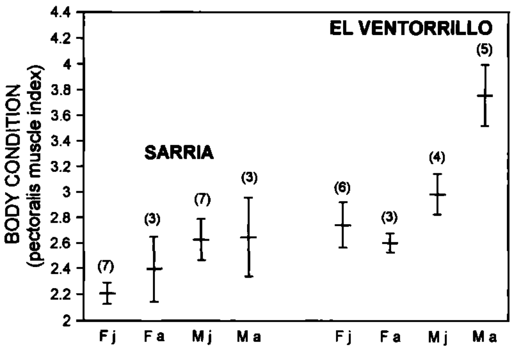

FIG. 2. The effect of locality and sex/age (dominance factor) on body condition in Great Tits. Values are adjusted means (±SE) controlling for the effect of tarsus length and the proportion of time spent foraging at artificial feeders, with samples sizes in parentheses. Fj, juvenile females; Fa, adult females; Mj, juvenile males; Ma, adult males.

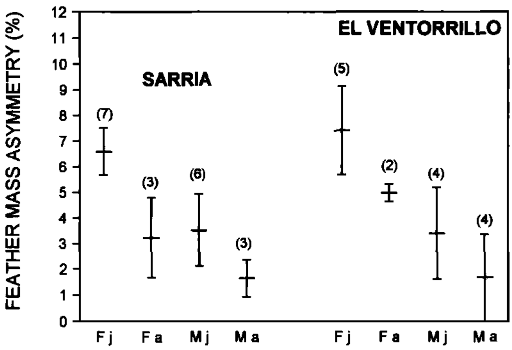

FIG. 4. The effect of locality and sex/age (dominance factor) on feather mass asymmetry of induced feathers in Great Tits. Values are adjusted means (±SE) controlling for the effect of pectoralis muscle thickness, with samples sizes in parentheses. Fj, juvenile females; Fa, adult females; Mj, juvenile males; Ma, adult males.

TABLE 1. Morphological measurements ($\bar{x}$ ± SD) of Great Tits captured during winter 1994/1995 at El Ventorrillo (n = 18) and Sarriá (n = 20), Spain.

Variable	El Ventorrillo	Sarriá	t	P
Tarsus length (mm)	19.4 ± 0.81	19.5 ± 0.73	0.58	0.563
Wing chord length (mm)	75.0 ± 2.81	73.7 ± 2.71	1.48	0.147
Tail length (mm)	62.8 ± 2.96	62.5 ± 3.61	0.23	0.816
Body mass (g)	17.2 ± 1.03	16.8 ± 1.12	1.18	0.246

Patterns of covariation among variables (body size, percentage of time spent foraging at feeder, body condition, induced feather growth, and feather mass asymmetry) within each locality were revealed by principal components analyses after rotated the initial factors by the Varimax procedure. Rotations were performed because the rotated factor loadings were conceptually simpler than the unrotated ones. Only principal components with eigenvalues larger than 1 were considered. We used Box's M test to check for homogeneity of covariance matrixes for multiple dependent variables. All statistical analyses were carried out using STATISTICA 5.0 of StatSoft (StatSoft Inc. 1996).

RESULTS

Great Tits captured at El Ventorrillo (n = 18) and Sarriá (n = 20) did not differ significantly in tarsus length, wing length, tail length, or body mass (Table 1).

Arthropod availability.—Arthropod abundance was significantly lower in the pine foliage at El Ventorrillo ($\bar{x}$ = 0.52 ± SD of 1.08 per sample, n = 20) than at Sarriá ($\bar{x}$ = 2.62 ± 4.21, n = 13; Mann-Whitney test, Z = 2.65, P = 0.008), but it was similar on the ground (El Ventorrillo, $\bar{x}$ = 2.60 ± 3.50, n = 20; Sarriá, $\bar{x}$ = 2.47 ± 2.83, n = 17; Z = 0.17, P = 0.864). The size distribution of arthropods was significantly different between the two localities (χ^2 = 11.08, df = 1, $P < 0.001$), the major difference being that the proportion of prey longer than 2 mm was higher at Sarriá (44.4% out of 63 prey items) than at El Ventorrillo (17.2% out of 64 prey items). Therefore, the overall biomass of arthropods was highest in Sarriá.

Use of supplemental food and intensity of aggression.—The proportion of time Great Tits spent foraging at feeders (of the 45 h of videotape sampling) was significantly higher at El Ventorrillo than at Sarriá (F = 19.57, df = 1 and 30, $P < 0.001$; Fig. 1) and was not consistently associated with dominance (linear contrast, F = 0.98, df = 1 and 30, P = 0.331). The interaction term locality × dominance approached significance (F = 3.98, df = 1 and 30, P = 0.055); planned comparisons analyzing the effect of dominance separately at each locality showed a nonsignificant effect at Sarriá (F = 0.46, df = 1 and 30, P = 0.504) and a significant effect at El Ventorrillo (F = 4.94, df = 1 and 30, P = 0.034). Although at El Ventorrillo the proportion of time spent foraging at feeders was on average 12 times higher than at Sarriá, this proportion was very low (<4%; see Fig. 1). Moreover, no Great Tits occurred at artificial feeders at Sarria in 98% of the 45 h sampled, whereas this proportion was 80.2% at El Ventorrillo.

A gross estimate of the influence of artificial feeders on the energy budget of Great Tits showed that on average, Great Tits obtained 0.6% of their energy requirements from feeders at Sarriá and 6.2% at El Ventorrillo (using data on caloric content of peanuts [Cummings and Wuycheck 1971], an efficiency of energy assimilation of 88% [Karasov 1990], the allometric equation provided by Bryant et al. [1985], an intake rate of 0.03 g of peanuts per min [unpubl. data], and the percentage of time Great Tits foraged at feeders [Fig. 1]).

The number of aggressive displacements suffered by each individual at feeders was significantly higher at El Ventorrillo than at Sarriá (El Ventorrillo, $\bar{x}$ = 6.90 per 45 h, median = 6, n = 18; Sarriá, $\bar{x}$ = 0.05 per 45 h, median = 0, n = 20; Z = 4.91, $P < 0.001$). Overall, birds at El Ventorrillo suffered 1.54 aggressive displacements per individual per 10 h, and at Sarriá 0.01 (i.e. birds at El Ventorrillo experienced 154 times more aggressive displacements).

In summary, Great Tits devoted a low proportion of their time foraging on supplemental food, but they were more dependent on artificial feeders, and they experienced more competitive pressure from conspecifics at feeders, in the locality with lower natural food availability and lower temperatures (El Ventorrillo). The effect of the dominance hierarchy on access to supplemental food was only discernible at the locality with the most severe environmental conditions.

Body condition.—The percentage of time spent foraging at artificial feeders (the covariate) did not covary significantly with pectoralis muscle thickness (i.e. a measure of body condition; $R^2 = 0.009$, $F = 0.32$, df = 1 and 28, $P = 0.574$), but pectoralis muscle thickness was positively associated with bird size (i.e. the relationship between tarsus length and muscle index; $R^2 = 0.335$, $F = 5.16$, df = 1 and 28, $P = 0.031$). Body condition was significantly higher at El Ventorrillo than at Sarriá (ANCOVA, $F = 10.87$, df = 1 and 28, $P = 0.003$; Fig. 2) after controlling for the effect of proportion of time spent foraging at feeders and differences in body size among birds. Pectoralis muscle thickness differed significantly with respect to dominance (sex/age ordination, $F = 11.13$, df = 1 and 28, $P = 0.002$ using a linear contrast). The interaction term locality × dominance was not significant ($F = 2.45$, df = 1 and 28, $P = 0.129$). This pattern held for both localities and hierarchy levels (parallelism test, $F = 1.93$, df = 14 and 14, $P = 0.116$). Partitioning the variance by factors and covariates, locality explained 21.9%, dominance (sex/age ordination) 25.5%, body size (tarsus length) 15.6%, proportion of time foraging at feeders 1.1%, and the interaction locality × dominance 8.0% of the variation in body condition (as measured by pectoralis muscle thickness).

In summary, body condition was dependent on bird size, was higher at the locality with more severe environmental conditions, and was not significantly and consistently associated with the amount of time devoted to feeding at artificial feeders. Dominance status was positively and consistently related to body condition at the two localities.

Growth rate of induced feathers.—Growth rates of induced feathers are shown in Figure 3. Induced feather growth rate was higher at Sarriá (ANCOVA, $F = 40.80$, df = 1 and 29, $P < 0.001$) but was not related to dominance hierarchy (linear contrast, $F = 0.50$, df = 1 and 29, $P = 0.484$). The locality × dominance interaction was significant ($F = 4.65$, df = 1 and 29, $P = 0.039$; Fig. 3). Post-hoc comparisons of means (Tukey HSD test for unequal sample sizes) showed that there were no significant differences at Sarriá among sex/age classes ($P > 0.6$ in six tests), whereas growth rate of induced feathers was higher in adult males than in the other three sex/age classes at El Ventorrillo ($P < 0.050$). Pectoral muscle index (covariate) was not related significantly to daily growth of induced feathers ($R^2 = 0.036$, $F = 1.08$, df = 1 and 29, $P = 0.308$). The parallelism test of the relationship between body condition and induced feather growth rate across the levels of locality and dominance factors was not significant (interaction factors × covariate; $F = 0.49$, df= 7 and 22, $P = 0.825$). Partitioning the variance by factors and covariate, body condition explained only 2.3%, locality 67.3%, dominance 4.8%, and the interaction locality × dominance 2.8% of the variation observed in growth rate of induced feathers.

In summary, growth rate of induced feathers was not dependent on body condition, was slower in the population inhabiting the locality with higher environmental harshness (El Ventorrillo), and changed in a different way among dominance levels in the two localities, being higher only in adult males under harsh environmental conditions.

Asymmetry of induced feathers.—Feather mass asymmetry did not change significantly between localities (ANCOVA, $F = 0.24$, df = 1 and 25, $P = 0.628$), but it decreased significantly with increasing dominance status (linear contrast, $F = 5.45$, df = 1 and 25, $P = 0.028$; Fig. 4). The interaction term locality × dominance was not significant ($F = 0.25$, df = 1 and 25, $P = 0.620$). Feather mass asymmetry did not covary significantly with pectoralis muscle thickness ($R^2 = 0.094$, $F = 2.62$, df = 1 and 25, $P = 0.118$). The interaction between this covariate and the locality and dominance factors also was not significant (parallelism test, $F = 0.58$, df = 7 and 18, $P = 0.760$). Partitioning the variance by factors and covariates, body condition explained only 7.2%, locality 0.0%, dominance 21.5%, and the interaction locality × dominance 2.1% of the variance in asymmetry of induced feathers. That is to say, mass asymmetry of induced feathers was not associated with body condition, nor did it change between localities, but it was directly associated with dominance (higher asymmetry in less-dominant birds).

Synthetic analysis of covariation among parameters.—The covariance matrices of the variables we considered (see Table 2) differed significantly between localities (Box's M test, $M =$

TABLE 2. Significant factor loadings ($P < 0.01$) from principal components analysis based on Great Tits captured at El Ventorrillo ($n = 15$) and Sarriá ($n = 19$), Spain.

Variable	PC1	PC2	PC3
El Ventorrillo			
Tarsus length	0.83		
% of time foraging at feeders	0.68		
Pectoralis muscle thickness	0.94		
Induced feather growth rate	0.82		
% symmetry of induced feathers		0.99	
Eigenvalue	1.51	1.50	
% variance explained	54.40	22.40	
Sarriá			
Tarsus length		0.90	
% of time foraging at feeders			0.95
Pectoralis muscle thickness		0.81	
Induced feather growth rate	0.87		
% symmetry of induced feathers	0.87		
Eigenvalue	1.51	1.50	1.11
% variance explained	30.20	30.00	22.20

39.74, $\chi^2 = 32.98$, $P = 0.005$). Therefore, the covariation pattern among variables describing bird size (measured by tarsus length), access to supplemental food, body condition, feather growth rate, and asymmetry was different at Sarriá and El Ventorrillo. The covariation among these variables was summarized in two different principal components analyses (Table 2).

At El Ventorrillo (the locality with higher environmental harshness), the first principal component (54% of total variance) included four significant variables, showing that larger Great Tits spent more time foraging on feeders, had a thicker pectoralis muscle (i.e. better body condition), and grew the induced feathers at a higher rate (Table 2). The second principal component (22% of total variance) included only feather-mass asymmetry (i.e. this variable was independent of the others).

At Sarriá, three significant components (eigenvalues > 1) were extracted. The first component (30% of total variance) showed that Great Tits with higher growth rates of induced feathers also grew their feathers more asymmetrically. The second component (30% of total variance) indicated that larger Great Tits had a thicker pectoralis muscle. Finally, the third component (22% of total variance) was significantly related only to percentage of time spent at feeders. Therefore, in the less-stressful locality, the use of supplemental food did not affect body condition, and body condition did not affect growth of induced feathers (i.e. nutritional status).

DISCUSSION

The growth rate of induced feathers was lower at the wintering locality that was colder, contained a lower availability of natural food, and at which Great Tits experienced stronger competitive pressure from conspecifics (i.e. they spent more time at feeders and experienced a 150-fold increase in hostile interactions at El Ventorrillo vs. Sarriá). Although protein reserves (measured as pectoralis muscle thickness) were higher at El Ventorrillo than at Sarriá, the difference did not parallel the difference between the two localities in growth rate of induced feathers. Moreover, protein reserves were not consistently correlated with induced feather growth across individuals at both localities. Thus, nutritional status had no clear and straightforward effect on growth of induced feathers (Murphy and King 1991, Murphy 1992).

The important point, however, is that the effect of environmental stress on feather growth varied according to the competitive ability of individuals (i.e. dominance status). The enhanced access to supplemental food by adult males at El Ventorrillo seemed to compensate for higher environmental stress, because these birds achieved a higher feather growth rate more similar to that observed at Sarriá, the locality with a milder climate. This was not the case for the three other sex/age classes. The higher dominance of adult male Great Tits, which appeared comparatively immune to the demands of the autumn and winter conditions, also has been described for the molting period (Gosler 1994) and is consistent with the view that dominant individuals are in good condition in all circumstances. The addition of supplemental food in autumn/winter probably had a marked effect on the subordinate fraction only at the locality with milder climate (i.e. Sarriá), because subordinates attained the same level of feather growth rate as adult males (see also Grubb 1989, Grubb and Cimprich 1990). Therefore, we conclude that under mild environmental conditions (i.e. coastal Mediterranean climate), all individuals manage reasonably well to fulfill the energetic and nutritive demands brought about by autumn and winter conditions; when environmental conditions deteriorate and competition for food increases, however, only the top-ranking birds succeed.

Our results that protein reserves increase with increasing dominance apparently contrast with studies that have shown that subordinate individuals carry larger fat stores than dominant individuals (e.g. Ekman and Lilliendahl 1993, Witter and Swaddle 1995, Gosler 1996). However, the acquisition of fat stores and protein reserves are subjected to different processes and are used under different time scales. Fat reserves are generated and used on a short-term basis in response to proximate energetic requirements (e.g. nocturnal fasting, unpredictable food, lower ambient temperatures; Blem 1990, Bednekoff et al. 1994, Bednekoff and Houston 1994). One way subordinates have to overcome periods of reduced food access owing to displacement at feeders by dominants is to gain large amounts of fat in short periods when food access is not constrained. The higher fat reserves of subordinates may help to cope with periods of food inaccessibility due to intraspecific interactions. Dominants do not need to carry large fat stores because they have good access to food even during harsh periods (Ekman and Lilliendahl 1993, Clark and Ekman 1995, Gosler 1996). Moreover, fat reserves have additional costs that could affect winter survival, i.e. diminished maneuverability and increased risk of predation (Witter and Cuthill 1993, Ekman and Lilliendahl 1993, Witter et al. 1994, Clark and Ekman 1995, Gosler et al. 1995, Metcalfe and Ure 1995). On the other hand, protein reserves are gathered on a long-term basis and result from good nutritional condition obtained through unrestricted access to food of high quality (Blem 1990, Murphy 1996b). Foraging in the better feeding places (with respect to both food abundance and quality) during long periods (e.g. autumn/winter) and under low food availability is achieved mainly by birds with high positions in the dominance hierarchy. Therefore, dominant birds are able to maintain a good body condition gained during longer time periods.

Although the effect of locality was strong on growth rate of induced feathers (67% of total variance), it had no influence on the asymmetry of induced feathers (0% of variance). We know of no hypothesis that explains this contrasting result, especially considering that dominance has a clear effect on increments in feather asymmetry. One possibility is that the developmental stability of regenerating feathers outside of the normal molting period is lower due to physiological stress. This stress would be attributable to low food availability with high protein content (e.g. arthropods and other foods with sulfur amino acids) because malnutrition may occur when food is abundant but of poor quality (Murphy 1996b). Ambient temperatures below the critical lower temperature (i.e. 18 to 21°C in small passerines; Calder and King 1974, Kendeigh et al 1977) also may exacerbate physiological stress by increasing thermoregulatory demands. These differences would impose a common threshold on fluctuating asymmetry. Only factors that increase the stress experienced by individuals would reduce developmental stability. Our results suggest that dominance is one of these factors.

The marked effect of dominance on asymmetry of induced feathers shows that not all individuals in the population are subjected to similar levels of stress. As shown in Figure 4, the efficiency of developmental stability mechanisms was lower in juvenile females than in adult females, and in both age classes of females compared with males. This pattern did not change between localities. A likely explanation for this is that subordinate individuals had a more limited and uneven access to food (Shawcross 1982, De Laet 1985, Ficken et al. 1990, Ramenofsky et al. 1992) and therefore suffered more frequent episodes of starvation, especially early in the morning after fasting all night. The limitations on food access imposed by dominant individuals on subordinates probably destabilize the physiological processes involved in feather growth, thus increasing asymmetry of induced feathers. Our results agree with Clarke's (1995) review in that fluctuating asymmetry in induced feathers showed a greater sensitivity to stress that resulted from dominance relationships than did the classic measure of growth rate of induced feathers.

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LITERATURE CITED

BEDNEKOFF, P. A., H. BIEBACH, AND J. R. KREBS. 1994. Great Tit fat reserves under unpredictable temperatures. Journal of Avian Biology 25:156–160.

BEDNEKOFF, P. A., AND A. I. HOUSTON. 1994. Optimizing fat reserves over the entire winter: A dynamic model. Oikos 71:408–415.

BEDNEKOFF, P. A., AND J. R. KREBS. 1995. Great Tit fat reserves: Effects of changing and unpredictable feeding day length. Functional Ecology 9:457–462.

BLEM, C. R. 1990. Avian energy storage. Current Ornithology 7:59–113.

BRYANT, D. M., C. J. HAILS, AND R. PRYS-JONES. 1985. Energy expenditure by free-living Dippers (*Cinclus cinclus*) in winter. Condor 87:177–186.

CALDER, W. A., AND J. R. KING. 1974. Thermal and caloric relations of birds. Pages 259–413 *in* Avian biology, vol. 4 (D.S. Farner, and J.R. King, Eds.). Academic Press, New York.

CARACO, T., C. BARKAN, J. L. BEACHAM, L. BRISBIN, S. L. LIMA, A. MOHAN, J. A. NEWMAN, W. WEBB, AND M. L. WITHIAM. 1989. Dominance and social foraging: A laboratory study. Animal Behaviour 38:41–58.

CARRASCAL, L. M., AND E. MORENO. 1992. Proximal costs and benefits of heterospecific social foraging in the Great Tit, *Parus major*. Canadian Journal of Zoology 70:1947–1952.

CARRASCAL, L. M., AND J. L. TELLERÍA. 1985. Estudio multidimensional del uso del espacio en un grupo de aves insectívoras forestales durante el invierno. Ardeola 32:65–113.

CLARK, C. W., AND J. B. EKMAN. 1995. Dominant and subordinate fattening strategies: A dynamic game. Oikos 72:205–212.

CLARKE, G. M. 1992. Fluctuating asymmetry: A technique for measuring developmental stress of genetic and environmental origin. Acta Zoologica Fennica 191:31–35.

CLARKE, G. M. 1995. Relationships between developmental stability and fitness: Application for conservation biology. Conservation Biology 9: 18–24.

COOPER, R. J., AND R. C. WHITMORE. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology 13:29–37.

CUMMINGS, K. W., AND J. C. WUYCHECK 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen Internationale Vereinigung Limnologie 18.

DE LAET, J. F. 1985. Dominance and anti-predator behaviour of Great Tits *Parus major*: A field study. Ibis 127:372–377.

DESROCHERS, A. 1989. Sex, dominance, and microhabitat use in wintering Black-capped Chickadees: A field experiment. Ecology 70:636–646.

DRENT, P. J. 1983. The functional ethology of territoriality on the Great Tit (*Parus major*). Ph.D. thesis, University of Groningen, Groningen, The Netherlands.

EKMAN, J., A. BRODIN, A. BYLIN, AND B. SKLEPKOVYCH. 1996. Selfish long-term benefits of hoarding in the Siberian Jay. Behavioral Ecology 7:140–144.

EKMAN, J. B. 1989. Ecology of non-breeding social systems of *Parus*. Wilson Bulletin 101:263–288.

EKMAN, J. B., AND C. E. H. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. Animal Behaviour 32:508–514.

EKMAN, J. B., AND K. LILLIENDAHL. 1993. Using priority to food access: Fattening strategies in dominance-structured Willow Tit (*Parus montanus*) flocks. Behavioral Ecology 4:232–238.

ENOKSSON, B. 1988. Age- and sex-related differences in dominance and foraging behaviour of Nuthatches *Sitta europaea*. Animal Behaviour 36:231–238.

FICKEN, M. S., C. M. WEISE, AND J. W. POPP. 1990. Dominance rank and resource access in winter flocks of Black-capped Chickadees. Wilson Bulletin 102:623–633.

GAUTHREAUX, S. A. 1978. The ecological significance of behavioural dominance. Perspectives in Ethology 3:17–54.

GINN, H. B., AND D. S. MELVILLE. 1983. Moult in birds. British Trust for Ornithology, Tring, United Kingdom.

GOSLER, A. G. 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. Bird Study 38:1–9.

GOSLER, A. G. 1993. The Great Tit. Hamlyn, London.

GOSLER, A. G. 1994. Mass-change during moult in the Great Tit *Parus major*. Bird Study 41:146–154.

GOSLER, A. G. 1996. Environmental and social determinants of winter fat storage in the Great Tit *Parus major*. Journal of Animal Ecology 65:1–17.

GOSLER, A. G., J. D. D. GREENWOOD, AND C. PERRINS. 1995. Predation risk and the cost of being fat. Nature 377:621–623.

GRUBB, T. C. 1989. Ptilochronology: Feather growth bars as indicators of nutritional status. Auk 106: 314–320.

GRUBB, T. C. 1995. Ptilochronology. A review and prospectus. Current Ornithology 12:89–114.

GRUBB, T. C., AND D. A. CIMPRICH. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: Evidence from ptilochronology. Ornis Scandinavica 21:277–281.

GRUBB, T. C., T. A. WAITE, AND A. J. WISEMAN. 1991. Ptilochronology: Induced feather growth in Northern Cardinals varies with age, sex, ambient temperature, and day length. Wilson Bulletin 103:435–445.

GRUBB, T. C., AND R. YOSEF. 1994. Habitat-specific nutritional condition in Loggerhead Shrikes (*Lanius ludovicianus*): Evidence from ptilochronology. Auk 111:756–759.

HERRERA, C. M. 1979. Ecological aspects of heterospecific flocks formation in a Mediterranean passerine bird community. Oikos 33:85–96.

HOGSTAD, O. 1988. Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. Ornis Scandinavica 19:169–174.

HOGSTAD, O. 1989. Social organization and dominance behavior in some *Parus* species. Wilson Bulletin 101:254–262.

HOGSTAD, O. 1992. Mate protection in alpha pairs of wintering Willow Tits, *Parus montanus*. Animal Behaviour 43:323–328.

JENNI, L., AND R. WINKLER. 1994. Moult and aging of European passerines. Academic Press, London.

JENNI-EIERMANN, S., AND L. JENNI. 1996. Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. Functional Ecology 10:62–72.

KARASOV, W. H. 1990. Digestion in birds: Chemical and physiological determinants and ecological implications. Studies in Avian Biology 13:391–415.

KENDEIGH, S. C., V. R. DOLNIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pages 127–204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge University Press, Cambridge, United Kingdom.

LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. Auk 104: 116–121.

LILLIENDAHL, K., A. CARLSON, J. WELANDER, AND J. B. EKMAN. 1996. Behavioural control of daily fattening in Great Tits (*Parus major*). Canadian Journal of Zoology 74:1612–1616.

LIMA, S.L. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. Ecology 67:377–385.

LUNDBERG, P. 1985. Dominance behavior, body weight and fat variations, and partial migration in European Blackbirds *Turdus merula*. Behavioral Ecology and Sociobiology 17:185–189.

MATTHYSEN, E. 1990. Nonbreeding social organization in *Parus*. Current Ornithology 7:209–249.

MERILÄ, J., AND M. BJÖRKLUND. 1995. Fluctuating asymmetry and measurement error. Systematic Biology 44:97–101.

METCALFE, N. B., AND S. E. URE. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society of London Series B 261:395–400.

MILLIKAN, G. C., P. GADDIS, AND H. R. PULLIAM. 1985. Interspecific dominance and the foraging behaviour of juncos. Animal Behaviour 33:428–435.

MORENO, E., AND L.M. CARRASCAL. 1991. Patch residence time and vigilance in birds foraging at feeders. Implications of bill shape. Ethology, Ecology and Evolution 3:345–350.

MURPHY, M. E. 1992. Ptilochronology: Accuracy and reliability of the technique. Auk 109:676–680.

MURPHY, M. E. 1996a. Energetics and nutrition of molt. Pages 158–198 *in* Avian energetics and nutritional ecology (C. Carey, Ed.). Chapman and Hall, New York.

MURPHY, M. E. 1996b. Nutrition and metabolism. Pages 31–60 *in* Avian energetics and nutritional ecology (C. Carey, Ed.). Chapman and Hall, New York.

MURPHY, M.E., AND J.R. KING. 1991. Ptilochronology: A critical evaluation of assumptions and utility. Auk 108:695–704.

NEWTON, S. F. 1993. Body condition of a small passerine bird: Ultrasonic assessment and significance in overwinter survival. Journal of Zoology (London) 229:561–580.

NILSSON, J. A., H. KÄLLANDER, AND O. PERSSON. 1993. A prudent hoarder: Effects of long-term hoarding in the European Nuthatch, *Sitta europaea*. Behavioral Ecology 4:369–373.

OBESO, J. R. 1987. Uso del espacio y alimentación de los *Parus* spp. En bosques mixtos de la Sierra de Cazorla. Ardeola 34:61–77.

PIPER, W. H., AND R. H. WILEY. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-thoated Sparrows (*Zonotrichia albicollis*). Behavioral Ecology and Sociobiology 26:201–208.

POLAK, M., AND R. TRIVERS. 1994. The science of symmetry in biology. Trends in Ecology and Evolution 9:122–124.

PÖYSÄ, H. 1988. Feeding consequences of the dominance status in Great Tit *Parus major* groups. Ornis Fennica 65:69–75.

RAMENOFSKY, M., J. M. GRAY, AND R. B. JOHNSON 1992. Behavioral and physiological adjustments of birds living in winter flocks. Ornis Scandinavica 23:371–380.

ROGERS, C. M. 1995. Experimental evidence for temperature-dependent winter lipid storage in the Dark-eyed Junco (*Junco hyemalis oreganus*) and Song Sparrow (*Melospiza melodia morphna*). Physiological Zoology 68:277–289.

SAITOU, T. 1979. Ecological study of social organization in the Great Tit, *Parus major* L. III. Home range of the basic flocks and dominance relationship of the members in a basic flock. Journal of the Yamashina Institute for Ornithology 11: 149–171.

SANDELL, M., AND H. SMITH. 1991. Dominance, prior occupancy, and winter residency in the Great Tit, *Parus major.* Behavioral Ecology and Sociobiology 29:147–152.

SHAWCROSS, J. E 1982. Agonistic behaviour over food and perch space in male *Quelea quelea.* Animal Behaviour 30:901–908.

STATSOFT, INC. 1996. STATISTICA for Windows. Tulsa, Oklahoma.

SVENSSON, L. 1992. Identification guide to European passerines, 2nd ed. Published by author, Stockholm, Sweden.

SWADDLE, J. P., AND M. WITTER. 1994. Food, feathers and fluctuating asymmetries. Proceedings of the Royal Society of London Series B 255:147–152.

SWADDLE, J. P., M. WITTER, AND I. C. CUTHILL. 1994. The analysis of fluctuating asymmetry. Animal Behaviour 48:986–989.

THEIMER, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate Dark-eyed Juncos, *Junco hyemalis.* Animal Behaviour 35:1883–1890.

WHITE, D. W., E. D. KENNEDY, AND P. C. STOUFFER. 1991. Feather regrowth in female European Starlings rearing broods of different sizes. Auk 108: 889–895.

WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London Series B 340:73–92.

WITTER, M. S., I. C. CUTHILL, AND R. H. C. BONSER. 1994. Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris.* Animal Behaviour 48:201–222.

WITTER, M. S., AND J. P. SWADDLE. 1995. Dominance, competition, and energetic reserves in the European Starling, *Sturnus vulgaris.* Behavioral Ecology 6:343–348.

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