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

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[ABSTRACT] [INTRODUCTION] [METHODS] [RESULTS] [DISCUSSION] [REFERENCES] [Acknowledgments] [OTHER LINKS]

Abstract.— Body condition and feather growth rate of Great Tits (*Parus major*) were studied in relation to dominance in two contrasting Mediterranean localites during late autumn and early winter. The two localities differed in altitude, ambient temperatures (100 vs 1500 m a.s.l., and 11.7 ºC vs 4.6 ºC, respectively) and arthropod availability. The two study areas were similarly food supplemented (husked peanuts) throughout the study period. Percentage of time spent at feeders was higher at El Ventorrillo (the locality with colder climate and less natural food availability), and was associated with dominance only in this locality. Number of aggressive displacements per hour suffered by each individual was higher (150-fold greater) in the area with less arthropod availability and lower temperatures. Protein reserves measured as pectoralis muscle thickness was higher at El Ventorrillo, and was positively and consistently related to dominance in both localities. Growth rate of induced feathers was slower in the locality that was colder and had less natural food availability (El Ventorrillo), but was not clearly and directly related to dominance in both localities. Only dominant adult males in El Ventorrillo could compensate the higher environmental harshness of this locality attaining a higher feather growth rate than the other sex-age classes. Feather mass asymmetry during autumn was not associated with body condition, did not change between localities, and was inversely and consistently related to dominance in both localities. The covariation pattern among variables describing bird size, access to supplemented food, body condition, feather growth rate and asymmetry was different in both localities. Only in the locality with colder temperatures and lower arthropod food availability (El Ventorrillo) larger, more dominant, Great Tits spent more time foraging on feeders, had a thicker pectoralis muscle (i.e. body condition), and grew the induced feathers at a higher rate.

INTRODUCTION

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 food access and body condition (e.g. Gauthreaux 1978, Piper and Wiley 1990, Lundberg 1985). The role of these variables in food access has been studied extensively (e.g. Krebs et al. 1972, 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 its 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 and Houston 1994a, b, Rogers 1995, Gosler 1996, Lilliendahl et al. 1996). However, several studies have suggested that fat reserves have costs in terms of winter survival, diminished maneuverability and increased predation risk (e.g. Lima 1986, McNamara and Houston 1990, Witter and Cuthill 1993, Ekman and Lilliendahl 1993, Witter et al. 1994, Gosler et al. 1995, Clark and Ekman 1995, Metcalfe and Ure 1995, Hake 1996). Therefore, fat storing may be subjected to different 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 depots and dominance in winter (e.g. Ekman and Lilliendahl 1993, Witter and Swaddel 1995, Gosler 1996).

Protein reserves are not viewed as short-term energy stores because they are not easily mobilized and are not maintained as special depots. Muscle proteins are used only after both glycogen and lipid reserves are nearly or completely exhausted (Blem 1990 and references therein). 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 are assembled into feather proteins (Murphy 1996a). The breadth of feather growth bars is increasingly being used as an indicator of long-term nutritional status in winter populations (Grubb 1989, Grubb and Cimprich 1990, Waite 1990, Grubb 1991, White et al. 1991, Hogstad 1992, Nilsson et al. 1993, Brodin and Ekman 1994, Hill and Montgomerie 1994, Grubb 1995, Ekman et al. 1996). Moreover, fluctuating asymmetry on the growth of right and left side feathers also 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 daily rate and to a greater total length and mass at higher ambient temperatures (Grubb et al. 1991; but see Grubb 1995). A significant seasonal effect also appears, with more rapid growth 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 1994). 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 all these factors is as important as the 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 and 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 access, body condition, and nutritional/ physiological state of Great Tits (*Parus major*). The Great Tit is a widely distributed species throughout the Palearctic region, although its winter ecology has been studied most frequently in northern latitudes or areas with very cold climate (Ekman 1989, Hogstad 1989, Matthysen 1990, Gosler 1993, 1996, Bednekoff and Krebs 1995, and references therein; but see Herrera 1979 and Carrascal and Moreno 1992).

Two different Mediterranean populations have been monitored at two contrasting wintering areas. The two localities differ in mean ambient temperature, and in 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 are 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 where small passerines have usually been studied. We predict 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

predict that in the colder area with lower food availability, Great Tits should rely more intensely on supplemented 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 predict that dominant individuals should have higher levels of indices that measure long-term nutritional status (e.g. protein reserves and induced feather growth) due to their better competitive abilities when interacting for access to food.

Additionally, we test if 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 less food availability, in less dominant individuals, and in individuals with lower body condition (see Swaddle and Witter 1994).

STUDY AREAS AND METHODS

Study areas.—Field work was carried out from November 1994 to January 1995 at two field stations, El Ventorrillo and Desert de Sarriá (hereafter Sarriá). The area at El Ventorrillo was a 6 ha mixed montane coniferous forest of *Pinus sylvestris, Castanea sativa,* and *Acer* spp. of continental cold Mediterranean climate (1500 m a.s.l., 40o45'N 04O01'W, Sierra de Guadarrama, Central Spain). The area at Sarriá occupied 3 ha of orchards and a mixed coniferous forest of *Pinus halepensis* and *Cedrus* sp. of coastal mild Mediterranean climate (100 m a.s.l., 41o25'N 02o10'W, Barcelona, NE Spain). Mean daily minimum temperatures, and mean daily temperatures during the study period were, respectively, 9.9 oC / 11.7 oC in Sarriá and 1.2 oC / 4.6 oC in El Ventorrillo (meteorological data were obtained from the weather stations closest to each plot —at less than 5 km—) .

Arthropod availability.—During the sampling period, Great Tits mainly fed on arthropods and seeds found in the ground and outer parts of tree canopy (Herrera 1979, Carrascal and Tellería 1985, Obeso 1987). The relative abundance of arthropods was measured in the ground and pine foliage (twigs and needles) in both localities. Arthropod abundance was evaluated by carefully searching and counting invertebrates larger than 1 mm over 2 min in pine foliage and on the ground (see Cooper and Whitmore 1990). We also annotated the size of each arthropod counted considering the following length categories: 1-2 mm, 3-5 mm, and 6-10 mm. Samples were obtained by random sampling in the pine foliage and on the ground in both study areas. The most common taxa in the ground samples (and therefore those more probably consumed by Great Tits) were Arachnida, Diptera, and Hemiptera, and in the foliage Diptera, Arachnida, and Coleoptera.

Box-feeders and bird trapping.—Supplemented food (husked peanuts) was available throughout the study period (i.e. feeders were replenished before they were emptied). Feeders were wooden boxes with one side (20 x 11 cm) covered by a 4.8 mm mesh plastic net allowing birds access to food. Feeders had the net covering one side so a bird feeding on it had to be clinging back lateral. They were suspended from pine branches approximately 50 cm below the canopy and 2-4 m above ground. To gather food, birds remained handling the peanuts through the plastic net to obtain small pieces. Average time spent on feeders per foraging bout was approximately 100 s (Moreno and Carrascal 1991). To equate the amount of food provided at the two field stations, equal number of feeders per ha were established (four feeders at El Ventorrillo and two feeders at Sarriá).

During the first two weeks of November we trapped, using [especially designed funnel-traps](#), 20 Great Tits in Sarriá (three adult males, three adult females, seven juvenile males and seven juvenile females) and 18 in El Ventorrillo (six adult males, three adult females, four juvenile males and five juvenile females). The distribution of the four categories of sex-age did not significantly differ between both localities (chi2 = 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). The period of adult Great Tit molt extends from June to September, and is complete. Nearly all juveniles also molt rectrices during this period (Gosler 1993, Jenni and Winkler 1994, J.C. Senar pers. obs.). Therefore, all the birds had completed postbreeding molt at the sampling period. We determined body mass to the nearest 0.01 g with an electronic balance. Tarsus length was measured to the nearest 0.01 mm with a digital caliper. Tail length and wind chord was measured with a ruler to the nearest 1 mm.

Ptilocronology.—Before releasing each bird at the capture site, we plucked the right and left fifth rectrix (R5, L5). Because the extraction of the outermost pair of the twelve rectrices could affect the maneuverability of birds while flying, we selected the second of the outermost rectrices. Birds were recaptured 45 to 60 days later and 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 lack of feather sheaths (Ginn and Melville 1983), and lack of blood in the part of the shaft within the follicle. We examined original and induced feathers for length, mass and growth bar width. Average [growth bar](#) width was calculated for the first 10 growth bars clearly visible from the distal part on each feather (usually beginning 3 to 4 mm from the distal 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 end of 10 growth bars. The distance between the two marks was then measured with a caliper to the nearest 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 of all feathers). This value was divided by ten to give an estimate of the mean rate of feather growth per day.

Daily growth rate of induced feathers was estimated as the average of left and right feathers growth rates and was expressed in mm/day. Daily growth bar width of the original (summer) feathers did not significantly differ between Sarriá and El Ventorrillo (F = 0.05, df = 1 and 36, P = 0.830), and was not related to induced feather growth either in Sarriá (r = 0.104, n = 20, P = 0.662) or in El Ventorrillo (r = 0.300, n = 18, P = 0.226). In order to standardize results among conspecifics controlling for intraspecific differences prior to the experimental removal of feathers (uncontrolled differences in food intake rate, body condition, health status, etc. in summer grown feathers), we also calculated an index by dividing the daily growth bar width of the induced feather (DGI) by the daily growth bar width of the original feather (DGO; index DGI/DGO; Grubb 1989, Hogstad 1992, Nilsson et al. 1993). As results of induced feather growth rates using mm/day and DGI/DGO were highly consistent in ANCOVAs performed in the next section (Results), we will only show results obtained with mm/day data to attain simplicity (see Ekman et al. 1996 for a similar approach).

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 estimations (differences between right-left feathers), and asymmetry estimations were not significantly repeatable (checked performing the 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 can not distinguish true asymmetry from measurement error (violation of point 2 in Swaddle et al. 1994).

To overcome this problem we used the masses of right and left 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 weight was done after the completion of the first weight of all feathers). Repeatabilities (r_I; see Zar 1984; Lessells and Boag 1987) of the weights of left (r_I = 0.98) and right (r_I = 0.99) feathers were very high (n = 38 birds). Estimated asymmetry was also very repeatable, as it was significantly higher than expected from the estimated measurement error (F = 3.453, df = 37 and 74, P < 0.001; mixed model ANOVA proposed by Swaddle et al. 1994). The asymmetry of feathers (difference of weights 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 (one-sample 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 percentage asymmetry index by dividing the absolute difference in weight between left (L) and right (R) feathers by their mean:

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

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

Body condition.—Ultrasound was used for estimations of [pectoral muscle mass](#) following the protocol proposed by Newton (1993). We used a portable Krautkrämer device. 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). Throughout the study period the Great Tits were captured several times ($n = 3$ to 35) using funnel-traps; ultrasound measurements and body masses were obtained. All estimates obtained for each individual bird on different days were averaged.

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 estimation of pectoral muscle thickness has not been significantly associated with an index of the visible amount of subcutaneous fat in the furcular depression in the Great Tit at El Ventorrillo during autumn-winter (L.M. Carrascal unpubl. data; $R^2 = 0.04$, $n = 63$ individual birds sampled in 3 consecutive years, $P = 0.100$). Therefore, our estimation of muscular thickness provides an index of body condition not related to fat reserves, and can be seen as a relatively stable estimation of body condition within the sampling period, and probably associated with muscular strength and regeneration of induced feathers by providing the amino acids which are assembled into feather proteins (Gosler 1991).

Use of supplemental food and intensity of aggressions.—Estimation of differential Great Tit competitive aggressiveness and intensity of use of supplemental food between the two localities was obtained by video-taping the feeders and recording total time spent feeding and the number of aggressive displacements experienced by individuals. Tripod-mounted zoom-videocameras were located at 2 to 4 m from box-feeders. Colour bands in the legs of the Great Tits were clearly visible, so it was possible to identify individual birds. As a general measure of competitive pressure 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 were able to obtain a gross measure of intake rate by pooling the data for all individuals. We noted the approximate size and the number of small pieces of peanuts Great Tits extracted from box-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 also Gosler 1996). Great Tit males 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 in El Ventorrillo where Great Tit dominance hierarchy was established as male-adult > male-juvenile > female-adult > female-juvenile (total number of dyadic interactions $= 179$; from the dyadic interactions observed between male-juveniles and female-adults, in 75 % of occasions males displaced females, and in 25 % of occasions females displaced males). Individual dominance scores could only be calculated for El Ventorrillo population (ten levels for 18 birds). Interaction rates were too low to provide adequate data for Sarriá population. The lack of information on dominance hierarchy in Sarriá precluded the analysis of the effect of dominance scores on box-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 dominance hierarchy, as the ordination of sex and age classes explained 91.2% of variance observed in El Ventorrillo in dominance scores ($F = 166.69$, df $= 1$ and 16, $n = 18$ birds, $P < 0.001$).

Statistical analyses.—Biometrical differences between the two populations were examined by means of *t*-tests. The effects of locality and dominance were analyzed with two-way ANCOVAs, using a linear contrast for the dominance factor. Although Figures 1-4 show original non-transformed data, [ANCOVA](#)s were performed with variables arc-sin-transformed (in the case

of percentages) or Box-Cox-transformed (in the case of feather mass asymmetry) to attain homocedasticity 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 non-zero asymmetry value; Swaddle et al. 1994). Due to the lack of normality and homocedasticity in the number of aggressive displacements suffered by individuals, the difference between localities in this variable was analyzed by means of the non-parametric Mann-Whitney test. The same non-parametric test was used with data on arthropod availability.

Patterns of covariation among variables (body size, percentage of time spent foraging in feeders, body condition, induced feather growth, and feather mass asymmetry) within each locality were revealed by principal components analyses after having 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 higher than 1 were considered. To check for homogeneity of covariance matrixes for multiple dependent variables we used the Box M test. As the Box M test is very sensitive to deviations from the normal distribution, we verified that all variables did not significantly differ from normality by means of the Shapiro-Wilk's test (StatSoft Inc. 1996). All statistical analyses were carried out using STATISTICA 5.0 of StatSoft.

RESULTS

Biometrical measurements of the populations of Sarriá and El Ventorrillo were not significantly different in either tarsus length, wing length, tail length or body mass (see Table 1).

Arthropod availability.—Arthropod abundance was significantly lower in the pine foliage (twigs and needles) of El Ventorrillo than in Sarriá (Mann-Whitney test: $Z = 2.65$, $p = 0.008$; mean $\pm$ one SD: El Ventorrillo 0.52 ± 1.08, $n = 20$; Sarriá 2.62 ± 4.21, $n = 13$), but it was similar on the ground (Mann-Whitney test: $Z = 0.17$, $p = 0.864$; mean $\pm$ one SD: El Ventorrillo 2.60 ± 3.50, $n = 20$; Sarriá 2.47 ± 2.83, $n = 17$). The size distribution of arthropods was significantly different between the two localities ($chi2= 11.08$, df $= 1$, $p < 0.001$), as the percentage of prey longer than 2 mm was significantly higher in Sarriá (44.4% out of 63 prey items) than in El Ventorrillo (17.2% out of 64 prey items). Therefore, arthropod availability was higher in Sarriá.

Use of supplemental food and intensity of aggressions.—Percentage of time spent foraging at feeders (of the 45 hours of videotape sampling) was significantly higher at El Ventorrillo (ANOVA: $F = 19.57$, 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 x Dominance was marginally significant ($F = 3.98$, df $= 1$ and 30, $p = 0.055$); planned comparisons analyzing the effect of dominance carried on separately within each locality showed a non-significant 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 in El Ventorrillo the percentage of time spent foraging at feeders was on average 12 times higher, the percentage of time spent foraging at feeders was very low (< 4% ; see Figure 1). Moreover, there was no Great Tit feeding on artificial feeders in Sarria in 98% of the 45 h sampled, while this percentage dropped to 80.2 % in El Ventorrillo.

A gross estimation of the influence of artificial feeders on the energy budget of Great Tits in both localities show that Great Tits obtained on average 0.6% of their energy requirements from feeders in Sarriá, and 6.2% in El Ventorrillo (using data on caloric content of peanuts from Cummins and Wuycheck 1971, an efficiency of energy assimilation of 88% —Karasov 1990—, the allometric equation provided by Bryant et al. 1985, the intake rate of 0.03 g of peanuts per minute obtained in

feeders —see Methods— and the percentage of time Great Tits foraged in feeders).

Number of aggressive displacements suffered by each individual at box-feeders was significantly higher in El Ventorrillo than in Sarriá (Mann-Whitney test: $Z = 4.91$, $p < 0.001$; Sarriá: mean= 0.05 per 45 h, median = 0, $n = 20$, inter quartile range = 0; El Ventorrillo: mean= 6.90 per 45 h, median = 6, $n = 18$, inter quartile range = 10). Overall, birds in El Ventorrillo suffered 1.54 aggressive displacements per individual per 10 h, and in Sarriá 0.01 (i.e. birds in El Ventorrillo experienced 154 times more aggressions).

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

Body condition.— The percentage of time spent foraging in artificial feeders (covariate) did not significantly covary 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 (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 in El Ventorrillo than in Sarriá (ANCOVA: $F = 10.87$, df = 1 and 28, $p = 0.003$; Fig. 2) after controlling for the effect of percentage of time spent foraging in 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 x 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, we obtained that locality explained 21.9 %, dominance (sex-age ordination) 25.5 %, body size (tarsus length) 15.6 %, percentage of time spent foraging at feeders 1.1%, and the interaction Locality x Dominance 8.0 % of the variation observed in body condition (pectoralis muscle thickness).

In summary, body condition (measured as pectoral muscle reserves) was dependent on bird size, was better in the locality with more severe environmental conditions, and was not significantly and consistently associated with the amount of time devoted to feeding in artificial feeders. Dominance hierarchy was positively and consistently related to body condition in the two localities.

Growth and asymmetry of induced feathers.—Feather growth rates of induced feathers are shown in Fig. 3. Induced feather growth rate significantly differed between localities, being higher in Sarriá (ANCOVA: $F = 40.80$, df = 1 and 29, $p < 0.001$), but it was not related to dominance hierarchy (linear contrast: $F = 0.50$, df = 1 and 29, $p = 0.484$). The interaction Locality x Dominance was significant ($F = 4.65$, df = 1 and 29, $p=0.039$; Fig. 3). Post-hoc comparisons of means (Tukey honest significant differences for unequal sample sizes) showed that there were no significant differences in Sarriá among sex-age levels ($p > 0.6$ in the six tests), whereas growth rate of induced feathers was higher in adult males than in the other three sex-age classes in El Ventorrillo ($p < 0.050$). Pectoral muscle index (covariate) did not significantly relate 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 x covariate; $F = 0.49$, df= 7 and 22, $p = 0.825$). Partitioning the variance by factors and covariate, we obtained that body condition only explained 2.3 %, locality 67.3 %, dominance 4.8 % and the interaction Locality x Dominance 2.8 % of the variability observed in induced feather growth rate.

In summary, induced feather growth 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 studied localities, being higher only in adult males under harsh environmental conditions.

Feather weight asymmetry did not significantly change between localities (ANCOVA: $F = 0.24$, df = 1 and 25, $p = 0.628$), but it significantly decreased with increasing dominance level (linear contrast: $F = 5.45$, df = 1 and 25, $p = 0.028$; Fig. 4). The interaction term Locality x Dominance was not significant ($F = 0.25$, df = 1 and 25, $p = 0.620$). Feather weight asymmetry did not significantly covary with pectoralis muscle thickness ($R^2 = 0.094$, $F = 2.62$, df = 1 and 25, $p = 0.118$). The interaction between this covariate and factors (locality and dominance) was not significant (parallelism test: $F = 0.58$, df = 7 and 18, $p = 0.760$). Partitioning the variance by factors and covariates, we obtained that body condition only explained 7.2 %, locality 0.0 %, dominance 21.5 % and the interaction Locality x Dominance 2.1% of the variance. That is to say, mass

asymmetry of induced feathers was not associated with body condition, nor did it change between localities, but was directly associated with dominance (higher asymmetry in less dominant birds).

Synthetic analysis of covariation among parameters.— The covariance matrixes of studied variables (those in Table 2) significantly differed between both localities (Box M test: $M = 39.74$, Chi$2 = 32.98$, $P = 0.005$). Therefore, the covariation pattern among variables describing bird size (measured by tarsus length), access to supplemented food, body condition, feather growth rate and asymmetry was different in Sarriá and El Ventorrillo. The covariation among these variables was summarized in two different principal components analyses (Table 2).

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

In Sarriá, three "significant" components (eigenvalues >1) were extracted. The first component (30% of total variance) shows that those Great Tits with higher growth rates of induced feathers, also grew the feathers more asymmetrycally. The second component (30% of total variance) indicates that larger Great Tits had thicker pectoralis muscles. Finally, the third component (22% of total variance) is significantly related only to percentage of time spent at feeders. Therefore, in the less stressful locality, the use of supplemented food did not affect body condition, and body condition did not affect growth of induced feathers (i.e. nutritional status).

DISCUSSION

The comparison of the two contrasting wintering localities shows a reduction in induced feather growth rate at the colder locality, with less natural food availability, and with a stronger competitive pressure (Great Tits spent more time feeding at box-feeders, and there was about 150-fold greater number of hostile interactions at El Ventorrillo). Although protein reserves (measured as pectoralis muscle thickness) was higher in El Ventorrillo than in Sarriá, this difference did not parallel the contrast between the two localities in induced feather growth rate. Moreover, it was not consistently correlated with induced feather growth across individuals in both localities. Thus, nutritional status had no clear and straightforward effect on induced growth rate (Murphy and King 1991, Murphy 1992).

The important point, however, is that the effect of environmental stress on feather growth varied according to the differential competitive ability of individuals (i.e. their dominance status). The enhanced access to supplemented food by adult males at El Ventorrillo (Fig. 1) seems to compensate for higher environmental stress, since they achieved a higher feather growth rate more similar to those observed at Sarriá, the locality with mild climate. This was not the case for the three other age/sex classes. The greater dominance of Great Tit adult males, which appear as comparatively immune to the demands of the autumn/winter, has also been described for the moulting period (Gosler 1994), and is consistent with the view that dominants are in good condition in all circumstances. The addition of supplementary food in autumn/winter probably had a marked effect on the subordinate fraction only in the locality with mild climate (Sarriá), as subordinates were able to attain the same level of feather growth rate as adult males (see also Grubb 1989, Grubb and Cimprich 1990). It can therefore be concluded that under mild environmental conditions (coastal Mediterranean climate), all individuals manage reasonably well to fulfill the energetic and nutritive demands of the autumn/winter, but when environmental conditions deteriorate and competition for access to food increases, only top ranking birds succeed.

The result of this paper of an increasing level of protein reserves with increasing dominance apparently contrasts with those studies that have shown that subordinates carry larger fat depots than dominants (e.g., Ekman and Lilliendahl 1993, Witter and Swaddle 1995, Gosler 1996). Nevertheless, the acquisition of fat depots 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, unpredectability of food access, decrease in ambient temperature; Blem 1990, Bednekoff and Houston 1994a, b). One way subordinates have to overcome periods of reduced food access, due to dominance displacements at feeding points, 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 depots because they have assured food access even in harsh periods (Ekman and Lilliendahl 1993, Clark and Ekman 1995, Gosler 1996). Moreover, fat reserves have additional costs that could decrease winter survival, diminishing maneuverability and increasing predation risk (e.g. Lehikoinen, E. 1986, McNamara and Houston 1990, Witter and Cuthill 1993, Ekman and Lilliendahl 1993, Witter et al. 1994, Clark and Ekman 1995, Gosler et al. 1995, Metcalfe and Ure 1995, Hake 1996). On the other hand, protein reserves are gathered on a long-time basis, and are the result of good nutritional condition obtained through unrestricted food access to high quality foods (Blem 1990, Murphy 1996b). Foraging in the better feeding places (both with respect to food abundance and quality) during long periods (e.g. autumn-winter), and under low food availability, is mainly attained by birds with high positions in the hierarchy. Therefore, dominant birds are those that do not need to carry large fat reserves obtained on a short-term basis, but which are able to obtain a good body condition gained during longer time periods.

Although the effect of locality was strong on induced growth rate (accounting for 67 % of total variance), it had no influence on the asymmetry of induced feathers (0 % of variance accounted for by this effect). At the moment we know of no hypothesis for explaining this contrasting result, especially considering that dominance had a clear and significant effect on increments in feather asymmetry. One possible explanation is that regeneration of feathers outside the normal moulting period may have a lower developmental stability due to physiological stress. This physiological stress would be attributable to the very low availability of food with high proteinic content (*e.g.* arthropods and other foods containing sulfur-amino acids) because malnutrition may occur when food is abundant but of poor quality (Murphy 1996b). Ambient temperatures many degrees below the critical lower temperature (18-21°C in small passerines; Calder and King 1974, Kendeigh et al 1977) may also exacerbate physiological stress because physiological processes would displace towards thermoregulation. These differences would impose a common threshold of fluctuating asymmetry. Only other factors that increase the experienced stress would reduce developmental stability. Our results suggest that one of these factors is the dominance hierarchy.

The marked effect of dominance on induced feather asymmetry points out that all individuals within the population are not subjected to a similar level of stress. As shown by Fig. 4, the efficiency of developmental stability mechanisms was lower in juvenile females than in adult females, and in these than in males. This pattern did not change between localities. Probably, the most subordinate individuals have a more limited and uneven access to food sources (e.g. Shawcross 1982, De Laet 1985, Ficken et al. 1990, Ramenofsky et al. 1992), suffering more frequent episodes of starvation, especially early in the morning after 15 h of cold without feeding. The limitations on food access imposed by dominant individuals on subordinates probably destabilize physiological processes involved in feather growth, thus increasing asymmetry of induced feathers. The comparison of our results using growth, rate and asymmetry is in agreement with Clarke's (1995) review, in the sense that fluctuating asymmetry shows a greater sensitivity (a spaced decreasing trend) to stress introduced by the dominance relationships among individuals, than the classical measure of induced growth rate.

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Table 1. Tarsus, wing chord, tail length and body mass (mean+se) of individually marked Great Tits in El Ventorrillo and

Sarriá.

	El Ventorrillo (n = 18)	Sarriá (n = 20)	t	P
Tarsus length (mm)	19.4±0.81	19.5±0.73	0.584	0.563
Wing chord length (mm)	75.0±2.81	73.7±2.71	1.482	0.147
Tail length (mm)	62.8±2.96	62.5±3.61	0.234	0.816
Body mass (g)	17.2±1.03	16.8±1.12	1.180	0.246

Table 2. Principal components analyses performed with the studied variables in Sarriá (*n* = 19 birds) and El Ventorrillo (*n* = 15 birds; one and three individual birds lacked asymmetry estimations respectively). Only significant factor loadings (correlations between variables and components) at *P* < 0.01 are shown.

EL VENTORRILLO	PC1	PC2
Tarsus length	0.83	
% of time foraging in 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	**54.40**	**22.40**

SARRIA	PC1	PC2	PC3
Tarsus length		0.90	
% of time foraging in 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	**30.20**	**30.00**	**22.20**

Fig. 1. The effect of locality and sex-age (dominance factor) on the percentage of time spent feeding at box-feeders (mean±se). Sample sizes in parentheses. Fj: juvenile females; Fa: adult females; Mj: juvenile males; Ma: adult males.
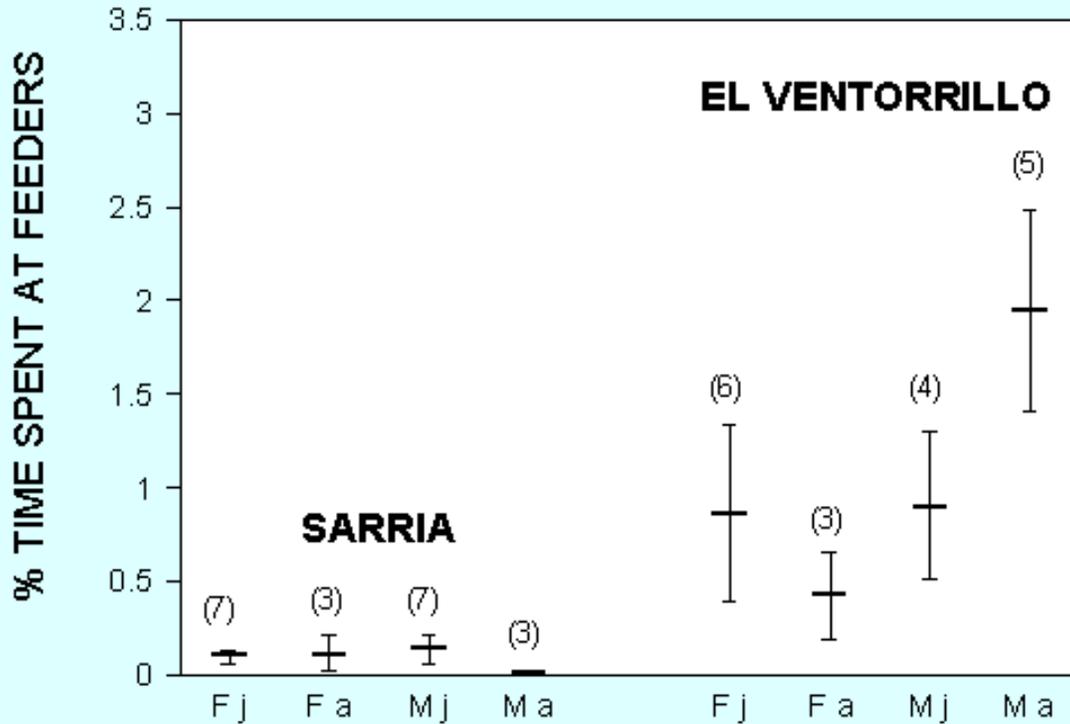

Fig. 2. The effect of locality and sex-age (dominance factor) on body condition (measured as pectoralis muscle thickness index). Vertical bars represent adjusted means (mean±se) controlling for the effect of tarsus length and percentage of time spent foraging in artificial feeders. Figures in brackets show sample size for each group. Fj: juvenile females; Fa: adult females; Mj: juvenile males; Ma: adult males.
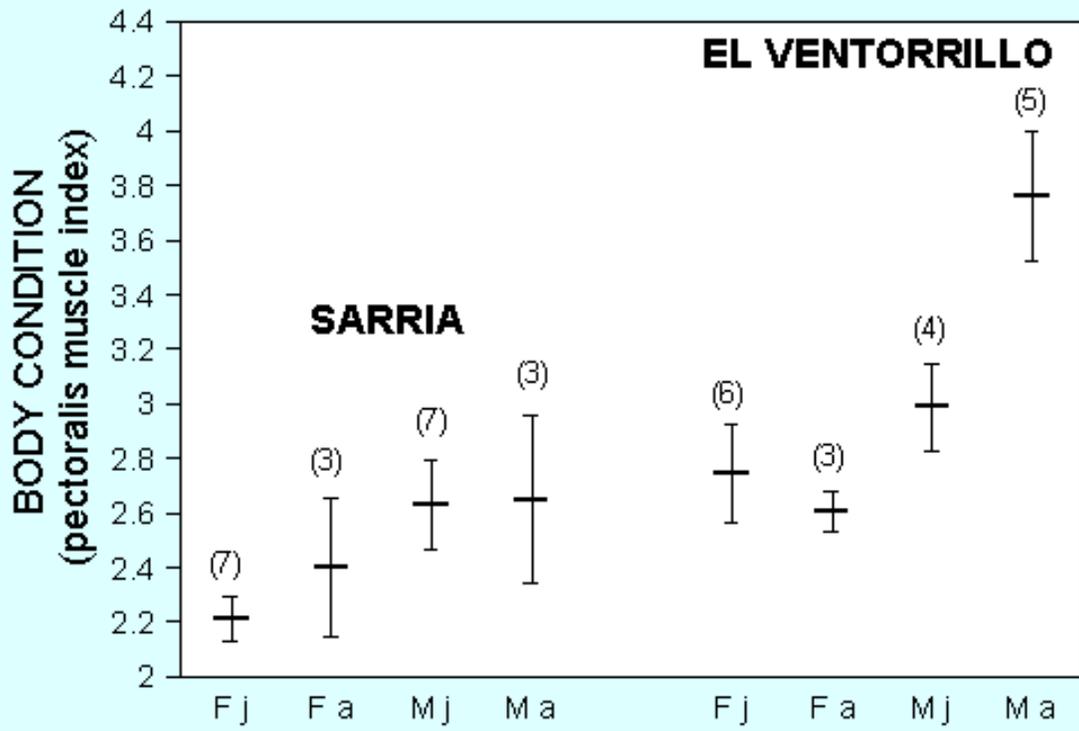
Fig. 3. The effect of locality and sex-age (dominance factor) on induced feather growth rate. Vertical bars represent adjusted means (mean+se) controlling for the effect of pectoralis muscle thickness. Figures in brackets show sample size for each group. Fj: juvenile females; Fa: adult females; Mj: juvenile males; Ma: adult males.
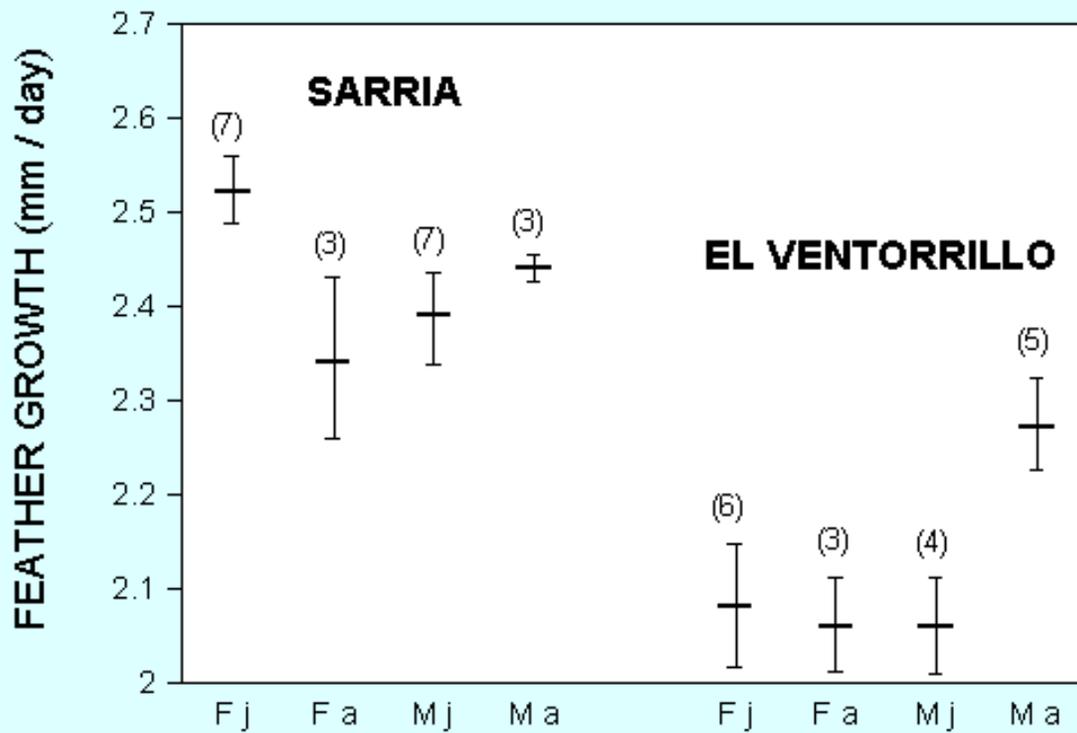
Fig. 4. The effect of locality and sex-age (dominance factor) on feather mass asymmetry of induced feathers. Vertical bars represent adjusted means (mean$\pm$se) controlling for the effect of pectoralis muscle thickness. Figures in brackets show sample size for each group. Fj: juvenile females; Fa: adult females; Mj: juvenile males; Ma: adult males.

FEATHER MASS ASYMMETRY (%)

SARRIA

EL VENTORRILLO
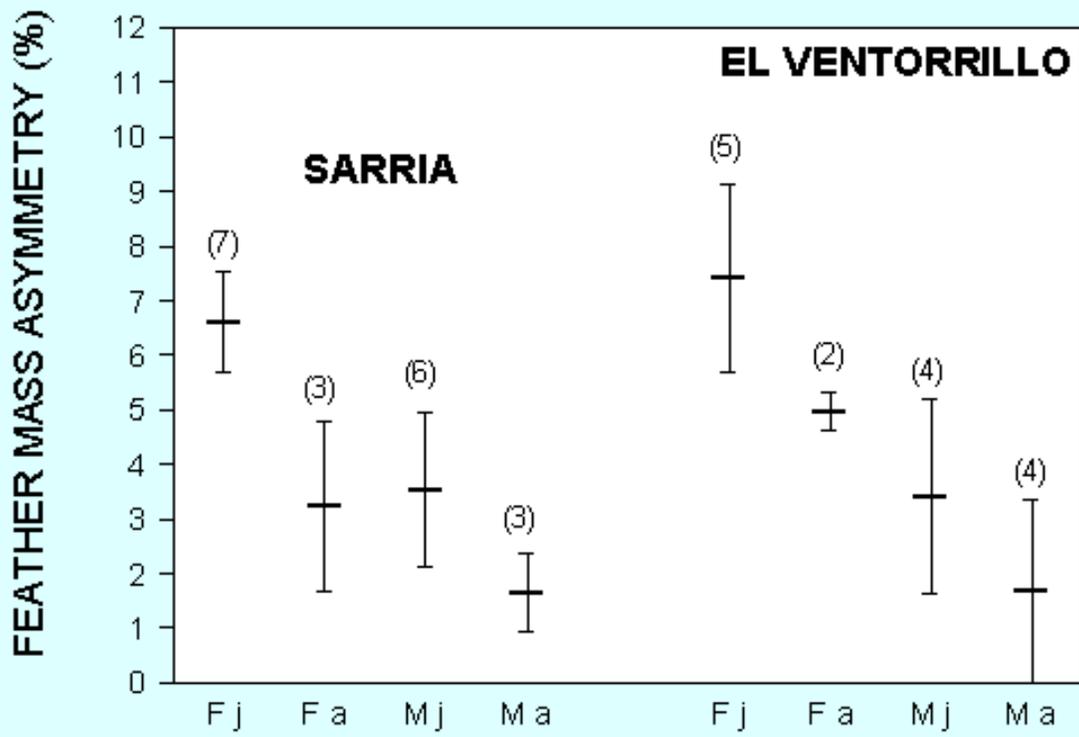
Varimax rotation: This rotation is aimed at maximizing the variances of the squared normalized factor loadings across variables for each factor; this is equivalent to maximizing the variances in the columns of the matrix of the squared normalized factor loadings. This is the method that is most commonly used and referred to as varimax rotation.

Box M: This is a multivariate test of the homogeneity of variances and covariances for multiple dependent variables or covariates. Use the Variables radio buttons to specify whether or not to include the covariates in this tests. The Box M test is very sensitive to deviations from the normal distribution and its results should be viewed with some skepticism. If this test is significant, then it means that the variance/covariance matrices in the different between-group cells in the design are significantly different from each other (see Anderson, 1958. *An introduction to multivariate statistical analysis*. New York: Wiley). In that case, one should probably examine the within-group variance/covariance matrices for any major heterogeneity problems; however, violations of this homogeneity of variances/covariances assumption usually do not seriously threaten the validity of the multivariate results.