

# Should congruence between intra- and interspecific ecomorphological relationships be expected? A case study with the great tit, *Parus major*

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## SUMMARY

We studied the relationship between leg morphology and posture while feeding in a population of great tits (*Parus major*) under controlled conditions to investigate to what extent morphology and ecology are linked at the individual level. From predictions generated at the interspecific level within the genus *Parus* (Moreno & Carrascal 1993), we tested whether intra- and interspecific ecomorphological relationships are consistent. Within our population, neither leg bone lengths nor leg muscle morphology were related to the feeding posture of individuals. However, differences in body weight were correlated with inter-individual differences in time spent hanging. These results demonstrate that the association between intra- and interspecific ecomorphological relationships is not uniform. We argue that, at the intraspecific level, body weight overrides the significance of other traits that have a functional meaning at the interspecific level (i.e. leg segment lengths, muscular morphology), due to isometric variation of morphological traits (muscular and skeletal) with body mass. Thus, the discrepancy between the ecomorphological associations at intra- and interspecific levels is the result of a problem of scale (morphological changes in evolutionary time and isometric variation of morphological traits with body mass in ecological time).

## 1. INTRODUCTION

The existence of a relationship between ecology and morphology is usually accepted as a result of evolution by natural selection being the paradigm underlying ecomorphological studies. However, some limitations of ecomorphological analyses have also been pointed out. Thus, it has been argued that morphology provides little information about niche utilization by a single individual or even a population (Ricklefs & Miles 1994; but see Grant 1986; Gosler 1987; Werner & Sherry 1987), although recent studies on ecological plasticity of morphological designs have demonstrated the importance of morphology in setting different species-specific upper and lower limits to performance (Díaz 1994; Carrascal *et al.* 1995). Few attempts have been made to study correlations among morphology, performance and ecology at the population level (but see Boag & Grant 1981; Smith 1987; Gustafsson 1988; Illius *et al.* 1995). In addition, little attention has been paid to the understanding of why or when intra- and interspecific congruence in morphology–ecology relationships might be expected (Emerson & Arnold 1989; Emerson 1991).

Moreno & Carrascal (1993) demonstrated that leg morphology and foraging behaviour are causally linked in four European tit species (*Parus* spp.). In the light of the ecomorphological hypothesis that variation in morphology correlates with differences in ecology, this paper addresses the question of whether inter-

individual variation in leg morphology of the great tit (*Parus major*) covaries with inter-individual differences in hanging, probably associated with abilities appropriate for exploiting different substrates (i.e. exploitation of the outer tree parts requires more hanging than the exploitation of the inner tree parts; Holmes *et al.* 1979; Laurent 1986; Carrascal *et al.* 1990).

Evidence has shown many times that some morphological, physiological and even behavioural characteristics of animals regularly change with changes in body mass (McMahon 1975*a, b*; Norberg 1995). While intra- and interspecific differences in morphological scaling relationships are not unusual (Lande 1979), most ecomorphological studies do not account for the likely confounding effects of body mass (but see Emerson *et al.* 1994). In this study we first consider the possibility that some differences between individuals in the hindlimb morphology might be due to scaling effects. Second, we test ecomorphological hypotheses causally linking feeding behaviour and leg morphology. We have identified deviations of the regression slope of each morphological trait on body mass from that expected exponent for geometric similarity (isometry; McMahon 1975*a*). Only in those cases where the slope of regression of any morphological trait with body mass deviates significantly from that expected by isometry could an ecomorphological relationship be observed. Thus, although a tight parallelism between ecomorphological relationships at inter- and intraspecific levels could be expected as a proof of natural selection shaping morphological design, we also identify a circumstance under which

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congruence between ecomorphological patterns at inter- and intraspecific levels are not expected to emerge due to the lack of sufficient morphological variation at the interspecific level above that predicted under isometry (geometric similarity).

## 2. PREDICTIONS AND THEORETICAL ANALYSES

### (a) *Ecomorphological predictions*

Considering functional properties of morphological traits together with functional implications of body weight, an increase in hanging performance (i.e. time spent hanging per foraging bout while feeding) would be associated with the following (see Moreno & Carrascal 1993; Carrascal *et al.* 1994 and references therein for more details):

1. Lighter body weight. While hanging, the main force acting on the bird is the force of gravity pulling the body downwards. It should be expected, therefore, that the greater the weight the less time individuals spend hanging while feeding, as the bigger will be the force of gravity pulling on heavier bodies.

2. Shorter leg segments. The shorter the leg bone segments, the shorter the resistance lever arms (moment arms) around the joints, which reduces the moments the muscles need to set up to maintain the leg elements flexed at a given position (for more details see Palmgren 1932; Norberg 1979).

3. An increase in both the distance from the head of the fibula to the insertion point of the iliofibularis muscle (IMI) and the distance from the head of the tarsometatarsus to the insertion point of the tibialis cranialis muscle (IMT). The iliofibularis and tibialis cranialis muscles are the main flexors of the knee and intratarsal joints, respectively (Raikow 1985). Upon contraction these muscles exert a torque on the fibula and tarsometatarsus with respect to the knee and intratarsal joints, respectively. For each muscle this torque is equal to the product of the force and its moment arm. The further the insertion of these two muscles the longer the moment arm around the joints, which increases the torque on the fibula and tarsometatarsus, thereby increasing the mechanical advantage (effectiveness of action) of the muscles (see Palmgren 1932; Richardson 1942; Norberg 1979).

4. The iliofibularis and tibialis cranialis muscles should be able to develop more force. From the above statement that upon contraction the iliofibularis and tibialis cranialis muscles exert a torque on the fibula and tarsometatarsus with respect to the knee and intratarsal joints, respectively, this torque being equal to the product of the force and its moment arm, the bigger the force developed by those muscles the bigger the torque on the fibula and tarsometatarsus. This will increase the effectiveness of the action of both muscles.

### (b) *Isometric variation of morphological traits with body mass*

As in this paper ecomorphological analyses are performed with adult full-grown individuals, isometric

relationships (geometric similarity) between morphological traits and body mass are expected (Gould 1975; Klingenberg 1996). Thus, the following relations can be defined considering the dimensionality of morphological variables (McMahon 1975*a* and references therein):

1. Linear measurements ( $L$ ; leg segments, and IMI and IMT distances):

$$L \propto M^{1/3}, \quad (1)$$

and taking logarithms,

$$\log L = \log a + 0.33 \log M$$

where  $M$  equals body mass.

2. Area measurements ( $S$ ; muscular force  $F$  is a function of the cross-sectional area of the muscle; see equation (8) below):

$$F \approx S \propto M^{2/3}, \quad (2)$$

and taking logarithms,

$$\log F = \log a + 0.67 \log M.$$

Considering these isometric relationships, the above mentioned predictions relating hanging performance to leg morphology (predictions 2–4) could only be observed if the slope of the regression of each morphological trait with body mass significantly deviates from that expected (0.33 or 0.67 depending on whether morphological traits are linear or area dimensions).

Prediction 2 (shorter leg segments) would be observed if, and only if, the regression slope of log length segments on log body mass is lower than 0.33. Under this circumstance leg segments would be shorter than expected by isometric variation to overcome the gravity force, promoting a reduction of the resistance lever arms around the joints.

Prediction 3 (increase in the IMI and IMT distances) would be observed if the regression slope of log IMI and IMT distances on log body mass is higher than 0.33. Therefore, IMI and IMT distances are expected to be longer than expected by isometric variation with body mass. The further the insertion of the iliofibularis and tibialis cranialis muscles into the fibula and tarsometatarsus, the more effective will be the forces flexing the legs to overcome the gravity force.

Prediction 4 (an increase in the force developed by the iliofibularis and tibialis cranialis muscles) would be observed if the regression slope of the log of muscular forces on log body mass is higher than 0.67. Therefore, muscular forces are expected to be greater than expected by isometric variation with body mass to overcome the gravity force.

### (c) *A synthetic formulation of deviations from geometric similarity*

Hanging emerges from the coordinated function of several systems acting in concert (Bennet 1989). In this study we have considered muscular forces, muscle insertions, and bone lengths as elements of the flexor systems of the knee and the ankle. Therefore, eco-

morphological relationships should arise if flexor systems deviate from the geometric similarity, considering the combined action of their elements.

Summarizing the above mentioned predictions and models, muscular forces performed by the leg flexor muscles ( $F_m$ ) are directly related to the gravity force acting upon the hanging birds ( $F_g$ ), directly related to the length of leg bones ( $L_b$ ), and inversely related to the distance between the articular joints and the point of insertion of flexor muscles ( $L_i$ ). This relationship can be expressed as:

$$F_m \propto \frac{F_g L_b}{L_i},$$

and rearranging for  $F_g$  gives:

$$F_g \propto \frac{F_m L_i}{L_b}. \quad (3)$$

Considering the isometric relationships expressed in equations (1) and (2), and that  $F_g$  is proportional to body mass ( $M$ ), it is clear that equation (3) is an inequality as its right part equals to  $M^{2/3}$  ( $M^{2/3} \cdot M^{1/3}/M^{1/3} = M^{2/3}$ ). To maintain the proportionality in equation (3), a deviation from isometry has to be introduced on every element in the right part of the equation. The deviation from isometry may be accounted for by introducing new exponents affecting the relationships expressed in equations (1) and (2). Thus, equation (3) has to be rewritten if the skeleto-muscular system acting on the two more distal leg segments is expected to overcome the gravity force while hanging:

$$F_g \leq \frac{F_m^x L_i^y}{L_b^z}, \text{ or } M \leq \frac{M^{x \cdot 2/3} M^{y \cdot 1/3}}{M^{z \cdot 1/3}}, \quad (4)$$

where  $x$ ,  $y$  and  $z$  are coefficients of deviation from isometry ( $Q$ ; for muscular forces, distances of insertion of flexor muscles and length of leg segments, respectively). Working with exponents in equation (4), the following expressions are obtained,

$$\frac{2}{3}x + \frac{1}{3}y - \frac{1}{3}z \geq 1 \quad (5)$$

or

$$2x + y - z \geq 3, \quad (6)$$

and thus  $x > 1$ ,  $y > 1$  and  $z < 1$  which agrees with the predictions stated in the previous section.

Therefore, the three components of each flexor system are taken into account in a synthetic model (equation (4)), against which we can test whether deviations from isometry may counteract the gravity force to aid hanging performance. The coefficients  $Q$  of deviation from isometry ( $x, y, z$ ) can be calculated from the slopes ( $b$ ) of the regression models of the log of each morphological trait with log body mass ( $\log$  [morphological trait] =  $\log a + b \log$  [body mass]); lengths,  $b = 0.33 Q$ ; muscular forces,  $b = 0.67 Q$ .

From the above mentioned expressions and reasoning, we expect morphological variation in leg morphology to be able to overcome the gravity force to

facilitate hanging performance if, and only if, the deviations from geometric similarity in morphological traits comply with the statement in equation (6). If the coefficients of deviation from isometry for the fibula and tarsometatarsus systems do not add to  $> 3$ , no significant relationship between intraspecific morphological variation in leg morphology and hanging performance can be expected.

### 3. MATERIAL AND METHODS

#### (a) Experimental procedure

Experiments were carried out during December and January 1991–92 and 1992–93 in outdoor aviaries at El Ventorrillo Field Station (1500 m above sea level, Sierra de Guadarrama, Central Spain). Seventeen adult individuals (nine males and eight females, over one year old; aged following criteria in Svensson 1992) were mist-netted and colour-banded at the field station the week before the experiments were performed. Prior to the experiments birds were kept in a 2 (high)  $\times$  2  $\times$  3 m aviary with an *ad libitum* diet of peanuts, sunflower seeds (both offered in open trays), and water with vitamins for at least 2 d. For experiments we used another 2  $\times$  2  $\times$  3 m aviary where one feeder was erected. The feeder was a wooden box with the bottom side (20  $\times$  11 cm) covered by a 4.8 mm mesh plastic net allowing birds access to food (peanuts). When the feeder was erected, the posture required for feeding was hanging (back down).

All individuals were starved for 1 h before the trials, so they were highly motivated to feed. We then released each individual into the experimental aviary. We sampled each individual during three time periods of 1 h on three different days. The minimum interval between successive experiments with the same individual was 72 h. Samples were taken between 0900–1500 GMT. We divided this period into three subperiods (0900–1100; 1100–1300; 1300–1500). Each individual was sampled once in each subperiod. The number of hanging events and their duration were recorded. The repeatability of the duration of hanging events was  $r = 0.14$  ( $F_{16,314} = 3.99$ ,  $p < 0.001$ ; Lessells & Boag 1987). This low value of repeatability may be due to the fact that hang duration varies between the maximum performance of hanging and unexpected interruptions of hanging events not directly related with such maximum performance. To overcome this problem, we have selected the three longest hanging times for each individual bird. Reanalysing the repeatability for the maximum hanging time we obtained  $r = 0.57$  ( $F_{16,32} = 3.18$ ,  $p = 0.003$ ). Moreover, the average hanging time using the whole sample for each bird and the mean of the three maximum hanging times were highly correlated ( $r = 0.96$ ,  $n = 17$ ,  $p < 0.001$ ). This average maximum time spent hanging could be referred to as a measurement of hanging performance. Only one bird was tested at a time. Between trials birds were removed from the sampling aviary.

#### (b) Mensural characters and data analyses

We dissected iliofibularis and tibialis cranialis muscles from all individuals. We selected these two muscles as they represent the two main muscles closing the knee and intratarsal joints (Raikow 1985), and because of their direct relationships with feeding behaviour (Richardson 1942; Norberg 1979; Moreno & Carrascal 1993). The gross morphology of the muscles was studied under a stereomicroscope at magnifications of  $\times 5$ –20, aided by an iodine muscle stain to enhance visibility of the muscle tissue (Bock

Table 1. *Morphometrical data from the great tit individuals used in this study**(n, sample size;  $\bar{x}$ , mean; s.d., standard deviation.)*

variable	<i>n</i>	$\bar{x}$	s.d.
body mass (g)	17	18.74	1.04
femur length (mm)	17	15.41	0.42
tibiotarsus length (mm)	17	27.54	0.64
tarsometatarsus length (mm)	17	19.82	0.53
IMI distance (mm)*	17	5.23	0.13
IMT distance (mm)†	17	2.96	0.18
angle of pinnation of iliofibularis muscle (degrees)	17	13.06	2.25
angle of pinnation of tibialis cranialis muscle (degrees)	17	7.21	1.29
force iliofibularis muscle (N)	17	0.0014	0.00015
force tibialis cranialis muscle (N)	17	0.0034	0.00033

\* Measured as the distance from the head of the fibula to the distal point of the insertion of the iliofibularis muscle.

† Measured as the distance from the head of the tarsometatarsus to the distal point of the insertion of the tibialis cranialis muscle.

& Shear 1972). We calculated the force ( $F$ ) developed by these muscles (in N) upon contraction (table 1) by the following equation:

$$F = k m \cos^2 \alpha / (\rho l), \quad (7)$$

where  $k$  is a constant for the unit of force development (N m<sup>-2</sup>; Bock 1974),  $m$  is the muscle's dry mass (kg),  $\rho$  is the muscle's density (assumed to be 1060 kg m<sup>-3</sup>; Bennett 1995),  $l$  is the muscle's mean fibre length, and  $\alpha$  is the mean pinnation angle (the angle between the muscle fibre and the line of action of the whole muscle) in degrees. This equation was obtained by combining and simplifying the formulae provided by Bock (1974) and Biewener (1992):

$$F = k C \cos \alpha \quad (8)$$

$$C = m \sin(2\alpha) / (2 \rho l \sin \alpha) \quad (9)$$

where ( $C$  is the cross-section).

Fibre lengths and pinnation angles of the muscles were determined with the aid of a digitizer tablet, the former being recorded to the nearest 0.001 mm and the latter in degrees. Muscle mass was recorded with a precision balance to the nearest 0.0001 g.

Measurements of the hindlimb bones were also taken (table 1). Biometrical variables measured were maximum femur length, maximum tibiotarsus length, maximum tarsometatarsus length, distance from the head of the fibula to the insertion point of the iliofibularis muscle (IMI) and distance from the head of the tarsometatarsus to the insertion point of the tibialis cranialis muscle (IMT). We used a digital calliper to measure leg bone lengths to the nearest 0.01 mm. IMI and IMT distances were obtained with the aid of a micrometric device coupled to a binocular microscope ( $\pm 0.05$  mm).

As body mass is an important morphological variable for explaining feeding ecology (e.g. Grant 1986; Benkman 1988; Carlson 1992) we weighed individuals prior to each experiment (table 1). For the statistical analyses we averaged the mass of each individual the three times it was used in the experiment. We have used body mass instead of a synthetic measure of body size as the former is the variable against which the force of gravity is pulling down while hanging.

The scaling of each biometrical variable with body mass was analysed by means of linear regression. As both dependent and independent (body mass) variables were subjected to mensural errors, ordinary least-squares regression is not adequate (Ricker 1972; Sokal & Rohlf 1981). As an alternative regression model we have used ordinary major axis regression, which minimizes the square of the vertical distances from the points to the regression line. Working with

variables in logarithms, this method is adequate when both dependent and independent variables are measured in different units (e.g. units for length, cross-section and mass; Jolicoeur & Mosimann 1968; Jolicoeur & Heusner 1971). Regression statistics and their standard errors were calculated using the nonlinear estimation module of Statistica (StatSoft 1996).

Average time spent hanging was regressed with the length of the three leg segments, the two muscular insertion distances and the forces of the two leg flexor muscles by means of multiple regression analyses. Partial correlations were obtained for each one of these seven morphological traits (in log). We also tested for the relationship between body weight and time spent hanging (both in log) by means of ordinary major axis regression.

#### 4. RESULTS

##### (a) *Test of isometric variation of morphological traits*

The slopes of the regressions of the leg length segments are significantly lower than those expected under isometry (geometric similarity; table 2). For IMI and IMT distances the regression slopes are not higher than those predicted by isometry (for IMI distance the slope is even significantly lower than that expected;  $p < 0.001$ ). The regression slopes of the muscular forces of the iliofibularis and tibialis cranialis muscles do not significantly differ from those expected under isometry. Therefore, only for leg length segments are deviations from an isometric relationship with body mass big enough to allow the emergence of ecomorphological patterns.

Combining the coefficients of deviation from the geometric similarity ( $Q$ ; table 2) according to equation (5),  $2x + y - z = 2.69$  for tibiotarsus length, IMI distance and force of the iliofibularis muscle (flexor system of the tibiotarsus), and  $2x + y - z = 2.87$  for tarsometatarsus length, IMT distance and force of the tibialis cranialis muscle (flexor system of the tarsometatarsus). In conclusion,  $2x + y - z$  is not greater than 3 in any case, showing that there is no sufficient morphological variation between individuals to promote clear associations between morphology and hanging performance (apart from that expected by

Table 2. Regression models (ordinary major axis method) of the morphological variables (in log) with log body mass (M), and expected deviations of regression slopes (b) from isometry (geometric similarity)

(Ho is the regression slope expected under isometry; Q is the coefficient of deviation from the expected Ho; s.e., standard error; sample size, n = 17 in all cases.)

variables	regression model log variable = log $\alpha + b \cdot \log M$				deviation from isometry		
	r	b	s.e. b	p	Ho	Q* expected deviations	p
femur length	0.62	0.13	0.044	< 0.001	0.33	0.39 b < Ho	< 0.001
tibiotarsus length	0.45	0.08	0.019	< 0.001	0.33	0.24 b < Ho	< 0.001
tarsometatarsus length	0.57	0.12	0.021	< 0.001	0.33	0.36 b < Ho	< 0.001
IMI distance	0.16	0.03	0.039	0.414	0.33	0.09 b > Ho	0.999
IMT distance	0.50	0.29	0.120	0.027	0.33	0.87 b > Ho	0.254
force iliofibularis muscle	0.48	0.95	0.448	0.050	0.67	1.42 b > Ho	0.536
force tibialis cranialis muscle	0.45	0.79	0.409	0.073	0.67	1.18 b > Ho	0.768

\*  $Q = b/Ho$ .

Table 3. Results of multiple regression analysis of mean maximum time spent hanging (in log) and the seven morphometrical variables

(Standardized regression coefficients ( $\beta$ ), partial correlations (r) and significance levels are shown.)

variables (in log)	$\beta$	r	p
femur length	0.30	0.19	0.580
tibiotarsus length	0.07	0.04	0.899
tarsometatarsus length	-0.74	-0.45	0.169
IMI distance	0.05	0.04	0.894
IMT distance	-0.71	-0.47	0.148
force iliofibularis muscle	-0.15	-0.11	0.739
force tibialis cranialis muscle	0.44	0.27	0.417

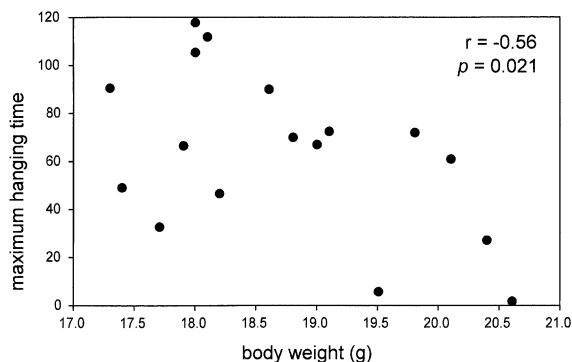


Figure 1. The relationship between mean hanging time and body weight for the 17 great tit individuals.

geometric similarity due to inter-individual differences in body size). Thus, we should not expect significant relationships between leg morphology and average time spent hanging.

(b) Within-species ecomorphological associations

Table 3 shows the results of multiple regression analysis of the seven morphometrical variables on average maximum time spent hanging. No morphometrical variable was significantly correlated with hanging performance. The multiple regression model was not significant ( $F_{7,9} = 1.17, p = 0.405$ ; adjusted multiple  $R^2 = 0.068$ ).

Body weight (in log) was significantly related to average time spent hanging, in accordance with prediction 1; lighter individuals tended to spend more time hanging than heavier individuals (figure 1).

Several authors have pointed out that some feeding differences between individuals are sex-related (Werner & Sherry 1987; Suhonen & Kuitunen 1991). Considering that some great tit populations have been shown to be sexually dimorphic in body weight (Gosler 1987), we performed an ANCOVA with maximum time spent hanging (in log) as the dependent variable, sex as the factor (independent variable) and log body weight as the covariate. There was no significant difference in mean hanging time between sexes once the effect of body weight was removed ( $F_{1,14} = 0.28, p = 0.603$ ).

5. DISCUSSION

Only the prediction relating body weight to hanging performance was supported by our results; lighter individuals tended to spend more time hanging than heavier individuals. Leg length segments, muscular forces, and distances of insertion of the main flexor muscles were not correlated with hanging performance. Our results at the intraspecific level showed that for both the tibiotarsus and tarsometatarsus flexor skeletal-muscular system, there is no deviation from isometry, thus precluding a functional relationship between morphology and behaviour at an intraspecific level. However, Moreno & Carrascal (1993) demonstrated that leg morphology and preferred posture used while feeding were causally related at the interspecific level within the four tit species they studied (one of these being the great tit). Therefore, results at the intraspecific and interspecific levels are not consistent.

The following question now emerges: should one expect these inconsistencies between predictions generated from comparisons among species and results obtained at intraspecific level? Recently, Ricklefs & Miles (1994) questioned whether one can predict that the relationship between intraspecific and interspecific ecomorphological relationships is uniform. Emerson & Arnold (1989) even stated that there are no strong theoretical grounds for expecting similar results at the

intra- and interspecific levels, and Emerson (1991) pointed out the need for substantial empirical work to determine such expectancies.

We argue that at an intraspecific level, body mass overrides the significance of other traits that have a functional meaning at an interspecific level (i.e. leg segment lengths, muscular morphology). That is to say, the discrepancy between the ecomorphological associations at intra- and interspecific levels may be the result of a problem of scale. In fact, between-species and within-species ranges of variation in leg segments and insertion of muscles are clearly different (compare data in table 1 with those in Moreno & Carrascal (1993)).

Apart from the different ranges of morphological variation among species and within species, the problem of scale is also related to the different processes that operate in ecological time at the level of variation among individuals of the same population and age group (intraspecific scaling, Gould 1975; static allometry, Klingenberg 1996), and at an interspecific level along the evolutionary course (evolutionary allometry, Klingenberg 1996). Evolutionary processes leading to the associations between traits (e.g. body mass and leg length) may change in different lineages manifested as evolutionary novelties. These evolutionary novelties may disrupt the patterns of covariation between morphological traits determined by intraspecific scaling. For example, revisiting the data in Moreno & Carrascal (1993) we obtain a regression slope for the insertion of the tibialis cranialis muscle in the tarsometatarsus on body mass that does not differ from the expected slope under isometry ( $b = 0.28$ ,  $s.e. = 0.12$ ,  $n = 5$ , four *Parus* spp. and the closely related *Aegithalos caudatus*) and is similar to that observed in this paper within the great tit (see table 2). Nevertheless, a careful inspection of this interspecific regression pattern shows that the blue tit (*Parus caeruleus*) has a very high residual value (0.125), many times higher than the most positive one (0.04) observed in the analysis of the 17 individual great tits. This contrasting pattern between the inter- and intraspecific levels is due to the emergence of an evolutionary novelty in this trait from the ancestral state (see figure 3 and discussion in Moreno & Carrascal (1993)). This may be the reason why Moreno & Carrascal (1993) found that the heavier great tit used hanging postures in significantly higher proportions than the lighter crested tit. Therefore, at the interspecific level, morphological changes may be introduced as drastic evolutionary novelties in some species whose variation is not related to scaling with body mass (allometric variation within an evolutionary lineage).

Considering the results of this study, it may be of value to test allometric models accounting for size differences among species or individuals within species prior to testing ecomorphological hypotheses, even more so when interpreting the functional basis of performance and resource use. In some occasions the use of morphological variation as a predictor of ecological differences among species has been criticized (Wiens & Rotenberry 1980; Wiens 1989 (and references therein), 1991). Nevertheless, these critical

papers do not examine whether interspecific differences in the studied morphological traits exist independent of the mere variation exclusively attributable to differences in body size (see, nevertheless, Tobalske 1996). Before accepting the null hypothesis of any ecomorphological analysis (lack of association between ecology and morphology) it would be necessary to check whether there is sufficient morphological variation above that predicted by existing geometric similarity.

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