# Morphological evolution and changes in foraging behaviour of island and mainland populations of Blue Tit (*Parus caeruleus*) – a test of convergence and ecomorphological hypotheses

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## Summary

We study the leg morphology and feeding postures of two subspecies of the Blue Tit (*Parus caeruleus*; Tenerife island and the Iberian Peninsula) and the Coal Tit (*Parus ater*; Iberian Peninsula). We search for evidence supporting the hypothesis of convergent evolution in morphological and ecological traits and we discuss the role of ecomorphological hypotheses as predictors of foraging differences at the intraspecific level. To overcome the problems introduced by environmental characteristics not related to locomotion and competition, we make observations under controlled situations to manage food quality and food access. We determine that the island Blue Tit has a longer tarsometatarsus, larger foot span and a more proximal insertion of the tibialis cranialis muscle (flexor of the tarsometatarsus) than the mainland Blue Tit. These morphological differences are consistent with the more frequent use of hanging and clinging 'head-up' postures by the Iberian Blue Tit. Several ecomorphological hypotheses obtained at the interspecific level with other taxa, have proved to be of high predictive value for explaining ecological differences considering morphological evolution. The Tenerife Blue Tit and the Iberian Coal Tit clearly show close convergence in both feeding postures and leg structure, although some differences in morphology were found between these two species. Convergence in foraging methods between the island Blue Tit and the mainland Coal Tit can be explained without considering current interspecific competition as a determinant of niche space.

*Keywords*: convergence; ecomorphology; leg structure; foraging behaviour; *Parus caeruleus*

## Introduction

Several studies have analysed geographic variation in avian foraging behaviour in relation to vegetation and bird community structure (Emlen, 1981; Maurer and Whitmore, 1981; Moreno, 1981; Landres and MacMahon, 1983; Sabo and Holmes, 1983; Wiens *et al.*, 1987; Block, 1990). Wiens *et al.* (1987) and Petit *et al.* (1990) suggested that variations in foraging behaviour within species are due to simple functional responses associated with differences in local environmental conditions. Availability of suitable foraging perches, availability and dispersion of food resources, biotic pressures (e.g. competition, predation) and the weather interact to influence local patterns of foraging (Wiens, 1989; Block, 1990). Sabo and Holmes (1983) called for the study of avian foraging niches across multiple sites, thereby allowing for a more comprehensive examination of niche theory (considering the pre- and post-competitive space). All these studies have reinforced the role of physical and biotic selection pressures determining the spatial niche

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and foraging behaviour of species, but have ignored the role of morphological variation when considering ecomorphological patterns (Leisler and Winkler, 1985; Bock, 1990).

Geographic variation in both morphological traits and foraging behaviour have been used to test hypotheses about convergence in bird assemblages. The analysis of convergence in ecological or morphological traits has been subjected to much debate and many studies have shown that it is a relatively infrequent phenomenon which is difficult to study due to the problem of differences in environmental factors (e.g. Wiens, 1989; for birds). In the absence of a potential competitor, convergence has usually been regarded as evidence of the effects of interspecific competition. In this case, convergent evolution in morphological traits is referred to as character release (Grant, 1972). Nevertheless, convergence should also be expected to occur if evolutionary distant species respond to the same set of environmental conditions in a similar way (see the review by Wiens, 1989). Moreover, island populations may undergo morphological convergence with a potential competitor and morphological divergence from the mainland population of its species for a variety of non-competitive genetic reasons (e.g. limitation of gene flow, founder effect; Cockburn, 1991). Therefore, if resource distribution, foraging opportunities and genetic constraints differ between two areas (e.g. island and mainland), convergence is more readily attributable to oportunistic responses of a species to differences in resources than to the presence or absence of a potential competitor.

In this paper we present a comparative study of the leg morphology and feeding postures used by two subspecies of the Blue Tit (*Parus caeruleus*) which evolved under different geographical and ecological conditions (insularity without another congeneric species and on the mainland with other *Parus* species present). Geographic variation in the external morphology of the Blue Tit has been studied by Snow (1954), Grant (1979) and Martin (1991). These authors clearly showed a clinal increase of bill thinness and relative tarsometatarsus length from northeastern to southwestern populations over the geographical range of the Blue Tit. Several hypotheses have been proposed to explain these differences in body measurements: competitive release (Lack and Southern, 1949), climatic variation (Allen's rule; Snow, 1954, Partridge and Pring-Mill, 1977), ecological conditions (e.g. habitat use; Martin, 1991) and a combination of these factors (Grant, 1979).

The morphological variation within the Blue Tit, with populations (subspecies) subjected to different evolutionary pressures (ecological, climatic, competitive and limited gene flow), offers the opportunity to test ecomorphological hypotheses usually obtained by comparing the morphology and ecology of different species and convergent evolution in morphological and behavioural traits. Our main goals are the following:

(1) To test, at intraspecific level, several ecological predictions derived from morphofunctional models related to different aspects of leg morphology, for example, length of leg segments (Partridge, 1976; Winkler and Bock, 1976; Norberg, 1979 and references therein), insertion of leg flexor muscles (Richardson, 1942), toe length and foot span (Palmgren, 1936; Partridge, 1976; Norberg, 1979) and the structure of the soles of the feet (Leisler and Thaler, 1982).

(2) To test if evolution under insularity and in allopatry with one broadly recognized potential competitor (the Coal Tit, *P. ater*) have produced niche shifts (as reflected by changes in foraging postures and morphology) indicative of convergent evolution (Partridge and Pring-Mill (1977) have demonstrated no convergence in the way the beak is used by Canarian Blue Tits and English Coal Tits, in spite of the similarity in bill morphology).

To attain these goals we made field observations under controlled and comparable situations of food quality, food access and escape distance to the nearest refuge (specially designed box-feeders). With this procedure we tried to overcome the problems of classic ecomorphological and

convergence studies, in which patch and environmental characteristics not related to foraging and competition (e.g. food availability, predation risk) are ignored or assumed to be similar among foraging substrates and geographical areas (Wiens, 1989).

## Material and methods

### Species and study area

We studied two populations of Blue Tit (*Parus caeruleus*) belonging to two different subspecies: (*Parus caeruleus ogliastroe*, Central Spain and *Parus caeruleus teneriffae*, Canary Islands) and one population of Coal Tit (*P. ater*).

Field work with *P. c. ogliastroe* and Coal Tit was carried out from October 1991 to January 1992, in a 6 ha mixed forest of *Pinus sylvestris, Castanea sativa, Acer* spp. and *Populus* sp. (El Ventorrillo, 1500 m a.s.l., 40°45'N 04°01'W, Sierra de Guadarrama, Madrid). Foraging behaviour of *P. c. teneriffae* was studied from November 1991 to February 1992, in a woodland of *Pinus canariensis* with abundant undergrowth of *Erica arborea* and *Ilex canariensis* and some plantations of *Pinus radiata* and *Eucaliptus* spp. (La Esperanza, 1100 m a.s.l., 28°26'N 16°22'W, Tenerife).

### Field procedure

To analyse foraging behaviour, we designed three types of feeder (types U, D and L) differing in the posture necessary to obtain the food. Feeders were wooden boxes with one side (20 × 11 cm) covered by a 4.8 mm mesh plastic net allowing birds access to food. When erected, feeder type U had the net on top and the posture required for feeding was standing (back up). Feeder type D had the net on the bottom and the posture required for feeding was hanging (back down). Feeder type L had the net covering one side so a bird feeding on it had to be clinging to the side (back lateral). Feeders were filled with husked peanuts, spaced 0.5–0.75 m apart and suspended from pine branches approximately 50 cm below the canopy. Five feeding points were established in each study area, spaced 75–150 m apart. At each point two feeders were erected, one feeder type U and one feeder type D, thus the bird had to choose between feeding standing or hanging (the use of each feeder requires opposite postures from a functional point of view and very much resembles postures that birds use in the wild while foraging). A second trial was performed with feeder type L at each feeding point, in which a bird had to choose between feeding clinging head up (head above the feet, feet placed at the same level), head down (head below the feet) or head lateral (one leg extended above and the other flexed below the longitudinal axis of the body). Prior to sampling, birds were allowed 3 weeks to familiarize themselves with the feeders. We assumed, therefore, that all the birds had experience of feeders.

Behaviour at feeders was recorded at each feeding station for sampling periods of 40–60 min. Sampling began when one individual came into the feeders and began to eat. Time spent in each posture in each trial was recorded until the bird abandoned the feeding point. The use of feeders and feeding postures were expressed as percentages. To avoid competitive effects on the choice of the type of feeder, only records of solitary birds (no other birds on the same tree), feeding more than 15 s, were used for statistical analysis. Sample records at feeders obtained per individual (colour banded) were averaged (10 Blue Tits and 14 Coal Tits in Sierra de Guadarrama and 15 Blue Tits in Tenerife).

### Mensural characters

The following mensural characters were measured on skin specimens: length of toes I (hind) and III (front), length of claws I and III and sole perimeter of toes I and III (all the former measurements were taken with the aid of a digitizer table – to ± 0.05 mm – and a camera lucida

microscope attachment). Four additional measurements were taken on skeletal specimens: tarsometatarsus, tibiotarsus, femur lengths (with a digital caliper to ± 0.01 mm) and distance from the head of the tibiotarsus to the distal point of the insertion of the tibialis cranialis muscle (with a micrometric device coupled to a binocular microscope, to ± 0.05 mm). Data on external morphology were obtained from the collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain) and Natural History Museum (Tring, UK). We measured only specimens collected in Tenerife and Sierra de Guadarrama. Skeletal measurements were obtained from individuals collected by us in Tenerife (coniferous forested areas in La Esperanza and Vilaflor) and Central Spain (mainly Sierra de Guadarrama).

### Data analysis

The statistical tests employed were the two-tailed *t*-test for morphological characters, the Mann–Whitney U-test for behavioural data at feeders (Sokal and Rohlf, 1981) and the non-parametric rank test comparing one data series with an expected median. Due to size differences between the Coal Tit and the two subspecies of Blue Tit, we divided each biometrical (linear) variable by the cube root of the body weight in the comparisons of morphological measurements between the Coal and Blue Tits.

## Results

### Morphology

Morphometrical data of Blue Tits from Tenerife and Sierra de Guadarrama are shown in Table 1. Body weight did not significantly differ between the two populations. Of the three leg bones,

Table 1. Morphometrical measurements of Blue Tits from Tenerife (Canary Island) and Guadarrama (Iberian Peninsula)

|  | Tenerife | | | Guadarrama | | | |
|---|---|---|---|---|---|---|---|
|  | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | *p* |
| Body mass (g)[a] | 10.3 | 0.25 | 12 | 10.3 | 0.96 | 14 | 0.946 |
| Femur length (mm, bone) | 12.4 | 0.58 | 6 | 12.1 | 0.34 | 13 | 0.234 |
| Tibia length (mm, bone) | 24.0 | 1.07 | 6 | 23.4 | 0.83 | 13 | 0.178 |
| Tarsus length (mm, bone) | 17.7 | 0.87 | 6 | 16.4 | 0.57 | 13 | 0.001 |
| Relative insertion of |  |  |  |  |  |  |  |
| M. tibialis cranialis (%)[b] | 15.9 | 0.54 | 6 | 17.6 | 0.95 | 8 | 0.002 |
| Hind toe length (mm) | 7.1 | 0.52 | 13 | 6.4 | 0.38 | 10 | 0.002 |
| Front toe length (mm) | 9.1 | 1.07 | 13 | 7.8 | 0.94 | 9 | 0.008 |
| Hind claw length (mm) | 5.3 | 0.30 | 13 | 4.7 | 0.53 | 10 | 0.002 |
| Front claw length (mm) | 4.1 | 0.31 | 13 | 3.8 | 0.40 | 10 | 0.167 |
| Foot span (mm)[c] | 25.6 | 1.60 | 13 | 22.7 | 1.70 | 9 | 0.000 |
| Complexity index of toe pads[d] | 1.2 | 0.05 | 11 | 1.3 | 0.08 | 9 | 0.120 |

$\bar{x}$, mean; SD, standard deviation; *n*, sample size. Significance of differences (*p*) between the two populations were determined by two-tailed *t*-tests.

[a] Body weights of Tenerife obtained using Grant (1979) and authors own data.

[b] Measured as the distance from the head of the tarsometatarsus to the distal point of the insertion of the tibialis cranialis muscle divided by tarsometatarsus length.

[c] Measured as the sum of the lengths of both front and hind claws and toes.

[d] Measured as the sum of the sole perimeters of front and hind toes divided by the sum of their lengths.

femur and tibiotarsus lengths did not significantly differ between the two subspecies, while the tarsometatarsus length was significantly longer in the Tenerife Blue Tits. The insertion of M. tibialis cranialis onto the cranial surface of the tarsometatarsus was proportionally more distal in the individuals from Sierra de Guadarrama than in individuals from Tenerife. Back and front toes were significantly longer in Tenerife Blue Tits. The hind claw was significantly longer in Tenerife individuals, while there was no statistical difference between the two subspecies in the length of the front claw. Thus, the Blue Tits from Tenerife had longer foot spans. Soles of the feet (measured as the complexity of pads of front and hind toes) did not significantly differ between the two subspecies.

*Foraging postures at feeders*

In trial UD (feeding standing vs feeding hanging) the frequency of use of the hanging posture by the Tenerife Blue Tit did not significantly differ from that expected by chance (hypothesized median: 0.5; non-parametric test for random location: $Z = 1.294, p = 0.196$), while in Sierra de Guadarrama, the Blue Tit hung (back down) in a higher proportion than that randomly expected ($Z = 2.591, p = 0.01$). Moreover, Blue Tits from Sierra de Guadarrama used the hanging posture in a higher proportion than Blue Tits from Tenerife (Table 2). On feeder type L, Blue Tits in Tenerife used the head lateral clinging posture more frequently than Blue Tits in Guadarrama, the trend there being reversed for clinging head up (Table 2). To feed in a clinging head down posture is uncommon in both populations (4.4% in Tenerife Tits and 0.1% in Guadarrama Tits).

*Convergence in morphology and foraging postures.*

Differences in leg morphology between the Coal Tit and the two subspecies of Blue Tit are shown in Table 3 (tests have been performed using relative lengths – dividing each linear variable by the cube root of the body weight). Relative femur and tibiotarsus lengths of Coal Tit were not significantly different from that of the Canary and Iberian Blue Tits. Relative tarsometatarsus length was longer in the Coal Tit than in the Iberian Blue Tit, but the Tenerife Blue Tits and Coal Tits were not statistically different in this leg dimension. The insertion of M. tibialis cranialis on tarsometatarsus was more distal in the two subspecies of the Blue Tit than in the Coal Tit, although the Blue Tit from Tenerife was more similar to the Coal Tit, than to the Blue Tit from Sierra de Guadarrama. Relative lengths of toes, claws and foot spans were longer in the Coal Tit than in the Iberian Blue Tit, while the Blue Tit from Tenerife was very similar to the Coal Tit (morphological measurements only reached the level of statistical significance in relative length of hind claw – longer in the Coal Tit). The complexity index of the pads of the front and hind toes was significantly higher in the two subspecies of the Blue Tit than in the Coal Tit.

Table 4 shows the selection of foraging postures by the Coal Tit in Sierra de Guadarrama and

Table 2. Use of different postures at feeders (selection trials of UD and L feeders)

| | Tenerife | | Guadarrama | | |
| --- | --- | --- | --- | --- | --- |
| | $\bar{x}$ | SD | $\bar{x}$ | SD | $p$ |
| Hanging in UD trials (%) | 42.7 | 24.3 | 80.0 | 22.9 | 0.002 |
| Clinging head up in L trials (%) | 46.4 | 16.2 | 91.3 | 9.0 | 0.000 |
| Clinging head lateral in L trials (%) | 49.3 | 17.0 | 8.7 | 9.0 | 0.000 |

Differences between the two Blue Tit populations were obtained using Mann–Whitney tests (two-tailed tests). $\bar{x}$, mean; SD, standard deviation. Sample sizes: Tenerife=15 individuals, Guadarrama=10 individuals.

comparisons between the Coal Tit and the two subspecies of Blue Tit are also shown. The use of the hanging posture (trial UD) by the Coal Tit in Sierra de Guadarrama did not significantly differ from that observed in the Canary Blue Tit. Nevertheless, difference in selection of a hanging posture between the Coal and Blue Tits in Sierra de Guadarrama was highly significant: the Blue Tit hung while feeding more frequently than the Coal Tit. The Coal Tit clung on feeder type L in a similar way to the Tenerife Blue Tit. The comparison between the Blue and the Coal Tits in Sierra de Guadarrama showed that Coal Tit used the head lateral clinging posture more frequently, while using the head up posture less often.

## Discussion

### *Testing ecomorphological hypotheses*

The results show that the Tenerife Blue Tit foraged at feeders using different postures than those of the Guadarrama Blue Tit (foraging postures of the two subspecies under artificially controlled situations agree with field observations: 29.8% of foraging manoeuvres hanging in Guadarrama

Table 3. Morphological measurements of Coal Tits from Sierra de Guadarrama and results of *t*-tests (*p*-values, two-tailed) comparing morphological variables between Coal Tits and Blue Tits from Tenerife and Sierra de Guadarrama

|  | $\bar{x}$ | SD | $n$ | Tenerife $p$ | Guadarrama $p$ |
|---|---|---|---|---|---|
| Body mass (g) | 9.5 | 0.53 | 11 | 0.000 | 0.000 |
| Femur length (mm, bone)[a] | 11.9 | 0.43 | 6 | 0.983 | 0.166 |
| Tibia length (mm, bone)[a] | 23.2 | 0.86 | 5 | 0.903 | 0.134 |
| Tarsus length (mm, bone)[a] | 17.3 | 0.68 | 6 | 0.609 | 0.000 |
| Relative insertion of |  |  |  |  |  |
|   M. tibialis cranialis (%) | 13.9 | 0.73 | 6 | 0.000 | 0.000 |
| Hind toe length (mm)[a] | 6.9 | 0.37 | 10 | 0.866 | 0.001 |
| Front toe length (mm)[a] | 8.6 | 0.82 | 10 | 0.495 | 0.024 |
| Hind claw length (mm)[a] | 5.6 | 0.30 | 10 | 0.001 | 0.000 |
| Front claw length (mm)[a] | 4.2 | 0.27 | 10 | 0.079 | 0.011 |
| Foot span (mm)[a] | 25.3 | 1.08 | 10 | 0.510 | 0.000 |
| Complexity index of toe pads | 1.1 | 0.03 | 10 | 0.001 | 0.001 |

$\bar{x}$, mean; SD, standard deviation; $n$, sample size.
[a] *t*-tests performed with variables divided by the cube root of body weight (to avoid size effect).

Table 4. Use of different postures at feeders (selection trials of UD and L feeders) and results of Mann–Whitney tests (two-tailed tests) comparing the Coal Tit with the two Blue Tits populations

|  | $\bar{x}$ | SD | Tenerife $p$ | Guadarrama $p$ |
|---|---|---|---|---|
| Hanging in UD trials (%) | 44.4 | 38.1 | 0.861 | 0.022 |
| Clinging head up in L trials (%) | 48.7 | 18.5 | 0.662 | 0.000 |
| Clinging head lateral in L trials (%) | 52.0 | 16.9 | 0.694 | 0.000 |

$\bar{x}$, mean; SD, standard deviation. Sample size for Coat Tit is 14.

($n = 57$), vs 9.5% in Tenerife ($n = 74$)). Data also show differences in mensural characters of the hind limb between the two subspecies. We will try to analyse whether morphological differences are consistent with changes in foraging techniques on the basis of ecomorphological (form–function) patterns already established at the interspecific level with arboreal birds. Several ecomorphological hypotheses and predictions will be analysed.

*Leg length and insertion of muscle tibialis cranialis.* Birds which hang upside down should have short tarsi and a long lever arm for the tibialis cranialis muscle (flexor of the tarsometatarsus) (Palmgren, 1932; Richardson, 1942; Partridge, 1976; Norberg, 1979). Short tarsometatarsi reduce the effort needed to hold the body close to the substrate while hanging. A longer lever arm for the tibialis cranialis muscle increases the effectiveness of action of the muscle closing the intratarsal joint. Our results are consistent with this prediction. The Blue Tit in Sierra de Guadarrama showed shorter tarsometatarsus length and longer distance from the head of this bone to the insertion point of M. tibialis cranialis than the Blue Tit in Tenerife. Accordingly, the former subspecies fed hanging significantly more often than the latter.

Species which cling in a nuthatch-like manner (one foot above and the other below the longitudinal axis of the body, i.e. clinging in a head lateral posture in this study) would be expected to have long legs (Winkler and Bock, 1976; Leisler and Winkler, 1985). Having long legs is advantageous because the longer the leg, the higher the possibility of being able to flex and extend them to a greater degree thus attaining a better equilibrium on vertical surfaces (one leg can be strongly extended and the other strongly flexed so that the centre of gravity can be brought below the extended leg). Our results fit this prediction as the Blue Tit in Tenerife used a clinging head lateral posture at feeder type L (lateral) more frequently than the Blue Tit in Guadarrama, having accordingly longer tarsometatarsus length. Differences in femur and tibiotarsus lengths were not significant, so leg lengthening in the Blue Tit is mainly attained by the increase in tarsometatarsus length. Promptov (1956) also stated that in arboreal passerines, the lengthening of the leg affects the tarsometatarsus mainly, the tibiotarsus to a lesser degree and the femur length least of all.

*Foot dimensions.* In hanging birds, greater foot span is an adaptation for perching on slender substrates (e.g. pine needles). This is for maximizing the amount of needles the bird is able to grasp, hereby increasing its ability to make the needle bunch a firm perch. Enlargement of foot span is mainly due to the lengthening of the hind and front toes and the hind claw. Conversely, having short opposable front and hind toes and claws is advantageous for strength when hanging from thin twigs and from the edges of broad-leaves (Palmgren, 1936; Partridge, 1976). On the other hand, a longer hind toe and hind claw are considered adaptations for clinging in a head lateral posture with one leg flexed and the other leg extended (Richardson, 1942; Rüggeberg, 1960; Partridge, 1976; Leisler and Thaler, 1982). Morphological differences in foot dimensions between the two Blue Tit subspecies (larger foot in Tenerife; not clearly shown by Martin (1991)) are consistent with differences in habitat occupancy and clinging postures. The Iberian Blue Tit exclusively inhabits and forages in broad-leaved forests and trees (Carrascal; 1985; Carrascal and Tellería, 1985), while in Tenerife it reaches very high densities in forests of *Pinus canariensis* and uses pines for foraging (Carrascal, 1987). The use of clinging in a head lateral posture is also significantly lower in the Iberian population. Moreover, the different contribution of the front and hind digits to the foot span is partially supported by the non-significant difference in the front claws between the Tenerife and Guadarrama Blue Tits.

*Structure of foot soles.* Pads, papillae and folds of the sole form a set of features which are adapted to the substrate by increasing friction and surefootedness (Lennerstedt, 1974). Conifer-

dwelling species should have the underside of the toes and the soles of the feet forming protruding tubercles with the pads separated by deep furrows for gripping around individual needles (Leisler and Thaler, 1982). Although the complexity of the foot sole has been qualitatively related to the extensive use of coniferous needles in four *Regulus* species (Leisler and Thaler, 1982; Keast and Saunder, 1991; the four species do not completely segregate in habitat selection and habitat use, i.e. coniferous vs broad-leaved trees; Becker, 1977; Robinson and Holmes, 1982; Carrascal, 1985), in the two Blue Tit subspecies analysed in this paper the data do not fit the prediction. This result shows that habitat shift and the structure of foot soles have not co-evolved in the recent evolutionary process within the Blue Tit, in spite of the extensive use of pines by populations from Tenerife (they also reach high densities in the broad-leaved forests – laurisilva; Martín, 1987). Moreover, the soles of the Coal Tit (a typical species of coniferous forests) showed a lower complexity index than those of the mainland Blue Tit (a characteristic species of broad-leaved forests; Snow, 1955; Perrins, 1979). Therefore, the ecomorphological significance of foot-sole structure related to habitat use cannot be generalized to *Parus* species (in spite of its high functional significance in the lighter *Regulus* species).

The pattern of divergence in leg morphology between the two Blue Tit subspecies does not reflect allometric consequences of selection on body size (a parallel increase in leg length due to an increase in body size) because both subspecies do not differ in body weight. The results of this study clearly demonstrate that pedal locomotory characters are closely associated to how birds forage and that differences in foraging postures used by the two Blue Tit subspecies are consistent with morphological variations in the hind limb. Several ecomorphological hypotheses obtained at the interspecific level have proved to be of high predictive value for explaining ecological differences when considering morphological changes between populations belonging to the same species. Therefore, testing form–function models which compare different populations of the same species subjected to morphological change, may cast light on the widespread applicability of ecomorphological hypotheses and the potential value of morphology predicting niche shifts and community-wide parameters from an alternative (non-competitive) point of view.

*Testing convergence between the island Blue Tit and mainland Coal Tit*

In a recent review on bird community ecology, Wiens (1989) found that convergence in morphological and behavioural traits is apparently atypical. Considering the species presently studied, Patridge and Pring-Mill (1977) showed, by means of field and laboratory observations of feeding skills, that the Canary Blue Tit does not show convergence with the English Coal Tit in the way the bill is used while feeding, in spite of their resemblance in beak morphology. However, our quantitative analyses of foraging behaviour under suitable controlled situations clearly showed a close convergence in feeding postures between the Tenerife Blue Tit and the Iberian Coal Tit. A similar result was found in leg morphology, although resemblance in foot structure is less significant. However, the leg morphology of the Tenerife Blue Tit, when different to that of the Coal Tit, tended to that of the latter species rather than to the morphology of the Iberian Blue Tit. The tighter convergence in behaviour than in morphology is probably due to the fact that morphology is constrained by the different phylogeny of each species under comparison (the Coal Tit and the Blue Tit are representative species of the two main, distant linages within *Parus*; Sheldon *et al.*, 1992) and by the different times the Tenerife Blue Tit and the European Coal Tit have had to evolve (Terborgh and Robinson, 1986).

Differences in foraging postures and morphology between the two Blue Tit subspecies and convergence with the Coal Tit may be explained considering competitive release in the island environment. Perhaps, competitive release in Tenerife during evolutionary time (subspeciation process) shifted the morphological evolution of the Blue Tit towards the morphology of the Coal

Tit, allowing the colonizers of Tenerife to broaden their foraging postures and habitat use (Grant (1979) argued that the absence of the pine-dwelling Coal Tit from the Canary Islands facilitated this evolutionary shift). Nevertheless, this is only one hypothesis among many others (the competitive exclusion hypothesis was rejected by Snow (1954) and Partridge and Pring-Mill (1977) when considering beak morphology).

Among the alternative ecological hypotheses is the geographical morphological variation related to climate. The lengthening of tarsometatarsus and the enlargement of the foot could be an expression of Allen's rule affecting the size of extremities in hotter and wetter environments (see Snow, 1954; Partridge and Pring-Mill, 1977; for beak length). Allen's rule seems to be supported by our results, considering that lengthening of the leg has only affected the most distal (and external) leg segments (tarsometatarsus and toes), with a lower and non-significant increase in the length of the internal leg segments (femur and tibiotarsus). Nevertheless, Martin (1991) pointed out that Allen's rule seems an unlikely explanation, because Blue Tit populations inhabiting northern Africa have longer tarsometatarsus length than Blue Tits from the Canary Islands (both geographical areas are at similar latitude).

Another alternative, non-competitive, hypothesis is related to the adaptation to particular features of the island environment (pine forests of *Pinus canariensis*). Island populations are usually relatively closed and they are free to develop responses to local environmental conditions more directly than mainland populations (due to the restricted gene flow; Wiens, 1989; Cockburn, 1991). This hypothesis was exemplified by Martin (1991) with the Blue Tit. He found that morphological similarity in tarsus, bill and wing lengths could be greater between geographically distant populations that face similar ecological conditions, than between geographically close populations subjected to different ecological conditions (e.g. habitat structure and floristic composition). Moreover, the intermediate foot morphology of the Tenerife Blue Tit between mainland Blue and Coal Tits, could be a reflection of their broad habitat width that precludes a fine-tuning between morphology and the use of a particular habitat (Winkler and Leisler, 1985; the Tenerife Blue Tit inhabits both coniferous and broad-leaved forests; Martín, 1987).

In any case, the ecological shift showed by the Tenerife Blue Tit towards the foraging postures of the mainland Coal Tit (due either to interspecific competition or to ecological factors or a combination of both of them, e.g. Grant (1979)) is associated with morphological changes which occurred during evolutionary time, considering functional relationships between ecology, behaviour and morphology. Therefore, convergence in foraging methods between Blue and Coal Tits can be explained without considering present interspecific competition (competitive release) as a determinant of current niche space.

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