

LEG MORPHOLOGY AND FEEDING POSTURES IN FOUR *PARUS* SPECIES: AN EXPERIMENTAL ECOMORPHOLOGICAL APPROACH¹

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Abstract. The foraging behavior of four *Parus* species feeding at artificial feeders was studied, while controlling for ecological variables related to patch characteristics (food quality, food access, and escape distance to the nearest refuge). Hindlimb morphology (osteology and myology) was analyzed and compared with foraging postures at feeders. Using the Long-Tailed Tit as an appropriate outgroup for comparison, and considering functional changes associated with morphological changes, we demonstrated the existence of clear ecomorphological patterns relating foraging postures and hindlimb morphology in the four *Parus* species studied. The Blue Tit uses hanging postures preferably and its hindlimb morphology is modified for helping leg flexion. The Crested Tit more often stands and its hindlimb morphology is modified to aid leg extension. Great and Coal Tits are ecologically and morphologically intermediate between the two former species. Our results show morphology as a determinant of locomotion mode. Since foraging postures are tightly associated with substrate use, then morphology should be considered when studying pressures determining community organization. Our proposed integrative method for dealing with ecomorphology can be valuable in demonstrating the adaptiveness of morphological structures in phylogenetically and ecologically related species.

Key words: ecomorphology; feeding postures; hindlimb; morphology; myology; osteology; *Parus*; tits.

INTRODUCTION

The main assumption of ecomorphological hypotheses is that morphology of an organism can predict its ecology (behavior), and many papers have shown strong correlations between morphology and ecology (e.g., Karr and James 1975, Leisler and Winkler 1985, Wainwright 1988, Losos 1990, Moreno and Carrascal, *in press*). However, the results of some studies have failed in finding congruent ecomorphological relationships (e.g., Wiens and Rotenberry 1980, Wiens 1989) within a broader pool of species likely affected by different selective regimes. In contrast to these studies, we presently demonstrate that ecomorphological studies, if conducted with closely related species, in somewhat controlled conditions, can demonstrate significant ecomorphological patterns.

We investigate the ecomorphology of four phylogenetically closely related species of *Parus* (*P. major*, *P. caeruleus*, *P. cristatus*, and *P. ater*; Sheldon et al. 1992) that co-occur in a mixed Mediterranean woodland of central Spain based on the following premises: (1) a knowledge of functional morphology should underlie ecomorphological studies (Bock 1990) and (2) morphological variables should be treated as parts of functional complexes (Leisler and Winkler 1985). Bones and muscles should be studied as parts of functional systems (Bock 1974). We investigate the relation of

foraging modes to leg morphology (osteology and myology). Norberg (1979) found that proportions of leg segments are associated with foraging differences in tits, and Leisler and Winkler (1985) showed that differences in hindlimb proportions among congeners are related to differences in foraging. We will extend this work with an analysis of leg musculature and feeding trials. To partially control for food quality, food access, and escape distance to the nearest refuge, we provided wild birds with special feeders. The possible bias resulting from these factors is usually ignored in purely descriptive studies, although it could obscure ecomorphological patterns. Finally we include a tentative phylogenetic analysis of the morphological and ecological (feeding postures) evolution within the genus *Parus*.

MATERIALS AND METHODS

Field work was carried out from October 1990 to January 1991, and from October 1991 to January 1992, in a 6-ha mixed forest of *Pinus sylvestris*, *Castanea sativa*, *Acer* spp., and *Populus* spp. (El Ventorrillo, 1500 m above sea level (a.s.l.), Sierra de Guadarrama, Madrid).

To detect interspecific variability in foraging postures, we designed two types of feeders (types U and D) 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. The posture required for feeding was

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standing (back up). Feeder type D had the net on the bottom, and the posture required for feeding was hanging (back down). Five feeding stations were established in the study area. At each station feeders U and D were erected (spaced 0.5 m apart), thus the bird had to choose between feeding standing or feeding hanging. We selected these two types of feeders for two reasons: (1) the use of each type of feeders requires opposite postures from a functional point of view, and (2) both postures very much resemble those that tits use in the wild while foraging, and represent postures referred to in the literature as tightly related to the use of different foraging substrates (e.g., Holmes et al. 1979, Laurent 1986, Carrascal et al. 1990). Feeders were filled with husked peanuts and suspended from pine branches \approx 50 cm below the canopy. Each year the birds were allowed 3 wk to familiarize themselves with feeders prior to sampling. We assume, therefore, that all birds had experience with the feeders.

Four *Parus* species (Coal Tit *P. ater*, Blue Tit *P. caeruleus*, Crested Tit *P. cristatus*, Great Tit *P. major*) used feeders commonly. Because birds had been netted and color-banded, we were able to identify them when they used the feeders. Samples obtained per individual were averaged prior to statistical analyses. Behavior 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 at each feeder (U or D) was recorded until the bird abandoned the feeding point. The use of feeders was expressed as percentages (%U + %D = 100%). To avoid competitive effects on the choice of the type of feeder, only records of solitary birds (no other birds on the same tree) lasting > 15 s were used for statistical analyses.

We dissected the hindlimb of two specimens of each *Parus* species, and we stained the muscle tissue with an iodine solution (Bock and Shear 1972). The gross morphology of the muscles was studied under a binocular dissecting microscope (5–20 \times). Anatomical nomenclature follows Baumel et al. (1979). Measurements of the hindlimb bones of 17 specimens of Great Tits, 6 Coal Tits, 5 Crested Tits, and 15 Blue Tits were taken. Biometrical variables measured were maximum femur length, maximum tibiotarsus length, maximum tarsometatarsus length, and distance from the head of the tibiotarsus to the distal point of the insertion of the tibialis cranialis muscle (IMT). To eliminate size effects we divided leg bone lengths by the cube root of the body mass. IMT distance was normalized by dividing by tarsometatarsus length because of the high functional meaning of this ratio (Richardson 1942, Norberg 1979).

We have used the Long-Tailed Tit (*Aegithalos caudatus*) as the most appropriate outgroup for comparison (it belongs to the family most closely related to the Paridae) on the basis of Sibley and Ahlquist's (1990) phylogenetic hypothesis. One spirit specimen of this

species was dissected and 11 skeletons were measured (the same measurements taken for other tit species).

Statistical tests employed were one-way analysis of variance and the *t* test for means (percentages were arcsine transformed; Sokal and Rohlf 1981).

MORPHOLOGICAL ANALYSIS

Muscles and bones

A detailed description and illustration of the hindlimb myology in *Parus atricapillus (montanus)* were given by Palmgren (1932). Muscular structure in the four *Parus* species is similar to that of this reference species. Thus, only muscles different from the reference species or differing among the four *Parus* species studied are described. Names of muscles are preceded by "M."

M. iliotibialis cranialis.—The most cranial muscle of the leg originates by an aponeurosis from the crest of the neural spine of the last two dorsal vertebrae and the most caudal end of the neural spine of the third dorsal vertebra in Great and Crested Tits. In the Coal and Blue Tits this origin is advanced to almost the whole neural spine of the third dorsal vertebra. In all species studied the origin becomes fleshy caudally from the anterior margin of the ilium. Fibers, in a nearly parallel-fibered arrangement, run down the thigh to insert by a flat tendon onto the craniomedial surface of the head of the tibiotarsus.

M. gastrocnemius.—Pars intermedia and pars externa in the species studied are as described for *P. atricapillus* (Palmgren 1932). Pars interna, however, varies among species. In the Crested Tit it arises by two distinct heads. An anterior superficial head arises in part from the tibiotarsal inner cnemial crest, while a band of fibers (the patellar band) originates from the patellar tendon, extending around the cranial surface of the knee. Following Raikow (1978), the size of the patellar band in the Crested Tit is 0.5 (i.e., 50% of the distance between the patellar crest and the patella). The posterior head of pars interna originates from the medial surface of the head of the tibiotarsus, partially underlying the anterior head. The two heads distally fuse into a tendon that distally joins with those of pars intermedia and pars externa to give rise to a common tendon of insertion. This passes over the tibial cartilage and over the hypotarsus and inserts on the caudolateral surface of the tarsometatarsus. The Coal Tit lacks the patellar band of pars interna, although the superficial (anterior) and deep (posterior) heads of origin are present. In the Blue and Great Tits, however, pars interna originates only by the anterior head.

M. fibularis brevis.—It originates by two heads. In Great and Crested Tits a tibial head arises as a small tendon from the caudodistal margin of the tibiotarsal outer cnemial crest. Distally it joins a fleshy fibular head, which originates from the fibular shaft craniolaterally, beginning distal to the insertion point of M.

TABLE 1. Mean (\bar{X}), standard error (SE), and sample size (n) of biometrical variables for the four tit species and for the Long-Tailed Tit. Linear dimensions are in millimetres; masses are in grams. Horizontal lines above means denote homogeneous groups not different statistically at $P < .05$ for morphological variables (Scheffé a posteriori test performed only with *Parus* species).

	Tit species				Long-Tailed Tit
	Blue	Great	Coal	Crested	
Body mass					
\bar{X}	11.2	18.6	9.3	11.6	7.1
SE	0.17	0.33	0.17	0.40	0.12
n	15	17	6	5	11
Leg length/(body mass)^{1/3}					
\bar{X}	23.2	23.7	24.9	25.1	25.4
SE	0.14	0.08	0.26	0.23	0.6
n	13	14	5	5	9
Tarsometatarsus/(body mass)^{1/3}					
\bar{X}	7.4	7.4	8.2	8.3	8.5
SE	0.06	0.04	0.09	0.09	0.08
n	13	14	6	5	11
Distance of insertion of <i>M. tibialis cranialis</i>/tarsomet. length					
\bar{X}	17.6	14.6	13.9	13.2	13.5
SE	3.4	2.6	3.0	3.6	0.30
n	8	10	6	5	10

iliofibularis. The belly runs down the crus to give rise to a tendon that passes across the intratarsal joint to insert on the lateral edge of the head of the tarsometatarsus. In Blue and Coal Tits the arrangement of *M. fibularis brevis* is as in the Great Tit, but the tibial head is big and fleshy.

Differences in skeletal characters are shown in Table 1. The relative length of the leg (femur + tibiotarsus + tarsometatarsus lengths) differed significantly among tit species ($F = 33.6$, $df = 3, 33$, $P < .001$). Blue and Great Tits having shorter legs than Crested and Coal Tits. Significant differences were also found in tarsometatarsus length ($F = 20.05$, $df = 3, 34$, $P < .001$) with Great and Blue Tits having shorter tarsometatar-

sus than that of Coal and Crested Tits. The insertion of the *M. tibialis cranialis* onto the cranial surface of the tarsometatarsus is proportionally more distal in the Blue Tit than in the other three tits ($F = 37.22$, $df = 3, 25$, $P < .001$).

Expected performance consequences from morphological traits

There are differences among the tits studied in both leg muscles and bone lengths. The following consequences for performance can be expected considering functional properties of the morphological traits (Table 2).

The *M. iliotibialis cranialis* is the main protractor of the femur (Cracraft 1971, Raikow 1985). The more advanced the position of its origin on the dorsal vertebrae, the longer the lever arm around the hip joint (Richardson 1942, Moreno 1991), thereby increasing the force of its protracting action on the femur (i.e., closing the hip joint).

The *M. gastrocnemius* is the main extensor of the tarsometatarsus (Raikow 1985). The greater its physiological cross section, the greater the force developed by the muscle extending the ankle, as the force increases with the number of fibers acting in parallel (Bock 1974).

M. fibularis brevis counteracts the forces of tarsometatarsal extension created by the toe flexors (Cracraft 1971), thereby aiding tarsometatarsal flexion and serving to maintain the position of this bone once it is flexed (Moreno 1990). The bigger the number of fleshy heads of origin (increased cross-sectional area), the bigger its effectiveness in flexing and maintaining a flexed position of the tarsometatarsus (Bock 1974).

M. tibialis cranialis is the main flexor of the tarsometatarsus (Raikow 1985). The further the insertion of this muscle on the cranial surface of the tarsometatarsus, the longer the lever arm around the intratarsal joint (Richardson 1942, Norberg 1979), which increases the force of its action closing the ankle.

TABLE 2. Morphological variables, character states, and ecological predictions about the hanging frequency of four *Parus* species considering their morphological differences. PA: Coal Tit; PCA: Blue Tit; PCR: Crested Tit; PM: Great Tit.

Morphological variable	Character state	Functional implications	Expected ecological ordination of species for hanging
<i>M. iliotibialis cranialis</i>	Advanced origin up to the third dorsal vertebrae	Increases lever arm around the hip joint Increased force for flexing femur	PCA = PA > PM = PCR
<i>M. gastrocnemius</i>	One head of origin in pars medialis	Decreases force for extending the ankle	PCA = PM > PA > PCR
<i>M. fibularis brevis</i>	Two fleshy heads of origin	Increases force for flexing the ankle	PCA = PA > PM = PCR
<i>M. tibialis cranialis</i>	Insertion more distal onto the tarsometatarsus	Increases the lever arm around the intratarsal joint Increased force for tarsometatarsal flexion	PCA > PM = PA = PCR
Tarsometatarsus and leg lengths	Shortening	Decreases the force needed to hold the body to the substrate	PCA = PM > PA = PCR

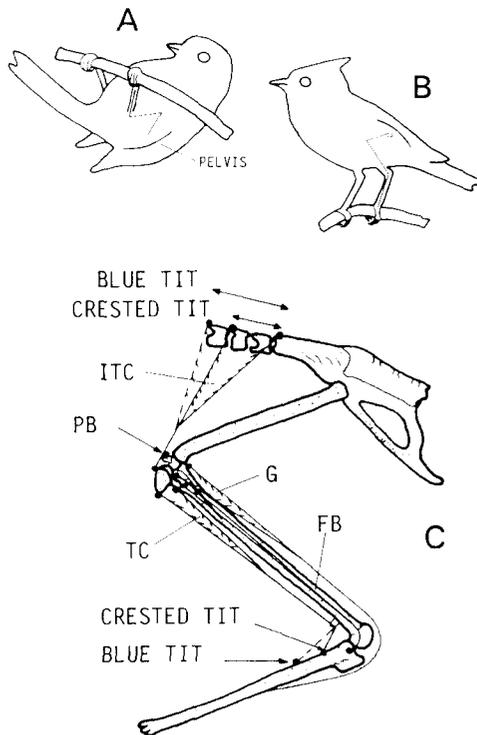


FIG. 1. Schematic representation of the leg bones in a "hanging" Blue Tit (A; at this posture the force of gravity tends to open the angle of the leg joints) and in a "standing" Crested Tit (B; the force of gravity tends to close the angle of the leg joints). Part C represents the relative position of the leg muscles differing among tits: *M. iliotibialis cranialis* (ITC) originates up to the third dorsal vertebra in the Blue (and Coal) Tit (---) while it arises from the second dorsal vertebra in the Crested (and Great) Tit. *M. gastrocnemius* (G) has a patellar band (PB) arising from the patella in the Crested Tit; such a patellar band is absent in the rest of the species studied. *M. tibialis cranialis* (TC) inserts onto the cranial surface of the tarsometatarsus the most distally in the Blue Tit (---) and the most proximally in the Crested Tit (Coal and Great Tits are intermediate). *M. fibularis brevis* (FB) has a fleshy tibial head in the Blue (and Coal) Tit while in the Crested (and Great) Tit such a tibial head is tendinous.

Shorter legs are often found in hanging species (Spring 1965, Norberg 1979, Carrascal et al. 1990). The shorter the leg bone segments, the shorter the distance between the center of gravity of the bird and the foraging surface, which reduces the effort needed to hold the body close to the substrate while hanging, optimizing the efficiency of the musculature supporting the body mass (see Winkler and Bock 1976, and Norberg 1979 for a detailed functional analysis).

From these expectations, and considering morphological differences among the four tit species altogether, the following suggested order can be made from the most hanging species to the least: Blue Tit, Great Tit, Coal Tit, Crested Tit (see Table 2 for details). Fig. 1 shows a synthesis of morphological variation among the tit species studied, and the association between

morphological syndromes and predicted foraging postures.

SELECTION OF FORAGING POSTURES AT FEEDERS

Tit species differed significantly in the mean proportion of time spent at feeder type D in feeder trials (percent of hanging; Fig. 2) ($F = 8.97$, $df = 3, 54$, $P < .001$). The Blue Tit used feeder type D (hanging) in a higher proportion than the other three *Parus* species; the Crested Tit spent the lowest proportion of time hanging. The Blue Tit used feeder type D significantly more than expected randomly (hypothesized mean: 50%), with the converse being true for the Crested Tit. Great and Coal Tits used both feeder types in proportions not differing from random. These results show that the ranking of the four tit species according to hanging frequency is consistent with the above predicted order derived from morphofunctional hypotheses (Table 2, Fig. 2).

DISCUSSION

Our results demonstrate that all tit species studied are able to use feeder type U and feeder type D (to be standing and to be hanging). However, there exist differences in the "preferred" foraging postures among the four *Parus* species as demonstrated by the percentage of time spent at each feeder in the feeder trial. We have also shown that such foraging differences can be predicted considering functional changes related to morphological changes at the hindlimb level.

Within the *Parus* studied, the Blue Tit is the species with the shortest legs. It has the main flexor muscles of the hip and intratarsal joints (*M. iliotibialis cranialis* and *M. tibialis cranialis*, respectively) modified in the direction that increases the force of their action (i.e., closing the joints). *M. fibularis brevis* is also modified to strengthen its action maintaining the tarsometatarsus at its position once it is flexed. Pars interna of *M. gastrocnemius*, the main extensor of the ankle, is, on the contrary, partially atrophied in the Blue Tit. This morphological pattern fits the mechanical requirements for hanging, i.e., morphological design should tend to counteract the force of gravity (the main force acting upon the bird while hanging; Fig. 1), which pulls the body downwards and tends to open the leg joints.

The Crested Tit has the longest legs. The main extensor muscle of the ankle, *M. gastrocnemius*, is modified by the addition of extra fibers to its pars interna, increasing ankle extension, as the force exerted by a muscle is related to its number of fibers (Bock 1974). Leg flexor muscles are not as well developed as in the Blue Tit (decreased leg flexion power). This hindlimb morphology better fits the mechanical requirements for standing, i.e., morphological design should tend to counteract the force of gravity, which, while standing, tends to close the leg joints (Fig. 1).

The Great Tit shows a mixture of characters. It shares with the Blue Tit characters that favor hanging (short

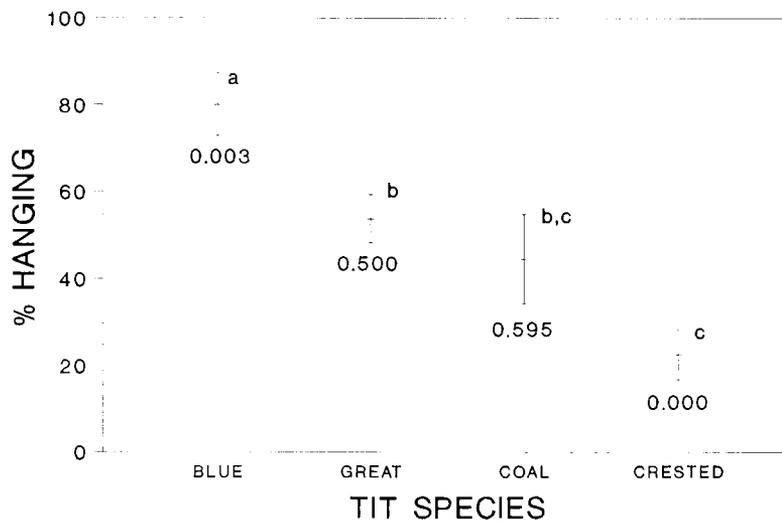


FIG. 2. Percentage of feeding postures in the trial (UD; standing vs. hanging). Vertical bars denote mean \pm 1 SE. The probability of Type I error in the t test comparing each data series with the hypothesized mean 50% (random use of feeder types U and D) is listed below each bar. Similar small letters near bars denote homogeneous groups not statistically different at $P < .05$ (Scheffé a posteriori test). Sample sizes: Blue Tit = 10, Great Tit = 20, Coal Tit = 14, Crested Tit = 14.

legs and pars interna of *M. gastrocnemius* arising from only one head). *M. iliotibialis cranialis*, *M. fibularis brevis*, and the insertion point of *M. tibialis cranialis* onto the tarsometatarsus, however, as in the Crested Tit, favor standing. This morphological pattern likely explains the use of feeder types U and D in proportions not differing from random. The Coal Tit also shares "hanging" characters with Blue Tits (*M. iliotibialis cranialis* and *M. fibularis brevis*) and "standing" characters with Crested Tits (relative long legs and short distance of insertion of *M. tibialis cranialis* onto the tarsometatarsus). This morphology, like that of the Great Tit, might explain the use of feeder types U and D in proportions not different from random. In summary, in Great and Coal Tits the same foraging behavior (proportion of feeding postures in trial UD) can be achieved with different hindlimb morphologies. This suggests that some phylogenetic constraints might underlie such morphological differences.

The results of this study show clear relationships between leg morphology and foraging modes. Although all species studied share a general morphological pattern allowing a wide behavioral repertoire (presumably through their common evolutionary history), there are subtle differences in both muscular morphology and skeletal proportions that can explain behavioral differences between them (presumably indicative of an adaptive relationship). In Fig. 3 we develop a tentative historical transformation analysis of the morphological (hindlimb)—ecological (foraging postures) characters exhibited by the *Parus* studied (these four tit species are representative of the two main lineages of the genus; Sheldon et al. 1992 complemented with data of Gill et al. 1989). The continuous skeletal variables have been coded into two discrete characters based on groups

identified by the Scheffé a posteriori tests. The derived character states of both skeletal and muscular traits were determined using the outgroup comparison method with Aegithalidae as the appropriate outgroup. Although the Long-Tailed Tit did not use the feeders (it is mainly an insectivorous species during winter; Perrins 1979, Carrascal and Tellería (1985) and Laurent (1986) have shown that this species hangs less than the Blue Tit and more than the Crested Tit (i.e., intermediate value). Therefore, it is plausible to hypothesize an unspecialized postural selection as the primitive behavioral character state for *Parus* (using Felsenstein's [1985] algorithm, and branch lengths from Sheldon et al. 1992 for estimating character states at nodes, the basal node for the *Parus* species studied is 49%).

Given the leg morphology of the Long-Tailed Tit (*M. iliotibialis cranialis* originates from the two last dorsal vertebrae, pars medialis of *M. gastrocnemius* originates in two heads lacking the patellar band, *M. fibularis brevis* having only a fibular head, relatively long leg, and short distance of insertion of *M. tibialis cranialis* onto the tarsometatarsus) and data from the literature (Raikow 1978, Bentz 1979, Moreno 1990, Moreno 1991, Moreno and Carrascal, *in press*), the following transformational events can be hypothesized (Fig. 3):

- 1) *M. iliotibialis cranialis* advanced its point of origin (from the two last dorsal vertebrae to the last three), and *M. fibularis brevis* developed a tibial fleshy head (derived state of the characters) have independently occurred in branches leading to Coal and Blue Tits (Fig. 3A).

- 2) Pars medialis of *M. gastrocnemius* reduced its heads of origin from two to one head, and a shortening of the leg bone segments (derived state of the charac-

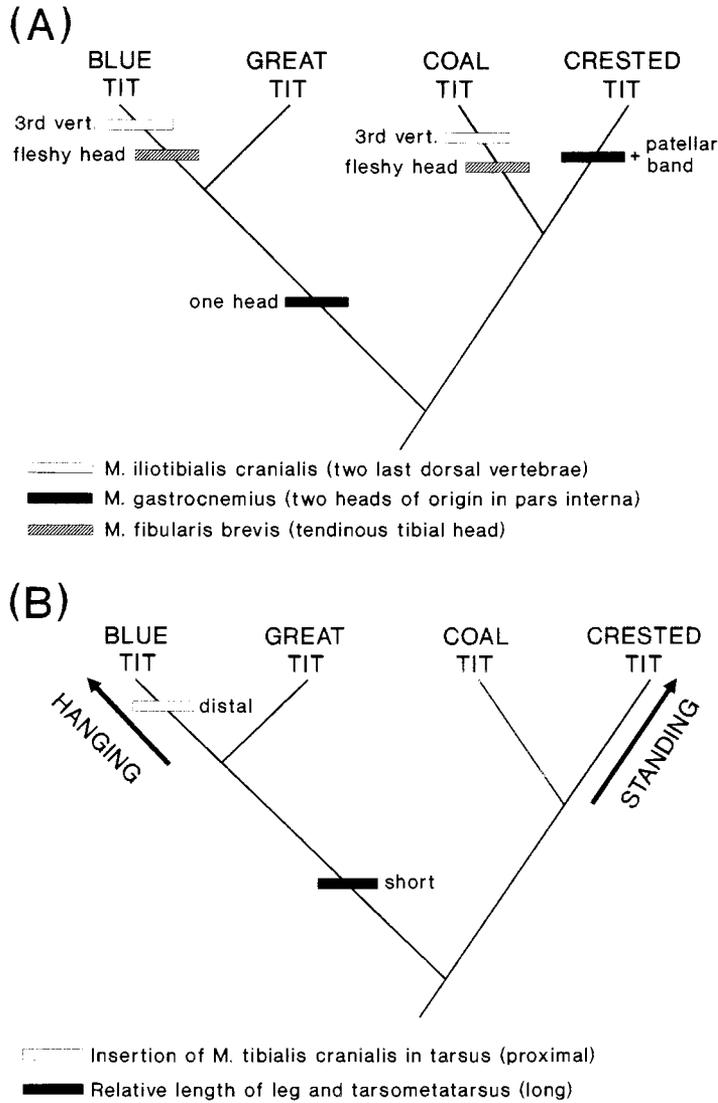


FIG. 3. Hypothesized morphological-ecological character state evolution in the genus *Parus*. *Aegithalos caudatus* (Aegithalidae) has been used as the outgroup for determining primitive character states. Horizontal bars represent the probable acquisition of a derived character state from the hypothesized ancestral state in *Parus*. Primitive character states are shown in parentheses for each morphological variable under the phylogenetic tree (branch lengths and tree topology obtained from Gill et al. 1989 and Sheldon et al. 1992); these characters are interpreted as primitive because they occur also in the outgroup. (A) Muscular characters. (B) Skeletal and ecological characters. Thick arrows denote hypothesized evolutionary change in foraging posture selection from an unspecialized primitive condition to a specialized "hanging" or "standing" situation.

ters) has occurred in the branch leading to the clade including Blue and Great Tits (synapomorphies; Fig. 3A).

3) A change in the insertion point of *M. tibialis cranialis* to a more distal position on the tarsometatarsus (derived state) has occurred in the branch leading to the Blue Tit.

4) The appearance of a patellar band added to the superficial head of origin of pars medialis of *M. gastrocnemius* (derived state) has occurred in the branch leading to the Crested Tit.

Considering functional changes associated with morphological changes, these hypothesized transforma-

tions in the character states are congruent with both the increased hanging proportion observed in the Blue Tit, and the increased standing proportion in the Crested Tit in our trials (Fig. 3A, B). On the other hand, historical constraints can explain differences found in morphology between Great and Coal Tits in spite of their similar foraging behavior. Results obtained with the latter two species demonstrate the importance of considering bones and muscles as inseparable parts of functional systems in ecomorphological studies (important suggestion made by Bock [1974] but ignored by many ecomorphologists). The Coal Tit, with relatively long legs (shared trait with the Crested Tit), is

able to hang as much as the Great Tit which has relatively shorter legs (shared trait with the Blue Tit) because some of its leg muscles are modified for helping leg flexion, thereby favoring its "hanging" abilities.

It also should be noticed that the only morphological difference between the Crested Tit and the Long-Tailed Tit (i.e., the addition of the patellar band to the gastrocnemius muscle) is important enough to drive differences in foraging behavior (a reduction in hanging performance). Moreover, the convergent changes in Coal and Blue Tit lineages in the lever arm change of the *M. iliotibialis cranialis* and the addition of the fleshy tibial head of the *M. fibularis brevis* are especially strong evidence of the adaptive nature of this complex.

Our results clearly show morphology as a determinant of the locomotion mode in the species concerned. If foraging postures are tightly associated with substrate use as has already been demonstrated (e.g., Holmes et al. 1979, Carrascal and Tellería 1985, Laurent 1986), then morphology should be considered when studying pressures determining community organization. This aspect is not usually taken into account in such ecological studies. For example, in recent papers on the organization of the *Parus* guild (Alatalo and Moreno 1987, Suhonen et al. 1992, 1993), differences in foraging sites between species are viewed in the light of predation risk, food resource distribution, and interspecific competition, without considering that morphology may influence the organization of the tit guild in terms of species distribution over different tree parts. In the *Parus* guild, differences in substrate use between the Coal and the Crested Tits (outer parts of branches in tree tops vs. inner parts of branches at medium heights) could be explained considering the presently demonstrated difficulty of the Crested Tit in using hanging postures, which are required for foraging at the needles of coniferous trees.

In this study we illustrate an integrative method when dealing with ecomorphology (morphological analysis [bones and muscles together] + experimental trials + phylogenetic relationships). We show how field studies undertaken under controlled conditions can be a valuable tool in comparing the behavioral abilities of ecologically related species, and in demonstrating the adaptiveness of morphological structures (Pounds 1988, Moermond and Howe 1989, Losos 1990).

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