Ecological plasticity of morphological design: an experimental analysis with tit species

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Abstract: To determine whether behavioural plasticity in foraging modes is contingent upon the morphology of the species, we analyzed the variability in frequency of use of foraging postures (standing versus hanging) under the selection pressure of predation risk. We studied the leg morphology of two contrasting tit species (Blue Tit, *Parus caeruleus*, and Crested Tit, *P. cristatus*). Results demonstrated that the leg morphology of the Blue Tit provides it with greater ecological plasticity in terms of foraging posture than that of the Crested Tit. Observed interspecific differences in ecological plasticity are not attributable to interspecific differences in morphological variability (between individuals within species). The morphofunctional bases of ecological plasticity in foraging posture are discussed. Morphological design may be considered an important factor in explaining niche width and potential for niche shifts, as morphology might determine the range of ecological "space" within which a species is allowed to move. The same niche shift in different species could represent different costs when morphological constraints are considered in relation to behavioural performance.

Résumé : Pour déterminer si la plasticité du comportement de quête de nourriture est fonction de la morphologie de l'espèce, nous avons analysé la variabilité dans la fréquence des postures d'alimentation (debout ou suspendus) soumises à la pression de sélection imposée par les risques de prédation. Nous avons choisi deux espèces de mésanges à pattes de morphologies différentes (la Mésange bleue *Parus caeruleus* et la Mésange huppée, *P. cristatus*) comme sujets expérimentaux. Les résultats ont démontré que la morphologie de ses pattes assure à la Mésange bleue une plasticité écologique plus grande en lui permettant plus de postures alimentaires. Les différences interspécifiques de plasticité écologique ne sont pas attribuables à des différences interspécifiques de variabilité morphologique (entre individus d'une même espèce). Les bases morpho-fonctionnelles de la plasticité écologique des postures de quête de nourriture sont examinées. La structure morphologique est probablement un facteur déterminant de l'étendue et du potentiel de déplacement de la niche écologique et la morphologie peut déterminer aussi l'étendue de l'«espace» écologique à l'intérieur duquel une espèce peut fonctionner. Le même déplacement de niche chez des espèces différentes peut entraîner des couts différents lorsque les contraintes morphologiques sont examinées en fonction de la performance comportementale.
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Introduction

The ecomorphological approach attempts to explain foraging behaviour and habitat use in relation to morphology. Ecomorphological patterns have usually been interpreted in the context of biomechanical models that predict the behaviour of species (i.e., locomotion modes, habitat, and substrate use; Winkler and Bock 1976; Norberg 1979; Leisler and Winkler 1985). Recent progress in ecomorphological studies has been achieved by considering phylogeny in comparative analyses (e.g., Losos 1990; Winemiller 1989) and through extension of ecomorphological patterns to a broad spectrum of taxa. Nevertheless, ecomorphological associations (i.e., correlational analysis of form and biological role; Bock 1990;

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Motta and Kotrschal 1992; Ricklefs and Miles 1994) do not tell anything about the extent to which morphology constrains ecological breadth. Evolutionary models of specialization pose costs for the specialist (Futuyma and Moreno 1988), as they sacrifice versatility in exchange for increased proficiency in the task for which it is specialized. Feeding specializations are widely distributed among animals, and several mechanisms have been found to explain such functional stereotypy (e.g., plastic behavioural responses of consumers to their resources, Whitfield 1990; competition, Smith 1990), at least at the intraspecific level.

In this paper we study the variability in foraging mode (posture preference while feeding) of the morphologically and behaviourally contrasting Blue and Crested tits (*Parus caeruleus, P. cristatus*) in respect to predation risk. In a previous study, Moreno and Carrascal (1993) demonstrated that within this genus, foraging behaviour and leg morphology (bones and muscles) are closely and causally related, Blue and Crested tits using substantially different body positions when feeding. Hanging upside down is associated with a

morphology that enhances leg flexion, i.e., shorter legs (mainly a shorter tarsometatarsus), the main flexor muscles of the hip (iliotibialis cranialis) and intratarsal (tibialis cranialis) joints originating and inserted, respectively, farther away from the articulation (facilitating effective flexing of the joints), and the fibularis brevis muscle with two fleshy heads of origin (which strengthens its action, maintaining the tarsometatarsus in its position once it is flexed). In contrast, standing upright requires hind-limb modifications for aiding leg extension: longer legs (mainly the tarsometatarsus), and the muscle gastrocnemius with extra heads of origin, which facilitates ankle extension (for morphological details and the functional role of these characters see Moreno and Carrascal 1993). Crested and Blue tits are at opposite extremes in both leg morphology and feeding postures in the genus *Parus*, the former being a "standing" species and the latter a "hanging" species.

Here we address the possibility that plasticity in foraging behaviour may be contingent upon the average phenotype of the species, that is, whether differences in morphological design allow different ecological ranges in terms of feeding postures in the two taxa of tits. To ensure that variation in ecological opportunities associated with feeding behaviour is appropriately investigated, the use of foraging postures is analyzed under either reduced or increased perceived predation risk, experimentally controlling for food quality, food access, and escape distance to the nearest refuge.

Material and methods

Study area, species, and feeders
Fieldwork was carried out during three consecutive autumn – winter periods (1989 – 1992) in a 6-ha mixed forest of *Castanea sativa*, *Acer granatensis*, *Populus* spp., and *Pinus silvestris* (elevation 1500 m; El Ventorrillo, Sierra de Guadarrama, Madrid, central Spain). Within the area nine feeding stations were established at least 50 m apart. Each consisted of one or two feeders measuring 20 × 11 cm, filled with husked peanuts, hanging from a pine branch either 0.5 or 2 m below the canopy (see below).

We designed three types of feeders (up, down, and lateral) made of wood except for one side, which was covered by a 4.8 mm mesh plastic net allowing birds access to food. Each type of feeder differed in the position of the net, thereby affecting the posture of the bird required for feeding. The "up" feeder type had the net on top, and the posture necessary to obtain the food was standing (upright). The "down" feeder type had the net on the bottom, and the posture required for feeding was hanging (upside down). The "lateral" feeder type had the net on one side, and the posture required for feeding was clinging (dorsum parallel to the net). We selected these types of feeders because their use required different, and in part antagonistic, postures from a functional point of view, and also because these postures closely resemble those that tits use for foraging on different foraging substrates in the wild (Holmes et al. 1979; Carrascal et al. 1990). Each year the birds were given 3 weeks to familiarize themselves with the feeders prior to sampling. We assume, therefore, that all birds had had experience with the feeders. Blue and Crested tits were chosen as the focal species because of their differences in "preferred" foraging posture, and the con-

trasting myological and skeletal morphology of the hind limb within the genus *Parus* (Moreno and Carrascal 1993).

In the three autumn – winter study periods, 28 Blue Tits and 17 Crested Tits were captured and colour-banded, facilitating identification of individual birds at the feeders. Samples obtained were averaged for each individual prior to statistical analyses. Behaviour at the feeders was recorded at each feeding station for sampling periods of 60 min. The first bird entering the feeding station was selected as the focal individual. Activity was recorded until the focal bird left the feeder (continuous recording method for sequences of behaviour; Martin and Bateson 1986). Only records of solitary birds were used, to avoid the unknown effects of interspecific and intraspecific social interactions on both feeding posture selection and time spent foraging at feeders. Samples were taken from 08:00 to 15:00 GMT. Only records lasting more than 15 s were used for statistical analyses. Behavioural data were collected with the Psion Organiser II computer programmed as an event recorder using The Observer (Noldus Information Technology, Wageningen, the Netherlands).

Procedures
The experimental design of this study rests on the assumption that tit species perceive distance to cover as a function of predation risk (for woodland passerines see Ekman and Askenmo 1984; Lima 1985; Ekman 1987; Hogstad 1988; Díaz and Asensio 1991). The farther the feeding patch from cover, the longer the escape distance and the higher the probability of being preyed upon while flying to a secure place. We predict that time spent at feeders should be shorter and vigilance greater at a patch more exposed to predation (see Barnard 1980; Lendrem 1983; Holmes 1984; Caraco et al. 1988; Hogstad 1988; Cassini 1991). To test this prediction, we manipulated the perceived predation risk. We erected one feeder of the lateral type either 0.5 m ("near") or 2 m ("far") below the canopy. At each feeding point the feeder was placed at a given position one day and switched to the other position the following day. The lateral feeder type was selected for this experiment to avoid habituation to a particular feeding box (up or down) used in the experiments with feeding posture selection.

Within the study area Sparrowhawks (*Accipiter nisus*) and Tawny Owls (*Strix aluco*) are common predators of small passerines. These raptors were observed flying just a few metres from the feeders. Blue and Crested tits responded to the presence of these predators by immediately flying towards the canopy and by alarm calling. We considered that birds were scanning the surroundings for the presence of predators when they raised the tip of the beak to eye level or higher (for a similar methodological approach see Hogstad 1988). Time spent foraging at feeders and the number of scans and scan duration were recorded for solitary focal individuals.

To measure the degree of ecological plasticity in selecting feeding postures by the two species, we developed an experimental design. Birds had to make a decision between feeding in the preferred posture and feeding at the safest patch (minimizing the risk of being preyed upon). Two different types of feeders (up and down; posture required while feeding: standing versus hanging) were erected at each feeding point in three different trials: (1) both up and down near (control

Table 1. Percentages of time spent hanging while foraging on box feeders in the three different trials.

| | | % time hanging | | | |
	n	x̄	SD	Z	P
Blue Tits					
Control	18	77.8	39.1		
Down−far / up−near	20	10.3	30.3	4.618	<0.001
Down−near / up−far	26	96.2	19.6	2.181	0.029
Crested Tits					
Control	17	23.0	39.5		
Down−far / up−near	16	3.1	12.5	1.991	0.046
Down−near / up−far	16	45.3	37.1	2.009	0.045

Note: Control: both up and down feeder types near (posture selection under no conflict risk situation); down−far / up−near: riskier hanging on down feeder type versus safer standing on up feeder type; down−near / up−far: riskier standing versus safer hanging. For a description of feeder types see Material and methods. Z and P values are from Mann−Whitney U tests of the comparisons with the controls; n is the sample size.

trial: posture selection under no conflict risk), (2) up−near and down−far (safer standing versus riskier hanging), and (3) up−far and down−near (riskier standing versus safer hanging).

Time spent feeding at each type of feeder was recorded. For each sample record, the percentage of time spent hanging upside down (use of the down feeder type) was calculated. Ecological plasticity in feeding posture was measured as the difference between the percentage of time spent feeding while hanging upside down in the down−near / up−far and up−near / down−far trials. We used nonparametric tests (Mann−Whitney U test and rank test for random location for the comparisons of a data series with an expected median) because of lack of normality and homoscedasticity in the data.

Results

We found significant differences in the mean proportion of time spent hanging (use of the down feeder type) between the two species in the control trial (down / up−near) (Mann−Whitney U test, two-tailed, Z = 3.447, P < 0.001; Table 1). The Blue Tits used the down feeder type (hanging upside down) more often than did the Crested Tit. Nevertheless, the two species did not differ significantly in variance of hanging frequency (Levene's test for homogeneity of variances, P = 0.98).

The vigilance proportion (seconds spent vigilant per minute of feeding) was significantly higher in Crested Tits when feeding far from cover than when this species was near (Mann−Whitney U test, one-tailed, P = 0.017), whereas Blue Tits showed no significant difference between these positions, although a trend towards more vigilance when far from cover was consistent with the prediction (one-tailed test, P = 0.09; Table 2). Time spent at feeders was significantly lower for Blue Tits in the far than in the near position (one-tailed test, P = 0.033). There was no statistical difference between positions for the Crested Tit (one-tailed test,

P = 0.236; Table 2). Therefore, birds responded to the increase in predation risk by modifying their feeding behaviour, the Crested Tits increasing the vigilance proportion and the Blue Tits decreasing the time spent at feeders.

In the down−near / up−far trial, Blue and Crested tits spent more time hanging (use of the down feeder type under safer conditions) than in the control situation (Mann−Whitney test, two-tailed, P = 0.029 and 0.045, respectively; Table 1). The interspecific difference in use of hanging when the up feeder type was exposed to a higher predation risk (down−near / up−far trial) remained significant (Blue Tits > Crested Tits; Mann−Whitney test, two-tailed, Z = 5.113, P < 0.001).

Distance to cover affected the mean proportion of time spent at the down feeder type (hanging with back down; Table 1). In the down−far / up−near trial, the two tit species used the down feeder type (hanging) less than in the control situation (Mann−Whitney test, two-tailed, P < 0.001 for the Blue Tits and P = 0.046 for the Crested Tits). The two species did not differ significantly in the proportion of time spent hanging in this trial (Mann−Whitney test, two tailed, Z = 0.846, P = 0.398). Differences between percentages of time spent hanging in the up−near / down−far and down−near / up−far trials were 85.9% for the Blue Tits and 42.2% for the Crested Tits.

Discussion

Results show that the Blue Tit is ecologically more plastic in terms of feeding postures than the Crested Tit; that is, ecological plasticity is not fixed for different morphological designs in these two *Parus* species (see Moreno and Carrascal 1993).

The niche-variation hypothesis (Van Valen 1965; Van Valen and Grant 1970) predicts that animals which have more variable feeding habits should also be more variable morphologically. Interspecific differences in morphological variability within species could be related to the observed differences in ecological plasticity (e.g., Grant et al. 1985; but see Díaz 1994). However, the two species studied here showed no significant differences in variance of the three morphometrical traits associated with foraging posture (applying Levene's test for homogeneity of variances to data in Moreno and Carrascal 1993: P = 0.36 for tarsometatarsus length; P = 0.81 for total leg length; P = 0.47 for relative distance from the head of the tibiotarsus to the distal point of the insertion of the tibialis cranialis muscle). Moreover, qualitative characters favouring hanging did not vary within any of these tit species (Moreno and Carrascal 1993). Therefore, the interspecific differences in ecological plasticity in foraging posture cannot be attributed to interspecific differences in morphological variability, and our experimental data do not support the niche-variation hypothesis relating generalized foraging habits to morphological variability (Van Valen and Grant 1970).

Within the ecomorphological pattern defined for our *Parus* species (Moreno and Carrascal 1993), it is clear that to have a "hanger" morphology gives the bearer increased ecological breadth compared with a bird with a "standing" morphology. If, as several authors have pointed out and is generally assumed (e.g., Alatalo and Moreno 1987), hang-

Table 2. Vigilance proportions (seconds spent vigilant per minute on the feeders) and times at the feeders for the two tit species 0.5 m (near) and 2 m (far) from pine foliage, and results of Mann—Whitney U tests (Z and P) comparing near and far distributions (one-tailed tests) (n is the sample size).

	Near			Far				
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	Z	P
Vigilance proportion (s/min)								
Blue Tits	19	18.9	10.5	16	21.4	8.4	1.34	0.090
Crested Tits	17	19.8	10.4	16	28.6	10.1	2.12	0.017
Time at feeder(s)								
Blue Tits	15	120.9	75.5	10	70.2	44.0	1.83	0.033
Crested Tits	17	46.4	45.8	16	49.2	36.4	0.72	0.235

ing postures are energetically more costly, it seems likely that species adapted to use an energetically costly posture (hanging) may nonetheless use an energetically less taxing posture (standing).

The Blue Tit's morphology consistently enables it to hang as efficiently as to stand, or at least provides a relatively high degree of plasticity in foraging posture, which may be advantageous when some individuals may be "penalized" (e.g., at increased risk of predation). On the other hand, the leg morphology of the Crested Tit does not seem to allow it to use feeders requiring hanging as efficiently as feeders that have to be exploited in a standing posture. From a functional perspective, modifications in the iliotibialis cranialis, tibialis cranialis, and fibularis brevis muscles increase their effectiveness (to flex the hip and the ankle; for details see Moreno and Carrascal 1993) when they contract, as the lever arm around each joint increases. This means that these joints are able to flex more efficiently when the bird is hanging, which may well decrease the energy costs of hanging. On the other hand, a shorter leg is advantageous for hanging, as it decreases the force (energy consumption) the leg musculature has to exert to maintain the body close to the substrate. Thus, differences in ecological breadth accruing to different adaptive morphologies are not "all or none" propositions, but a matter of "degree."

Our results also show that the morphological design of a species should be considered an important factor in explaining niche width, as morphology might determine the range of ecological "space" in which a species can operate effectively, considering morphofunctional interactions (see also Díaz 1994). If different morphologies impose different penalties upon the degree of deviation from an ecomorphological pattern, then niche shifts and variations in niche width among species might not always be due to interspecific dominance status, but may have a morphologically determinant or determined basis as well (e.g., Carrascal et al. 1990). That is, the same niche shift in different species could represent different costs, when morphological constraints are considered in relation to behavioural performance.

In conclusion, to find differences in ecological plasticity related to distinctive morphological designs and to understand them in a functional context can be of importance in explaining niche shifts and changes in niche width and over-

lap at the community level. Morphology may be useful as a predictor not only of the between-species component of mean performance (classical ecomorphology; Ricklefs and Miles 1994), but also of the within-species component (i.e., ecological plasticity) associated with the behavioural repertoire of each species, setting different species-specific upper and lower limits to performance. Future studies should analyze the relationship between morphological gradients and ecological plasticity in more species with well-established phylogenetic relationships to further our understanding of how morphological evolution has constrained the evolution of ecological breadth.

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