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Learning the ecological niche

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A cornerstone of ecological theory is the ecological niche. Yet little is known about how individuals come to adopt it: whether it is innate or learned. Here, we report a cross-fostering experiment in the wild where we transferred eggs of blue tits, *Cyanistes caeruleus*, to nests of great tits, *Parus major*, and vice versa, to quantify the consequences of being reared in a different social context, but in an environment otherwise natural to the birds. We show that early learning causes a shift in the feeding niche in the direction of the foster species and that this shift lasts for life (foraging conservatism). Both species changed their feeding niches, but the change was greater in the great tit with its less specialized feeding behaviour. The study shows that cultural transmission through early learning is fundamental to the realization of ecological niches, and suggests a mechanism to explain learned habitat preference and sympatric speciation in animals.

Keywords: ecological niche; cultural transmission; learning; speciation; foraging conservatism; habitat preferences

1. INTRODUCTION

Ecological theory states that each species has a unique niche, which encompasses its habitat and its use of resources in the presence of competition and other biotic interactions (Hutchinson 1959; Krebs 2001; Begon *et al.* 2005). The theory suggests that niches of closely related species are usually separated, facilitating coexistence by reducing competition if food is limited. Classic textbook examples are habitat use by Galápagos finches (Grant 1986; Grant & Grant 2003) and the spatial segregation in trees by small passerine bird species foraging in mixed flocks, such as warblers (MacArthur 1958; Price *et al.* 2000) and titmice (Lack 1971; Alatalo *et al.* 1987; Suhonen *et al.* 1994). However, although feeding niches are well documented, little is known about how individuals come to adopt them, whether they are innate and fixed at birth or else learned (Immelmann 1975; Marchetti & Price 1989; Davis & Stamps 2004; Tonniss *et al.* 2005). Here, we report a cross-fostering experiment in the wild where we transferred eggs of blue tits, *Cyanistes caeruleus*, to nests of great tits, *Parus major*, and vice versa, to quantify the consequences of being reared in a different social context, but in an environment otherwise natural to the birds (Slagsvold *et al.* 2002).

In the breeding season, blue tits and great tits feed on an abundance of caterpillars in trees and bushes. In winter, the two species forage together in mixed species flocks with little overlap in feeding niches, the blue tit feeding mainly high in trees on twigs and buds, and the great tit mainly on the ground or on the trunks and thicker branches of trees (Lack 1971; Suhonen *et al.* 1994). We cross-fostered young birds between the two species in a woodland near Oslo, Norway, and observed their foraging behaviour at two times of the year, in early autumn soon after they became independent, and in early spring before breeding started.

2. MATERIAL AND METHODS

Cross-fostering of blue tits and great tits has been carried out since 1997 in an area of 1.6 km², with about 450 nest boxes in mixed deciduous–coniferous woodland near Oslo (60°00'N, 10°38'E; Slagsvold & Hansen 2001; Slagsvold *et al.* 2002). The research has been approved by the appropriate authorities of Norway regulating research with animals. We determined which birds owned the territories and boxes in March and April 2005, and observed foraging in early spring (8–30 April), and also in early autumn (16 August–30 September) in 2005. In spring, we focused on all known cross-fostered birds and observed a similar number of unmanipulated (control) birds inhabiting the nearest territories to the cross-fostered ones. The cross-fostered and control birds reared in our nest boxes could be identified by a unique combination of colour rings. As controls, we also included immigrants that were captured and ringed (usually by mistnetting in autumn) and which were aged by plumage as first year (juvenile) or older birds (adult) assumed to be in their second year of life.

In autumn, the location of adult birds was less predictable than in spring because individuals were less territorial and juveniles foraged in flocks. We therefore attempted to record the foraging behaviour of every bird encountered as we visited all parts of the study area and so sample sizes were more variable between treatment groups in autumn than in spring. Over the years, there were too many nestlings to assign a unique combination of colour leg rings to each. Hence, in 2005, we assigned each of the four treatment groups a unique subset of colours and made use of 12 different combinations in each group. Unringed juveniles were included as controls, and we assumed that juveniles with the same ring combination (or those unringed) were different individuals if seen in different flocks. Yearlings and adults were sexed from their breeding behaviour in March–June (e.g. only females build nests and incubate). Juveniles observed in the autumn were not sexed.

The sex ratio and age in years ($\log x + 1$ transformed) of focal birds did not differ among treatment groups in either the spring sample ($n = 101$, 56% males; χ^2 -test, $p = 0.52$; range

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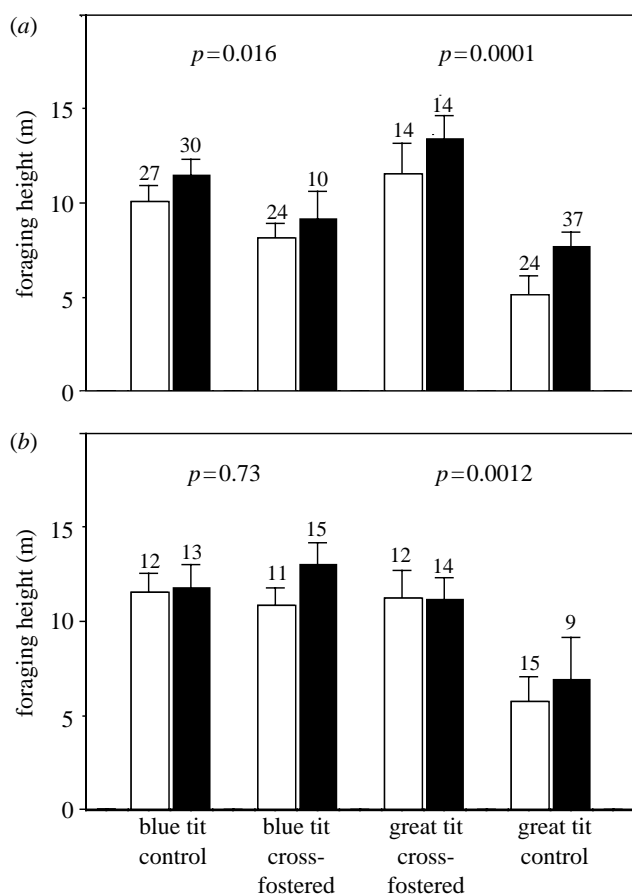


Figure 1. Foraging height (mean + s.e.m.) for blue tits and great tits: (a) in August–September, and (b) in April. Open bars, juveniles; filled bars, older birds. Cross-fostered birds were reared by the other species. Sample sizes are shown above bars. The p -values refer to t -tests between cross-fostered birds and controls. Age of focal bird had no significant effect in these comparisons.

1–7 years old; ANOVA, $p=0.26$) or the autumn sample (68% males, $n=92$, only possible to sex adults; χ^2 -test, $p=0.93$; range 0–4 years old, $n=180$; ANOVA, $p=0.33$). Similarly, the date of observation did not differ among the treatment groups in either spring (ANOVA, $p=0.46$) or autumn ($p=0.27$).

The observation period began after we identified the focal bird from its leg rings. We collected a total of 120 s of foraging observations (usually a consecutive period), only once per bird per season. If the focal bird moved out of sight or engaged in activities other than foraging before the 120 s elapsed, we spent a further 10 min in the area in an effort to resight it, accepting foraging observations that lasted at least 5 s. Observation bouts were longer for blue tits than for great tits in spring (ANOVA, $n=101$, $p=0.0041$), but not in autumn (same test, $n=180$, $p>0.05$). However, there was no significant difference in observation time between cross-fostered birds and controls for either the spring or the autumn data (ANOVA, same samples, $p>0.05$).

Foraging height, measured with a Suunto height recorder, was calculated as the mean of the heights at the start and end of the observation period. Most control blue tits fed from buds and leaves, or twigs with a diameter less than 2 cm (usually much thinner), whereas most control great tits fed from the trunk and branches thicker than 2 cm or on the ground. We graphed the mean percentage of time spent foraging in twigs to illustrate the results, but used a logistic

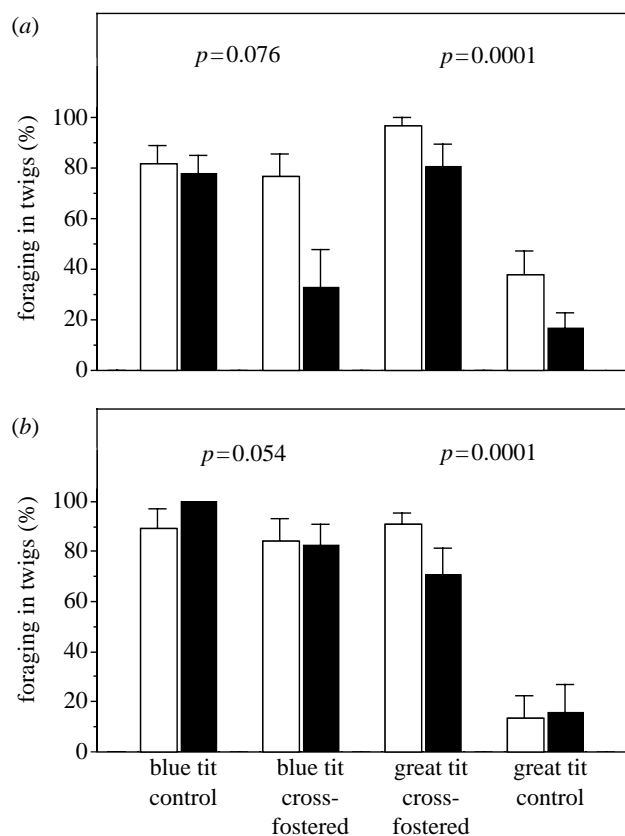


Figure 2. Percentage of time foraging in twigs (mean + s.e.m.) for blue tits and great tits: (a) in August–September and (b) in April. Sample sizes and symbols as in figure 1, except that p -values refer to logistic regression for great tits where age of focal bird had a significant effect (p -value refers to the model with both treatment and age included), and to U -tests in the other comparisons where age did not have any significant effect.

regression on whether or not the bird spent any time in twigs because most birds either were in twigs all the time, or not at all. The statistical tests are two-tailed.

3. RESULTS

As a first step, we confirmed the prerequisite that there was a marked difference in foraging ecology between blue tits and great tits in our populations of unmanipulated (control) birds. Control blue tits foraged higher above the ground than control great tits both in autumn (t -test, $t_{176}=4.58$, $p=0.0001$; figure 1a) and in spring ($t_{47}=4.00$, $p=0.0002$; figure 1b), and they also spent more time foraging in twigs in autumn (U -test, $z=-6.04$, $n_1=57$, $n_2=61$, $p=0.0001$; figure 2a) and in spring ($z=-5.75$, $n_1=25$, $n_2=24$, $p=0.0001$; figure 2b).

If foraging behaviour is influenced by early learning, the behaviour of cross-fostered birds should differ from controls of the same species and be more similar to their foster species. This was confirmed in foraging heights, although the effect was stronger in great tits than in blue tits (figure 1). Factorial ANOVA of foraging height showed a significant effect of treatment (cross-fostered versus control) both for the autumn ($p=0.030$) and the spring ($p=0.004$) data, and the interaction term between species and treatment was also significant for both periods (autumn, $p=0.0001$; spring, $p=0.014$; table 1). In autumn, juveniles foraged at lower heights than adults

Table 1. Differences in foraging behaviour between blue tits and great tits, and between two treatments (cross-fostered and control). (Interaction term is included only when significant. Statistics are given as F -values for foraging height (factorial ANOVA), and χ^2 -values for foraging in twigs (logistic regression). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.)

dependent variable	season	n	factor		
			species	treatment	interaction
foraging height	autumn	180	0.02	4.81*	28.61***
	spring	101	12.07***	8.58**	6.29*
foraging in twigs	autumn	180	0.00	8.48**	16.47**
	spring	101	16.32***	18.54***	—

($F_{1,172} = 4.64$, $p = 0.033$), but there was no interaction effect of age with species or treatment ($p > 0.05$). In spring, there was no effect of age, and the sex of the focal bird did not add significantly to the model in any period ($p > 0.05$).

The cross-fostered birds also changed the amount they foraged in twigs in the direction of the foster species; more so for the great tit than for the blue tit (figure 2). Logistic regression of whether or not a bird foraged in twigs showed a significant effect of treatment in both periods (autumn, $p = 0.004$; spring, $p < 0.0001$), and a significant interaction between species and treatment for autumn ($p < 0.0001$; table 1), but not for spring ($p > 0.05$). In autumn, juveniles tended to forage more often in twigs than adults ($\chi^2_1 = 6.52$, $p = 0.011$), but there was no interaction effect of age with species or treatment ($p > 0.05$). As with foraging height, there was no effect of age in spring or sex of the focal bird in any period ($p > 0.05$).

The above global analyses showed that juveniles were no more affected by cross-fostering when compared with adults because neither any interaction term between age and treatment nor any interaction between species, treatment and age was significant. In a more detailed test, we compared the foraging height and the proportion of time spent foraging in twigs, of a cross-fostered bird with its actual age in years (age $\log x + 1$ transformed; range: in blue tits, 0–4 years in autumn and 1–4 years in spring; in great tits, 0–4 years in autumn and 1–7 years in spring). If cross-fostered blue tits adjusted their foraging behaviour in the direction of conspecific controls over their lifespan, the correlations should have been positive. This was not the case as correlations were non-significant or negative (height in autumn, Pearson's $r = 0.14$, $n = 34$, $p = 0.44$; spring, $r = 0.20$, $n = 26$, $p = 0.32$; twigs in autumn, Spearman's $r_s = -0.45$, $n = 34$, $p = 0.010$; spring, $r_s = -0.07$, $n = 26$, $p = 0.74$). Likewise, we would expect significant, negative correlations in the case of cross-fostered great tits, but this was not found (height in autumn, $r = 0.28$, $n = 28$, $p = 0.15$; spring, $r = 0.02$, $n = 26$, $p = 0.94$; twigs in autumn, $r_s = -0.18$, $n = 28$, $p = 0.36$; spring, $r_s = -0.20$, $n = 26$, $p = 0.31$). We conclude that early learning from a different species caused a shift in the normal feeding niche that lasted for life.

4. DISCUSSION

Feeding niches may result from both morphological and behavioural differences among species. Blue tits are better adapted anatomically than great tits to forage from buds and leaves of tiny twigs because they have longer and stronger feet which allow them to hang upside down more easily while foraging than great tits (Moreno & Carrascal

1993; Rytkönen & Krams 2003). A genetically fixed and specialized morphology may explain why blue tits were less affected by cross-fostering than great tits. Blue tits are socially subordinate to great tits, but the shifts of feeding niches in our study cannot be explained by social dominance rank. Although cross-fostered birds tended to lose fights over food at common feeding sites in winter with control birds of the same species and sex (Hansen & Slagsvold 2004), they were free to choose feeding locations in their respective breeding territories in spring where they were socially dominant (Hansen & Slagsvold 2003). Moreover, in both tit species, males are socially dominant to females and this was also true for cross-fostered males versus control females in winter (Hansen & Slagsvold 2004). Yet, our statistical analysis indicated neither any influence of sex on foraging behaviour in autumn or spring nor any significant interaction between sex and treatment.

Studies of tits in captivity show not only that feeding skill and choice of foraging site have strong innate biases (Partridge 1974, 1979), but also that the birds may learn new feeding techniques and food items after they become independent (Fisher & Hinde 1949; Rowe *et al.* 2004). Therefore, it was remarkable in our study that early learning had such a strong and lasting effect on the foraging behaviour of birds in the wild. We expected that cross-fostered birds would shift their foraging niche by trial-and-error, back to the normal niche for the species, assuming that control birds had the optimal foraging patterns in the local environment. In contrast, the foraging behaviour of the parents, and possibly other individuals perceived as conspecifics, seemed to be imprinted on the young ones, probably because juveniles avoid costly trial-and-error learning by copying behaviour that has proven to be successful for their parents (Galef & Laland 2005). Our study is therefore consistent with recent findings that animals may be reluctant to include new prey items in their diets (Marples *et al.* 1998; Marples & Kelly 1999; Thomas *et al.* 2004), which may be explained by the advantages of search images, the experience with prey handling and the informational costs of a generalist foraging strategy (Dall & Cuthill 1997; Marples *et al.* 2005). The present study shows that such dietary conservatism may also be found in a food generalist (the great tit) and include not only prey types but also feeding sites (learned foraging habitat preference). Strong foraging conservatism means that, in order to benefit from early experience, a bird should prefer to settle in a habitat that is similar to its natal rearing site, and also to be philopatric to its breeding area once settled (Stephens 1991; Beltman & Metz 2005). If foraging efficiency

increases with social learning of prey types and the location of those prey, our results provide an ultimate explanation for why birds are imprinted on their natal habitat (Davis & Stamps 2004).

Recent theory and models suggest that learned habitat preference is even more potent a force in sympatric speciation than genetic-based habitat preference (Beltman & Metz 2005). Once populations become behaviourally imprinted on certain habitats, reproductive isolation may occur and subsequently facilitate genetic divergence among groups (Beltman *et al.* 2004; Tonnies *et al.* 2005). The idea that learning promotes speciation (Immelmann 1975; Beltman *et al.* 2004; Beltman & Metz 2005) is supported by our findings because cross-fostering had a greater influence on foraging in great tits than in blue tits and speciation has been much greater in the great tit group than in the blue tit group, although blue tits branched off earlier than did the great tit group (Gill *et al.* 2005). The theory (Beltman & Metz 2005) also predicts two endpoints to evolution: specialists with genetic and fixed habitat preferences or generalists with flexible (learned) preferences. Great tits use a much broader range of habitats for breeding than blue tits (Lack 1971) and show a greater reliance on early learning, consistent with the prediction.

In sum, our study provides the first experimental evidence from the wild that the behavioural components serving to separate niches of closely related species are not fixed at birth, but that cultural transmission through early learning is fundamental to the realization of ecological niches, and its influence lasts for life. We also discovered that two closely related species differed in their sensitivity to such early learning. The results provide new insights into how animals come to exploit their environment, suggesting a mechanism to explain learned habitat preference and sympatric speciation.

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