Research

Social learning in birds and its role in shaping a foraging niche

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We briefly review the literature on social learning in birds, concluding that strong evidence exists mainly for predator recognition, song, mate choice and foraging. The mechanism of local enhancement may be more important than imitation for birds learning to forage, but the former mechanism may be sufficient for faithful transmission depending on the ecological circumstances. To date, most insights have been gained from birds in captivity. We present a study of social learning of foraging in two passerine birds in the wild, where we cross-fostered eggs between nests of blue tits, *Cyanistes caeruleus* and great tits, *Parus major*. Early learning causes a shift in the foraging sites used by the tits in the direction of the foster species. The shift in foraging niches was consistent across seasons, as showed by an analysis of prey items, and the effect lasted for life. The fact that young birds learn from their foster parents, and use this experience later when subsequently feeding their own offspring, suggests that foraging behaviour can be culturally transmitted over generations in the wild. It may therefore have both ecological and evolutionary consequences, some of which are discussed.

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

1. INTRODUCTION

Social learning is widely used among vertebrates to acquire information about a fluctuating environment [1–3]. In birds, there is ample opportunity for social learning because parents may provide care for their offspring for several weeks, and because birds may join conspecific or mixed species flocks, allowing both vertical and horizontal transmission of behaviour. Here, we briefly review the literature on social learning in birds. Most insights on social learning in animals come from studies in captivity, and the role of social learning in nature remains rather poorly understood [4,5]. We therefore conducted a study of social learning in the wild, where we cross-fostered eggs of blue tits, *Cyanistes caeruleus*, to nests of great tits, *Parus major*, and vice versa, enabling us to quantify the consequences of being reared in a different social context but in an environment otherwise natural to the birds. To our knowledge, the study is the most extensive of its kind of any animal group. Here we report on foraging behaviour and on the foraging niche.

One contribution of 26 to a Discussion Meeting Issue 'Culture evolves'.

(a) *Social learning in birds*

Social learning may be involved in migration of some, but not all, avian species, where inexperienced birds may be guided by adults to find suitable migration routes and wintering areas. This knowledge has been successfully used to train naive, captive-reared endangered birds during migration using a microlight aircraft as 'foster parents' [6]. Social learning early in life may also be important in habitat selection [7,8], and birds may use 'public information', viz. the breeding performance of other species, in choice of habitats and nest sites [9].

On the other hand, little social learning seems to be involved in nest building. Some species build quite complex nests, yet conditioning probably is a sufficient developmental mechanism, with only a limited repertoire of stereotyped movements needed [10]. In a few birds, males may build courtship display sites (bowers) and for these, there is some circumstantial evidence that social learning is involved in the choice of decoration objects [11].

Social learning has a role in the recognition of predators [12,13] and brood parasites [14]; conservation strategies for endangered species attempt to teach inexperienced birds [13]. Alarm calls are considered to be quite stereotypic. Social learning may be involved in responding to such calls [13,15], but not necessarily in producing them [16], although great tits seem to learn from foster parents of another species (blue tits) in the wild [17].

Convincing examples of social learning in birds come from studies of song. Some details about the ontogeny of song have been well studied such as the brain pathways for vocal learning, the sensitive period during which a juvenile must learn songs, and which individuals the juvenile learns from [18,19]. Apparently, the strongest cases of 'production learning' come from vocal mimics copying calls of other species and environmental sounds [20]. Such mimicry is not confined to song birds [19]. Most experiments with song have been done in captivity but song copying also occurs in the wild, e.g. many birds have song dialects, and the dialects in a given local area may change over time. A few experimental studies on song copying in the wild suggest horizontal transmission, e.g. adult pied flycatchers, *Ficedula hypoleuca*, may pick up and sing novel playback songs [21].

Social learning is also important for mate choice in birds, primarily by vertical transmission through sexual imprinting early in life [22,23]. Most data are from studies in captivity, but there is some support from experiments in the wild [24–26], where sexual imprinting as a juvenile lasts for life [27]. However, sexual imprinting does not seem to be equally important in all species: pied flycatchers did not imprint on blue tit or great tit foster parents in the wild [28]. Mate choice and species recognition seem to have a strong genetic basis in the flycatcher and may be linked to the sex chromosomes [29]. A challenge is to understand the variation in the degree of sexual imprinting among species [28]. Interestingly, male pied flycatchers raised by tits did include tit song elements in their song repertoire, suggesting that different mechanisms are involved in the development of mate choice preferences and song acquisition [30].

In addition to sexual imprinting early in life, using parents as role models when choosing a mate, birds may use social information gained later in life such as 'public information' and eavesdropping by observing the mating choices of other individuals [31]. Costs and benefits may differ between the sexes, and so also their use of information [32], e.g. females may modify their song preferences by attending to the vocal behaviour of other females [33]. There is some evidence for mate choice copying in polygynous birds but results are more mixed in monogamous birds [34–36].

Many bird species also depend on social learning to learn aspects of foraging such as feeding sites [8,37], food items [38–40], hunting skills [41], handling and feeding techniques [42,43], and tool use [44]. Social learning of foraging may take place early in life, using parents as role models [8,40,45], and later in life by observing others [20,43,46]. The efficiency of learning may depend on whether the demonstrator is rewarded and on which other birds are present [47], e.g. in the presence of familiar birds, males and females [48], and producers and scroungers [49].

Social learning in birds, such as that involved in foraging, may only be owing to social learning in the weakest sense, e.g. learning of foraging sites through stimulus and local enhancement, rather than any true imitation; see [20] for definitions of levels and mechanisms of learning. There is little evidence for true imitation in the wild [20,50], although an increasing number of experimental studies suggests that birds are capable of motor imitation and production imitation [20,51]. New Caledonian crows, *Corvus moneduloides*, are the most sophisticated tool manufacturers other than humans. The behaviour is primarily based on trial-and-error learning but offspring also seem to learn from observing their parents [44,52]. Apparently, the social learning is sufficient to cause consistent differences in tool designs between separate geographical sites in the wild without any obvious ecological correlates [53]. Note that even relatively simple ways of social learning might lead to faithful transmission of behaviours [20,54,55], and that even with imitation, ecological and physiological factors may be important for faithful transmission [5,56].

Teaching was previously treated as a high-order intentionality attribute, largely restricted to humans. In recent years, it has been viewed as a functional category of behaviours serving to promote the learning of others [57]. The strongest evidence of teaching in wild birds may be the 'food' calls uttered by parents when arriving with food to the nestlings [58], and when foraging on preferable food items with the offspring after leaving the nest [40].

We conclude that although social learning is expected to be common in birds, strong evidence mainly exists for predator recognition, song, mate choice, and foraging. Although mainly lower level learning mechanisms may be involved in foraging, these may be sufficient both for vertical and horizontal transmission of behaviours.

(b) *Experimental testing*

Strong evidence for social learning requires controlled experiments in the laboratory and in the field [57,59–61]. The classical method has been to compare the behaviour of an animal allowed to observe a conspecific, with an animal not allowed to observe another, using a single transmission event [20,50]. An improvement is to apply 'diffusion' experiments, in which founder behaviours are experimentally manipulated and their spread across multiple individuals tested [62]. This method has been applied with success in fish, birds and mammals [62], and has shown that birds use social learning when responding to predators [12], and when developing foraging behaviour [38,42,43,63].

Cross-fostering in animals with parental care and translocation in species without parental care are powerful methods to study the influence of early learning, as shown by the famous studies of filial imprinting in geese by Lorenz [64]. More recently, these methods have been successfully applied to a range of taxa, from fish [65,66] to mammals [67], although the focus has been on song learning and sexual imprinting in birds, as mentioned above. Perhaps, this is because it is relatively easy to cross-foster birds' eggs when compared with the more limited tools for studying vertical transmission in mammals.

2. CROSS-FOSTERING EXPERIMENTS ON TITS

We conducted a large-scale, long-term, heterospecific, cross-fostering experiment of blue tits and great tits in

the wild, showing that many behaviours are affected, including sexual imprinting on the foster species [26,27], alarm calls [17], song [68] and foraging [8]. Blue tits and great tits live in sympatry in large parts of their breeding ranges. The two species forage in mixed flocks except during breeding, with little overlap in feeding niches. Outside the breeding season, the blue tit feeds mainly high in trees on twigs and buds, whereas the great tit feeds mainly on the ground or on the trunks and thicker branches of trees [69]. We have shown previously that the foraging height and amount of foraging on twigs during autumn and early spring shifts in the direction of the foster species as a result of early learning [8]. Here, we ask whether such learning influences the type and size of prey delivered to offspring in the breeding season. The answer is not obvious because the two species may overlap in food choice during breeding, causing competition [70]. In addition, studies of foraging of hand-reared tits in captivity indicate a strong genetic predisposition to the foraging habitat [71]. In the present study, we filmed cross-fostered and control parents as they delivered prey to young.

(a) Fieldwork and video analyses

Our study was conducted in a woodland area near Oslo over 4 years (2005–2008), and was approved by the Norwegian Animal Care Committee. Each year, about 500 nest boxes were available for breeding, of which about 110 were used annually by blue tits and 80 by great tits. Local recruits were given a unique colour combination of rings. Because of a possible difference in habitat of origin, immigrants (= not raised in our nest boxes) may have provided different prey items than the local recruits. Hence, the immigrants were excluded from all analyses except for an analysis within pairs presented in the electronic supplementary material. We compared prey items delivered by cross-fostered birds versus controls (= birds reared by parents of their own species). We also took several other variables into account: sex, age of parent, year, date of filming, brood size and geographical position of the nest site. The broods were filmed only once, for 1.5 h when about 10–12 days old. The tits are single prey loaders, and we estimated the length (l) and width (w) of each prey item in proportion to bill length of the focal parent (e.g. $l = 0.5$ means that prey length was half of parent bill length). Notice, therefore, that this is not an absolute measure. Prey volume was calculated using $s = \pi(0.5w)^2 l$ [72]. Type of prey was recorded as green, white or brown larvae, spider, adult Diptera ('fly'), adult Lepidoptera or 'others' (see electronic supplementary material for further details).

(b) Statistical analyses

We used the mean prey volume for each individual as a single sample. The volumes of individual prey items were log-transformed for statistical analyses (and when calculating the mean values) but for easy interpretation in the figures, we back-transformed the log values. Statistical tests were two-tailed. The statistical analyses of prey volume, and the proportion of a given prey
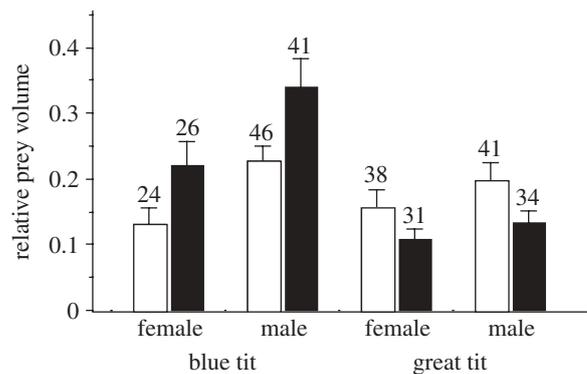

Figure 1. Mean (+s.e.) volume of prey items provided by female and male blue tit and great tit parents. Open bars, controls; filled bars, cross-fostered (reared by the other species). Prey volume was estimated from length and width of prey relative to bill length of parent. Sample size (number of parents) is shown above the bars.

type, were done in two steps. Initially, we tested for random effects using general linear models (GLM) in R [73] because a few birds and nest boxes were filmed in more than 1 year. Hence, to account for repeated measures, bird identity and nest-box number were treated as random factors. Fixed effects tested were: species, sex, age (yearling or older), year, date, brood size, altitude, longitude and latitude (position of nest site on the study area). The analysis showed that including random effects did not result in model improvement (see electronic supplementary material). Hence, in the final analyses reported below, random effects were excluded and we used GLM-ANOVA (analysis of variance) in SPSS v. 17.0.

(c) Results

The main factors of interest were species and treatment. Hence, to test for interaction, we started with a global ANOVA for prey volume including only these factors. The analysis showed a significant main effect of species ($F_{1,277} = 22.9$, $p < 0.0001$), but not of treatment ($F_{1,277} = 0.05$, $p = 0.83$). However, there was a highly significant interaction between the two variables ($F_{1,277} = 16.9$, $p = 0.0001$) because cross-fostered blue tits provided larger prey than controls, but it was the reverse in great tits, with cross-fostered birds providing smaller prey than controls, as predicted (figure 1).

Because of the interaction, separate ANOVAs were conducted on each species and we included the following potentially confounding variables: treatment, year, date of filming, sex, age (first year or older), brood size, altitude, longitude and latitude of nest site. Forward stepwise selection was used, and variables, and interactions between these, were included only if significant at the 5 per cent level. In blue tits ($n = 137$), the final model included treatment ($F_{1,130} = 22.2$, $p < 0.0001$), year ($F_{3,130} = 11.4$, $p < 0.0001$), sex ($F_{1,130} = 7.88$, $p = 0.006$) and brood size ($F_{1,130} = 4.12$, $p = 0.045$). No second-order interactions were significant. In great tits ($n = 144$), the final model included treatment ($F_{1,136} = 6.71$, $p = 0.011$), year ($F_{3,136} = 5.03$, $p = 0.002$), date of filming
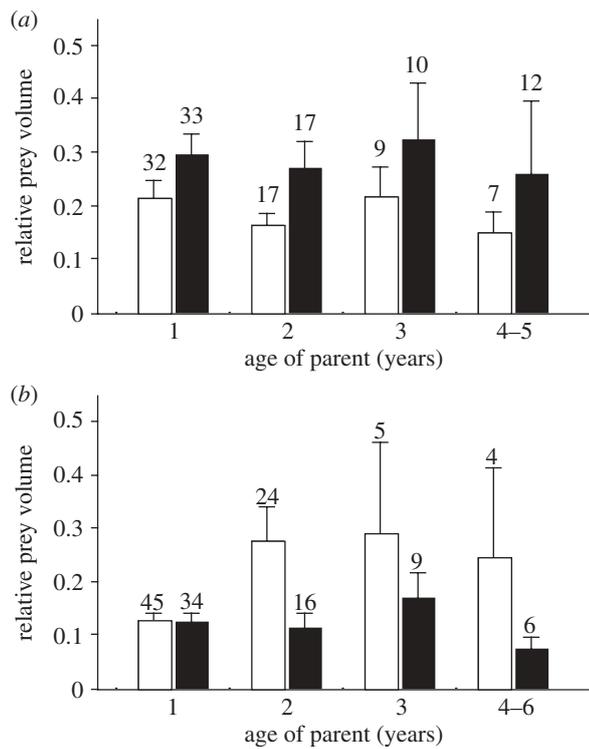
Figure 2. Mean (+s.e.) volume of prey items provided by (a) blue tit and (b) great tit parents in relation to the age of parent. Open bars, controls; filled bars, cross-fostered (reared by the other species). Prey volume was estimated from length and width of prey relative to bill length of parent. Sample size (number of parents) is shown above the bars.
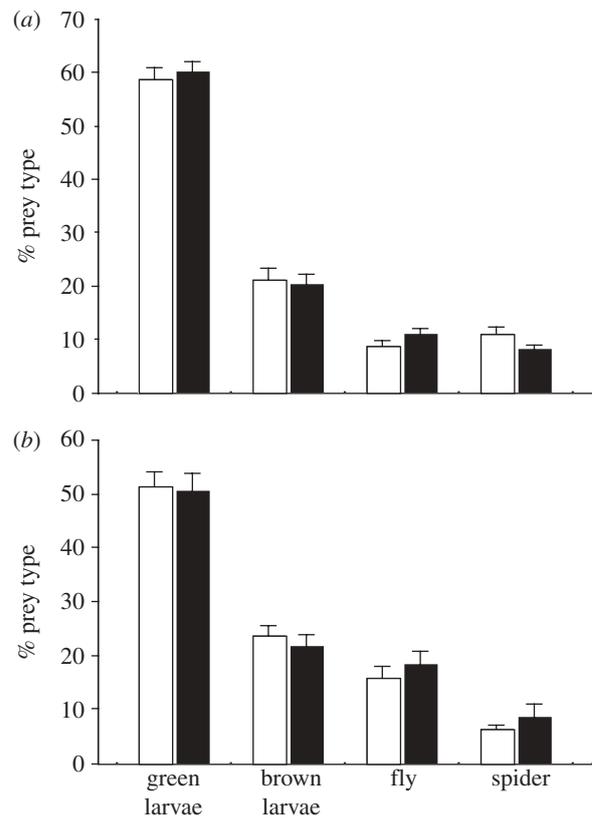

Figure 3. Mean proportion (+s.e.) of various prey types provided by (a) blue tit and (b) great tit parents. Open bars, controls (70 blue tits, 79 great tits); filled bars, cross-fostered (reared by the other species; 67 blue tits, 65 great tits).

($F_{1,136} = 5.57$, $p = 0.020$), age ($F_{1,136} = 4.24$, $p = 0.041$) and the interaction between treatment and age ($F_{1,136} = 6.36$, $p = 0.013$). See electronic supplementary material for the global ANOVA analysis for both species combined.

Prey volume was smaller for cross-fostered great tits than controls (figure 1), except for yearlings (figure 2). Apparently, this was because controls collected disproportionately smaller prey early in life compared with later, whereas cross-fostered birds provided small prey at all ages (figure 2). To test this in more detail, we compared individual birds filmed when they were 1 year old and when they were older (mean value in case of more than 1 year of filming as older). Prey volume did not change significantly in either cross-fostered or control blue tits, nor in cross-fostered great tits (paired t-tests, all ps > 0.20, $n = 8$–12), only in control great tits ($t_{17} = 3.90$, $p = 0.001$).

In our analyses, prey volume was estimated from length and width of the prey relative to bill length of the parent. To obtain a rough estimate of absolute prey volumes, we used mean (absolute) values of bill length recorded separately for each of the two species (for details see electronic supplementary material). The mean volumes of prey provided by the control birds were roughly 0.10 and 0.24 cm^3 for blue tit and great tit controls, respectively, and 0.16 cm^3 for the cross-fostered birds of both species. Thus, great tit controls provided larger prey than blue tits, but with cross-fostering, the difference disappeared and both groups provided prey intermediate in volume to the two control groups.

The main prey provided by the two tit species were green larvae, followed by brown larvae, flies and spiders (figure 3). Blue tits provided more green larvae than did great tits (blue tits: mean values of 59%, s.d. = 18, $n = 137$; great tits: 51%, s.d. = 26, $n = 144$; $t_{277} = 3.17$, $p = 0.002$). Blue tits also provided more spiders (U-test, $z = -2.39$, $p = 0.017$), but fewer flies ($z = -2.62$, $p = 0.009$) than did great tits, whereas no difference existed between the species in the proportion of brown larvae ($z = -0.89$, $p = 0.38$). For the latter prey types, the Mann–Whitney U-test was used because of deviations from normality.

A global ANOVA for the proportion of green larvae showed a significant main effect of tit species ($F_{1,277} = 10.1$, $p = 0.002$), but not of treatment ($F_{1,277} = 0.003$, $p = 0.96$), or the interaction between the two variables ($F_{1,277} = 0.19$, $p = 0.66$). We also analysed the proportion of green larvae for each species separately, including all potentially confounding variables as above, but there was no significant effect of cross-fostering even though there were a few other significant main effects (for blue tits: date of filming and longitude of nest site; for great tits: year of filming; tests not shown). See electronic supplementary material for a global ANOVA for both species combined.

Cross-fostered blue tits ($n = 67$) provided a higher proportion of flies than controls ($n = 70$; U-test, $z = -2.19$, $p = 0.029$), whereas no significant differences existed between the two groups in proportion
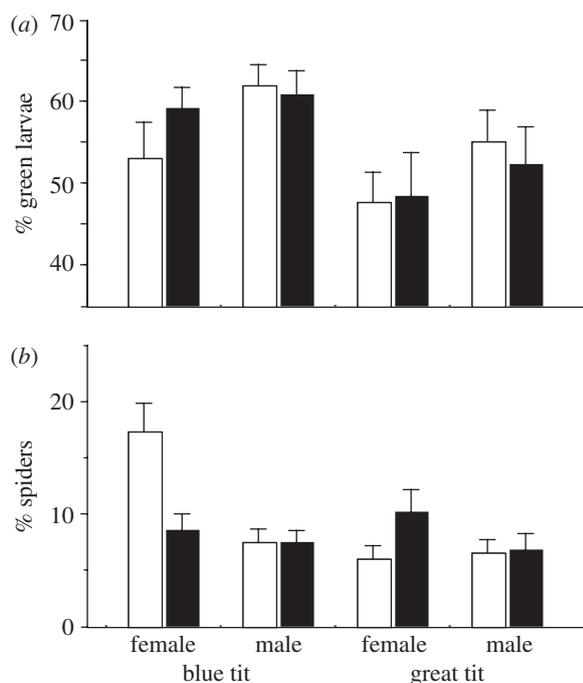
Figure 4. Mean (+s.e.) proportion of (*a*) green larvae, and (*b*) spiders, provided by female and male blue tit and great tit parents. Open bars, controls; filled bars, cross-fostered (reared by the other species). Sample sizes as in figure 1.

of brown larvae ($z = -0.38$, $p = 0.70$), or spiders ($z = -1.13$, $p = 0.26$). However, cross-fostered females ($n = 26$) provided relatively fewer spiders than control females ($n = 24$; $z = 2.57$, $p = 0.010$; figure 4). In great tits, no difference was found between cross-fostered birds ($n = 65$) and controls ($n = 79$) in the proportion of brown larvae ($z = -0.67$, $p = 0.50$), flies ($z = -0.56$, $p = 0.58$), or spiders ($z = -1.07$, $p = 0.29$).

Any difference in habitat quality surrounding the nest sites used by cross-fostered birds versus controls cannot account for our results. For instance, there was an effect of cross-fostering on prey volume even when comparing the prey provided by each member of a pair, where one parent was cross-fostered and the other parent was not (see electronic supplementary material). Furthermore, the differences in foraging between cross-fostered birds and controls cannot be explained by differences in body size. In blue tits, cross-fostered birds and controls had similar body size; in great tits, the cross-fostered birds tended to be slightly larger than the controls (T. Slagsvold 1997–2008, unpublished data). Larger birds may prefer larger prey, yet in our study, cross-fostered great tits provided smaller prey than controls.

3. SIGNIFICANCE OF THE EXPERIMENT
(a) *Social learning of foraging*
The social learning hypothesis was supported. Great tits in the wild typically provide much larger prey to offspring than blue tits. Hence, we predicted that blue tits reared by great tit foster parents would bring larger prey items than control blue tits, and this was confirmed. The opposite prediction was confirmed for cross-fostered great tits; they provided

smaller prey items than control great tits. Our study shows that not only does early social learning influence foraging during the non-breeding season [8], but also during the breeding season. The effect of social learning seemed to be equally strong in both species, although earlier work [7,8] indicated that the response was stronger in the species with the more generalist diet (the great tit) than the one with the more specialized food niche (the blue tit).

Cross-fostering had a greater impact on the size of prey chosen than on the type of prey. However, our classification of prey types was quite coarse, and if we had been able to identify species of green larvae or other insects more precisely, more differences between the treatment groups might have been apparent. Nevertheless, cross-fostered blue tits provided more flies than the conspecific controls as would be predicted with social learning because, control great tits provided more flies than blue tits.

Another explanation for the lack of a pronounced difference in prey types between cross-fostered birds and conspecific controls may be an effect of genetic predispositions. This explanation is supported by the fact that cross-fostered birds of both species provided food items intermediate in (absolute) size to those provided by the controls of the two species. However, such intermediate patterns would also be expected if strong innovative and trial-and-error learning are involved, behaviours that are commonly seen in tits [74–76]. Trial-and-error learning may lead individuals to prefer food they can deal with more easily, and learning of such skills would presumably be rapid and early. Hence, the changes in food preferences reported here may only be due to social learning in the weakest sense, e.g. learning of foraging sites through stimulus and local enhancement [77] rather than imitation. Further studies are needed to see whether the young tits pick up foraging techniques from their parents, and whether they are influenced by the specific prey items provided by the parents.

Individual-based learning would probably shift the foraging technique and the choice of food items by the cross-fostered birds in the direction of the conspecific controls, i.e. to fill the feeding niche to which the species is morphologically and physiologically adapted. However, if innovation and trial-and-error learning were important in the tits, it must have been restricted primarily to a short time-window early in life because we neither found a significant effect of age in the present study, nor in a previous study where an effect of cross-fostering on foraging location was detectable already in the autumn soon after the young had left the parents [8].

Our results suggest that early social learning lasts for life. Recent studies indicate that animals in general are reluctant to include new prey items in their diets [78,79], and avoid new nutritional stimuli [80]. Such dietary conservatism may be adaptive because the food items chosen by parents have already proven to be successful. Thus, early social learning in life may help the offspring to identify favourable food items, avoid other items, and develop search images more efficiently [81–83].

(b) Ecological and evolutionary consequences

The fact that young birds learned from their foster parents, and used this experience later in life when subsequently feeding their own offspring, suggests that foraging behaviour can be culturally transmitted over generations in the wild, and may therefore have both ecological and evolutionary consequences. Recently, it has been recognized that non-genetic factors, such as phenotypic plasticity and epigenetics ('inclusive heritability' [84]), must be included in order to more fully understand phenotypic evolution [5,84,85]. According to theory, phenotypic plasticity may accelerate evolutionary change, depending on whether the genotypes that are already fitter have a proportionally higher gain in fitness owing to plasticity than those of the genetically less-fit individuals [4,86]. Social learning may be favoured in fluctuating environments and when prey capture is difficult [1,2]. Throughout the year, blue tits and great tits forage on a wide variety of food items that have evolved counter-measures to predation, like mimicry and camouflage [82,87]. However, we do not know to what extent the individual tits gained in fitness from the social learning; it is not always obvious that social information is more valuable than personal information [4].

A cornerstone of ecological theory is that each species has a unique niche, which encompasses its habitat and use of resources in the presence of competing species and other biotic interactions [88]. A primary characteristic of the ecological niche involves exploitation of food. Much is known about animal foraging [89], and feeding niches are well documented in many species, yet little is known about how individuals come to adopt the niches [90,91]. According to the present study, social learning may be important, even in two species that appear to have quite distinct foraging niches [69]. Our findings indicate strong phenotypic plasticity and hence suggest an ability of the focal populations to adapt rather quickly to environmental changes, such as those involving climate and anthropogenic factors [2,92]. Knowledge of the ontogeny of foraging preferences may also help to understand patterns of competition among species, viz. juveniles may learn from their parents early in life to avoid excessive overlap with the foraging niches of competing species.

Early social learning, combined with dietary conservatism later in life, may influence natal dispersal and the use of micro- and macro-habitats, and explain a preference for the natal habitat [7,93]. In turn, this may influence reproductive isolation, potentially causing hybridization and speciation [91,94]. A social learning mechanism for foraging, rather than a strong genetic control, may reduce problems that hybrids face when the two parental species feed on different types of food [95].

Other consequences of the foraging niche may include plumage colour caused by variation in levels of carotenoids in the diet [96,97], breeding time, growth rate and risk of predation. Foraging behaviour may thus have a strong influence on life history and fitness traits such as reproductive success and survival

[89,98]. We are currently addressing some of these questions in our long-term cross-fostering project.

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