Immigrants and locally recruited birds differ in prey delivered to their offspring in blue tits and great tits

Tore Slagsvold [a,*], Karen L. Wiebe [b]

[a]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

[b]Department of Biology, University of Saskatchewan, Saskatoon, Canada

*Correspondence: T. Slagsvold, Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway.

E-mail address: tore.slagsvold@ibv.uio.no (T. Slagsvold).

Natal dispersal is common in animals but the fitness cost of moving from the natal area is less well understood. One reason for a fitness cost is that foraging skills and prey preference learned early in life may be less efficient if the individual settles in a new, unfamiliar habitat. In a four-year study, we found that immigrant parent blue tits *Cyanistes caeruleus* and great tits *Parus major* were inferior food providers compared to local recruits. In blue tits, immigrants provided smaller prey items than local recruits, whereas in great tits, the immigrants provided fewer green larvae, but relatively more brown larvae, to the offspring than local recruits. We also found that immigrant females laid later or smaller clutches than females locally recruited. The results are consistent with the hypothesis that natal dispersal carries costs related to the learning of foraging skills. However, alternative explanations are that the differences were caused by genetic and/or quality differences between the two groups of birds. We discuss various ecological and behavioural traits that may influence, and be influenced by, the mismatch of foraging between natal and breeding habitats. In altricial birds, yearlings will not have previous foraging experience during breeding and in addition, immigrants will not have spent a long post-fledging period in the new local habitat with their parents. If there are foraging-habitat mismatches as a result of dispersal, researchers should include natal origin in models of optimal foraging, time budgets, reproductive success, and survival because performance may be directly related to the early learning environment rather than genetic differences.

Keywords:

Foraging, habitat selection, natal dispersal, prey choice, social learning

Dispersal is a fundamental component of an individual's life history and plays an important role in the population dynamics of mobile species (e.g. Gamelon et al., 2017). Animals often move from their natal area to reproduce, perhaps to gain benefits such as access to more or better resources, and to reduce inbreeding (Foerster et al., 2003; Szulkin & Sheldon, 2008) and competition (Cotto et al., 2014; Hovestadt et al., 2014; Blyton et al., 2015). Costs of natal dispersal are less well understood but may involve factors such as increased energy expenditure and predation risk while traveling through unknown or unsuitable habitats, slower settlement, loss of social rank and support from kin, increased competition, and exposure to new predators and diseases after settlement in the new area (Duckworth & Badyaev, 2007; Bonte et al., 2012; Knowles et al., 2014; Aguillon & Duckworth, 2015). Costs and benefits of dispersal may differ among and within species, leading to variation in which animals move longer distances before settling. Knowledge of origin may help to understand variation in traits within a local population, including life history traits (Wilkin et al., 2007; Auld & Charmantier, 2011). Identifying differences in behaviour related to origin may also help understanding phenotypic plasticity and the ability of individuals to adapt to environmental changes.

Immigrating individuals may differ in behaviour and reproduction from those that settle in their natal area (i.e., local recruits) for several reasons. First, immigrants may be less well adapted to the local environment as a result of genetic differences caused by adaptation to different environments (Dhondt et al., 1990; Porlier et al., 2012). Second, immigrants may differ in quality from local recruits because of migration and settling biases caused by competition in the respective areas. For instance, local recruits which have familiarity with an area may have an advantage over immigrants (Pärt, 1994). The extent of dispersal may also differ in relation to personality (Dingemanse et al., 2003; Van Overveld et al., 2014), which in turn may cause differences in behaviour between immigrants and local recruits, possibly influencing competition and mate choice. Third, immigrants may have experienced a different habitat in their natal area than the local recruits and early learning may then affect subsequent behaviour and breeding biology.

Learning may occur individually as a result of trial-and-error or by observing others (i.e., social learning). Social learning may occur early in life, using parents as role models, but may also occur later by observing others. In birds, many species depend on social learning for such things as feeding sites, food items, hunting skills, handling and feeding techniques, and tool use (Slagsvold & Wiebe, 2011). Early social learning may help offspring to identify favourable food items, and to develop search images (Dall & Cuthill, 1997; Marples et al., 2005). Aversion to particular food objects may also be socially transmitted (Curio, 1993). After a period of learning, birds may be reluctant to include new prey items in their diets (Marples et al., 1998; Thomas et al., 2004).

Although foraging efficiency in a new location likely has strong fitness consequences, there is little information on how foraging is affected by dispersal (Fletcher et al., 2015). For instance, juveniles that need to learn foraging skills may delay natal dispersal and drive population-divergence patterns (Rutz et al., 2012). In social animals, foraging skills acquired as a juvenile may be compromised if settling in a new habitat where such skills do not conform to the foraging habits of the local social group (Van de Waal et al., 2013). Costs of dispersal may depend on the ability of the individual to learn appropriate prey types and foraging techniques when the new habitat differs from the natal habitat and this ability will likely depend on the amount of time the individual has to experience the environment. For example, first year breeding birds which settle in a new habitat may have less efficient foraging compared to older breeders which will have experience from at least one year of previous breeding and foraging. In comparison to first year immigrants, local first year recruits will have some foraging experience in the local habitat which they would have gained during the post-fledging period, although they will all lack experience in the habitat from the spring period prior to hatch.

Here we examine whether food provisioning of nestlings differed between immigrants and local recruits in two species of passerine birds, the blue tit *Cyanistes caeruleus* and the great tit *Parus major*, in a study area in Norway. Previously we showed with a field experiment which cross-fostered offspring between these two species of tits in the same study area, that juveniles learn foraging behaviour from their parents, and that this behaviour is fairly fixed for life (Slagsvold & Wiebe, 2007, 2011). Here we assume that larger prey items are preferred over smaller ones, and that green larvae are preferred because they are larger on average than brown larvae, spiders and flies (Wiebe & Slagsvold, 2015), and may help the bird to develop a bright yellow carotenoid-rich plumage (Partali et al., 1987). In another study area in Norway, the proportion of green versus brown larvae in the diet of great tits was lower in coniferous than in deciduous woodlands (Slagsvold & Lifjeld, 1985). In the present study, we assumed that the natal habitats of the local recruits and immigrants differed on average (see methods) and so we expected that the two groups of birds would differ in prey delivery to their brood as a result of foraging experience gained as a juvenile. If immigrant great tits to our study area had been reared in a more conifer-dominated forest relative to the natal habitat of local recruits, we would predict that the immigrants would provide relatively fewer green larvae to their offspring, but more alternative prey.

Recently it has been shown that individual tits may improve some aspects of their foraging behaviour later in life through local enhancement learning (Aplin et al., 2013, 2015). Thus, we tested whether the differences found in food provisioning between immigrants and local recruits was greater for first year than for older birds. A reduced difference with age was also expected if mortality was biased in relation to origin and foraging behaviour. For instance, in our study area, immigrants have lower social rank at feeding sites during winter than local recruits (Hansen & Slagsvold, 2004), and may therefore suffer higher mortality.

Genetic differentiation between populations at this northern latitude is small (Lemoine et al., 2016) because blue tits and great tits are partial migrants and may disperse over long distances. Whereas genetic differences between immigrants and local recruits are unlikely in our population, there is a potential settling bias because the habitat of the study area is of relatively high quality (see below) and so competition for a territory may be strong. Therefore, we studied whether immigrants and local recruits differed in body size and body condition. If there are settling biases, parents that settle early should have better territories and provision higher quality food items than those that settle late and so we tested for differences in food provisioning between birds that had arrived already in autumn and those that first appeared in the breeding season. In the present study, we also accounted for differences in territory quality by comparing food provisioning within pairs where one parent was an immigrant and one was a local recruit. Finally, we compared correlates of fitness, namely clutch initiation date and clutch size, between the groups.

METHODS

Study Species and Study Area

In Norway, both tit species are partial migrants; many juveniles leave in autumn but most adults remain near the territory throughout the year (Haftorn, 1971). Most pairs are formed several weeks before breeding and both species and sexes defend a resource territory throughout the breeding season (Perrins, 1979). The offspring leave the nest when 18-21 days old, and then spend 2-3 weeks near the nest being fed by the parents which they follow closely (Slagsvold et al., 2013). In Norway, coniferous forest is readily used by breeding great tits but it tends to be avoided by blue tits (Haftorn, 1971). Seeds are common in the diet year-round but the main prey delivered to offspring are caterpillar larvae.

We studied prey deliveries of blue tits and great tits from 2005-2008 near Oslo (59°56'N, 10°32'E) on a 1.6 km^2 site that is part of a larger woodland area interspersed with farmland and settlements. Deciduous trees dominate but there are also coniferous trees (spruce *Picea abies* and pine *Pinus silvestris*) standing alone or in patches throughout the whole study area. Of the deciduous species, some (birch *Betula* spp., grey alder *Alnus incana*, and willow *Salix* sp) are also widespread in southern Norway whereas others (ash *Fraxinus excelsior*, hazel *Corylus avellana*, maple *Acer platanoides*, and elm *Ulmus glabra)* are much less common and depend on rich soil and south-facing slopes characteristic of our study area. Hence, the study area is an unusual ´habitat island´ of luxuriant deciduous forest within an area of conifer-dominated forests (taiga) at this northern latitude.

Each year, about 500 nest boxes were available and about 90-120 were used by blue tits, and 80-100 by great tits. Unringed birds were assumed to be immigrants because each year we ringed all nestlings and a detailed study of breeding sites used by the tits showed that more than 97% of the tits in the local population used our nest boxes for breeding. Ringing of nestlings started in 1999 and probably most local recruits were already ringed when the present study started in 2005.

Fieldwork and Video Analyses

Of the fledging tits (700-1200 per year), typically 5-15% were found in the study area in a subsequent breeding season (Slagsvold et al., 2002). Yearling tits seem to settle mainly in two waves, one in autumn and one in late winter (Farine & Sheldon, 2015). Each autumn (September – November), we caught and ringed most birds in the study area by mist netting. We trapped again in spring to ring individuals not marked in autumn, probably mostly birds that had first settled in late winter. Locally recruited birds were given a unique combination of colour rings, as were many immigrants which were aged as first year or older based on plumage colour. We also recorded wing length, tarsus length, and body mass. In birds, wing length may be a superior measure of body size than tarsus length (Gosler et al., 1998). Body condition was calculated as the residual of mass on wing length. In spring, unringed birds still not caught were considered to be yearlings because of our extensive catching in autumn, because almost all older birds stayed in their territory for life, and because most of the ringed, local recruits that first appeared in spring were yearlings, probably returning from migration. When analysing food provisioning, we compared yearlings present in autumn with birds not observed until spring.

We also recorded date of first egg, clutch size, and hatching date for all nests. When analysing laying time and clutch size in relation to food provisioning, we focused on the females only because male quality seems to have little effect on these traits (Slagsvold & Lifjeld, 1990). We also analysed the proportion of great tit parents that survived from one breeding season to the next. Small sample size precluded analysis of survival of blue tits. Because of our extensive fieldwork, we assumed that any bird that was alive was recoded.

In previous studies, we video-filmed provisioning by some parents which were feeding experimentally cross-fostered heterospecific young (see Slagsvold & Wiebe, 2007, 2011 for details) but here we only included birds reared by conspecifics and feeding conspecific nestlings. Broods were filmed once for 1.5 hours in favourable weather when nestlings were 10-12 days old, using analog Sony Hi8 Handicams. A filming period of this length seems to be sufficient for obtaining reliable data (García-Navas & Sanz, 2012; Pagani-Núnez & Senar, 2013). Each year, the films were analysed in random order, and always by the same person (K.L.W), who did not know the origin of the birds. We used the first 20 food deliveries for each parent if available, and excluded cases with fewer than five identifiable items. Most of a video was analysed to get the required sample. In the main analyses, a parent bird was only included once. If a parent was filmed in more than one year, we used the last year of filming to reduce the bias of young birds and analysis showed that conclusions did not change with or without these observations. Sample sizes were 147 blue tits (123 immigrants, 24 local recruits), and 146 great tits (102 immigrants, 44 local recruits). The percentage of first year birds did not differ between immigrant and local recruit in blue tits (59% vs. 54%, $\chi^2 = 0.03$, $P = 0.86$) or in great tits (58% vs. 55%, $\chi^2 = 0.04$, $P = 0.85$). The percentage of males was also similar between immigrants and local recruits for blue tits (36% vs. 58%, $\chi^2 = 3.39$, $P = 0.066$) and great tits (40% vs. 48%, $\chi^2 = 0.44$, $P = 0.51$).

The tits are single prey loaders, and from the videos we estimated length (l) and width (w) of each prey item relative to the bill length of the focal parent and prey volume was calculated using $s = \pi(0.5w)^2l$ (Slagsvold & Wiebe, 2011). Type of prey was recorded as green or brown larvae, spider, adult Diptera or adult Lepidoptera, or unidentified (the latter were few, <1%). In the present study, the few (<3%) whitish larvae were combined with the green and we used three groups: green larvae, brown larvae, and all other items. In the rare cases the camera's clock did not work, we calculated percentages of the various prey types but not feeding rate. When a parent entered so fast that it was impossible to record prey type and size, we included the visit when calculating feeding rate. Hence, sample sizes may differ slightly between tests.

Statistical Analyses

We analysed provisioning behaviour using linear mixed models in SPSS v. 24. Pair identity was included as a random factor. Because some dependent foraging variables were strongly correlated, we only analysed a subset in more detail (prey volume, feeding rate of green larvae, brown larvae and all other items). We were primarily interested in the effect of origin of focal parent on the foraging variables and its interactions with age and sex but we included year as a random factor to account for annual variation in provisioning variables. We also included filming date and brood size. Thus, initial models for each provisioning variable included six independent variables (origin of focal bird, year, sex, age, date of filming and brood size), and the two-way interactions terms between origin and each of the five other variables. We deleted interaction terms and factors if they were not significant. Because food provisioning may be related to territory quality (Wilkin et al., 2009), in a separate analysis we controlled for variation related to traits of the territory and brood by comparing members of a pair where one parent was an immigrant and the other a local recruit. We used a paired *t*-test in this case. For all models, we calculated as dependent variables the proportions of prey items delivered in each of the three categories of prey types, and calculated an overall mean prey volume after log transforming the volumes of the individual prey items to achieve normality. Feeding rates (visits per hour) were also log (or log x+1) transformed for statistical analyses. To maximize sample size, we used data for all the immigrants and local recruits from the study area during the period 2003 – 17 to analyse laying date (N = 2432) and clutch size (N = 2319) of first nesting attempts. Statistical tests were two-tailed with significance set at $\alpha = 0.05$.

Ethical Note

The study complies with the current laws of Norway, and was approved by the Directorate for Nature Management in Norway (2006/1890, 2007/3295), and the animal welfare committee of Norway (reference numbers 2006/14549, 2007/8921).

RESULTS

Differences in Morphology

We performed two-way ANOVAs with sex and origin as factors to see whether yearling local recruits and immigrants differed in morphometric measures. In both species, females are smaller than males and with sex in the model, there was no relationship between origin and wing length in blue tits (origin: $F_{1,51} = 0.65$, $P = 0.42$, sex: $F_{1,51} = 26.3$, $P < 0.001$, origin*sex: $F_{1,51} = 0.10$, $P = 0.76$), or condition (origin: $F_{1,51} = 0.16$, $P = 0.69$, sex: $F_{1,51} = 0.23$, $P = 0.63$, origin*sex: $F_{1,51} = 0.31$, $P = 0.58$). Similarly, for great tits, origin was not related to wing length (origin: $F_{1,66} = 0.33$, $P = 0.57$, sex: $F_{1,66} = 42.7$, $P < 0.001$, origin*sex: $F_{1,66} = 0.05$, $P = 0.83$), or body condition (origin: $F_{1,66}$

= 0.002, $P = 0.96$, sex: $F_{1,66} = 0.60$, $P = 0.44$, origin*sex: $F_{1,66} = 0.004$, $P = 0.95$). Results were similar for analyses of tarsus length in relation to origin (data not shown). Therefore, we did not include morphometric variables in the subsequent analyses.

Effects of Individual Traits and Reproductive Timing

Natal origin had a significant effect on some aspects of provisioning when other variables were controlled in the linear mixed models (Tables 1 - 3). For blue tits, immigrants provided smaller prey than local recruits (Table 2, Fig. 1). The significant interaction term between age and origin for prey volume, and for feeding rate of brown larvae, was caused by first year immigrants providing smaller prey and delivering brown larvae relatively less frequently.

In great tits, there was no corresponding effect of origin on prey size but there was a strong effect on the feeding rate of green larvae (Table 1 and 3), and an interaction with age ($P = 0.001$, Table 3). The interaction was caused by a lower feeding rate of green larvae by immigrants than by local recruits for first year compared to older birds (first year birds, $t_{71} = 3.99$, $P < 0.001$; older birds, $t_{56} = 0.77$, $P = 0.44$). Back-transformed mean values for first year birds were 4.5 and 9.6 green larvae per hour for immigrants and local recruits, respectively (Fig. 2). The lower percentage of green larvae for all great tit immigrants (40% vs. 53%) was largely compensated by a higher percentage of brown larvae (31% vs. 21%, Table 1). For feeding rate of brown larvae, the significant interaction between origin and age was primarily caused by a difference among older and not by younger birds (Fig. 2). No significant interaction was found between origin and sex of parent in either species, and sex had only a significant main effect for two of the provisioning variables, both in blue tits (Table 2, 3). There was no significant interaction between origin and date of filming, or origin and brood size (Table 2, 3).

Of the juvenile blue tits we filmed, only 28% ($N = 72$) of immigrants were caught in autumn compared to 54% ($N = 13$) of the local recruits ($\chi^2 = 2.36$, $P = 0.12$). For great tits the numbers were 47% ($N = 58$) for immigrants and 79% ($N = 24$) for local recruits ($\chi^2 = 6.07$, $P = 0.014$). Hence, on average, yearling immigrants tended to settle later in the study area than local recruits. Sample sizes of local recruits were too small to include time of settlement as a factor in the models above, but no significant effect of time of settlement on provisioning was found for first year birds of either species when taking origin of the focal bird into account (**two**-way ANOVAs on the six variables in Table 1, all *P*-values > 0 .18) and there were no interactions (all *P*-values > 0.25).

Provisioning within Pairs

Within pairs of blue tits, the immigrant parent provided smaller prey items than its locally-recruited mate (Table 4) primarily when both parents were first year birds (paired *t*-test: $t_5 = 5.25$, $P = 0.003$) but not when older ($t_8 = 1.26$, $P = 0.24$). The feeding rate with ′other prey items′ was higher for the immigrant partner (Table 4) with a similar effect of age. In great tits, the immigrant parent provided fewer green larvae per hour than its locally recruited mate (Table 4). This held for first year birds ($t_{11} = 2.82$, $P = 0.017$), but not for older birds ($t_4 = 0.13$, $P = 0.90$). The three significant values in Table 4 also held true if taking sex of the respective parents into account in repeated measures ANOVAs (results not shown).

Annual Survival

No significant differences were found between immigrants and local recruits of great tit parents in survival from one breeding season to the next (all birds: immigrants 45%, $N = 86$; local recruits 51%, $N = 43$; $\chi^2 = 0.19$, $P = 0.66$; yearlings only: $N = 89$; $\chi^2 = 0.77$, $P = 0.38$). This was also the case if taking year, sex and age (first year or older) into account in a logistic regression analysis, or when also entering the interaction terms between origin and each of these three variables (all P - values > 0.34). We also studied whether survival was selective in relation to provisioning. However, there were no significant relationships between survival and either prey volume, or feeding frequency of green larvae, nor when taking year and interactions between year and the provisioning variable into account (all P - values > 0.28).

Reproduction

For the total sample (2003-**17**) for blue tit females, an ANOVA model which included year to account for annual phenological differences indicated that mean laying date of immigrants (30.5 April ± 6.3 SD, $N = 1243$) was later than for local recruits (29.4 April ± 6.6 SD, $N = 154$; $F_{1,1394} = 5.40$, $P = 0.020$; year: $F_{14,1394} = 93.5$, $P < 0.001$). The interaction between the two was not significant. For great tit females, mean laying date was similar for immigrants and local recruits (immigrants: 3.3 May ± 7.8 SD, $N = 868$; local recruits: 3.2 May ± 7.2 SD, $N = 167$; $t_{1033} = 0.99$, $P = 0.32$). However, the interaction between study year and origin was significant (origin: $F_{1,1031} = 0.41$, $P = 0.52$; year: $F_{14,1031} = 40.3$, $P < 0.001$; year*origin: $F_{14,1031} = 2.13$, $P = 0.009$), meaning that in some years immigrants laid slightly later on average, in other years slightly earlier, than local recruits.

For blue tits, clutch size was similar for the two groups of females (immigrants: 9.35 ± 1.59 SD, N = 1175; local recruits: 9.25 ± 1.67, SD *N* = 143) (ANCOVA; origin: $F_{1,1314} = 1.15$, $P = 0.28$; year: $F_{14,1314} = 4.57$, $P < 0.001$; laying date: $F_{1,1314} = 116.6$, $P < 0.001$). No interactions were significant. For great tit females, mean clutch size was significantly lower for immigrants than for local recruits (immigrants: 7.79 ± 1.54 SD, *N* = 839, local recruits: 8.15 ± 1.54 SD, *N* = 162; origin: $F_{1,996} = 4.16$, $P = 0.042$; year: $F_{14,996} = 4.24$, $P < 0.001$; laying date: $F_{1,996} = 30.3$, $P < 0.001$; year*laying date: $F_{14,996} = 4.09$, $P < 0.001$).

DISCUSSION

We found that in two species of passerine birds, provisioning behaviour differed between immigrants and local recruits; in great tits, immigrants provided fewer green larvae, but relatively more brown larvae, to their offspring than local recruits, whereas in blue tits immigrants provided smaller prey items than local recruits. We also found that immigrant females laid later or smaller clutches than females locally recruited. Although alternative explanations for these differences may include genetic differences, or differences in individual quality, we suggest the main cause was differences in acquired foraging behaviour due to differences in natal habitat because our study area is an unusual ´habitat island´ of luxuriant deciduous forest within an area of conifer-dominated forests.

Genetic and Quality Differences

Provisoning differences between immigrants and local recruits might have been caused by genetic differences between populations such as that which exists between tit populations in Corsica that differ in timing of breeding (Porlier et al., 2012). Although we cannot exclude genetic differences, they are less probable at the higher latitudes of our study area where tits are more migratory and gene flow is greater (Lemoine et al., 2016). Irrespective of genes, early environmental conditions might affect physiology and morphological development, causing life-long impacts on performance (**i.e.,** the ´silver spoon effect´; for great tits, see Wilkin & Sheldon, 2009). However, immigrants and local recruits did not differ in body size or body condition. Furthermore, a recent analysis showed that immigrants and locally recruited great tits on our study area did not differ in various measures of ´personality´ linked to fear and aggression (Skaraas, 2016). The habitat is of good quality and supports a high density of tits, meaning that only good competitors are likely able to compete with locally raised birds to settle. Hence, there is no reason to assume that the immigrants were of inferior physical quality.

Differences in territory quality cannot explain the results because birds settling in the autumn are predicted to have better territories than those settling later in the season, but we found no differences in foraging patterns related to timing of settlement. Indeed, differences in territory, season, weather or brood demands cannot explain differences in provisioning between immigrants and local recruits because foraging differences remained in the comparison between pair members when these factors were the same for each parent. Finally, in our study area, immigrants tend to be socially subordinate to local recruits at feeding sites in winter (Hansen & Slagsvold, 2004). However, for great tits, we did not find any significant differences in annual survival rate between immigrants and local recruits.

Differences Related to Early Learning

Apparently, the deciduous habitat of our study area made it of higher quality for tits than the conifer-dominated taiga forests most common at this northern latitude in Fennoscandia. Verhulst et al. (1997) found that even in deciduous forests with relatively short dispersal distances (Tilgar et al., 2010), 94% of great tit immigrants came from distances > 2 km. This is probably also the case for blue tits, which have similar migratory behaviour as great tits in Norway (Haftorn, 1971). Therefore, because the rich forest patch of our study area is smaller than 2 km across, many immigrants to the study area probably had experienced a different foraging substrate early in life than local recruits.

The proportion of green versus brown larvae in the diet of great tits seems to be lower in coniferous than in deciduous woodlands (Slagsvold & Lifjeld, 1985). If immigrant great tits to our study area had been reared in a more conifer-dominated forest relative to the natal habitat of local recruits, we therefore predicted that the immigrants would provide relatively fewer green larvae to their offspring, but more alternative prey, than local recruits, and this is what we found.

In birds, females generally disperse longer distances than males (Paradis et al., 1998; Tilgar et al., 2010; Michler et al., 2011; Ortego et al., 2011) and hence may be more likely to breed in unfamiliar habitats. However, we did not find that the sexes differed in provisioning behaviour related to origin. It is hard to predict which sex generally has more opportunity to learn to exploit novel foraging niches. In captivity, juvenile female blue tits were twice as likely as other sex and age classes to acquire a novel foraging skill from social learning (Aplin et al., 2013). In captive great tits, females were better than males at using information from the environment when discriminating prey (Hansen et al., 2010), and when exploiting food stored by another species (Brodin & Urhan, 2015).

In altricial birds, offspring may gain some experience of appropriate prey types during the nestling stage based on items the parents feed them in the nest. After fledging, further experience is gained of prey types, where to forage, and how to handle prey items. Blue tits and great tits bring caterpillars to their young but even first year local recruits may lack foraging experience with this important prey for the breeding period because such prey are often abundant only during a narrow time window in spring (Van Noordwijk et al., 1995; Reed et al., 2013). If so, all first year birds, but particularly the immigrants should improve their foraging behaviour with age.

Consistent with this idea, the difference in provisioning between immigrants and local recruits was greater among first year birds than among older birds. This difference in provisioning may have been caused by a higher mortality of individuals with ´poor´ foraging ability from the first to the second year of life. However, for great tits, there was no difference in survival rate between immigrants and local recruits and no bias in survival related to characteristics of parental food provisioning (prey volume and feeding frequency of green larvae). In willow tits *Poecile montanus*, immigrant males had lower survival during winter than philopatric males (Pakanen et al., 2016). Instead, in our species, some learning of local conditions seems to have occurred in our population from one breeding season to the next but we recommend future longitudinal studies of changes in foraging patterns within individuals over time.

In many birds, foraging skills improve during the first years of life (Hand et al., 2010; Zimmer et al., 2011). Learning is adaptive when conditions encountered later in life are unpredictable and it may occur by both individual trial-and-error and social learning. Social learning is often relatively fast and efficient (Boogert et al., 2014; Aplin et al., 2015). The degree to which individuals may learn foraging behaviours from their mate after settling in a new habitat is unknown. In tits, mate-guarding males follow females closely during her fertile period (Hansen et al., 2009). However, there is probably less contact between partners during incubation and nestling-feeding, and as shown here, differences still existed in provisioning between partners when the two birds had different origin.

In our previous study of tits, early social learning seemed to account for more than trial-and-error learning, and subsequent social learning, because cross-fostered birds maintained the novel foraging niche of their foster parents over years (Slagsvold & Wiebe, 2007, 2011). One reason may be that most cross-fostered birds became sexually misimprinted on the foster species and this seemed to last for life (Slagsvold et al., 2002; Hansen et al., 2008). Although we did not expect strong age-related effects, our analyses here revealed a stronger difference in food provisioning between immigrants and local recruits for first year birds than for older birds.

When comparing bird species, the effect of diet breadth on the foraging costs of dispersal is difficult to judge. Generalists can take advantage of a greater diversity of food types than specialists and be more opportunistic, using the most common prey. However, generalists may be more dependent on previous learning to forage optimally than specialist species which may show more innate food preferences and foraging techniques. Because blue tits in Norway are more specialized on deciduous forests than are great tits (Haftorn 1971), we expected the difference in provisioning might actually be more pronounced in great tits (diet generalists) compared to blue tits (specialists, García-Navas et al., 2013) because our mainly deciduous study area should have been more familiar to dispersing blue tits. However, the results between the species were hard to compare because immigrant great tits provided fewer green larvae, and relatively more brown larvae, than local recruits, whereas in blue tits, immigrants provided relatively smaller prey than local recruits.

In general, we suggest that the mismatch between foraging skills in the breeding versus the natal habitat will be exacerbated when (1) the areas with different habitats are relatively small and patchy on the landscape such that a dispersing bird is likely to land in a novel habitat type; (2) foraging conditions have large seasonal variation and differ greatly between the autumn period when some learning by juveniles may occur compared to the spring or summer period when breeding occurs; (3) the bird is short-lived and has less time to learn as an immature and to improve skills in subsequent breeding seasons; and (4) foraging behaviour is either fixed and innate or any learning occurs mainly during a short time window during early development after which time behaviours are quite fixed.

Most animals prefer to settle in habitats that match those they have experienced in early life (Davis, 2008). However, this preference may be reduced if the juvenile experiences relatively poor conditions (e.g. little food) in the natal area (Stamps et al., 2009; but see Fletcher et al., 2015). Thus, immigrant tits originating from a relatively poor coniferous forest may still benefit from settling in a rich deciduous woodland as long as the net gain in food supply outweighs any foraging inefficiency costs.

The dietary differences we found are probably conservative because we were only able to classify prey to coarse groups and not species. An obvious next step will be to study whether immigrants forage in different microhabitats compared to local recruits.

The lower proportion of green larvae in the diet of immigrant great tits suggests that these birds foraged less often in the green foliage. Larvae colour probably reflects crypsis and the need of background matching. In blue tits, immigrants provided on average smaller prey than local recruits, suggesting the two groups focused on different species of larvae.

Fitness Differences

Because foraging behaviour differed between immigrants and local recruits we expected that there could be consequences for correlates of fitness such as timing of egg laying and clutch size. The reproductive differences might arise because foraging directly impacts the energy available for egg formation or, alternatively, because the two groups of females might respond differently to the local environmental cues about food abundance depending on familiarity. For blue tit females, mean laying date was slightly later for immigrants than for local recruits but for great tits, the difference in timing between the groups varied with year. For blue tits, clutch size was similar for the two groups of females but for great tits, mean clutch size was significantly lower for immigrants than for local recruits, suggesting a cost of dispersal. Other studies of tits have also documented lower clutch size for immigrants compared to local recruits (Wilkin et al., 2007; Auld & Charmantier, 2011). Clutch size in tits is partly heritable, and assuming that optimal cutch size has evolved mainly in deciduous forests and at lower latitudes, it may explain why great tits lay too many eggs in some areas with coniferous forest (Dhondt et al., 1990), and forests at high latitude (Rytkönen & Orell, 2001). However, clutch size is also affected by environmental factors including female condition and nest box size (Slagsvold & Lifjeld, 1990; Møller et al., 2014).

Some studies have reported negative fitness effects associated with long-distance dispersal in male but not in female passerines, including great tits (Pärn et al., 2009; Van Overveld et al., 2015), but with an opposite result in blue tits (García-Navas et al., 2014). However, most previous studies have been unable to distinguish potential effects of dispersal from effects of social status and phenotypic quality on fitness (Doligez & Pärt, 2008), and to our knowledge none has examined foraging. Studies that only examine natal dispersal distances within a study area may be at too small a spatial scale to detect fitness differences because juvenile tits may forage with their families at distances greater than 1 km from their natal territory (Van Overveld et al., 2011; Slagsvold et al., 2013) and hence may gain local experience over a fairly wide area.

If immigrants are poorer food providers, we predict that they would be avoided as partners and there might be assortative pairing according to origin. Assessing the origin of a potential mate could be difficult but it might be easy to assess its foraging skills or other indirect cues such as plumage colour or vocal dialect. Great tits raised in spruce forest were paler than those raised in deciduous forest (Slagsvold & Lifjeld, 1985). However, an experimental study of zebra finches *Taeniopygia guttata* suggested that learned foraging specializations did not affect female mate choice or pair formation (Boogert et al., 2010). In a highly mobile avian raptor, assortative mating was found in relation to natal habitat type although the reason for it was unknown (Fletcher et al., 2015).

In sum, differences between immigrant and local recruits in food provisioning were largely consistent with the hypothesis that the tits learn their foraging niche in their natal habitat type. However, we cannot rule out genetic differences between the groups related to origin. Our study suggests that dispersing individuals face foraging costs if they settle to breed in an unfamiliar habitat type. Therefore, the heterogeneity of habitat types on the landscape, and the ability of birds to learn foraging techniques during their lifetime, may affect decisions by juveniles such as the timing of independence from the parents, the extent to which social living is favoured, and natal dispersal distances. Learning new foraging techniques entails time and efficiency costs, so there will be selection for early social learning, combined with dietary conservatism later in life when the breeding habitat is similar to the natal habitat. If there are foraging-habitat mismatches as a result of dispersal, researchers should include natal origin in models of optimal foraging, time budgets, reproductive success, and survival because performance may simply be caused by differences in the early learning environment rather than by genetic differences.

AUTHOR CONTRIBUTIONS

T.S. and K.L.W. conceived and designed the study. T.S. collected the data in the field, K.L.W. analysed the videos. Both analysed the data and wrote the manuscript.

COMPETING INTERESTS

We have no competing interests.

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Table 1

Comparison of provisioning behaviour of immigrant and locally recruited **blue tits** and **great tits** in southern Norway during 2005 – 2008

	Immigrants			Local recruits			*t*-test	
Variable	Mean	SD	*N*	Mean	SD	*N*	*t*	*P*
Blue tit								
Prey volume[a]	-0.84	0.34	123	-0.71	0.39	24	1.70	0.092
Prey items per hour[a]	1.25	0.24	121	1.19	0.23	24	1.04	0.30
Green larvae per hour[b]	1.01	0.26	121	0.94	0.26	24	1.30	0.20
Brown larvae per hour[b]	0.56	0.37	121	0.57	0.39	24	.14	0.89
% green larvae	54.6	20.5	123	53.2	21.4	24	.30	0.77
% brown larvae	20.2	17.1	123	24.3	21.2	24	1.04	0.30
Great tit								
Prey volume[a]	-0.81	0.35	102	-0.77	0.39	44	.69	0.49
Prey items per hour[a]	1.13	0.22	91	1.17	0.24	40	1.10	0.27
Green larvae per hour[b]	0.78	0.28	91	0.92	0.25	40	2.66	0.009
Brown larvae per hour[b]	0.66	0.33	91	0.57	0.36	40	1.35	0.18
% green larvae	40.0	20.0	102	53.1	23.3	44	3.45	<0.001
% brown larvae	31.4	22.0	102	21.4	17.1	44	2.68	0.008

[a] Log (x) transformation.

[b] Log(x+1) transformed, where x = the number of the particular prey items provided per hour

Table 2

Linear mixed models for provisioning behaviour in blue tit parents

Dependent variable	Factor	DF	*F*	*P*	Parameter estimate	95% CI
Prey volume	Origin	1,90	4.45	0.038	0.09	0.07, 0.11
	Year	1,103	36.0	<0.001	-0.33	-0.35, -0.27
	Age	1,106	3.97	0.049	0.22	0.02, 0.42
	Origin*age	1,104	4.74	0.032	-0.23	-0.42, 0.03
	Sex	1,69	15.6	<0.001	-0.15	-0.22, 0.08
Feeding rate of green larvae	Origin	1,88	0.66	0.47	0.04	-0.15, 0.23
	Year	1,95	4.71	0.033	0.10	0.07, 0.13
	Date	1,86	7.07	0.009	-0.009	-0.014, -0.004
	Brood	1,109	6.24	0.014	0.027	0.006, 0.05
Feeding rate of brown larvae	Origin	1,105	3.27	0.073	0.13	-0.04, 0.30
	Origin*age	1,120	4.88	0.029	-0.08	-0.19, 0.03
	Age	1,123	0.69	0.41	0.17	-0.04, 0.38
	Brood	1,86	7.75	0.007	0.04	0.02, 0.06
Feeding rate of other items	Origin	1,110	1.56	0.21	0.08	-0.07, 0.23
	Year	1,96	7.61	0.007	0.15	0.04, 0.26
	Sex	1, 77	8.53	0.005	0.14	0.04, 0.23
	Age	1,140	5.31	0.023	-0.12	-0.21, -0.02

All models had pair as a random factor. The full model included six variables (origin of focal bird, year, sex, age, brood size and date) and the interactions between origin, year and age. Non-significant interactions and terms were deleted, stepwise for the final model.

Table 3
Linear mixed models (see footnotes Table 2) for provisioning behaviour in great tit parents

Dependent variable	Factor	DF	*F*	*P*	Parameter estimate	95% CI
Prey volume	Origin	1,96	0.53	0.46	-0.05	-0.18, 0.08
	Year	1,108	8.73	0.004	-0.18	-0.29, -0.07
	Brood	1,111	6.18	0.014	0.04	0.02, 0.06
Feeding rate of green larvae	Origin	1,112	6.98	0.009	0.07	0.038, 0.10
	Origin*age	1,126	10.8	0.001	-0.86	-0.96, -0.76
	Age	1,130	2.12	0.15	0.22	0.08, 0.35
Feeding rate of brown larvae	Origin	1,108	4.36	0.038	0.23	0.05, 0.41
	Origin*age	1,124	5.03	0.027	-0.08	-0.21, 0.06
	Age	1,129	0.58	0.45	0.17	-0.03, 0.36
	Brood	1,90	9.87	0.002	0.05	0.03, 0.07
Feeding rate of other items	Origin	1,131	0.33	0.57	0.05	0.03, 0.07
	Year	1,131	15.8	<0.001	0.24	0.12, 0.36
	Date	1,131	5.30	0.023	-0.008	-0.01, -0.007

Table 4

Comparison of provisioning behaviour within pairs of **blue tits** and **great tits**

	Immigrant		Local recruit		Paired *t*-test		
Variable	Mean	SD	Mean	SD	*t*	*N*	*P*
Blue tit							
Prey volume[a]	-0.89	0.40	-0.69	0.40	2.93	21	0.008
Green larvae per hour[b]	1.00	0.33	1.00	0.29	0.01	20	0.99
Brown larvae per hour[b]	0.51	0.36	0.59	0.40	1.39	20	0.18
Other items per hour[b]	0.83	0.33	0.61	0.33	3.15	20	0.005
Great tit							
Prey volume[a]	-0.69	0.31	-0.75	0.29	1.24	29	0.23
Green larvae per hour[b]	0.77	0.28	0.93	0.22	2.26	27	0.033
Brown larvae per hour[b]	0.65	0.29	0.63	0.37	0.23	27	0.82
Other items per hour[b]	0.65	0.36	0.57	0.32	0.86	27	0.40

[a] Log (*x*) transformation.

[b] Log(*x*+1) transformed, where *x* = the number of the particular prey items provided per hour.

Only pairs where one parent was an immigrant and one parent was a local recruit. For transformation of variables, see Table 2.

Figure Legends

Figure 1. Mean prey volume (+SE) by first year and older blue tit parents. Filled bars, immigrants; open bars, local recruits. Back-transformed log values are shown. For first year birds, sample size was 72 for immigrants and 13 for local recruits. For older birds values were 51 and 11 respectively.

Figure 2. Mean feeding rates (+SE) by first year and older great tit parents. Filled bars, immigrants; open bars, local recruits. To the left: total delivery rate which was equal to the sum of the delivery rate for all prey types (green larvae, brown larvae, and all other items). The separate data for the three groups of prey items are also shown. For first year birds, sample size was 51 for immigrants and 22 for local recruits. For older birds the values were 40 and 18 respectively.

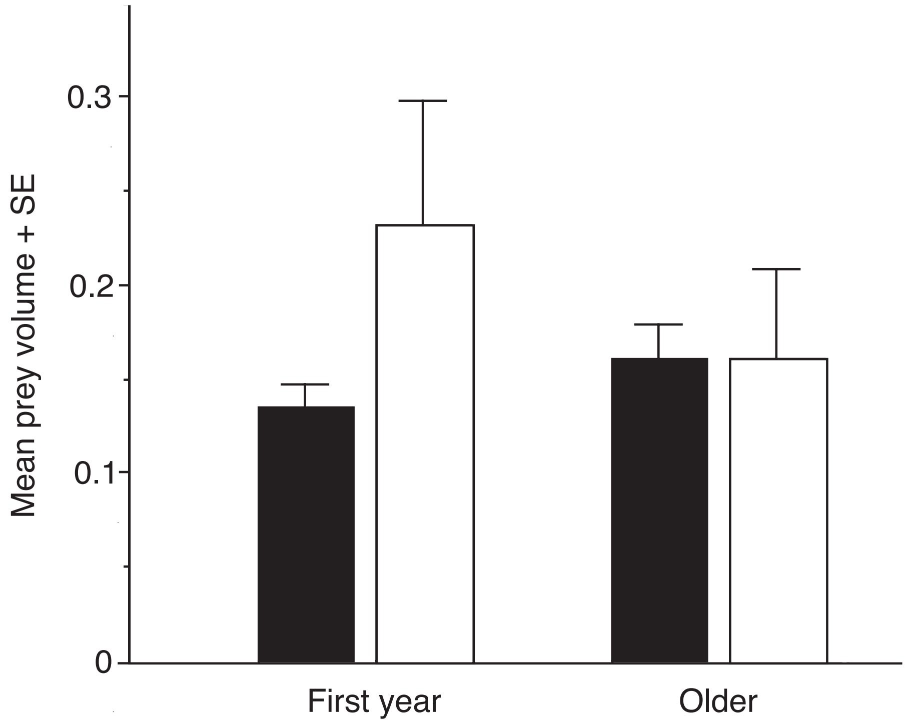

Figure 1

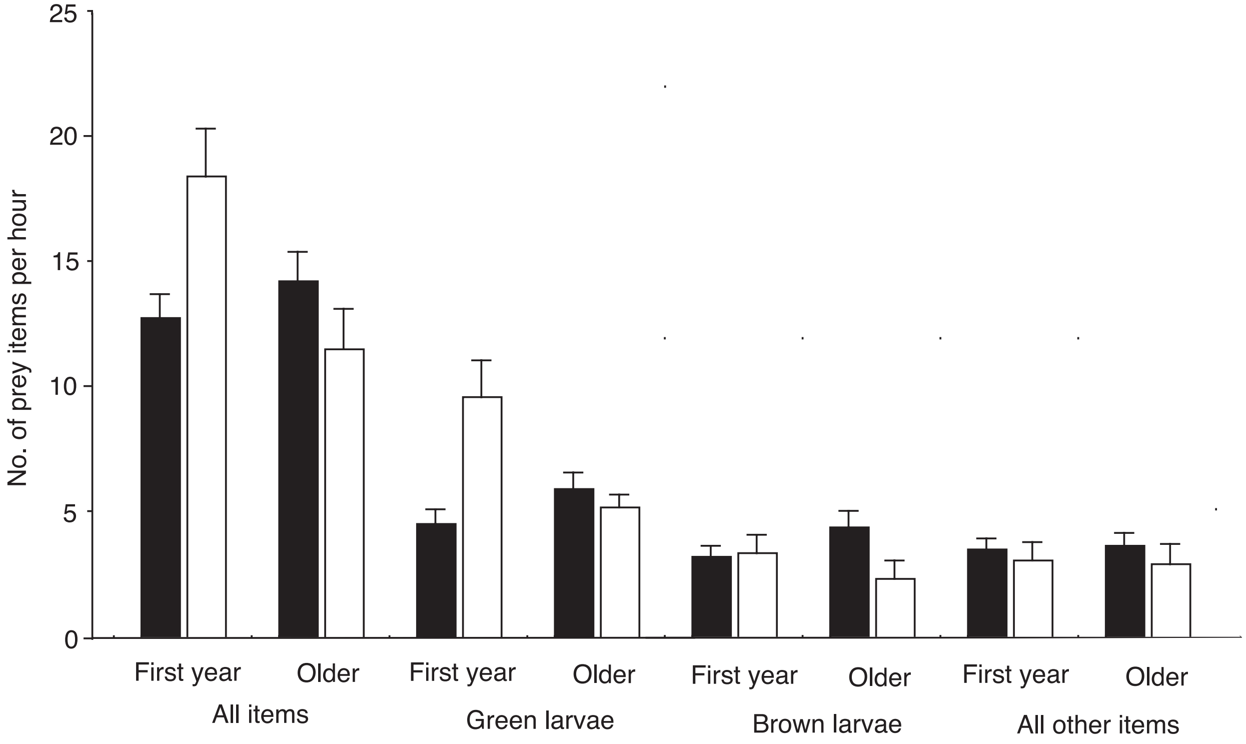
25
20
15
10
5
0
No. of prey items per hour
First year
Older
All items
First year
Older
Green larvae
First year
Older
Brown larvae
First year
Older
All other items

Figure 2