



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

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## ARTICLE INFO

### Article history:

Received 4 September 2017

Initial acceptance 26 September 2017

Final acceptance 18 December 2017

MS. number: 17-00712R

### Keywords:

foraging  
habitat selection  
natal dispersal  
prey choice  
social learning

Natal dispersal is common in animals but the fitness cost of moving from the natal area is not 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 4-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 postfledging 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.

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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, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003](#); [Szulkin & Sheldon, 2008](#)) and competition ([Blyton, Banks, & Peakall, 2015](#); [Cotto, Kubisch, & Ronce, 2014](#); [Hovestadt, Mitesser, & Poethke, 2014](#)). Costs of natal dispersal are not well understood but may involve factors such as increased energy expenditure and predation risk while travelling 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 ([Aguillon & Duckworth, 2015](#); [Bonte et al., 2012](#); [Duckworth & Badyaev, 2007](#); [Knowles, Wood,](#)

[Alves, & Sheldon, 2014](#)). Costs and benefits of dispersal may differ between and within species, leading to variation in which animals move longer distances before settling. Knowledge of an animal's origin may help us understand variation in traits within a local population, including life history traits ([Auld & Charmantier, 2011](#); [Wilkin, Garant, Gosler, & Sheldon, 2007](#)). Identifying differences in behaviour related to origin may also help us understand 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, Adriaensen, Matthysen, & Kempenaers, 1990](#); [Porlier, Garant, Perret, & Charmantier, 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 that are familiar with an area may have an advantage over immigrants ([Pärt, 1994](#)). The extent of dispersal may also differ in

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relation to personality (Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003; Van Overveld, Careau, Adriaensen, & Matthysen, 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, Kelly, & Thomas, 2005). Aversion to certain foods 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, Roper, & Harper, 1998; Thomas, Bartlett, Marples, Kelly, & Cuthill, 2004).

Although foraging efficiency in a new location is likely to have 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, Ryder, & Fleischer, 2012). In social animals, foraging skills acquired as a juvenile may be compromised if the animal settles in a new habitat where such skills do not conform to the foraging habits of the local social group (Van de Waal, Borgeaud, & Whiten, 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 probably depend on the amount of time the individual has to experience the environment. For example, first-year breeding birds that settle in a new habitat may be less efficient at foraging than older breeders which will have experience from at least 1 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 postfledging period, although they will all lack experience in the habitat from the spring period prior to hatching.

Here we examined 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, in which we 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 assumed 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, Liaaen-Jensen, Slagsvold, & Lifjeld, 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, Sheldon, & Morand-Ferron, 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; we therefore tested for differences in food provisioning between birds that arrived 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 sexes of both species 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, Eriksen, De Ayala, Husek, & Wiebe, 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 to 2008 near Oslo (59°56'N, 10°32'E) on a 1.6 km<sup>2</sup> 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 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 nestboxes were available; 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

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