



Lower settlement following a forced displacement experiment: nonbreeding as a dispersal cost in a wild bird?



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Dispersal is a key life history trait impacting ecological and evolutionary processes. Yet, the fitness consequences of dispersal remain poorly investigated. Using a displacement experiment of 616 individuals in a patchy population of collared flycatchers, *Ficedula albicollis*, we investigated behavioural responses to forced movement in terms of settlement, subsequent breeding performance and return rate. Newly arrived birds were caught and displaced between patches or released back in the patch of capture. We analysed (1) the probability of successful settlement within the study area, (2) for displaced birds, the probability of accepting the forced movement rather than returning to the patch of capture, (3) components of reproductive performance and (4) return rate in subsequent years according to experimental treatment. The probability of settling within the study area tended to be lower for displaced than control birds and was lower for immigrants than local birds. This suggests that displacement induced long-distance dispersal movements or nonbreeding, which could reflect costs of unfamiliarity with the environment. Nondispersers (individuals caught early in the breeding season in the same patch as their previous one) were more likely to return to their patch of capture, probably because of higher benefits of familiarity. Once individuals had settled, their breeding performance did not vary markedly between treatments, although displaced individuals that did not return to their patch of capture raised lighter young than other individuals. This could indicate a lower phenotypic quality of these individuals or, again, a cost of breeding in an unfamiliar environment. Finally, individuals that settled (and nondispersers) were more likely to return to the study area in subsequent years than individuals that disappeared (and immigrants/dispersers, respectively). Together, these results suggest that, in addition to the costs of transience, dispersal (here forced) may entail costs linked to settlement in an unfamiliar habitat.

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Dispersal is commonly defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood & Harvey, 1982). Dispersal determines the flow of individuals and genes, both within and among populations. As a consequence, dispersal influences processes as diverse as species distribution and range expansion, population dynamics and genetics, and community structure (Clobert, Baguette, Benton, & Bullock, 2012; Clobert, Danchin, Dhondt, & Nichols, 2001; Kokko & Lopez-Sepulcre, 2006) and is therefore widely recognized as a key life history trait. However, the fitness consequences of dispersal

often remain poorly understood (Clobert et al., 2001, 2012; Kokko & Lopez-Sepulcre, 2006; Pakanen, Koivula, Orell, Rytönen, & Lahti, 2016). Dispersal can entail both immediate and deferred costs on various fitness components linked to the three dispersal stages (departure, transience and settlement; Bonte et al., 2012). For example, dispersal is often assumed to entail a survival cost during the transience phase (Baker & Rao, 2004; Soulsbury, Baker, Iossa, & Harris, 2008). However, predicting the effects of dispersal on subsequent settlement and reproductive success in the novel habitat is less straightforward because these effects will depend on the balance between multiple possible costs and benefits (Johnson & Gaines, 1990; Lemel, Belichon, Clobert, & Hochberg, 1997). Suggested costs of dispersal after the transience phase (after arrival in the new breeding patch) include search costs for a suitable breeding territory/site in terms of energy and time spent searching

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or predation risk, but also unfamiliarity with the new breeding habitat and low level of adaptation to local conditions leading to suboptimal decision making in mate and/or site choice (Pärt, 1995; Stamps, Krishnan, & Reid, 2005; Yoder, Marschall, & Swanson, 2004).

So far, most studies investigating the fitness consequences of dispersal have been based on the direct comparison of fitness components between dispersers and nondispersers (see Belichon, Clobert, & Massot, 1996; Doligez & Pärt, 2008 for reviews). However, this approach is correlative and does not allow the direct fitness consequences of dispersal to be distinguished from the confounding effects of a third factor, such as phenotypic quality, that could affect both dispersal and fitness components (Clobert, Perrins, McCleery, & Gosler, 1988; Greenwood, Harvey, & Perrins, 1979). Experimental manipulations of dispersal may help us elucidate the causality of relationships between dispersal and fitness-related traits, but are often difficult to implement in wild populations and, therefore, remain rare. To date, most of these experiments are based on the translocation of individuals and are thus equivalent to a forced dispersal event, mimicking movement to a new habitat irrespective of the individual's actual motivation to do so. To our knowledge, most translocations have been performed in the context of conservation actions, in an attempt to establish new populations or re-establish extinct populations of endangered species (see Fischer & Lindenmayer, 2000; Seddon, Armstrong, & Maloney, 2007 for reviews), increasing the size of small and declining populations and/or 'rescuing' inbred populations by introducing new genes (Fisher, Lambin, & Yletyinen, 2009; Griffith, Scott, Carpenter, & Reed, 1989; Madsen, Shine, Olsson, & Wittzell, 1999). These mostly applied studies have provided crucial fundamental insights on the immediate costs that may prevent settlement (e.g. predation risk; Calvete, Villafuerte, Lucientes, & Osacar, 1997; Letty, Marchandeu, Reitz, Clobert, & Sarrazin, 2002). Nevertheless, many of them could not assess or ignored most settlement and postsettlement costs (Pierre, 2003; Stamps et al., 2005). Few experimental studies have investigated the potential reproductive costs associated with settlement in an unfamiliar environment by monitoring the breeding activity of displaced individuals (Burger, Nord, Nilsson, Gilot-Fromont, & Both, 2013; Burgess, Tremblay, & Marshall, 2012; Komdeur et al., 1995).

To investigate the behavioural and reproductive responses of individuals to forced dispersal, we performed a forced displacement experiment in a patchy population of a small hole-nesting migratory passerine bird, the collared flycatcher, *Ficedula albicollis*. Our study aimed at mimicking dispersal movements to provide fundamental insight into the consequences of dispersal. Birds were caught just after their arrival from their winter quarters and were either displaced, that is, released in a new patch within the study area (displaced group), or released back into the patch of capture (control group; Pärt, 1995). The displacement therefore occurred within a few kilometres, a distance much smaller than the migration distance (a few thousands of kilometres, from sub-Saharan Africa to Northern Europe), but comparable to the between-patch dispersal distance in our population (between a few hundred metres and a few kilometres (Doligez, Gustafsson, & Pärt, 2009; Pärt, 1990; Pärt & Gustafsson, 1989).

To investigate the consequences of forced movement and unfamiliarity with the breeding environment, we subsequently recorded (1) prebreeding decisions (probability of successful settlement to breed and, for displaced birds, probability of returning to the patch of capture), (2) for individuals caught again as breeders, the main variables related to breeding success (laying date, clutch size, incubation length, probability of fledging at least one young and number and condition of young) and (3) return rate to the study area in subsequent years as a proxy of local survival. We

tested whether these responses differed between experimental groups in relation to age, sex and dispersal status prior to the experiment. Social factors and habitat suitability may have a marked influence on settlement decisions of individuals and are also an important component of dispersal (e.g. Richardson & Ewen, 2016), and therefore we displaced individuals among already occupied and thus suitable habitat patches where conspecifics may provide social information (e.g. Doligez, Part, Danchin, Clobert, & Gustafsson, 2004). If habitat familiarity is advantageous, we could expect displaced individuals to be less likely to settle and/or to breed successfully in a new patch than individuals released in the patch of capture. Birds with higher local experience prior to displacement (i.e. old individuals/nondispersers) should also be more likely to return to their patch of capture than those with less experience (i.e. young individuals/dispersers). Finally, males could be more likely to return to their patch of capture than females, because familiarity is likely to be more beneficial in males (Pärt, 1994, 1995).

METHODS

Study Species and Study Site

The collared flycatcher is a short-lived, hole-nesting, migratory passerine bird that winters in sub-Saharan Africa. The experiment was performed in 1989–1990 and 2012–2013 in a patchy population breeding on the island of Gotland, Southern Baltic, Sweden (57°10'N, 18°20'E). In the study population, artificial nestboxes were regularly distributed in discrete woodland patches of varying size, several hundred metres to 12 km from each other, over an area of ca. 30 km² (Pärt & Gustafsson, 1989). Collared flycatchers are single-brooded in this population, although a replacement clutch can be laid if the first fails early.

Forced Displacement Experiment

Several patches (four in 1989, 1990 and 2013, eight in 2012) were thoroughly searched for at least 7 h each day from late April until early June to locate newly arrived males and females and attempt to catch them on the same or the next day(s). Upon arrival from winter quarters, males select a breeding territory and defend it to attract a female. During the breeding site selection process, both sexes frequently visit empty nestboxes, allowing us to catch them before nest building by using swing-door traps placed in empty boxes. Among the birds of a given age (yearlings/older birds) and sex category caught on a given day, we used a randomization-by-block design within each category to assign each individual to one of the following experimental treatments: the individual was released (1) in a patch other than the patch of capture ('displaced birds', $N = 144$ females and 337 males) or (2) into the same patch ('controls', $N = 44$ females and 91 males). Because we expected that a high proportion of displaced individuals would return to the patch of capture in this highly mobile species, we intentionally biased the sample towards displaced birds rather than controls (3/4 versus 1/4 of individuals caught, respectively). In 1989 and 1990, control individuals were either released immediately after capture or 2–3 h later to apply the same time delay between capture and release as for displaced individuals ('time controls'). The subsequent probability of settling and breeding in the patch of capture did not differ between the two control categories (see Pärt, 1995 for further details). Consequently, in 2012 and 2013, control individuals were systematically released 2–3 h after capture, and all control birds were pooled into one group for the analyses. We displaced and released an equivalent number of individuals from/to each patch to avoid modifying local patch density, because density may

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