



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

markedly affect individual dispersal decisions (Clobert et al., 2012). Displaced individuals were swapped between patches to maximize distance of displacement within the study area (range 2–9 km, mean \pm SE: 3.47 \pm 0.11). This distance matched the higher range of between-patch dispersal distance in our population (Doligez et al., 2009; Pärt, 1990; Pärt & Gustafsson, 1989). It remained trivial, however, compared to the migration distance (several thousands of kilometres). Therefore, the potential metabolic costs of flying to return to the patch of capture for displaced birds were likely to be negligible here.

Population monitoring during the breeding season, including systematic catching of all possible adults (see below), allowed us to determine whether experimental individuals subsequently settled to breed in the study area and, if so, in which patch, and, in particular, whether displaced individuals had returned to their patch of capture to breed. Individuals that were not subsequently caught during the breeding season in the study area were considered as 'disappeared' ($N = 267$ out of 616, i.e. 43%, including 45 controls and 222 displaced individuals). We excluded from the analyses individuals caught less than 4 days before the laying of the first egg in their nest. We assumed that, even though these individuals were caught visiting empty nestboxes, they had probably already mated, selected their breeding site and possibly started nest building (in another nestbox), which probably affected their response to forced dispersal and, in particular, their probability of returning to the patch of capture. Some individuals ($N = 26$ of 616, i.e. 4%) were manipulated in 2 consecutive years. In that case, we only used the data for the first manipulation to avoid any effect of previous manipulation on the individual's responses.

Population Monitoring and Dispersal Status

Each year since 1980, nestboxes were visited regularly throughout the season, allowing us to record detailed breeding parameters. Breeding birds were caught inside nestboxes and identified individually with aluminium rings, aged (yearling versus 2 years or more, based on their previous records in the population or plumage characteristics when previously unringed; Svensson, 1992), weighed (to the nearest 0.1 g) and measured (tarsus length to the nearest 0.1 mm). For all nests in nestboxes, young were ringed, weighed and measured a few days before fledging (when 12 days old). Because females incubate alone, breeding females were first caught during incubation while males were caught when feeding young aged 5–12 days; therefore, males could not be caught in cases of early breeding failure (at incubation or young nestlings). In our population, as in many other hole-nesting populations, the capture and identification of adults were therefore tightly linked to reproductive activity and success, with nearly all females breeding in nestboxes (i.e. > 90%) and all males breeding successfully up to the nestling stage (i.e. on average 70%) being caught every year. The fraction of nonbreeding birds in this population therefore remains unknown.

Dispersal was defined as a change of patch between the year of birth and first breeding (natal dispersal) or between consecutive breeding events (breeding dispersal), separated by a migration event (Doligez et al., 2009). This binary definition of dispersal (dispersers versus nondispersers) has been found to be biologically informative in previous studies on this population, with the propensity to change patch depending on patch quality as measured by the density and local reproductive success of conspecifics in the patch, and being moderately heritable (Doligez, Clobert et al., 2002; Doligez, Danchin, Clobert, & Gustafsson, 1999; Doligez et al., 2009; Doligez, Part, Danchin, Clobert et al., 2004; Doncaster, Clobert,

Doligez, Gustafsson, & Danchin, 1997). Here, we defined dispersal status of individuals used in the forced displacement experiment by comparing the patch of early capture (see above) with the previous patch (natal or previous breeding), assuming that the patch of capture was the patch chosen by individuals to settle. We cannot exclude that some individuals had not yet settled and were transient upon early capture, but among the 135 control individuals, only five (< 4%) finally settled in a different patch than the patch of capture, suggesting that most individuals had indeed settled before the early capture. We kept these individuals in our analyses here because we cannot identify and exclude the corresponding individuals that had not settled before the early capture among displaced individuals; nevertheless, the results remained qualitatively unchanged when excluding these individuals (results not shown). Immigrants, which are unringed individuals whose natal or previous breeding site was thus unknown (about 40% of adults caught each year), were included in the analyses (except when their age was uncertain), but were kept as a separate category compared to dispersers and nondispersers because they consisted of a mix of local birds previously missed and true, potentially long-distance, immigrants.

Statistical Analyses

We first investigated whether settlement decisions differed between individuals depending on the experimental treatment (displaced versus control individuals), dispersal status (as defined by the patch of capture, see above: immigrants, dispersers and nondispersers), sex and age class (yearlings versus older birds; we did not attempt to explore age effects at a finer scale because this would exclude most immigrant individuals whose exact age was unknown). In particular, (1) we compared the probability of successfully settling as a breeder in the study population following manipulation between displaced and control individuals while accounting for dispersal status and (2) for displaced individuals, we compared the probability of returning to the patch of capture (i.e. the probability of rejecting the displacement) between immigrants, dispersers and nondispersers. We included the individual's dispersal status in the analyses to account for familiarity level with the breeding patch because familiarity is likely to be a key factor influencing settlement decisions here (see Pärt, 1995).

We analysed the probabilities of successful settlement and return to the patch of capture using generalized linear mixed models with a binomial error and a logit link function. In both analyses, we accounted for sex and age class, which have previously been found to affect dispersal decisions in many species (Forslund & Pärt, 1995; Greenwood & Harvey, 1982; Paradis, Baillie, Sutherland, & Gregory, 1998), including the collared flycatcher (Doligez et al., 1999; Doligez, Pärt, & Danchin, 2004; Pärt, 1990, 1995; Pärt & Gustafsson, 1989), possibly reflecting sex and age differences in the costs and benefits balance of local experience. We also included as a covariate the date of capture (day 1 = 1 May), which can be expected to affect the probabilities of settlement and of return to the patch of capture. Time costs of searching for a breeding site indeed increase with the date in the season as a result of the decrease in reproductive success and increase in competition for available sites with time (Pärt, 1995). Because birds caught in patches located at the edge of the study area may have a higher probability of disappearing by dispersing out of the study area, we added as a cofactor the location of the plot of release as a binary variable (at the edge versus in the centre of the study area; Doligez et al., 2009). To control for possible temporal changes in environmental conditions that may affect settlement decisions (e.g. an increase in the number of nestboxes and patches available between the 1990s and recent years), year was also included as a

fixed effect in the models. We chose to consider year as a fixed effect because the experiment was run over two periods of 2 consecutive years, rather than in random years over the course of the study. Nevertheless, the results remained qualitatively unchanged when year was included as a random factor (results not detailed here). We included the patch of capture as a random effect to control for the nonindependence of individuals caught in the same patch; using the patch of release instead gave qualitatively similar results (results not detailed). For the probability of successful settlement, the starting model included the variables listed above as well as the pairwise interactions between the experimental treatment and dispersal status, age class, sex and patch location. For the probability of returning to the patch of capture (for displaced individuals only), in addition to the variables listed above, we added the distance of displacement, as well as the pairwise interactions between dispersal status and sex, age class and patch location. The probability of returning to the patch of capture for displaced birds did not differ according to the distance of displacement, since this distance was not retained in the best models (minimal difference in the Akaike's information criterion corrected for small sample sizes, AICc, between the best model and the first model including distance of displacement: 11.06), and is not considered further. Distance of displacement could not be included in the analysis of the probability of successful settlement because all control individuals have, by definition, a translocation distance of 0.

To test whether reproductive performance differed in relation to the experimental treatment, we compared laying date, clutch size, probability of success (probability of fledging at least one young) and fledging number and condition (body mass at 12 days old) between experimental groups but also nonexperimental individuals. Continuous variables (laying date, clutch size, body mass and fledging number for successful nests only) were analysed using linear mixed models. Probability of success was analysed using a generalized linear mixed model with a binomial error and logit link function. Because the costs and benefits balance in reproduction may differ not only between displaced and control individuals but also between displaced individuals depending on whether or not they returned to their patch of capture, our definition of an experimental treatment *sensu lato* included whether the individual returned to its patch of capture following displacement or not. The treatment *sensu lato* thus had four modalities: (1) experimental controls, (2) displaced individuals that returned to the patch of capture, (3) displaced individuals that did not return to the patch of capture, (4) nonexperimental individuals. Displaced individuals that returned to their patch of capture may indeed differ from controls in breeding variables due to the extra movement back to the patch of capture and possible associated time costs (e.g. to find a territory). Although no straightforward differences between dispersers and nondispersers in breeding variables have previously been found (Germain, 2014), we included dispersal status in the analysis of breeding variables to account for potential differences due to the manipulation.

For each breeding response variable, the starting model included the following explanatory variables as fixed factors: treatment *sensu lato*, dispersal status, sex, age class and year, as well as all two-way interactions between treatment and other explanatory variables except year. Nonexperimental individuals mated with experimental individuals were omitted from analyses to avoid any potential confounding effect via compensation for the treatment of their partner. We did not consider the treatment of the partner as a cofactor because of the low number of pairs with two experimental birds and thus unbalanced samples, leading to model convergence problems. For the analysis of nestling body mass, we also included nestling tarsus length to control for body size and

nestling number to control for brood size. The patch of breeding was included as a random effect to control for spatial variation in environmental conditions. Finally, we randomly selected one breeding event per individual when present in different years to avoid pseudoreplication. Indeed, we could not include individual as a random factor because the number of individuals with repeated observations was too low (56 of 1126, i.e. 5%) and models would not converge. Year was systematically retained in the most competitive models, except for the probability of returning to the patch of capture, but because this effect was not of primary interest here, we detail the year effect on all relevant variables in [Appendix 1, Table A1](#).

To explore the fate of 'disappeared' individuals (those that were not caught later on during the breeding season after the displacement experiment), we analysed the probability that individuals were caught as breeders in the study area in the years following the experiment (return rate in subsequent years) as a proxy of local survival. We compared return rate in subsequent years between individuals that successfully settled and those that disappeared. We analysed the return rate in subsequent years using generalized linear mixed models with a binomial error and a logit link function. The starting model included the successful settlement response to the experiment (settled to breed versus disappeared), dispersal status, age, sex, location of the plot of release, date of capture, year as well as pairwise interactions between the response to the experiment and dispersal status, age, sex and location of the plot of release. We also included the patch of capture as a random effect.

Whenever a sex effect was retained for any of the response variables, we explored whether it was due to the sampling bias between males and females because of the differential timing of capture (see above). To do so, we performed the analyses again after restricting the female data by excluding females whose males had not been caught because of early nest failure to eliminate the sampling bias between the sexes.

For each response variable, model selection was based on the AICc when the ratio of sample size to the number of parameters was lower than 40 (Johnson & Omland, 2004), with models showing lower AICc values being best supported by the data (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011). When several models performed equally well and showed AICc values that differed by less than 2 (Table 1), we averaged parameter estimates for the variables retained in this set of best models (Burnham & Anderson, 2002). To compare models with and without interactions and perform model averaging, we centred all predictors including categorical variables (Schielzeth, 2010). Such centring renders the main effects biologically interpretable even when involved in interactions and thus allows avoiding potential misinterpretation of main effects (Schielzeth, 2010). We further computed relative variable importance (RVI) for each explanatory variable as the sum of the Akaike weights w_i over all the best models including the variable considered. For each response variable, the candidate model set contained the more complex (starting) model including all the fixed effects and two-way interactions listed above and all possible models including a subset of these effects and interactions down to the null model containing only the intercept. All analyses were carried out in R statistical software version 3.0.3 (R Core Team, 2014), using the packages lme4 (Bates & Maechler, 2009) and MuMIn (Barton, 2015). The MuMIn package is known to overestimate the effects of components factors of interaction terms (Calcagno & de Mazancourt, 2010). However, alternative packages addressing this problem do not easily allow one to define a full model including only a subset of the two-way interactions, and full models including all two-way interactions did not converge in our case.

Table 1
Best models (based on selection by AICc) for each response variable

Model	K	LogLik	AICc	ΔAICc	wi
Probability of settling to breed in the study area (N=588)					
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year	11	-355.591	733.6	0.00	0.351
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year+Age*Experimental treatment	12	-355.228	735.0	1.36	0.178
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year+Sex*Experimental treatment	12	-355.240	735.0	1.38	0.176
Age+Date of capture+Dispersal status+Sex+Year	10	-357.435	735.3	1.61	0.157
Age+Date of capture+Dispersal status+Location of the breeding plot+Sex+Experimental treatment+Year	12	-355.472	735.5	1.85	0.139
Null model	2	-403.819	811.7	78.01	< 0.001
Starting model	18	-353.923	745.0	11.41	< 0.001
Probability of returning to the patch of capture (for displaced individuals) (N=241)					
Age+Dispersal status+Sex	6	-114.494	241.3	0.00	0.378
Age+Dispersal status+Sex+Age*Dispersal status	8	-112.524	241.7	0.32	0.321
Age+Dispersal status+Location of the plot of release+Sex	7	-114.303	243.1	1.74	0.158
Age+Dispersal status+Location of the plot of release+Sex+Age*Dispersal status	9	-112.256	243.3	1.94	0.143
Null model	2	-136.021	276.1	34.74	< 0.001
Starting model	23	-107.577	266.2	24.89	< 0.001
Laying date (N=719)					
Age+Dispersal status+Sex+Year	10	-2104.547	4229.1	0.00	1.000
Null model	3	-2190.644	4387.3	158.19	< 0.001
Starting model	25	-2101.601	4253.2	24.11	< 0.001
Clutch size (N=715)					
Age+Experimental treatment sensu lato+Year	8	-812.933	1645.9	0.00	0.493
Age+Sex+Year	6	-815.558	1647.1	1.25	0.264
Age+Sex+Experimental treatment sensu lato+Year	9	-812.638	1647.3	1.41	0.243
Null model	3	-834.459	1674.9	29.05	< 0.001
Starting model	25	-805.312	1660.6	14.76	< 0.001
Probability of success (i.e. of fledging at least one young) (N=657)					
Age+Sex+Experimental treatment sensu lato+Year+Sex*Experimental treatment sensu lato	13	-279.026	584.1	0.00	1.000
Null model	2	-331.202	666.4	82.35	< 0.001
Starting model	24	-275.936	599.87	15.82	< 0.001
Number of fledglings among successful nests (N=520)					
Age+Dispersal status+Year	9	-951.751	1921.5	0.00	0.458
Age+Year	7	-953.960	1921.9	0.42	0.371
Age+Dispersal status+Sex+Year	10	-951.737	1923.5	1.97	0.171
Null model	3	-975.702	1957.4	35.90	< 0.001
Starting model	25	-947.904	1945.809	24.30	< 0.001
Nestling body mass (N=2193)					
Number of Nestling+Tarsus length+Experimental treatment sensu lato+Year	12	-2991.135	6006.3	0.00	0.512
Age+Number of Nestling+Tarsus length+Experimental treatment sensu lato+Year	13	-2990.686	6007.4	1.10	0.295
Number of Nestling+Sex+Tarsus length+Experimental treatment sensu lato+Year	13	-2991.110	6008.2	1.95	0.193
Null model	4	-3278.488	6565.0	558.77	< 0.001
Starting model	28	-2985.112	6026.2	20.01	< 0.001
Return rate in subsequent years (N=588)					
Age+Response+Dispersal status+Age*Response+Dispersal status*Response	9	-349.242	716.8	0.00	0.540
Age+Response+Dispersal status+Dispersal status*Response	8	-351.100	718.4	1.65	0.236
Age+Response+Dispersal status+Sex+Age*Response+Dispersal status*Response	10	-349.091	718.6	1.77	0.223
Age+Response+Dispersal status+Date of capture+Age*Response+Dispersal status*Response	10	-349.148	718.7	1.88	0.174
Null model	2	-369.230	742.5	25.68	< 0.001
Starting model	17	-347.030	729.1	12.33	< 0.001

Best models based on AICc values (i.e. models with ΔAICc compared to the best model < 2), as well as null and starting models, for the probability of successfully settling and being caught as a breeder in the study area, the probability of returning to the patch of capture, breeding variables (laying date, clutch size, probability of success (i.e. of fledging at least one young) and, among successful nests, fledgling number and nestling body mass) and return rate in the years following the translocation experiment. K: number of parameters in the model; LogLik: log-likelihood; ΔAICc: difference in AICc to the best model; wi: Akaike weight.

Ethical Note

The data upon which this study is based were obtained following the Swedish guidelines for work on natural populations and under licences and permits from the Swedish Ringing Centre and Swedish National Board for Laboratory Animals, Stockholm.

RESULTS

Probability of Successfully Settling to Breed

The probability of successfully settling to breed depended on the individual dispersal status, age and sex (Table 2). Immigrants (i.e. previously unringed individuals) were less likely to settle than

dispersers and nondispersers (Table 2, Fig. 1). In addition, older birds were more likely to settle than yearlings (Table 2; fitted values ± SE: older birds: 0.27 ± 0.06; yearlings: 0.17 ± 0.04) and females were more likely to settle than males (Table 2; fitted values ± SE: females: 0.34 ± 0.08; males: 0.19 ± 0.05). However, when restricting the female data to females whose males had been caught (i.e. nests without early breeding failure, see Methods), the effect of sex was no longer supported (95% confidence interval, CI, of averaged parameters: -0.778; 0.144; RVI: 0.44; see Appendix 2, Table A2 for detailed model selection). This showed that the initial sex effect was due to the sampling bias between the sexes rather than reflecting a biological difference between them. Finally, late caught birds were less likely to settle than early caught birds (Table 2).

Table 2
Estimates \pm SE, 95% confidence intervals (CI) and relative variable importance (RVI) from averaged models of the effects retained in the best models for each response variable

Variable from averaged model	Estimates \pm SE	95% CI	RVI
Probability of settling to breed in the study area			
Intercept	0.21 \pm 0.12	-0.017; 0.439	–
Sex (male)*Experimental treatment (displaced individuals)	0.08 \pm 0.27	-0.586; 1.440	0.18
Age (yearling)*Experimental treatment (displaced individuals)	-0.07 \pm 0.25	-1.307; 0.517	0.18
Experimental treatment (displaced individuals)	-0.37 \pm 0.26	-0.885; 0.008	0.84
Age (yearling)	-0.60\pm0.20	-0.996; -0.199	1
Sex (male)	-0.79\pm0.22	-1.220; -0.360	1
Dispersal status (disperser)	-0.09 \pm 0.26	-0.601; 0.424	1
Dispersal status (immigrant)	-0.72\pm0.22	-1.150; -0.287	–
Date of capture	-0.06\pm0.02	-0.097; -0.018	1
Year (1990)	-0.19 \pm 0.29	-0.759; 0.377	1
Year (2012)	-0.97\pm0.30	-1.562; -0.384	–
Year (2013)	-1.33\pm0.28	-1.894; -0.764	–
Location of the breeding plot (edge patch)	-0.01 \pm 0.09	-0.512; 0.308	0.14
Probability of returning to the patch of capture (for displaced individuals)			
Intercept	1.32\pm0.33	0.662; 1.970	–
Age (yearling)*Dispersal status (disperser)	0.44 \pm 0.80	-0.937; 2.831	0.46
Age (yearling)*Dispersal status (immigrant)	0.80\pm1.04	0.012; 3.419	–
Age (yearling)	-1.51\pm0.40	-2.292; -0.734	1
Sex (male)	1.40\pm0.38	0.664; 2.145	1
Dispersal status (disperser)	-0.44 \pm 0.48	-1.378; 0.501	1
Dispersal status (immigrant)	-1.21\pm0.43	-2.051; -0.364	–
Location of the breeding plot (edge patch)	-0.08 \pm 0.25	-1.067; 0.520	0.30
Laying date			
Intercept	23.21 \pm 0.47	22.391; 24.234	–
Age (yearling)	1.13\pm0.37	0.405; 1.849	1
Sex (male)	-1.26\pm0.35	-1.944; -0.584	1
Dispersal status (disperser)	-0.07 \pm 0.46	-0.965; 0.829	1
Dispersal status (immigrant)	0.91\pm0.41	0.105; 1.720	–
Year (1990)	-3.43\pm0.51	-4.435; -2.430	1
Year (2012)	-5.65\pm0.50	-6.620; -4.679	–
Year (2013)	-1.07\pm0.48	-2.005; -0.130	–
Clutch size			
Intercept	6.28\pm0.03	6.224; 6.335	–
Experimental treatment sensu lato (displaced individuals not returned)	-0.02 \pm 0.10	-0.310; -0.234	0.55
Experimental treatment sensu lato (displaced individuals returned)	-0.02 \pm 0.08	-0.253; 0.175	–
Experimental treatment sensu lato (nonexperimental individuals)	-0.10 \pm 0.12	-0.379; 0.015	–
Age (yearling)	-0.21\pm0.06	-0.329; -0.095	1
Sex (male)	0.03 \pm 0.06	-0.052; 0.199	1
Year (1990)	0.12 \pm 0.09	-0.052; 0.283	1
Year (2012)	0.36\pm0.08	0.201; 0.513	–
Year (2013)	0.10 \pm 0.08	-0.051; 0.259	–
Probability of success (i.e. of fledging at least one young)			
Intercept	0.84 \pm 0.63	-0.401; 2.079	–
Sex (male)*Experimental treatment sensu lato (displaced individuals not returned)	2.22 \pm 1.34	-0.399; 4.842	1
Sex (male)*Experimental treatment sensu lato (displaced individuals returned)	0.40 \pm 0.89	-1.355; 2.147	–
Sex (male)*Experimental treatment sensu lato (nonexperimental individuals)	2.22\pm1.33	0.782; 4.256	–
Experimental treatment sensu lato (displaced individuals not returned)	-0.20 \pm 0.69	-1.553; 1.156	1
Experimental treatment sensu lato (displaced individuals returned)	0.44 \pm 0.68	-0.899; 1.778	–
Experimental treatment sensu lato (nonexperimental individuals)	-0.69 \pm 0.55	-1.775; 0.396	–
Age (yearling)	-0.52 \pm 0.23	-0.968; -0.080	1
Sex (male)	0.02 \pm 0.71	-1.367; 1.408	1
Year (1990)	-0.35 \pm 0.31	-0.960; 0.258	1
Year (2012)	1.70\pm0.42	0.874; 2.520	–
Year (2013)	0.95\pm0.35	0.262; 1.646	–
Number of fledglings among successful nests			
Intercept	5.05\pm0.12	4.826; 5.283	–
Age (yearling)	-0.32\pm0.15	-0.613; 0.0338	1
Sex (male)	-0.007 \pm 0.05	-0.307; 0.220	0.17
Dispersal status (disperser)	-0.02 \pm 0.14	-0.392; 0.313	0.63
Dispersal status (immigrant)	0.16 \pm 0.18	-0.0422; 0.588	–
Year (1990)	-0.59\pm0.22	-1.033; -0.153	1
Year (2012)	0.70\pm0.21	0.294; 1.123	–
Year (2013)	-0.13 \pm 0.20	-0.307; 0.220	–
Nestling body mass			
Intercept	14.11\pm0.07	13.983; 14.241	–
Experimental treatment sensu lato (displaced individuals not returned)	-0.65\pm0.26	-1.163; -0.146	1
Experimental treatment sensu lato (displaced individuals returned)	-0.18 \pm 0.19	-0.566; 0.197	–
Experimental treatment sensu lato (non-experimental individuals)	-0.07 \pm 0.18	-0.432; 0.289	–
Age (yearling)	-0.03 \pm 0.08	-0.333; 0.114	0.30
Sex (male)	-0.004 \pm 0.05	-0.238; 0.191	0.19
Year (1990)	-0.41 \pm 0.23	-0.871; 0.046	1
Year (2012)	0.31 \pm 0.23	-0.142; 0.753	–
Year (2013)	-0.16 \pm 0.23	-0.605; 0.282	–

Table 2 (continued)

Variable from averaged model	Estimates \pm SE	95% CI	RVI
Tarsus length	0.88\pm0.04	0.808; 0.954	1
Brood size	-0.08\pm0.04	-0.153; -0.011	1
Return rate in subsequent years			
Intercept	-0.81 \pm 0.10	-1.008; -0.622	-
Response to the experiment (individuals that settled to breed)*Age (yearling)	-0.76 \pm 0.47	-1.687; 0.028	0.80
Response to the experiment (individuals that settled to breed)*Dispersal status (disperser)	0.37 \pm 0.51	-0.623; 1.424	1
Response to the experiment (individuals that settled to breed)*Dispersal status (immigrant)	1.26\pm0.58	0.424; 2.302	-
Response to the experiment (individuals that settled to breed)	0.81\pm0.20	0.412; 1.214	1
Age (yearling)	0.57\pm0.22	0.149; 0.994	1
Sex (male)	-0.02 \pm 0.10	-0.499; 0.280	0.18
Dispersal status (disperser)	-0.56\pm0.25	-1.063; -0.061	1
Dispersal status (immigrant)	-0.88\pm0.23	-1.340; -0.421	-
Date of capture	0.001 \pm 0.008	-0.026; 0.041	0.17

Bold type indicates parameters with 95% confidence intervals that do not encompass 0. 95% confidence intervals correspond to the modality of the factor in parentheses in comparison to the reference modality (reference category: control birds for experimental treatment, control birds for experimental treatment sensu lato, individuals that disappeared for response to the experiment, older individuals for age, females for sex, nondisperser for dispersal, year 1989 for year, central plots for the location of the breeding plot).

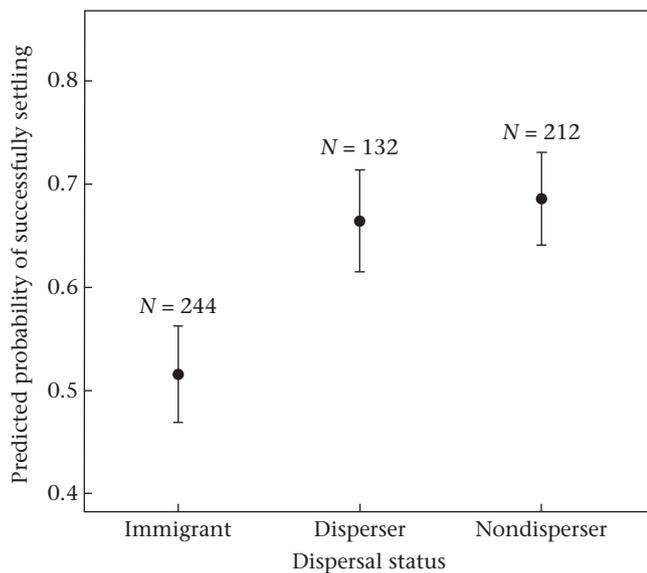


Figure 1. Probability of experimental individuals successfully settling and being caught as breeders in the study area after the experimental manipulation according to their dispersal status. Immigrants: unringed individuals upon early capture; dispersers: individuals that were caught early in a patch different from their previous (natal or breeding) patch; nondispersers: individuals that were caught early in their previous patch. The figure shows fitted values from model averaging \pm 95% confidence interval. Numbers are sample sizes.

In addition, the probability of successfully settling to breed in the study area tended to be lower for displaced individuals than control birds (fitted values \pm SE: displaced birds: 0.19 ± 0.04 ; control birds: 0.27 ± 0.07), although support for the treatment effect was limited (95% CI encompassed 0 but RVI was 0.84; Table 2). Interactions between treatment and age or sex retained in one of the best models were not supported (Table 2).

Probability of Returning to the Patch of Capture

Among displaced individuals that successfully settled in the study area, the probability of returning to the patch of capture also depended on individual dispersal status, age and sex (Table 1). Immigrants were less likely to return to the patch of capture than nondispersers but did not differ from dispersers (Table 2; fitted values \pm SE: immigrants: 0.57 ± 0.09 ; dispersers: 0.72 ± 0.09 ; nondispersers: 0.79 ± 0.07) and yearlings were less likely to return than older individuals (Table 2; fitted values \pm SE: yearlings:

0.51 ± 0.09 ; older birds: 0.82 ± 0.05). The probability of returning to the patch of capture also depended on the interaction between age and dispersal status, although this interaction received little support (Table 2, Fig. 2). In addition, males returned more often to the patch of capture than females (Table 2; fitted values \pm SE: females: 0.54 ± 0.09 ; males: 0.80 ± 0.05). This effect of sex remained strongly supported when restricting the female data to females whose males had also been caught, (95% CI of averaged parameters: 0.371; 1.988; RVI: 1; fitted values \pm SE: females: 0.57 ± 0.10 ; males: 0.81 ± 0.06 ; see Appendix 2, Table A3). Thus, this effect was not due to the sampling bias between the sexes. Finally, the effect of patch location (i.e. edge versus centre) was not supported (Table 2).

Breeding Variables

Laying date depended on dispersal status, age and sex (Table 1). Immigrants laid later than nondispersers and dispersers (95% CI: 0.116; 1.845; Table 2) with no difference between dispersers and

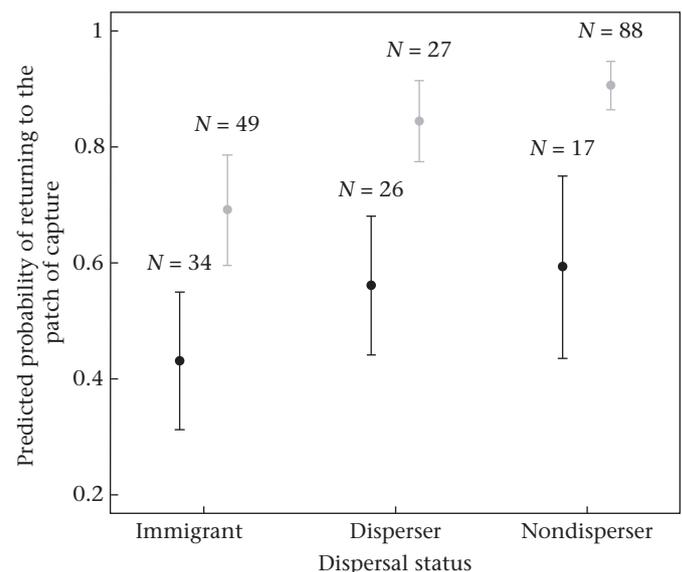


Figure 2. Among displaced individuals, the probability of returning to the patch of capture according to the interaction between dispersal status and age. Black dots: yearlings; grey dots: older birds. Immigrants: unringed individuals upon early capture; dispersers: individuals that were caught early in a patch different from their previous (natal or breeding) patch; nondispersers: individuals that were caught early in their previous patch. The figure shows the fitted values from model averaging \pm 95% confidence interval. Numbers are sample sizes.

nondispersers (Table 2; fitted values \pm SE for immigrants: 21.4 ± 0.6 ; dispersers: 20.8 ± 0.6 ; nondispersers: 21.0 ± 0.6). Yearlings also laid later than older birds (Table 2; fitted values \pm SE: 21.8 ± 0.1 and 20.3 ± 0.1 , respectively). Females had an earlier laying date than males (Table 2; fitted values \pm SE: 20.2 ± 0.6 and 21.9 ± 0.6 , respectively), but this sex effect was again due to the sampling bias between the sexes, because it was no longer supported when restricting the female data to females whose males had also been caught (95% CI of averaged parameters: -0.956 ; 0.319 ; fitted values \pm SE: females: 20.8 ± 0.5 ; males: 20.6 ± 0.5 ; see Appendix 2, Table A3).

Clutch size depended only on age (Table 1). Yearlings laid smaller clutches than older birds (Table 2; fitted values \pm SE: 6.17 ± 0.05 and 6.38 ± 0.04 , respectively). The effects of treatment sensu lato and sex were not supported (Table 2).

The probability of success (i.e. of fledging at least one young) depended on age with yearlings having a lower probability of success than older birds (Table 2; fitted values \pm SE: 0.79 ± 0.05 and 0.84 ± 0.04 , respectively) but depended also on the experimental treatment sensu lato in interaction with sex (Tables 1, 2). However, this interaction was not supported when restricting the female data to females whose males had also been caught (Appendix 2) and therefore only resulted from the sampling bias between the sexes.

Among successful nests, the final number of fledglings depended only on age (Table 1). Yearlings fledged fewer young than older birds (Table 2; fitted values \pm SE: 4.92 ± 0.16 and 5.20 ± 0.13 , respectively). The dispersal status and sex effect were not supported although they were retained in two and one of the best models, respectively (Table 2).

Finally, nestling body mass depended on treatment sensu lato (Table 1). Displaced individuals that did not return to the patch of capture raised lighter young than other birds, i.e. displaced individuals that returned, control and nonexperimental birds (Table 2, Fig. 3). Nestling body mass also increased with tarsus length (Table 2) and decreased with brood size (Table 2). Sex and age were not supported even though they were each present in one of the best models (Tables 1, 2).

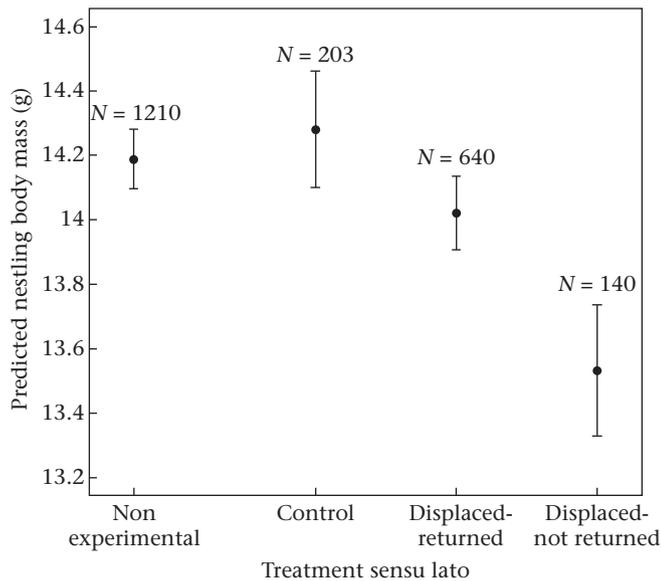


Figure 3. Nestling body mass according to treatment sensu lato: nonexperimental (i.e. unmanipulated birds), control (i.e. birds released in the patch of capture), displaced returned (i.e. displaced birds that returned to their patch of capture) and displaced stayed (i.e. displaced birds that did not return to their patch of capture). The figure shows fitted values from model averaging \pm 95% confidence interval. Numbers are sample sizes.

Return Rate in Subsequent Years

The probability of returning to the study area in the years following the experiment depended on the interaction between dispersal status and the response to the experiment in terms of successful settlement (i.e. whether the individual was caught as a breeder in the same season or whether it disappeared; Table 1). Immigrants and dispersers that disappeared were less likely to return to the study area in subsequent years than immigrants and dispersers that settled (Table 2, Fig. 4). Overall, individuals that settled to breed were more likely to return in subsequent years than individuals that disappeared (Table 2; fitted values \pm SE: 0.40 ± 0.03 and 0.25 ± 0.03 , respectively) and immigrants and dispersers were less likely to return than nondispersers (Table 2; fitted values \pm SE: 0.23 ± 0.03 and 0.30 ± 0.04 and 0.43 ± 0.04 , respectively). The interaction between age and response to the experiment was not supported (Table 2) even though it was retained in three of the four best models (Table 1). Finally, the effects of sex and date of capture were not supported (Table 2).

DISCUSSION

By experimentally displacing newly arrived collared flycatchers between habitat patches, we explored potential costs of small-scale movement (i.e. outside metabolic flight costs) and settlement in a new habitat on reproductive decisions. The experimental displacement slightly decreased the probability that an individual successfully settled and bred in the study area. A large proportion of experimental birds were not subsequently caught as breeders in the study area, and this was particularly the case for immigrants. Among displaced birds, nondispersers showed the highest probability of returning to the patch of capture, and immigrants the lowest. These results suggest that the forced displacement affected prebreeding decisions and that these decisions also depended on the individual's dispersal history, possibly reflecting differences in the cost–benefit balance of dispersal movements. Once settled, displaced individuals that did not return to their patch of capture raised lighter young than those that returned, even though laying

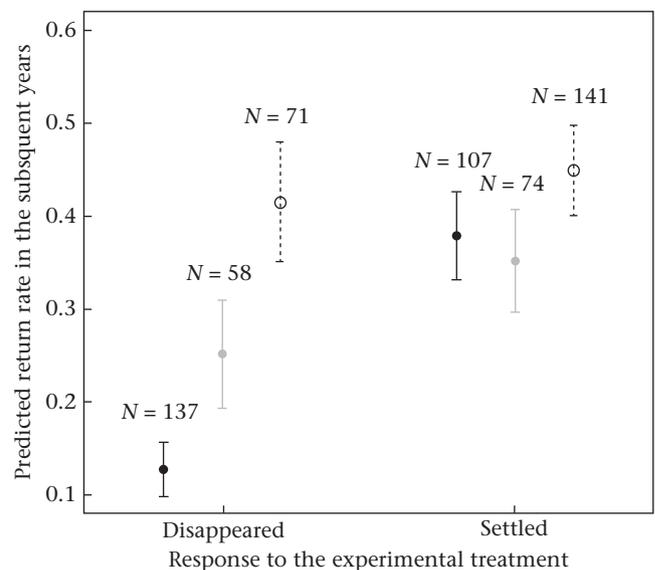


Figure 4. Return rate in the years following the translocation experiment according to the interaction between the response to the experimental treatment in terms of successful settlement and dispersal status. Black dots: immigrants; grey dots: dispersers; open dots: nondispersers. The figure shows fitted values from model averaging \pm 95% confidence interval. Numbers are sample sizes.

date, clutch size and fledging number did not differ between treatments. These results could be explained either by phenotypic differences between displaced individuals that did and did not return to their patch of capture, with individuals that did not return being lower quality individuals, or by a cost paid by displaced individuals that did not return, due to the lack of local knowledge with the breeding environment (Germain, Pärt, Gustafsson, & Doligez, 2017). Finally, immigrants and dispersers that disappeared after the forced displacement were less likely to return in subsequent years than those that had settled, while this was not observed among nondispersers, suggesting potential large-scale movements following the displacement.

Disappearance Following Displacement: Movements Rather Than Mortality?

Overall, about 44% of experimental individuals (i.e. 267 out of 611) disappeared after the manipulation, with higher disappearance among displaced individuals (46%) and immigrants (55%) than control (34%) and local individuals (36%), respectively. These figures are in line with the high rate of disappearance of released individuals observed in many translocation programmes performed for conservation purposes, particularly in avian species (Wolf, Griffith, Reed, & Temple, 1996). Disappearance from the release population/site may be due to mortality and/or large-scale movements of released animals out of the monitored area (Calvete & Estrada, 2004; Griffith et al., 1989; Mihoub, Le Gouar, & Sarrazin, 2009; Snyder, Pelren, & Crawford, 1999), two processes that are difficult to distinguish in our case. Here, nondispersers that had subsequently been caught as breeders in the year of the manipulation and those that had disappeared had similar return rates to the study area in subsequent years, suggesting that mortality was unlikely to explain disappearance among nondispersers. Immigrants (and to a lesser extent dispersers) that had disappeared were less likely to return to the study area in subsequent years than both immigrants (and dispersers) that had successfully settled and nondispersers. Although we cannot totally exclude a higher mortality for disappeared immigrants (and dispersers), the high rate of return of disappeared nondispersers supports the hypothesis that disappeared immigrants may have dispersed outside the study area following the experiment. Many of these immigrants were probably long-distance dispersers that came from outside the study area, and dispersers have been found to be more likely to disperse again (see Doligez & Pärt, 2008). Some of these disappeared immigrants could also have been transient individuals that had stopped on their way to their intended breeding site and resumed migration beyond the study area following the early capture. Large-scale postrelease movements by displaced individuals have previously been documented, particularly in highly mobile species such as birds (Coates, Stiver, & Delehanty, 2006; Kemink & Kesler, 2013; Le Gouar et al., 2008). Monitoring postrelease movements would be needed to assess the fate of the disappeared birds but requires using remote tracking over large areas, which remains difficult on small species such as the collared flycatcher (Ponchon et al., 2013). Further work therefore remains needed to compare postrelease movements of translocated and control individuals and identify the factors affecting these movements, and may be permitted in the near future thanks to rapid progress in the miniaturization of tracking devices.

Disappearance Following Displacement: Nonbreeding or Lack of Familiarity?

Alternatively, but not exclusively, the tendency for higher disappearance by displaced individuals than control ones may

reflect a cost of the lack of familiarity with the environment on settlement and/or early breeding success (Isbell, Cheney, & Seyfarth, 1990; Yoder et al., 2004). Displaced individuals, but also immigrants, could be expected to pay a higher dispersal cost due to unfamiliarity with the breeding environment compared to nondispersers or short-distance dispersers, both after settlement and during the movement and settlement process itself (Hansson, Bensch, & Hasselquist, 2004; Pakanen et al., 2016; Pascual, Carlos Senar, & Domenech, 2014). A lack of prior knowledge about the local environment regarding, for example, food sources or predation risk may affect the probability of acquiring a high-quality breeding site and/or mate (Brown, Brown, & Brazeal, 2008; Pärt, 1995; Saunders, Roche, Arnold, & Cuthbert, 2012; Yoder et al., 2004), which may eventually lead to nonbreeding; it may also decrease foraging efficiency, survival and reproductive performance once settled, which may eventually lead to early breeding failure (Danchin & Cam, 2002). Here, displacement may thus have induced nonbreeding or early breeding failure, which could represent a cost of the forced movement to an unfamiliar environment.

Such a cost of breeding in an unfamiliar environment after the settlement may be illustrated here by the later laying date of immigrants than dispersers and nondispersers, given that reproductive success decreases with increasing date in the season in this as in many other passerine species (for a review see Verhulst & Nilsson, 2008). Familiarity with the breeding environment has been proposed to be beneficial in different species (e.g. increased daily survival in cliff swallows, *Petrochelidon pyrrhonota*: Brown et al., 2008; increased fledging success in the piping plover, *Charadrius melodus*: Saunders et al., 2012) including in our study population (Pärt, 1994). Accordingly, we could therefore expect that, among displaced individuals, those with the highest familiarity with their former environment would be more likely to return to their patch of capture after the displacement. We indeed found that displaced nondispersers had a higher probability of returning to the patch of capture than displaced immigrants (with displaced dispersers in between). Benefits of familiarity were also suggested to be higher in males than females, predicting a higher probability of returning to the patch of capture for displaced males, because of the resource-holding mating system in this species (as in most bird species; Greenwood, 1980). The probability of returning to the patch of capture rate was indeed higher in displaced males than females, an effect already found and discussed in a previous study (Pärt, 1995). These results therefore suggest that the higher disappearance of displaced than control birds could be due to a lower probability of breeding successfully, and thus of being caught again, due to lower familiarity with the local environment.

This raises the question of the extent to which individuals may acquire familiarity with a new environment prior to breeding in this species. Prospecting towards the end of the breeding season has been shown to be frequent and to allow individuals to gather knowledge about the local environment (i.e. at the patch scale) to be used for settlement decisions in the next year (Doligez, Danchin, & Clobert, 2002; Doligez et al., 2004; Pärt & Doligez, 2003). These studies therefore suggest that prospecting may involve large-scale movements between patches allowing individuals to become familiar with different potential future breeding patches. However, little information is currently available regarding the identity of prospecting birds, and therefore it is not possible to assess here whether nonlocal individuals may have acquired knowledge about the patches they were displaced to later on through prospecting in the previous year. Understanding the role of familiarity with the local environment in shaping the response of individuals to forced movement therefore requires further work.

Reproductive Performance Following Forced Displacement

Once settled, however, displaced, control and nonexperimental individuals did not differ in laying date, clutch size and number of fledglings when successful, which could suggest low costs of unfamiliarity with the environment after settlement. Nevertheless, nestling body mass was lower for displaced individuals that did not return to the patch of capture than for other individuals. In this population, nestling body mass was found to correlate positively with juvenile survival and recruitment (Linden, Gustafsson, & Part, 1992). Hence, the lower nestling body mass may here still reflect an important cost of breeding in an unfamiliar environment, via, for example, lower foraging efficiency and/or lower quality territory (e.g. Pärt, 1991, 1994). Alternatively, but again not exclusively, the difference in nestling body mass could result from phenotypic differences between displaced individuals that did and did not return to the patch of capture. Phenotypic differences between dispersers and nondispersers have been widely described and are known to affect the balance between the costs and benefits of dispersal (Bonte, De Roissart, Wybouw, & Van Leeuwen, 2014; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Dufty & Belthoff, 2001). In particular, when local competition drives dispersal, dispersers may be less competitive individuals expected to access only lower quality nest sites and/or mates and achieve lower mating success than nondispersers (e.g. Clobert et al., 2001; Martin et al., 2008). In our case, phenotypic differences may have existed prior to the displacement and shaped the individual's probability of accepting the displacement. Phenotypic differences may also result from the displacement itself, for example as a result of the lack of familiarity with the breeding environment. In our population, parental body condition was positively related to the mean brood fledging mass (Germain, 2014). As a result, a lower parental body condition either before the displacement or resulting from the costs of breeding in an unfamiliar environment may explain the lower nestling mass for displaced individuals that did not return than for other individuals. Here, individuals responding differently to the experimental displacement (i.e. returning to the patch of capture or not) did not differ in terms of body condition index (as measured by the ratio of mass over tarsus length; results not given), but this index may not have reliably captured the relevant phenotypic differences between individuals. Fully assessing the impact of potential phenotypic differences here could first require identifying relevant proxies of individual quality, which may involve comparing more detailed phenotypic (e.g. physiological and behavioural) measures, but also long-term fitness, between displaced individuals that did and did not return to their patch of capture. Because many of the reproductive measures explored here did not differ between displaced individuals that did and did not return and control (or nonexperimental) individuals, a forced displacement at the beginning of the breeding season did not appear to impose strong reproductive costs although the long-term fitness consequences of the forced displacement remain to be explored. The forced movement itself imposed no cost after settlement since the success of displaced individuals that returned to their patch of capture did not differ from that of control individuals. Differences in breeding variables that may reveal a cost were only observed when individuals did not return to their patch of capture, which suggests that additional processes (unfamiliarity or phenotypic differences or both if phenotypic quality influences information gathering and familiarization with the environment) are involved in shaping possible postsettlement costs of a forced displacement. Although many factors are likely to shape individual variation in the motivation to disperse in natural situations (Clobert et al., 2001, 2012), our experimental results indicate that displacing individuals to a new environment can have consequences both on

settlement decisions (here, the probability of settling to breed) and subsequent breeding performance (here, nestling body mass) and also suggest a different cost - benefit balance of familiarity with the environment depending on dispersal history along with sex and age. Monitoring detailed movements of individuals after displacement to get information on individuals that failed to access resources for reproduction and/or moved outside the study area would be required to better understand the consequences of forced movements. Nevertheless, our study provides insights on factors driving individuals to settle in a new habitat and associated potential costs, independently from the dispersal transfer itself.

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APPENDIX 1. YEAR EFFECTS

Probability of Successfully Settling and Returning to Patch of Capture

The probability of settling as a breeder but not the probability of returning to the patch of capture among displaced individuals differed between years. The probability of settlement was lower in 2012 and 2013 than in 1989 and 1990 (fitted values \pm SE: 1989: 0.74 ± 0.04 ; 1990: 0.70 ± 0.05 ; 2012: 0.54 ± 0.05 ; 2013: 0.46 ± 0.05).

Breeding Variables

The year was systematically retained in the most competitive models explaining each of the breeding variables investigated (Table 1).

Table A1

Fitted values \pm SE from model averaging for each breeding variable and each year of the experiment

Breeding variable	1989	1990	2012	2013
Laying date	23.55 \pm 0.41	20.21 \pm 0.45	17.96 \pm 0.37	22.52 \pm 0.37
Clutch size	6.14 \pm 0.06	6.25 \pm 0.07	6.50 \pm 0.06	6.24 \pm 0.06
Probability of success	0.70 \pm 0.08	0.60 \pm 0.09	0.92 \pm 0.03	0.84 \pm 0.05
Number of fledglings among successful individuals	4.91 \pm 0.19	4.31 \pm 0.20	5.61 \pm 0.15	4.79 \pm 0.15
Nestling body mass	14.06 \pm 0.22	13.66 \pm 0.13	14.38 \pm 0.10	13.91 \pm 0.10

APPENDIX 2. RESTRICTED DATA SET

Whenever a sex effect was retained for any of the response variables, we explored whether it was due to the sampling bias between males and females because of the differential timing of capture. To do so, we performed the analyses again after restricting the female data by excluding females whose males had not been caught because of early nest failure, which eliminated the sampling bias between sexes.

Table A2

Best models (based on selection by AICc) for each response variable when restricting the female data to females whose males had also been caught

Model	K	LogLik	AICc	Δ AICc	wi
Probability of settling to breed in the study area (N=547)					
Age+Date of capture+Dispersal status+Experimental treatment+Year	10	-335.368	691.1	0.00	0.235
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year	11	-334.441	691.4	0.23	0.209
Age+Date of capture+Dispersal status+Experimental treatment+Year+Age*Experimental treatment	11	-334.878	692.3	1.10	0.135
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year+Sex*Experimental treatment	12	-333.901	692.4	1.24	0.126
Age+Date of capture+Dispersal status+Sex+Experimental treatment+Year+Age*Experimental treatment	12	-334.048	692.7	1.53	0.109
Age+Date of capture+Dispersal status+Location of the breeding plot+Experimental treatment+Year	11	-335.213	692.9	1.77	0.097
Age+Date of capture+Dispersal status+Year	9	-337.374	693.1	1.94	0.089
Null model	2	-377.303	758.6	67.48	<0.001
Starting model	17	-333.161	701.5	10.33	<0.001
Probability of returning to the patch of capture (for displaced individuals) (N=208)					
Age+Sex	4	-98.289	204.8	0.00	0.552
Age+Dispersal status+Sex	6	-97.003	206.4	1.65	0.242
Age+Date of capture+Dispersal status+Sex	5	-98.229	206.8	1.98	0.205
Null model	2	-112.444	228.9	24.17	<0.001
Starting model	17	-92.991	223.2	18.42	<0.001
Laying date (N=518)					
Age+Year	7	-1401.753	2817.5	0.00	0.598
Age+Sex+Year	8	-1401.150	2818.3	0.79	0.402
Null model	3	-1487.534	2981.1	163.56	<0.001
Starting model	25	-1398.078	2846.2	28.65	<0.001
Probability of success (i.e. of fledging at least one young) (N=481)					
Year	4	-114.406	236.8	0.00	0.549
Age+Year	5	-113.600	237.2	0.39	0.451
Null model	2	-132.913	267.8	31.01	<0.001
Starting model	24	-104.282	254.6	17.75	<0.001

Best models based on AICc values (i.e. models with Δ AICc compared to the best model < 2), as well as null and starting models, for the probability of successfully settling and being caught as a breeder in the study area, the probability of returning to the patch of capture, laying date and probability of success (i.e. of fledging at least one young). K: number of parameters in the model; LogLik: log-likelihood; Δ AICc: difference in AICc to the best model; wi: Akaike weight.

Table A3

Estimates \pm SE, 95% confidence intervals (CI) and relative variable importance (RVI) from averaged models of effects retained in the best models for response variable when restricting the female data to females whose males had also been caught

Variable from averaged model	Estimates \pm SE	95% CI	RVI
Probability of settling to breed in the study area			
Intercept	0.04 \pm 0.15	–0.259; 0.334	–
Sex (male)*Experimental treatment (displaced individuals)	0.56 \pm 0.54	–0.509; 1.624	0.13
Age (yearling)*Experimental treatment (displaced individuals)	–0.45 \pm 0.48	–1.396; 0.491	0.24
Experimental treatment (displaced individuals)	–0.47\pm0.23	–0.935; –0.012	0.91
Age (yearling)	–0.59\pm0.21	–1.008; –0.179	1
Sex (male)	–0.32 \pm 0.23	–0.778; 0.145	0.44
Dispersal status (disperser)	–0.005 \pm 0.27	–0.531; 0.520	1
Dispersal status (immigrant)	–0.74\pm0.23	–1.195; –0.295	–
Date of capture	–0.07\pm0.02	–0.110; –0.027	1
Year (1990)	–0.16 \pm 0.30	–0.747; 0.424	1
Year (2012)	–1.24\pm0.33	–1.888; –0.594	–
Year (2013)	–1.53\pm0.31	–2.152; –0.916	–
Location of the breeding plot (edge patch)	–0.12 \pm 0.22	–0.548; 0.306	0.10
Probability of returning to the patch of capture (for displaced individuals)			
Age (yearling)	–1.60\pm0.40	–2.376; –0.816	1
Sex (male)	1.18\pm0.41	0.371; 1.99	1
Dispersal status (disperser)	–0.29 \pm 0.51	–1.300; 0.712	0.24
Dispersal status (immigrant)	–0.73 \pm 0.46	–1.644; 0.182	–
Date of capture	–0.02 \pm 0.05	–0.103; 0.072	0.21
Laying date			
Age (yearling)	1.35 \pm 0.34	0.688; 2.020	1
Sex (male)	–0.32 \pm 0.32	–0.956; 0.319	0.37
Year (1990)	–5.79\pm0.47	–4.610; –2.735	1
Year (2012)	–1.40\pm0.47	–6.710; –4.869	–
Year (2013)	–3.67\pm0.48	–2.319; –0.471	–
Probability of success (i.e. to fledge at least one young)			
Age (yearling)	–0.47 \pm 0.36	–1.188; 0.245	0.45
Year (1990)	–0.08 \pm 0.39	–0.845; 0.682	1
Year (2012)	3.38\pm1.04	1.338; 5.424	–
Year (2013)	1.61\pm0.53	0.562; 2.651	–

Bold type indicates parameters with 95% confidence intervals that do not encompass 0.95% confidence intervals correspond to the modality of the factor in parentheses in comparison to the reference modality (reference category: control birds for experimental treatment, control birds for experimental treatment sensu lato, individuals that disappeared for response to the experiment, older individuals for age, females for sex, nondisperser for dispersal, year 1989 for year, central plots for the location of the breeding plot).