

## Research

### Natal dispersal does not entail survival costs but is linked to breeding dispersal in a migratory shorebird, the southern dunlin *Calidris alpina schinzii*

Veli-Matti Pakanen, Kari Koivula, Blandine Doligez, Lars-Åke Flodin, Angela Pauliny, Nelli Rönkä and Donald Blomqvist

V.-M. Pakanen (<https://orcid.org/0000-0003-4838-9927>) ✉ ([veli-matti.pakanen@oulu.fi](mailto:veli-matti.pakanen@oulu.fi)), K. Koivula and N. Rönkä, Ecology and Genetics Research Unit, Univ. of Oulu, Oulu, Finland. – V-MP, A. Pauliny and D. Blomqvist, Dept of Biological and Environmental Sciences, Univ. of Gothenburg, Gothenburg, Sweden. – B. Doligez, CNRS, Univ. Lyon 1, Dept of Biometry and Evolutionary Biology, UMR 5558, Villeurbanne, France. – L.-Å. Flodin, Rannevägen 12, Varberg, Sweden.

Oikos

2022: e08951

doi: 10.1111/oik.08951

Subject Editor: Wendt Muller

Editor-in-Chief: Dries Bonte

Accepted 8 April 2022



The costs and benefits of dispersal are often assessed by comparing fitness between dispersing and non-dispersing individuals. Importantly, individuals that disperse between their natal and first breeding site may subsequently be more likely to disperse between breeding sites compared to those that remained philopatric to their natal site. Such within-individual consistency in dispersal behaviour can bias local survival estimation, and thus the survival comparison between dispersing and non-dispersing individuals, if breeding dispersal leads to permanent emigration from the study area. We examined whether adult survival correlates with natal dispersal in a migratory shorebird, the southern dunlin *Calidris alpina schinzii*, in two isolated patchy populations where permanent emigration is expected to be extremely rare. To assess whether local adult survival could be biased by non-random breeding dispersal, we analysed between-patch breeding dispersal probability and quantified within-individual consistency in dispersal. Among females, natal dispersers were more likely to disperse again as adults compared to non-dispersers, while no difference was observed in males which were always highly site faithful. Yet, adult survival did not differ between natal dispersing and non-dispersing individuals in either sex. Breeding dispersal probability was higher in failed compared to successful breeders. Breeding dispersal often resulted in dispersal back to the natal patch, i.e. delayed natal philopatry. Our results suggest no survival costs of dispersal after first reproduction. Despite individual consistency, survival estimates of dispersing individuals were not biased because nearly all available breeding habitat was covered. We show that consistency in dispersal can occur even in site faithful species like the southern dunlin. Studies of the effects of dispersal on survival should therefore account for within-individual consistency in dispersal if not all available breeding habitat is monitored in open populations. In particular, delayed natal philopatry may lead to biased local survival estimates for immigrants when compared with philopatric individuals.

Keywords: breeding dispersal, dispersal benefits, dispersal costs, emigration, philopatry, site fidelity, within-individual consistency



[www.oikosjournal.org](http://www.oikosjournal.org)

© 2022 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Introduction

The evolution of dispersal is shaped by its costs and benefits on survival in the different phases of the dispersal process and on reproductive success after settlement (Clobert et al. 2001, 2012, Bowler and Benton 2005, Bonte et al. 2012). However, assessing these costs and benefits often remains challenging, because in most cases only survival and reproductive success correlates of dispersal are available. Thus, inferring causality relation with dispersal remains difficult. A large body of literature has quantified potential fitness consequences of dispersal by comparing survival, reproductive success and/or lifetime fitness measures (e.g. lifetime reproductive success) between dispersing and non-dispersing individuals after settlement (reviewed by Bélíchon et al. 1996, Doligez and Pärt 2008, Germain et al. 2017a). When the origin of individuals is known, comparison of fitness measures is usually done in relation to within-study area dispersal status (i.e. non-dispersing individuals are compared to within-study area dispersers; Waser et al. 2013) or dispersal distance (Serrano and Tella 2012). When the origin of dispersing individuals is unknown, immigrants that have settled in the study site are usually compared to locally born and recruited individuals (Pakanen et al. 2010). Overall, these studies show that dispersal is often associated with lower subsequent survival, suggesting that dispersal can bear survival costs also after the movement phase (Bélíchon et al. 1996, Doligez and Pärt 2008). In highly mobile species, inferring causal relationships between dispersal and fitness components, i.e. dispersal fitness costs, remains difficult because experimental manipulations of the dispersal status itself are not easy to implement in natural populations (Germain et al. 2017b). Thus, correlative approaches continue to be an important line of empirical research on dispersal evolution (Davidian et al. 2016, Barbraud and Delord 2020, Martinig et al. 2020).

The ability to reliably assess survival may be hampered by the practical constraints of the monitoring of open populations over spatially limited areas. Working in areas of small relative size compared to the actual dispersal distance distribution may prevent discriminating permanent emigration from mortality for a large fraction of monitored individuals that disappear (Marshall et al. 2004, Taylor et al. 2015). This may affect estimation of the survival correlates of dispersal if the probability to emigrate from the study area is linked to dispersal status. A commonly neglected issue is indeed that dispersing individuals may be more likely to disperse again as adults (i.e. non-random subsequent dispersal with respect to previous dispersal status, hereafter referred to within-individual consistency in dispersal). This may lead to higher chance of permanent emigration, and hence systematic underestimation of adult survival for dispersing compared to non-dispersing individuals (Doligez and Pärt 2008). This bias can be avoided by working in closed or semi-closed (isolated) study populations, but such opportunities are rare.

Within-individual consistency in dispersal behaviour could occur because of a (at least partial) genetic determinism on dispersal behaviour. A tendency to disperse or be site

faithful as juveniles would continue into the adult stage. In line with this, dispersal has been found to be heritable in different species (Doligez et al. 2009, Charmantier et al. 2011, Saastamoinen et al. 2018). Alternatively, however not exclusively, within-individual consistency may reflect the functional integration between dispersal and phenotypic traits that allow reducing dispersal costs. For example, dispersers and non-dispersers may differ in physiological, behavioural and/or morphological traits that allow coping with the costs of movement or settling in unfamiliar environments (Clobert et al. 2009, Korsten et al. 2013, Bize et al. 2017, Denoël et al. 2018). Empirical evidence has been accumulating for both processes (Clobert et al. 2001, 2009, Doligez and Pärt 2008, Cote et al. 2010, Cote and Clobert 2012, Edelaar and Bolnick 2012). Within-individual consistency in dispersal could thus be a widespread phenomenon, but it has received little attention when examining survival correlates of dispersal. This could be because dispersal is usually highest early in life, before the first breeding event (i.e. natal dispersal) compared to after it (i.e. breeding dispersal; Greenwood and Harvey 1982, Paradis et al. 1998).

In an earlier review, Doligez and Pärt (2008) found only five studies that examined within-individual consistency in dispersal behaviour. After that, further studies reporting within-individual consistency in dispersal behaviour have been published. Including studies reviewed by Doligez and Pärt (2008), we have found 16 published studies (on 12 different bird species) that investigated within-individual consistency in dispersal behaviour (Table 1). Within-individual consistency was found in all five studies that compared breeding dispersal probability between natal dispersing and non-dispersing individuals, but only in one out of six studies that tested the relationship between natal and breeding dispersal distances (Table 1; Pärt and Gustafsson 1989). In studies examining within-individual consistency between breeding dispersal events, it was found in six out of eight cases (Table 1). While these studies suggest a clear tendency for dispersal consistency throughout life, more studies are needed to unravel the underlying mechanisms of such consistency. The different genetic and phenotypic backgrounds between dispersing and non-dispersing individuals may, for example, lead to different decisions in response to cues that induce dispersal (Aragón et al. 2006, Pakanen et al. 2011a). Furthermore, dispersing and non-dispersing individuals may possess different amount of available information (e.g. habitats) for making dispersal decisions. For example, dispersing individuals also possess crucial information about their natal sites in addition to their first breeding site, and therefore breeding dispersal back to natal sites may be common (Balkiz et al. 2010, Péron et al. 2010).

Here, we examined within-individual consistency in dispersal behaviour and whether such consistency may affect our estimation of potential costs and benefits of natal dispersal on subsequent adult survival using lifetime individual histories of a migratory shorebird, the southern dunlin *Calidris alpina schinzii*. We make use of two closely monitored patchy populations that resemble closed populations.

Table 1. Studies testing for within-individual consistency in relation to (a) natal dispersal and (b) breeding dispersal. WIC indicates whether or not within-individual consistency was found. Studies are organized by the compared variable (dispersal probability or distance) and the type of comparison of groups (i.e. DP=dispersing versus non-dispersing, or IP=immigrants versus local recruits). Details gives the sex(es) in which within-individual consistency was found. See the Supporting information for details on the review of articles shown here.

Species	WIC	Type	Variable	Details	Reference
(a) Within-individual consistency from natal dispersal to breeding dispersal					
<i>Calidris temminckii</i>	yes	IP	Probability	♂♀	Pakanen et al. 2011a <sup>a</sup>
<i>Chroicocephalus ridibundus</i>	yes	DP	Probability	♂♀	Péron et al. 2010
<i>Phoenicopterus roseus</i>	yes	DP	Probability	♂♀	Balkiz et al. 2010 <sup>b</sup>
<i>Ficedula albicollis</i>	yes	IP+DP	Probability	♀	Doligez et al. 1999, 2002
<i>Parus major</i>	yes	IP	Probability	♀	Verhulst and Van Eck 1996
<i>Falco naumanni</i>	no		Distance		Serrano and Tella 2012
<i>Ficedula albicollis</i>	yes	IP	Distance	♂	Pärt and Gustafsson 1989
<i>Ficedula hypoleuca</i>	no	IP	Distance		Montalvo and Potti 1992
<i>Poecile montanus</i>	no	IP	Distance		Orell et al. 1999
<i>Poecile montanus</i>	no	IP	Distance		Pakanen et al. 2016b <sup>c</sup>
<i>Tyto alba</i>	no		Distance		van den Brink et al. 2012
(b) Within-individual consistency in breeding dispersal					
<i>Falco naumanni</i>	yes	DP	Probability	♂♀	Serrano et al. 2001
<i>Milvus migrans</i>	no		Probability		Forero et al. 1999)
<i>Tachycineta bicolor</i>	yes	DP	Probability	♀	Lagrange et al. (2017)
<i>Ficedula albicollis</i>	yes	DP	Probability	♀	Doligez et al. 2012
<i>Milvus migrans</i>	no		Distance		Forero et al. 1999
<i>Falco tinnunculus</i>	yes		Distance	♂♀	Vasko et al. 2011
<i>Falco naumanni</i>	yes		Distance	♂♀	Serrano et al. 2001
<i>Tyto alba</i>	yes		Distance	♂♀	van den Brink et al. 2012

<sup>a</sup> Comparison of return rates of successful and unsuccessful birds in two populations (Oulu and Kokkola), <sup>b</sup> same effect for unexperienced breeders and experienced breeders, <sup>c</sup> post-winter movement from wintering territories to nest sites.

They are geographically separated and genetically differentiated, breeding on the Baltic coastal meadows in Sweden and Finland (Blomqvist et al. 2010, Pakanen et al. 2016a, 2017, Rönkä et al. 2021). These study populations provide a highly suitable system to test for within-individual consistency in between-patch, within-population dispersal, and to compare adult survival estimates of natal dispersing and non-dispersing individuals, as permanent emigration should be extremely rare. Specifically, we tested whether natal dispersing individuals were more likely to disperse between patches as adults compared to non-dispersing individuals, accounting for sex, age and previous breeding success of the individual, which have been previously linked to breeding dispersal distance (Soikkeli 1970, Thorup 1999, Flodin and Blomqvist 2012). Finally, to investigate the role of the natal habitat in breeding dispersal decisions of natal dispersing individuals, we examined whether the breeding dispersal of natal dispersing individuals occurs more frequently back towards their natal site than to other sites.

## Material and methods

### Population monitoring and data collection

We collected long-term individual-based data from southern dunlin populations breeding in two coastal meadow networks: at the Bothnian Bay (ca 64°50'N, 25°00'E; eight breeding patches) from 2002 to 2018 and on the west coast of Sweden (57°55'N, 11°47'E–57°7'N, 12°14'E, seven breeding patches) from 1985 to 2015 (Fig. 1). Patch sizes

vary between 16 and 272 ha in size (Supporting information; Pakanen et al. 2017). Distances between patches range between 2.1 and 90.0 km and hence possible dispersal distances can extend from zero to 90 km within these study areas (Supporting information). These coastal meadows are always connected to the shoreline, which serves as a foraging area for adults and chicks.

Both study populations are situated hundreds of kilometers away from other populations along the coast (Pakanen et al. 2016a, 2017, Rönkä et al. 2021). Therefore, these isolated populations show little exchange of individuals with other populations (Blomqvist et al. 2010, Pakanen et al. 2017, Rönkä et al. 2021) and are genetically differentiated from other populations (Rönkä et al. 2021). Our study areas thus provide a unique system to study dispersal consequences, as permanent emigration should be extremely rare. Furthermore, nearly all movements within the study populations could be detected because we were able to localize and monitor almost all suitable breeding sites within the study populations, as the southern dunlin breeds only on habitat patches composed of short-vegetated meadows within an unsuitable matrix of mainly high vegetation such as reedbed or sandy dunes (Pakanen et al. 2017). In the Finnish study area, four managed areas that are not part of our main study area, have been censused during the study, and very few breeding observations have been made, none of these including colour ringed birds (Fig. 1). Thus, there is a very small chance that we missed individuals or dispersal movements, and the possibilities for short distance dispersal leading to movement outside of our study areas is expected to be minimal.

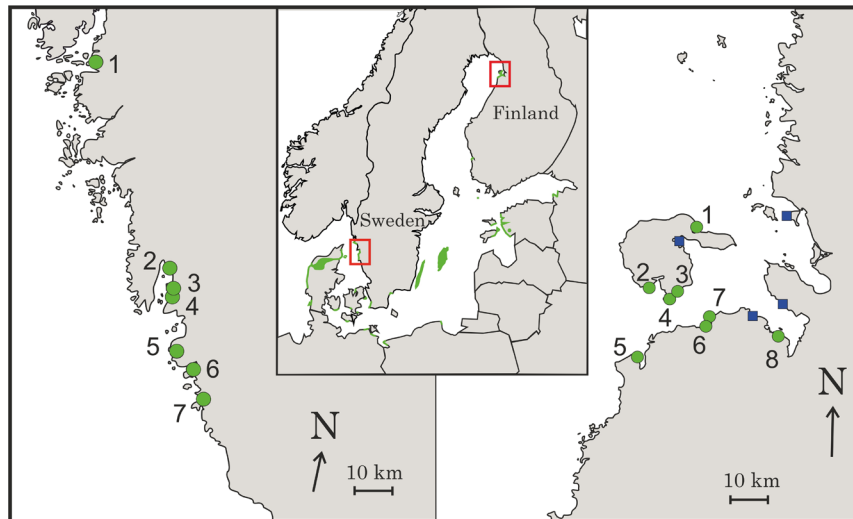


Figure 1. Location of the study areas in Sweden and Finland together with a distribution of Baltic dunlin breeding range (in green colour) in Fennoscandia (Helcom 2013, the Swedish Species Information Centre 2015, own observations). Locations of breeding patches are marked with green dots (Sweden: 1=Ödsmåls kile, 2=Torkelstorp, 3=Tjolöholm, 4=Ölmevalla, 5=Båtafjorden, 6=Klosterfjorden, 7=Getterön; Finland: 1=Pökönokka, 2=Kuivasäikkä, 3=Tömpä, 4=Isomatalla, 5=Tauvo, 6=Savilahti, 7=Säärennokka, 8=Pitkänokka). The breeding distribution in Sweden indicates areas that have regularly held breeding Baltic dunlins from the 1990s onwards. The blue squares in the Finnish study area map indicate four meadows that have harboured one breeding pair of dunlin during the study but held no breeding dunlin most of the time (map modified from Pakanen et al. 2017).

The first individuals arrive on the breeding sites in late March in Sweden and in late April in Finland (Blomqvist unpubl., Pakanen et al. 2018). Very few individuals start to breed when one year old; most start to breed when they are 2–3 years old (Pakanen et al. 2016a). The laying period starts from mid or late April in Sweden (Blomqvist, unpubl.) and usually in early May in Finland (Pakanen et al. 2016a). Failed nests can be replaced but double nesting is extremely rare and re-nesting always occurs in the same patch (Pakanen et al. 2014). Hatching success in the two populations is similar (Sweden 41%; Finland 49%) with most failure being caused by nest predation (Pauliny et al. 2008, Pakanen et al. 2011b). Juvenile survival (recruitment) is high and similar (in Sweden: 0.17; in Finland: 0.20) (Pakanen et al. 2016a, 2021). Previous studies on adult survival are lacking from the Swedish study population, but adult survival has been estimated to be on average 0.77 in the Finnish study population (Pakanen et al. 2016a). Southern dunlins start migration as soon as possible after breeding. They migrate to western Africa after staging at the Wadden sea (Thorup et al. 2009, Pakanen et al. 2018).

Field work entailed intensive territory and nest searching throughout the laying period in order to find all nesting attempts. We searched for nests and territories by systematically walking across the meadows and observing individuals (displaying, calling etc.). We considered nest scrapes to be a strong sign of a territory, and we revisited these sites regularly. We floated the eggs when found to estimate expected hatching dates (Liebezeit et al. 2007) and monitored nest fates until hatching or destruction to determine nest success. If a pair was present at the site (e.g. had a territory) but its nest or brood was never found, we considered it to be unsuccessful. We ringed chicks at or in close vicinity of

their nest with numbered steel rings (Finland and Sweden), or with combinations of a steel and colour rings (Sweden). We caught recruits as breeding adults when incubating or brooding chicks using mist-nests or cage traps (Pakanen et al. 2017). We gave these adults individually identifiable colour ring combinations, which made it possible to follow their movements and survival through resightings in subsequent years. Resightings of adults accumulated during the whole breeding season at the shoreline, on territories and nests, and with broods.

We took blood samples from adults and chicks for sexing and microsatellite analyses (Blomqvist et al. 2010, Rönkä et al. 2021). We sexed adults using molecular analyses (Griffiths et al. 1998). When DNA samples were not available (Sweden 1985–1996; Finland 2002–2003), we sexed adults using behaviour (e.g. display behaviour), morphological measurements or plumage characteristics (Soikkeli 1966). These methods yielded the same results. We determined the exact age using the year of hatching. In the Finnish population, adult birds were fitted with geolocators during 2013–2014 for the purpose of studying migration ecology and wintering site use (Pakanen et al. 2018). These tracking devices did not affect reproduction but affected survival especially when the individuals carried them for more than one year (Pakanen et al. 2015a, 2020).

### Definition of dispersal

We defined natal dispersal as a change of patch (site; Fig. 1) between the patch where an individual hatched and the patch where the individual first bred, and breeding dispersal as a change of patch between successive breeding attempts. We

included data from individuals that were found to be breeding at ages 1–4. Indeed, recapture probabilities increase up to age 4 (Pakanen et al. unpubl.), indicating that breeding probability is 100% by that age (Clobert et al. 1994, Sanz-Aguilar et al. 2009). Individuals first recorded breeding at ages 5–8 thus most likely had started to breed earlier but remained undetected before. Their natal dispersal status could thus have been inaccurately assessed, and we therefore excluded them (12 individuals in total out of 251 recruits).

## Adult survival

We examined adult survival using CJS–capture–recapture models (Lebreton et al. 1992). Our main variable of interest, the natal dispersal status (‘Status’; dispersing versus non-dispersing) of an individual was modelled as a permanent state. Using this binomial variable, the survival and recapture rates of individuals that dispersed between patches in the natal dispersal phase (dispersing individuals) were compared to those of individuals that returned to their natal patch to breed (non-dispersing individuals). In addition, our survival ( $\Phi$ ) model included population (‘Pop’: Sweden versus Finland) and sex of the individual (‘Sex’) as well as the interaction (:) between sex and dispersal status, because survival and the costs of dispersal may be sex-specific (Jönsson 1991, Bonte et al. 2012). Finally, we considered the time since first reproduction (‘Tsm’: time since marking, i.e. time since first reproduction) distinguishing survival 1) after first reproduction and 2) after the second reproduction to control for age-specific variation in survival. In addition, we included an interaction between time since marking and dispersal status to test whether the cost of dispersal is stronger after first breeding than after later breeding events.

Our recapture model ( $p$ ) included population (‘Pop’) and sex (‘Sex’) because field effort may have been different in these populations due to different configurations or constraints, and because sex affects the likelihood of being recaptured (Pakanen et al. 2016a). We also included dispersal status because dispersing individuals may have a lower likelihood of being recaptured due to e.g. higher breeding dispersal probability or lower breeding probability (Oro et al. 2011). Finally, we included an interaction between population and dispersal status because the effect of dispersal status on recapture probability may differ between populations.

Our starting model thus had the following form: [ $\Phi(\text{Pop}+\text{Sex}+\text{Status}+\text{Tsm}+\text{Sex}:\text{Status}+\text{Tsm}:\text{Status})$   $p(\text{Pop}+\text{Sex}+\text{Status}+\text{Pop}:\text{Status})$ ]. This model fitted the data (Bootstrapping goodness of fit,  $p = 0.10$ ,  $\hat{c} = 1.08$ ; White et al. 2002). Our model did not account for temporal variation in survival because a previous analysis based on a larger data set did not find support for differences between years (Pakanen et al. 2020). Analyses were performed in program MARK (White and Burnham 1999). In order to control for the effect of geolocators on survival (Pakanen et al. 2020), we added to each model an individual covariate (binary variable) distinguishing individuals that carried a geocator from year  $i$  to year  $i+1$  (1) from those that did not (0). Starting from

the full model, we explored all possible sub-models down to the constant model (i.e. with no effect).

## Breeding dispersal

We analysed between-patch breeding dispersal probability (a binary variable, disperse or not) using generalized linear mixed models (GLMM, with binomial errors and logit link) in R ver. 3.6.1 (<www.r-project.org>) using function *glmer* in package *lme4* (Bates et al. 2015). We explored the influence of natal dispersal status (Status: natal dispersing versus non-dispersing individual), sex, age (continuous variable ranging from 1 until 17), current breeding success (Success: hatched chicks or not), population (Sweden versus Finland) and two-way interactions of the above factors as fixed factors on subsequent breeding dispersal probability. A higher probability of breeding dispersal for natal dispersers compared to non-dispersers while accounting for other factors would indicate within-individual consistency in dispersal behaviour. We included breeding success because it has previously been shown as a major factor influencing breeding dispersal decisions (Switzer 1997), as well as the interaction between breeding success and natal dispersal status because natal dispersing individuals may differ from non-dispersing individuals in their probability to disperse after breeding failure (Pakanen et al. 2011a). We fitted all possible combinations of main effects. In addition, we included a maximum of one interaction into a model to prevent fitting too complicated models. We standardised all continuous variables [(value – mean)/standard deviation] to allow meaningful interpretation of interaction models (Schielzeth 2010). We included individual (ID) as a random factor because the data contained several dispersal/philopatry events for a given individual (mean 3.4, SD 2.7). In addition, we included breeding patch (Site) as a random factor to control for site specific variation in dispersal.

## Model selection

We ranked models using the (Quasi-) Akaike’s information criterion corrected for small sample size ((Q)AICc; Burnham and Anderson 2002). We considered models that were within  $\Delta(Q)AICc \leq 2$  as the best models. In the capture–recapture analysis, we accounted for model selection uncertainty by calculating model averaged survival estimates (Burnham and Anderson 2002). In the dispersal analysis, we discarded models that were more complex versions of the model with the lowest AIC (i.e. had additional parameters that are likely to be uninformative; Richards et al. 2011). This selection procedure resulted in a singular, best model.

## Probability of breeding dispersal back to natal site

For natal dispersers that dispersed again as adults, we calculated the probability of returning to their natal patch and compared this to an expected distribution under random breeding dispersal. When calculating the expected distribution, we assumed that dispersal is random with respect to the available space in

each patch, because it is not possible to formally count the number of possible territories (Pakanen et al. 2017). Indeed, dunlins are not strictly territorial and may breed close to each other. We used the size (ha) of the breeding patches to calculate the proportion of breeding habitat that each specific patch constituted of the total breeding habitat in the population. For each breeding dispersal event considered, the total available breeding habitat was calculated excluding the site from which the disperser originated. We then generated a random number between 0 and 1. If the random number was within the proportion of habitat that the natal patch constituted out of the total habitat for this dispersal event, the individual was considered to have dispersed back to its natal site. For example, if the natal patch comprised 20% of total available habitat, the individual was considered to have dispersed back to the natal site if the random number was 0.2 or lower. If the random number was larger than 0.2, the individual was considered to have dispersed elsewhere. We included only the first breeding dispersal event per individual. Random numbers were drawn 1000 times to calculate the expected distribution of the random probability to return to the natal patch, its mean and 95% confidence interval. We then examined whether the observed value fell within the confidence interval of the expected distribution.

## Results

The data included 239 recruits (94 natal dispersing and 145 non-dispersers or philopatric individuals; by population: Finland: 151 recruits; Sweden 88 recruits; see the Supporting information for further details on the data). The capture–recapture data included 873 encounters from these recruits (Finland 485, Sweden 388). These accumulated 632 observations of recruits after their first breeding event were used when analysing breeding dispersal (Finland 336, Sweden 296; see the Supporting information for further details on the data) from 178 different individuals (Finland 107, Sweden 71).

### Adult survival

The survival model retained, i.e. with the lowest QAICc, included only sex (Supporting information). Survival was higher in males (0.81; 95% CI 0.77–0.84) than in females (0.75, 95% CI 0.71–0.80) (Fig. 2). Models within 2 QAICc units also included time since marking and population, but their effects remained weak (i.e. 95% CI of partial regression coefficients included 0 for time since marking from model A2: 0.296, 95% CI –0.130, 0.721; partial regression coefficient for Population from model A6: –0.077, 95% CI –0.423, 0.269; Supporting information). Dispersal status was not retained in the best models (Supporting information), indicating a lack of difference in adult survival between natal dispersing and non-dispersing individuals (Fig. 2; there was also no support for interactions between natal dispersal status and sex: Supporting information).

Recapture probability differed between natal dispersers and non-dispersers, but this difference was not the same in

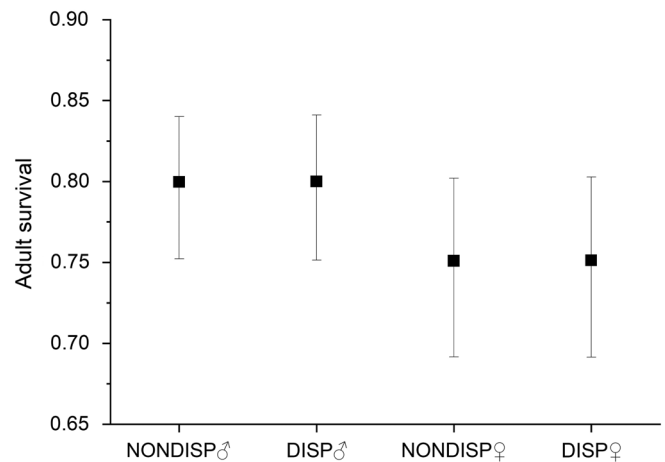


Figure 2. Adult survival probabilities of southern dunlin (and their 95% CI) according to natal dispersal status (NONDISP: non-dispersers and DISP: dispersers) and sex estimated for individuals recaptured at least once (time since marking class 2) that did not carry a geolocator.

both populations (interaction between dispersal status and population was retained in the best model for recapture probabilities: Table 2). In Finland, natal dispersing individuals had a lower recapture probability compared to non-dispersing individuals (recapture probability  $\pm$  SE in males: dispersing individual:  $0.861 \pm 0.037$ ; non-dispersing individual:  $0.932 \pm 0.022$ ), whereas the opposite seemed to be true in Sweden (dispersing male  $0.976 \pm 0.018$ ; non-dispersing male:  $0.923 \pm 0.021$ ). Recapture probabilities tended to be higher for males than females (Table 2).

### Breeding dispersal

The model with the lowest AICc indicated that breeding dispersal probability differed between natal dispersers and non-dispersers, but this difference depended on sex (interaction

Table 2. Model results for apparent adult survival ( $\Phi$ ) and recapture probabilities ( $p$ ) of southern dunlin. Parameter estimates are from the best model in Supporting information including additive (+) and interactive (: ) effects of the study population (Population), sex (Sex), dispersal status (Status) and geolocator attachment (Geolocator, yes or no).

Parameter	Coefficient	SE	–95% CI	+95% CI
<b>Survival probabilities</b>				
Intercept	1.121	0.123	0.879	1.363
Sex (male)	0.319	0.168	–0.010	0.647
Geolocator (geolocator)	–0.839	0.285	–1.398	–0.280
<b>Recapture probabilities</b>				
Intercept	3.195	0.757	1.711	4.679
Population (Finland)	–1.869	0.783	–3.404	–0.334
Sex (male)	0.506	0.311	–0.103	1.116
Status (philopatric)	–1.201	0.791	–2.750	0.349
Pop:Status	2.000	0.888	0.259	3.740

sex by natal dispersal status; Supporting information). Among females, natal dispersers were more likely to disperse than non-dispersers as adults, while no such difference was observed for males (Fig. 3, Table 3). Breeding dispersal probabilities of females that did not disperse as juveniles (non-dispersing) was low and similar to that of males (Fig. 3, Table 3). As expected, breeding dispersal probability was higher following breeding failure (i.e. nest did not hatch) compared to successful breeding (Fig. 3, Table 3; no support for an interaction between success and dispersal status or between success and sex: Supporting information). We found no difference in breeding dispersal probability between populations (Finland versus Sweden) even though more breeding dispersal observations were made in the Finnish population (23 breeding dispersal events out of a total of 336 observations, i.e. 6.8%) compared to the Swedish population (8 breeding dispersal events out of a total of 296 observations, i.e. 2.7%).

Among natal dispersers that dispersed again as breeders, over half of the breeding dispersal events (57%, i.e. 12 out of a total of 21 events) occurred back to the natal patch. This was higher than the expected probability under random breeding dispersal with respect to breeding habitat availability (i.e. relative size of the natal patch) which was 0.33 (95% CI 0.14–0.52; Fig. 4).

## Discussion

Dispersal is often assumed to entail survival costs. Here, we show that natal dispersal is not related to subsequent survival after first breeding in two populations of a long-distance migratory shorebird. Our results are thus in line with the view that mortality costs of dispersal are rare after first breeding. Hence, any mortality costs must occur essentially during the movement and settlement phases of dispersal (Devillard

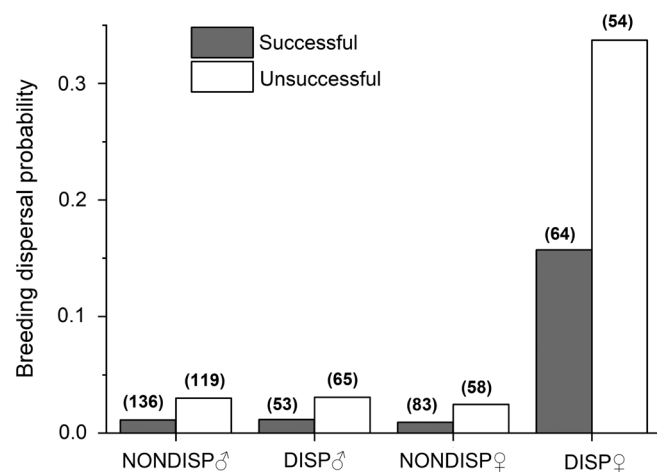


Figure 3. Between-patch breeding dispersal probabilities of southern dunlins according to natal dispersal status (NONDISP: non-dispersers and DISP: dispersers) and sex for successful (nest hatched) and unsuccessful (nest did not hatch) individuals as predicted by the best model (Table 3). The numbers indicate sample sizes.

Table 3. Analyses of between-patch breeding dispersal probabilities of the southern dunlin. Parameter coefficients and their 95% confidence intervals from a generalized linear mixed model (GLMM, binomial distribution, logit link). Statistically significant variables (95% CI excluding zero) in bold. Breeding dispersal was explained by fixed factors: Sex= male versus female, Status= natal dispersal status (natal dispersing individual versus non-dispersing individual), Success= previous breeding success. Random factors: ID= individual, Site= breeding site. See listing of all models in the Supporting information.

Parameter	Coefficient	SE	-95% CI	+95% CI
Intercept	-3.675	1.283	-1.161	-6.189
Sex(male)	0.196	1.249	2.644	-2.253
<b>Status(disperser)</b>	<b>2.999</b>	<b>1.194</b>	<b>0.659</b>	<b>5.339</b>
<b>Success(hatched)</b>	<b>-1.004</b>	<b>0.507</b>	<b>-0.011</b>	<b>-1.996</b>
<b>Sex:Status</b>	<b>-2.969</b>	<b>1.478</b>	<b>-0.072</b>	<b>-5.866</b>
Random factor	Variance	N (obs)	N (ID)	
ID	1.171	632	178	
Site	2.090		15	

and Bray 2009, Bonte et al. 2012, Hardouin et al. 2012, Waser et al. 2013, Pakanen et al. 2016b). Our results contrast with previous studies showing lower survival of natal dispersing individuals after first breeding (Bélichon et al. 1996, Doligez and Pärt 2008). Yet, out of 34 studies comparing adult survival between dispersers and non-dispersers (Supporting information), 12 (35%) found higher adult survival in philopatric (non-dispersing) individuals compared to dispersing individuals, while most (19 studies, 56%) found no differences according to dispersal status (Bélichon et al. 1996, Doligez and Pärt 2008, Supporting information). Our dunlin study is thus in line with the most common pattern.

Any dispersal costs in terms of survival should not be linked to direct energy costs of movement, since natal dispersal occurred within 2–80 km, a range of distance far below the yearly migratory movement of dunlins (Pakanen et al.

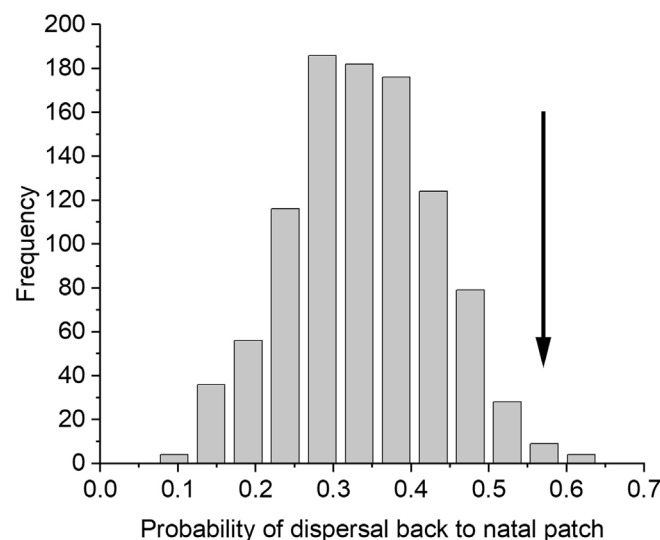


Figure 4. Expected (grey bars) and observed (arrow) breeding dispersal probability back to the natal patch for natal dispersers. Expected values were calculated by assuming random movement within available breeding habitat for each population.

2017, 2018). Potential survival costs within observed natal dispersal distances may result from increased energy expenditure and stress during the movement phase (Yoder et al. 2004, Bonte et al. 2012), selection of poorer territories and lower familiarity with the environment, and knowledge about the availability of resources such as food and roosting or breeding sites safe from predators (Pärt 1994, Brown et al. 2008, Piper 2011). In the present study, we detected no such long-term (i.e. adult) survival costs of natal dispersal. It is possible that breeding habitats in our dunlin populations are homogenous in terms of survival prospects (Oro et al. 2011). In particular, both dispersing and non-dispersing individuals breeding within a patch simultaneously share the same open shoreline habitats for foraging and may therefore also be under similar predation risk. Survival costs could be more pronounced after long-distance dispersal movements over hundreds of kilometers, which may result in incompatible phenologies (Burger et al. 2013) or a lack of other adaptations that are crucial for local survival (Hansson et al. 2004, Postma and van Noordwijk 2005). Such very long-distance dispersal events, however, remain rare; possibly as a result of counter-selection. In our case, this may have led to the nearly complete isolation of populations that can be considered closed, with no exchanges with other populations.

Importantly, we found that the breeding dispersal probability of female dunlins was higher among natal dispersing individuals than non-dispersing individuals, whereas breeding dispersal was rare among males in both groups. A female bias in individual consistency in dispersal is in line with many previous studies that investigated within-individual consistency in dispersal (Table 1), but also with the general sex-biased dispersal (Paradis et al. 1998, Trochet et al. 2016). In the southern dunlin, for example, females disperse longer distances especially after divorce (Flodin and Blomqvist 2012) whereas males are site faithful, most likely because they benefit from prior territory ownership (Oring and Lank 1984).

The within-individual consistency observed may partly reflect a genetic basis for dispersal (Saastamoinen et al. 2018). Dispersal is usually a response to a change in the environment (Clobert et al. 2008), and dispersing individuals may be characterized by more explorative phenotypes that are also more sensitive to environmental cues (Clobert et al. 2001, 2009, Doligez and Pärt 2008, Doligez et al. 2009, Cote et al. 2010, Charmantier et al. 2011, Pakanen et al. 2011a, Korsten et al. 2013). However, natal dispersing individuals had no stronger dispersal response to reproductive failure than non-dispersing individuals, which is perhaps the most important cue for breeding dispersal among birds (Doligez et al. 1999, Pakanen et al. 2011a). Lagrange et al. (2017) reported similar results in female tree swallows *Tachycineta bicolor*, which showed higher dispersal probabilities had they dispersed before, while breeding success affected dispersal of both previously dispersing and non-dispersing birds in a similar way. In our study populations, breeding dispersal was nevertheless very rare among females that did not disperse as juveniles (1 out of 141), and the difference in breeding dispersal propensity between unsuccessful and successful individuals was also

low (Fig. 3). Such a strong breeding patch fidelity suggests high reproductive benefits of returning to the same site to breed (e.g. due to familiarity with the site, mate fidelity or timing of breeding) or low benefits from breeding dispersal (Gerber et al. 2019).

Natal dispersing individuals that dispersed again as adults more often than random returned to their natal meadow, suggesting that within-individual consistency partly represents ‘delayed natal philopatry’. This is in line with previous studies on colonial breeders (Balkiz et al. 2010, Péron et al. 2010). Natal dispersers still have access to information about their natal site, where they were successfully raised, and this could also work as strong incentive to settle in that patch again (Pärt 1991). In the southern dunlin, the relatively short breeding season constrains breeding via lowered juvenile survival and renesting probability as the season progresses (Pakanen et al. 2014, 2016a), and may leave little time for movement, patch sampling and mating. Hence, previous experience from multiple sites may allow natal dispersers to be better informed about patch quality and thus more flexible in habitat selection, and consequently they could more easily disperse as adults compared to those that remained philopatric as juveniles.

While still relatively few studies have examined within-individual consistency in dispersal (Table 1, Doligez and Pärt 2008), most studies found evidence that natal dispersing juveniles were more likely to disperse again as adults (Table 1). Here, we show that within-individual consistency can occur even in species that are generally considered to be site faithful as adults, such as the southern dunlin (Soikkeli 1970, Thorup 1999, Flodin and Blomqvist 2012). Therefore, most studies addressing the survival costs of dispersal are vulnerable to the permanent emigration of dispersing individuals unless the entire population is monitored (Doligez and Pärt 2008). This can be particularly problematic when comparing survival of immigrants and philopatric individuals because delayed natal philopatry can bias the survival of immigrants whose natal sites are not monitored. More generally, this also implies that survival estimates can be biased in populations that receive immigrants (Chernetsov et al. 2009, Becker et al. 2018), and that survival estimated from individuals born within the study area should be less prone to biases due to permanent emigration (Pakanen et al. 2015b).

So far, some of the studies examining costs and benefits of dispersal have concluded that dispersing individuals or immigrants were, compared to non-dispersing/philopatric individuals, more likely to permanently emigrate from the study population as a consequence of breeding dispersal (Verhulst and Van Eck 1996, Chernetsov et al. 2009, Pakanen et al. 2011a), while many others have suggested that such permanent emigration of dispersing individuals or immigrants is likely to be rare (Pärn et al. 2009, Barbraud and Delord 2020, Luna et al. 2020). Only one study showed that lower survival of dispersing individuals was not the result of permanent emigration (Serrano and Tella 2012). Studies based on life-time reproductive success as a fitness measure have often found sex-specific costs of dispersal but rarely addressed the effect of



permanent emigration of adults (Gienapp and Merilä 2011, Tarwater and Beissinger 2012, van Overveld et al. 2015, Green and Hatchwell 2018). Biases in fitness estimates due to within-individual consistency in dispersal could be overcome by studying isolated populations that can be monitored almost entirely such as our study populations or closed island populations (Nevoux et al. 2013), but such opportunities are rare and dispersal is a key population parameter in most populations that are open. Open study populations that occur within a larger distribution range of the study species can be problematic. The level of underestimation of survival estimates caused by within-individual consistency in such populations will depend on the interplay between the relative size of the study area in comparison to dispersal distances (shaping the probability to disperse out of the study area), and factors that determine breeding dispersal probability of immigrants out of the area. Delayed natal philopatry may occur in all populations. However, it may be more likely in populations that have a patchy structure (such as in our study, Balkiz et al. 2010, Péron et al. 2010) because possibilities for movement will be more constrained by the spatial configuration of breeding habitat than in populations with more continuous breeding habitats. Efforts to estimate within-individual consistency in dispersal and its potential impact on fitness estimates are needed as it remains too often ignored.

*Acknowledgements* – We thank all the people that helped in the field. We thank Wendt Müller and Simeon Lisovski for valuable comments that improved the manuscript.

*Funding* – The Finnish study was funded by the Academy of Finland (128384, KK and 278759, VMP), The Finnish Foundation for Nature Conservation (VMP), the Faculty of Science, University of Oulu, Finland (NR), Finnish Cultural Foundation (VMP), the Finnish Environment Institute (KK), the Emil Aaltonen Foundation (NR and VMP), the Kone Foundation (VMP), the University of Oulu Scholarship Foundation (NR) and the Tauno Tönnig Foundation (VMP). The Swedish study was supported by Formas (21.5/2002-1037, 217-2005-817 and 215-2009-463, DB), funding from Oscar och Lili Lamms Minne (FO2009-0007 and FO2012-0039, AP), Stiftelsen Olle Engkvist Byggmästare (DB), Carl Tryggers Stiftelse (CTS 09:294, AP), Stiftelsen Lars Hiertas Minne (AP), as well as by the County Administration Board of Halland, Sweden.

## Author contributions

**Veli-Matti Pakanen:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Writing – original draft (lead). **Kari Koivula:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Blandine Doligez:** Formal analysis (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Lars-Åke Flodin:** Resources (equal); Writing – review and editing (equal). **Angela Pauliny:** Data curation (equal); Investigation (equal); Resources (equal);

Writing – review and editing (equal). **Nelli Rönkä:** Data curation (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Donald Blomqvist:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.b2rbnjsj2>> (Pakanen et al. 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Aragón, P. et al. 2006. Dispersal status dependent response to the social environment in the common lizard, *Lacerta vivipara*. – *Funct. Ecol.* 20: 900–907.
- Balkiz, Ö. et al. 2010. Experience-dependent natal philopatry of breeding greater flamingos. – *J. Anim. Ecol.* 79: 1045–1056.
- Barbraud, C. and Delord, K. 2020. Selection against immigrants in wild seabird populations. – *Ecol. Lett.* 24: 84–93.
- Bates, D. et al. 2015. Fitting linear mixed effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Becker, A. J. et al. 2018. Annual survival and breeding dispersal of a migratory passerine, the scissor-tailed flycatcher. – *J. Field Ornithol.* 89: 22–36.
- Bélíchon, S. et al. 1996. Are there differences in fitness components between philopatric and dispersing individuals? – *Acta Oecol.* 17: 503–517.
- Bize, P. et al. 2017. Negative phenotypic and genetic correlation between natal dispersal propensity and nest-defence behaviour in a wild bird. – *Biol. Lett.* 13: 20170236.
- Blomqvist, D. et al. 2010. Trapped in the extinction vortex? Strong genetic effects in a declining vertebrate population. – *BMC Evol. Biol.* 10: 33.
- Bonte, D. et al. 2012. Costs of dispersal. – *Biol. Rev.* 87: 290–312.
- Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biol. Rev.* 80: 205–225.
- Brown, C. R. et al. 2008. Familiarity with breeding habitat improves daily survival in colonial cliff swallows. – *Anim. Behav.* 76: 1201–1210.
- Burger, C. et al. 2013. Fitness consequences of northward dispersal as possible adaptation to climate change, using experimental translocation of a migratory passerine. – *PLoS One* 8: e83176.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Charmantier, A. et al. 2011. Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross. – *J. Evol. Biol.* 24: 1487–1496.
- Chernetsov, N. et al. 2009. Local survival rates of pied flycatchers *Ficedula hypoleuca* depend on their immigration status. – *Avian Ecol. Behav.* 16: 11–20.

- Clobert, J. et al. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. – *Biometrics* 50: 375–387.
- Clobert, J. et al. 2001. *Dispersal*. – Oxford Univ. Press.
- Clobert, J. et al. 2008. Evolution of dispersal. – In: Danchin, E. et al. (eds), *Behavioural ecology*. Oxford Univ. Press, pp. 125–147.
- Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecol. Lett.* 12: 197–209.
- Clobert, J. et al. 2012. *Dispersal ecology and evolution*. – Oxford Univ. Press.
- Cote, J. and Clobert, J. 2012. Dispersal syndromes in the common lizard: personality traits, information use and context-dependent dispersal decisions. – In: Clobert J et al. (eds), *Dispersal ecology and evolution*. Oxford Univ. Press, pp. 152–160.
- Cote, J. et al. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. – *Phil. Trans. R. Soc. B* 365: 4065–4076.
- Davidian, E. et al. 2016. Why do some males choose to breed at home when most other males disperse? – *Sci. Adv.* 2: e1501236.
- Denoël, M. et al. 2018. Dispersal and alternative breeding site fidelity strategies in an amphibian. – *Ecography* 41: 1543–1555.
- Devillard, S. and Bray, Y. 2009. Assessing the effect on survival of natal dispersal using multistate capture–recapture models. – *Ecology* 90: 2902–2912.
- Doligez, B. and Pärt, T. 2008. Estimating fitness consequences of dispersal: a road to ‘know-where’? Non-random dispersal and the underestimation of dispersers’ fitness. – *J. Anim. Ecol.* 77: 1199–1211.
- Doligez, B. et al. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. – *J. Anim. Ecol.* 68: 1193–1206.
- Doligez, B. et al. 2002. Costs of reproduction: assessing responses to brood size manipulation on life-history and behavioural traits using multi-state capture–recapture models. – *J. Appl. Stat.* 29: 407–423.
- Doligez, B. et al. 2009. ‘Heritability’ of dispersal propensity in a patchy population. – *Proc. R. Soc. B* 276: 2829–2836.
- Doligez, B. et al. 2012. Estimation and comparison of heritability and parent-offspring resemblance in dispersal probability from capture–recapture data using different methods: the collared flycatcher as a case study. – *J. Ornithol.* 152: 539–554.
- Edelaar, P. and Bolnick, D. I. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. – *Trends Ecol. Evol.* 27: 659–665.
- Flodin, L.-Å. and Blomqvist, D. 2012. Divorce and breeding dispersal in the dunlin *Calidris alpina*: support for the better option hypothesis? – *Behaviour* 149: 67–80.
- Forero, M. G. et al. 1999. Causes and consequences of territorial change and breeding dispersal distance in the black kite. – *Ecology* 80: 1298–1310.
- Gerber, B. D. et al. 2019. Extreme site fidelity as an optimal strategy in an unpredictable and homogeneous environment. – *Funct. Ecol.* 33: 1695–1707.
- Germain, M. et al. 2017a. Natal dispersers pay a lifetime cost to increased reproductive effort in a wild bird population. – *Proc. R. Soc. B* 284: 20162445.
- Germain, M. et al. 2017b. Lower settlement following a forced displacement experiment: nonbreeding as a dispersal cost in a wild bird? – *Anim. Behav.* 133: 109–121.
- Gienapp, P. and Merilä, J. 2011. Sex-specific fitness consequences of dispersal in Siberian jays. – *Behav. Ecol. Sociobiol.* 65: 131–140.
- Green, J. P. and Hatchwell, B. J. 2018. Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit *Aegithalos caudatus*. – *Proc. Natl Acad. Sci. USA* 115: 12011–12016.
- Greenwood, P. J. and Harvey, P. H. 1982. The natal and breeding dispersal of birds. – *Annu. Rev. Ecol. Syst.* 13: 1–21.
- Griffiths, R. et al. 1998. A DNA test to sex most birds. – *Mol. Ecol.* 7: 1071–1075.
- Hansson, B. et al. 2004. Lifetime fitness of short- and long-distance dispersing great reed warblers. – *Evolution* 58: 2546–2557.
- Hardouin, L. A. et al. 2012. Determinants and costs of natal dispersal in a lekking species. – *Oikos* 121: 804–812.
- Jönsson, P. E. 1991. Reproduction and survival in a declining population of the southern dunlin *Calidris alpina schinzii*. – *Wader Study Group Bull.* 61: 56–68.
- Korsten, P. et al. 2013. Genetic integration of local dispersal and exploratory behaviour in a wild bird. – *Nat. Commun.* 4: 2362.
- Lagrange, P. et al. 2017. Assessment of individual and conspecific reproductive success as determinants of breeding dispersal of female tree swallows: a capture–recapture approach. – *Ecol. Evol.* 7: 7334–7346.
- Lebreton, J.-D. et al. 1992. Modelling survival and testing biological hypothesis using marked animals: a unified approach with case studies. – *Ecol. Monogr.* 62: 67–118.
- Liebezeit, J. R. et al. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. – *Condor* 109: 32–47.
- Luna, Á. et al. 2020. Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls. – *PLoS One* 15: e0226089.
- Marshall, M. R. et al. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site – fidelity: study designs that may help. – *Anim. Biodiv. Conserv.* 27: 59–72.
- Martinig, A. R. et al. 2020. The new kid on the block: immigrant males win big whereas females pay fitness cost after dispersal. – *Ecol. Lett.* 23: 430–438.
- Montalvo, S. and Potti, J. 1992. Breeding dispersal in Spanish pied flycatchers *Ficedula hypoleuca*. – *Ornis Scand.* 23: 491–498.
- Nevoux, M. et al. 2013. The short- and long-term fitness consequences of natal dispersal in a wild bird population. – *Ecol. Lett.* 16: 438–445.
- Orell, M. et al. 1999. Immigration and gene flow in a northern willow tit *Parus montanus* population. – *J. Evol. Biol.* 12: 283–295.
- Oring, L. W. and Lank, D. B. 1984. Breeding area fidelity, natal philopatry and the social systems of sandpipers. – In: Burger, J. and Olla, B. L. (eds), *Shorebirds: breeding behavior and populations*. Plenum Press, pp. 125–147.
- Oro, D. et al. 2011. Comparing demographic parameters of philopatric and immigrant individuals in a long-lived bird adapted to unstable habitats. – *Oecologia* 165: 935–945.
- Pakanen, V.-M. et al. 2010. Impact of dispersal status on estimates of local population growth rates in a Temminck’s stint *Calidris temminckii* population. – *Oikos* 119: 1493–1503.
- Pakanen, V.-M. et al. 2011a. Breeding dispersal strategies following reproductive failure explain low apparent survival of immigrant Temminck’s stints. – *Oikos* 120: 615–622.
- Pakanen, V.-M. et al. 2011b. Nest predation and trampling as management risks in grazed coastal meadows. – *Biodivers. Conserv.* 20: 2057–2073.
- Pakanen, V.-M. et al. 2014. Informed reneesting decisions: the effect of nest predation risk. – *Oecologia* 174: 1159–1167.

- Pakanen, V.-M. et al. 2015a. No strong effects of leg-flagged geolocators on return rates or reproduction of a small long-distance migratory shorebird. – *Ornis Fenn.* 92: 101–111.
- Pakanen, V.-M. et al. 2015b. Estimating sex specific apparent survival and dispersal of little ringed plovers *Charadrius dubius*. – *Ornis Fenn.* 92: 172–186.
- Pakanen, V.-M. et al. 2016a. Grazed wet meadows are sink habitats for the southern dunlin *Calidris alpina schinzii* due to nest trampling by cattle. – *Ecol. Evol.* 6: 7176–7187.
- Pakanen, V.-M. et al. 2016b. Sex-specific mortality costs of dispersal during the settlement phase promote male philopatry in a resident passerine. – *Behav. Ecol. Sociobiol.* 70: 1727–1733.
- Pakanen, V.-M. et al. 2017. Between-patch natal dispersal propensity declines with increasing natal patch size and distance to other patches in two endangered southern dunlin *Calidris alpina schinzii* metapopulations. – *Ibis* 159: 611–622.
- Pakanen, V.-M. et al. 2018. Migration strategies of the Baltic dunlin: rapid jump migration in the autumn but slower skipping type spring migration. – *J. Avian Biol.* 49: e01513.
- Pakanen, V.-M. et al. 2020. Survival probability in a small shorebird decreases with the time an individual carries a tracking device. – *J. Avian Biol.* 51: e02555.
- Pakanen, V.-M. et al. 2021. Survival during the pre-fledging period rather than during post-fledging drives variation in local recruitment of an endangered migratory shorebird, the southern dunlin *Calidris alpina schinzii*. – *J. Ornithol.* 162: 119–124.
- Pakanen, V.-M. et al. 2022. Data from: Natal dispersal does not entail survival costs but is linked to breeding dispersal in a migratory shorebird, the southern dunlin *Calidris alpina schinzii*. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.b2rbnzs2j>>.
- Paradis, E. et al. 1998. Patterns of natal and breeding dispersal in birds. – *J. Anim. Ecol.* 67: 518–536.
- Pärn, H. et al. 2009. Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. – *J. Anim. Ecol.* 78: 1216–1225.
- Pärt, T. 1991. Philopatry pays: a comparison between collared flycatcher sisters. – *Am. Nat.* 138: 790–796.
- Pärt, T. 1994. Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. – *Anim. Behav.* 48: 401–409.
- Pärt, T. and Gustafsson, L. 1989. Breeding dispersal in the collared flycatcher *Ficedula albicollis*: possible causes and reproductive consequences. – *J. Anim. Ecol.* 58: 305–320.
- Pauliny, A. et al. 2008. Nest predation management: effects on reproductive success in endangered shorebirds. – *J. Wildl. Manage.* 72: 1579–1583.
- Péron, G. et al. 2010. Breeding dispersal in black-headed gull: the value of familiarity in a contrasted environment. – *J. Anim. Ecol.* 79: 317–326.
- Piper, W. H. 2011. Making habitat selection more ‘familiar’: a review. – *Behav. Ecol. Sociobiol.* 65: 1329–1351.
- Postma, E. and van Noordwijk, A. J. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. – *Nature* 433: 65–68.
- Richards, S. A. et al. 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. – *Behav. Ecol. Sociobiol.* 65: 77–89.
- Rönkä, R. et al. 2021. Genetic differentiation in an endangered and strongly philopatric, migrant shorebird. – *BMC Ecol. Evol.* 21: 125.
- Saastamoinen, M. et al. 2018. Genetics of dispersal. – *Biol. Rev.* 93: 574–599.
- Sanz-Aguilar, A. et al. 2009. Contrasting age-specific recruitment and survival at different spatial scales: a case study with the European storm petrel. – *Ecography* 32: 637–646.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. – *Methods Ecol. Evol.* 1: 103–113.
- Serrano, D. and Tella, J. L. 2012. Lifetime fitness correlates of natal dispersal distance in a colonial bird. – *J. Anim. Ecol.* 81: 97–107.
- Serrano, D. et al. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. – *J. Anim. Ecol.* 70: 568–578.
- Soikkeli, M. 1966. On the variation in bill and wing-length of the dunlin *Calidris alpina* in Europe. – *Bird Study* 13: 256–269.
- Soikkeli, M. 1970. Dispersal of dunlin *Calidris alpina* in relation to sites of birth and breeding. – *Ornis Fenn.* 47: 1–9.
- Switzer, P. V. 1997. Past reproductive success affects future habitat selection. – *Behav. Ecol. Sociobiol.* 40: 307–312.
- Tarwater, C. E. and Beissinger, S. R. 2012. Dispersal polymorphisms from natal phenotype– environment interactions have carry-over effects on lifetime reproductive success of a tropical parrot. – *Ecol. Lett.* 15:1218–1229.
- Taylor, C. M. et al. 2015. Using local dispersal data to reduce bias in apparent survival and mate fidelity. – *Condor* 117: 598–608.
- Thorup, O. 1999. Breeding dispersal and site-fidelity in dunlin *Calidris alpina* at Tipperne, Denmark. – *Dansk Ornitol. Foren. Tidsskr.* 93: 255–265.
- Thorup, O. et al. 2009. Migration and wintering of Baltic dunlins *Calidris alpina schinzii* with known breeding origin. – *Ardea* 97: 43–50.
- Trochet, A. et al. 2016. Evolution of sex-biased dispersal. – *Q. Rev. Biol.* 91: 297–320.
- van den Brink, V. et al. 2012. Melanic color-dependent antipredator behavior strategies in barn owl nestlings. – *Behav. Ecol.* 23: 473–480.
- van Overveld, T. et al. 2015. No evidence for correlational selection on exploratory behaviour and natal dispersal in the great tit. – *Evol. Ecol.* 29: 137–156.
- Waser, P. M. et al. 2013. Fitness consequences of dispersal: is leaving home the best of a bad lot? – *Ecology* 94: 1287–1295.
- Vasko, V. et al. 2011. Breeding dispersal of Eurasian kestrels *Falco tinnunculus* under temporally fluctuating food abundance. – *J. Avian Biol.* 42: 552–563.
- Verhulst, S. and Van Eck, H. M. 1996. Gene flow and immigration rate in an island population of great tits. – *J. Evol. Biol.* 9: 771–782.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: 120–139.
- White, G. C. et al. 2002. Advanced features of program MARK. – In: Fields, R. (ed.), Integrating people and wildlife for a sustainable future. Wildlife Society, pp. 368–377.
- Yoder, J. M. et al. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. – *Behav. Ecol.* 15: 469–476.