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
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 Bélichon 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 (Bélichon 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 constrains 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 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.
### 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.

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### 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 |     |      |          |         |                         |
| Calidris tataricus             | yes | IP   | Probability | ♂♂       | Pakanen et al. 2011a‡  |
| Chroicocephalus ridibundus     | yes | DP   | Probability | ♂♂       | Péron et al. 2010      |
| Phoenicopeterus roseus         | yes | DP   | Probability | ♂♂       | Balkiz et al. 2010b     |
| Ficedula albicollis            | yes | IP+DP| Probability | ♂         | Doligez et al. 1999, 2002|
| Parus major                    | yes | IP   | Probability | ♂         | Verhulst and Van Eck 1996|
| Falco naumanni                 | no  | IP   | Distance   | ♂         | Serrano and Tell 2012   |
| Ficedula albicollis            | yes | IP   | Distance   | ☀         | Pärt and Gustafsson 1989|
| Ficedula hypoleuca             | no  | IP   | Distance   | ☀         | Montalvo and Potti 1992 |
| Poecile montanus               | no  | IP   | Distance   | ☀         | Orell et al. 1999      |
| Poecile montanus               | no  | IP   | Distance   | ☀         | Pakanen et al. 2016b†   |
| Tyto alba                      | no  | IP   | Distance   | ☀         | van den Brink et al. 2012|
| (b) Within-individual consistency in breeding dispersal |     |      |          |         |                         |
| Falco naumanni                 | yes | DP   | Probability | ♂♂       | Serrano et al. 2001     |
| Milvus migrans                 | no  | DP   | Probability | ☀         | Forero et al. 1999      |
| Tachycineta bicolor            | yes | DP   | Probability | ☀         | Lagrange et al. (2017)  |
| Ficedula albicollis            | yes | DP   | Probability | ☀         | Doligez et al. 2012     |
| Milvus migrans                 | no  | IP   | Distance   | ☀         | Forero et al. 1999      |
| Falco tinnunculus              | yes | IP   | Distance   | ♂♂       | Vasko et al. 2011       |
| Falco naumanni                 | yes | IP   | Distance   | ♂♂       | Serrano et al. 2001     |
| Tyto alba                      | yes | IP   | Distance   | ♂♂       | van den Brink et al. 2012|

* Comparison of return rates of successful and unsuccessful birds in two populations (Oulu and Kokkola), † same effect for unexperienced breeders and experienced breeders, ‡ post-winter movement from wintering territories to nest sites.
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 renesting 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 (Φ) 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 geolocator from year 1 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 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 ± SE in males: dispersing individual: 0.861 ± 0.037; non-dispersing individual: 0.932 ± 0.022), whereas the opposite seemed to be true in Sweden (dispersing male 0.976 ± 0.018; non-dispersing male: 0.923 ± 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 (Φ) 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 |
|--------------------|-------------|-----|---------|---------|
| Survival probabilities |             |     |         |         |
| 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  |
| Recapture probabilities |            |     |         |         |
| 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 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. 2016b).

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    |
| Status(disperser) | 2.999   | 1.194| 0.659   | 5.339     |
| Success(hatched) | −1.004     | 0.507| −0.011  | −1.996    |
| Sex:Status      | −2.969      | 1.478| −0.072  | −5.866    |
| Random factor   |             |      |         |           |
| Variance ID     | 1.171       | 632  | 178     |           |
| Variance Site   | 2.090       | 15   |         |           |

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.

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.
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 (Oiring 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 migration (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.

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

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b2rbnzzs2> (Pakanen et al. 2022).

Supporting information

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

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