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Between-patch natal dispersal declines with increasing natal patch size and distance to other patches in the endangered Southern Dunlin *Calidris alpina schinzii*

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Natal dispersal has profound consequences for populations through the movement of individuals and genes. Habitat fragmentation reduces structural connectivity by decreasing patch size and increasing isolation, but understanding of how this impacts dispersal and the functional connectivity of landscapes is limited because many studies are constrained by the size of the study areas or sample sizes to accurately capture natal dispersal. We quantified natal dispersal probability and natal dispersal distances in a small migratory shorebird, the Southern Dunlin *Calidris alpina schinzii*, with data from two extensively monitored endangered metapopulations breeding in Sweden and Finland. In both metapopulations philopatry was strong, with individuals returning to or close to their natal patches more often than expected by chance, consistent with the patchy distribution of their breeding habitat. Dispersal probabilities were lower and dispersal distances were shorter in Sweden. These results provide a plausible explanation for the observed inbreeding and population decline of the Swedish population. The differences between Sweden and Finland were explained by patch-specific differences. Between-patch dispersal decreased with increasing natal patch size and distance to other patches. Our results suggest that reduced connectivity reduces movements of the philopatric Dunlin, making it vulnerable to the effects of inbreeding. Increasing connectivity between patches should thus be one of the main goals when planning future management. This may be facilitated by creating a network of suitably sized patches (20–100 ha), no more than 20 km apart from each other, from existing active patches that may work as stepping stones for movement, and by increasing nest success and prefledging survival in small patches.

Keywords: fragmentation, functional connectivity, gene flow, philopatry, wet-grassland.

Natal dispersal, defined as the movement from the site of birth to the site of first reproduction, is an essential part of life history among most taxa (Clobert *et al.* 2012). This behaviour is generally sex-biased and functions to avoid inbreeding, kin-competition and poor environmental conditions (Bowler & Benton 2005). Dispersal has important consequences at a population level, as it leads to interchange of individuals and genes between local populations. Gene flow shapes the genetic composition of populations by reducing genetic

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differentiation and maintaining genetic diversity mainly by counteracting the effects of drift and inbreeding (Frankham 2015). In the current context of human-induced environmental change, the process of habitat fragmentation has profoundly affected landscapes (Haddad *et al.* 2015). Fragmentation reduces the structural connectivity of a landscape by affecting patch size and the degree of patch isolation (distance between patches), factors that affect between-patch movement of individuals and hence functional connectivity (Hanski 1998, Moilanen & Nieminen 2002, Calabrese & Fagan 2004, Baguette & Van Dyck 2007, Kindlmann & Burel 2008). Increased isolation reduces movement by making it difficult to find or access other patches (Moore *et al.* 2008) but dispersal probability may increase with decreasing patch size (Bowler & Benton 2005).

The behaviour of animals within a landscape eventually determines how a reduction in structural landscape connectivity caused by fragmentation affects the functional connectivity of that landscape (Calabrese & Fagan 2004, Bélisle 2005, Kindlmann & Burel 2008). Thus, the effects may differ between taxa and life history strategies (Peacock & Smith 1997, Cushman 2006, Callens *et al.* 2011, Garrard *et al.* 2012). In birds, dispersal is less restricted in migratory than in resident species (Weatherhead & Forbes 1994, Paradis *et al.* 1998, Ceresa *et al.* 2015), but fragmented habitats may represent barriers to breeding dispersal of migratory birds even though they do not constrain their movement during migration (Lindsay *et al.* 2008). Hence, the level of structural connectivity may explain why among conspecific populations, some show high natal philopatry whereas others do not (Weatherhead & Forbes 1994, Hansson *et al.* 2002). By studying the dispersal patterns of a species, we can better understand the functional connectivity of a landscape and possibly even predict the movement of individuals and their responses to changes in the structural landscape, which can aid population management and the conservation of biodiversity (Calabrese & Fagan 2004, Van Houtan *et al.* 2010).

Unfortunately, many dispersal studies are limited by either the size of the study area or the sample size needed to accurately capture the natal dispersal distributions of a given species (Koenig *et al.* 1996). Without sufficient data, it is difficult to make generalizations about dispersal distributions, or to assess how reduced structural connectivity between breeding habitats might affect dispersal and ultimately gene flow. Here, we use two long-term datasets to quantify natal dispersal behaviour (sex-specific dispersal probabilities and distances) of the Southern Dunlin *Calidris alpina schinzii* (hereafter Dunlin), a small, long-distance migratory shorebird.

The Baltic population of the Dunlin breeds on pastures and mowed coastal meadows where it is a habitat specialist, confined to the grassland patches that have shorter grass (Thorup 1998). This species was common and widespread across the Baltic region in the beginning of the 20th century (Thorup 1997). Historically, the breeding habitats of the Dunlin were fairly continuous because of the widespread use of traditional farming practices, including maintenance of coastal meadows and pastures. Such environmental predictability selects for site fidelity (Ronce 2007), a phenomenon that is especially strong in adult Dunlins (Soikkeli 1970, Jackson 1994, Thorup 1999, Flodin & Blomqvist 2012). During the last century, these connected habitat systems have been fragmented due to drainage, eutrophication and other agricultural changes that have led to overgrowth of vegetation (Soikkeli 1967, Soikkeli & Salo 1979, Thorup 1997). As a result, suitable habitat can now only be found almost exclusively on pastures, which are clearly defined patches within an unsuitable habitat matrix. During this process of habitat loss and fragmentation, the Baltic Dunlin population declined severely and became one of the most endangered wader populations in Europe (Thorup 2006). As some populations along the Baltic Sea suffer from inbreeding (Blomqvist *et al.* 2010) and many of them show excess homozygosity (Rönkä 2016), it seems plausible that movement of individuals has become more restricted over time. However, previous information on natal dispersal of the Dunlin is limited by small study areas and small sample sizes (Soikkeli 1970, Jackson 1994), and nothing is known about how structural connectivity affects natal dispersal.

We studied natal dispersal in the Dunlin using data from two extensive individual-based studies that cover the entire metapopulations on the west coast of Sweden (Pauliny *et al.* 2008, Blomqvist *et al.* 2010, Flodin & Blomqvist 2012) and on the coast of the Bothnian Bay in Finland (Pakanen *et al.* 2011, 2014, 2016; Fig. 1). These populations are geographically widely separated from the other

Dunlins in the Baltic region (the Swedish population by 200 km, the Finnish population by 400 km; Fig. 1), and movement of individuals from these populations to other regions of the Baltic Sea, or vice versa, does not occur or is minimal (Blomqvist *et al.* 2010, Pakanen *et al.* 2016). In contrast to many previous studies of dispersal behaviour, we therefore were able to cover nearly all suitable habitat (in total 15 breeding patches covering *c.* 1100 ha) for our study populations and to mark nearly all locally born individuals and follow their breeding histories closely (in total 222 individuals).

We predicted that the patchy structure of the landscape reduces natal dispersal in the Dunlin. We thus assessed whether Dunlins are more philopatric than expected by chance given available habitat in other patches, assessed whether dispersal probability is linked to the size of the natal patch and the mean distance from the natal patch to other patches. Importantly, the Swedish population is closed and suffers from inbreeding (Blomqvist *et al.* 2010), whereas the Finnish population receives immigrants and does not show strong signals of inbreeding depression. For example, hatching rate of eggs and juvenile survival are both relatively high (Pakanen *et al.* 2016). Inbreeding depression in the Swedish population suggests that inbreeding avoidance mechanisms such as dispersal by one or both of the sexes are rare and/or insufficient to counteract losses of genetic variation. We therefore predicted that natal dispersal probability is lower in the Swedish population, and that dispersal distances are shorter and not sex-biased. Consequently, we assessed whether sex-specific dispersal probabilities and dispersal distributions differ between these metapopulations, and whether the structural connectivity of their landscapes is different.

METHODS

Data collection

Data were collected between 1985 and 2015 on the west coast of Sweden (between 57°55′N, 11°47′E and 57°7′N, 12°14′E) and between 2002 and 2016 in the Bothnian Bay of Finland (*c.* 64°50′N, 25°00′E; Fig. 1). The study areas included patches that have regularly held breeding Dunlins, and our sampling included the majority of patches and breeding pairs within these metapopulations. In both Sweden and Finland, we excluded a few patches that held only an occasional breeding

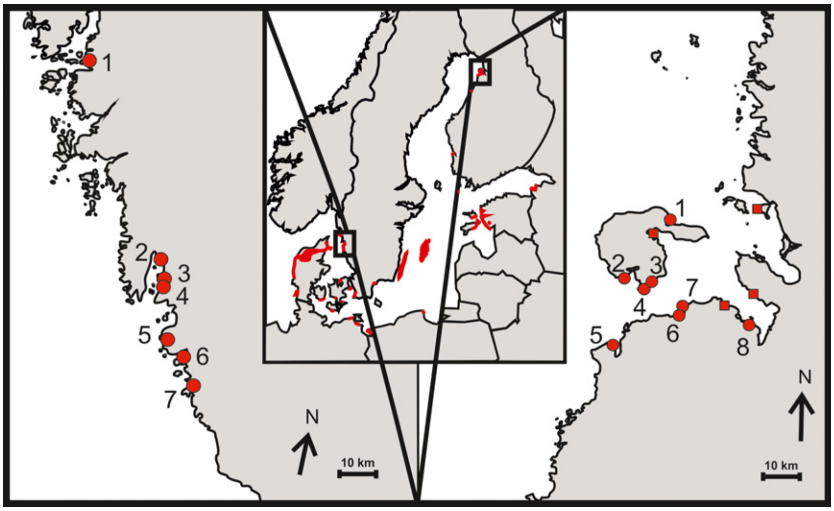

Figure 1. Study areas on the west coast of Sweden and the coast of Bothnian Bay, Finland. Locations of breeding patches are marked with dots, characteristics of patches are described in Table 1 (Sweden: 1 = Ödsmåls kile, 2 = Torkelstorp, 3 = Tjolöholm, 4 = Ölmevalla, 5 = Båtafjorden, 6 = Klosterfjorden, 7 = Getterön; Finland: 1 = Pökönnokka, 2 = Kuivasäikkä, 3 = Tömppä, 4 = Isomatala, 5 = Tauvo, 6 = Savilahti, 7 = Säärennokka, 8 = Pitkänokka). The Fennoscandian map shows the distribution of Baltic Dunlin breeding range according to Helcom (2013), The Swedish Species Information Centre (2015) and our own observations. The breeding distribution in Sweden indicates areas that have regularly held breeding Baltic Dunlins from the 1990s onwards. Squares show locations of four meadows in the Finnish metapopulation that have harboured one breeding pair of Dunlin during the study but held no breeding Dunlin most of the time.

record of a single pair (and which therefore held no breeding Dunlins in most years).

Because both studies aimed to collect meticulous individual-based data on reproduction, survival and movement, fieldwork that included ringing and capturing of individuals was done with as constant and as intensive effort as possible in all patches. Each patch was visited multiple times during the breeding season, but the smaller patches were visited less often than larger ones. Recapture probabilities of adults were similar and very high in both metapopulations (Sweden: 0.92, Finland: 0.92; V.-M. Pakanen, K. Koivula, L.-Å .Flodin, M. Larsson, A. Pauliny, N. Rönkä & D. Blomqvist unpubl. data), suggesting good coverage of the breeding populations. Fieldwork followed routines that started with territory searching early in the season (Sweden: early April, Finland: late April) and continued with nest searching until late in the season (Sweden: June, Finland: July). We recorded nest locations either on field maps or with GPS devices. We followed nest fates until nest failure or hatching, and ringed chicks with numbered steel rings (and colour rings in Sweden). Data on natal dispersal accumulated when these chicks recruited back to the breeding populations as adults. All adults were caught with mist-nests or cage traps when they were incubating eggs or brooding chicks (adults brooding freshly hatched chicks were only captured with cage traps in Sweden). Adults were sexed using morphological measurements and with DNA using the CHD gene (Griffiths *et al.* 1998). More detailed field methods can be found elsewhere (Pauliny *et al.* 2008, Blomqvist *et al.* 2010, Pakanen *et al.* 2011, 2014, 2016, Flodin & Blomqvist 2012).

We measured metapopulation- and patch-specific attributes that describe the structural landscape. For each patch, we calculated size (ha) and mean distance to other patches (km). For each metapopulation we calculated the range and mean of patch sizes and mean distances between patches. Mean distance to other patches is a better description of connectivity than the nearest neighbour distance because it does not ignore other patches (Moilanen & Nieminen 2002). Patch sizes were approximated based on the outlines of pastures and/or the suitable habitat for Dunlin. For example, large areas of Common Reed *Phragmites australis* within pastures were not included in the size estimates. Distances between patches were calculated as the distance between the mid-points of each patch.

Data analysis

We defined natal dispersal as movement from the natal nest to some other location (either within natal patches or to other patches) to breed for the first time. We examined natal dispersal in terms of (1) the probability to disperse to another patch, (2) dispersal distances throughout the metapopulation and (3) within-patch dispersal distances. Our data included 222 natal dispersal observations (Finland 144, Sweden 78).

Between-patch natal dispersal probability was analysed with two *a priori* sets of generalized linear models (GLMs, binomial errors and logit link) in R 3.0.3 (R Development Core Team 2014). We first applied a set of models including sex and metapopulation (Sweden vs. Finland) and their interaction. After this, we added the mean distance from the natal patch to other patches, the size of the natal patch and relevant interactions between factors. We ranked models with the Akaike information criterion corrected for small sample size (AICc). We considered models with ΔAICc ≤ 2 as the best models with equal contribution, and considered model selection uncertainty by averaging the coefficients with the function 'model.avg' in the package MuMIn (Bartón 2011).

We measured natal dispersal distance as the Euclidian distance between the natal nest and an individual's first nest. We used GLMs (gamma errors) to examine the effects of sex, metapopulation and their interaction on natal dispersal distance using all data. The results from these models should be treated with caution because the residuals deviated slightly from the normal distribution (see Supporting Information Fig. S1). In addition, we used a Wilcoxon rank-sum test to examine sex and metapopulation differences in dispersal distances, separately for dispersing and philopatric birds (those that recruited back to their natal patch).

Finally, we generated expected dispersal distributions based on the available area of each patch (as a proxy for the number of territories), assuming that an individual is free to settle anywhere in the patch. We first calculated the proportional size of each patch relative to the total area of all patches. Using all of the observed recruits originating from patch *i*, we then calculated the expected number of individuals dispersing from patch *i* to each of the available patches by multiplying the number of recruits originating from patch *i* with the relative area of each available patch. For each combination of between-patch movement, the expected numbers of individuals were assigned to have dispersed the distance between these given patches. For philopatric individuals, we assigned the mean observed dispersal distance within their natal patch. This method is a simplified version of a bootstrapping approach where the expected distribution is calculated by giving each observed recruit a chance to disperse to any territory within the landscape (Ortego *et al.* 2011). However, as Dunlins do not have strict territories, and because defining suitable territories is difficult, we were unable to apply this method. Using the generated expected distribution, we assessed whether the observed number of individuals that remained at or close to their natal patch (i.e. within 3 km, a distance class that includes all philopatric individuals of large sites) differed from the expected number of individuals by comparing these frequencies with a chi-square goodness-of-fit test.

RESULTS

Patch size ranged from 16 to 272 ha and did not differ between Sweden (mean 83.6 ha ± 28.5 se) and Finland (mean 64.7 ha ± 30.5 se, $W = 35$, $P = 0.451$; Table 1). The between-patch distance was larger in Sweden (32.6 km, 5.95 se, range 2.5–90.0) than in Finland (15.7 km, 1.47 se, range 2.1–29.8; mean distance log-transformed, $t_{47} = 2.00$, $P = 0.026$).

Natal philopatry was high in both metapopulations and sexes (Fig. 2). However, natal dispersal probability between patches was higher in Finland than in Sweden (Table 2a, Fig. 2). There was no interaction between sex and metapopulation (Table 2a). Dispersal probability declined with increasing natal patch size and increasing mean distance to other patches (Table 2b, Fig. 3). When the statistical model included these parameters, the difference between Finland and Sweden was no longer significant (Table 2b).

Natal dispersal distances were larger in Finland than in Sweden (Table 2c, Fig. 4). There was no difference in natal dispersal distance between the sexes, and no indication of an interaction between sex and metapopulation (Table 2c). A larger than expected proportion of individuals returned within 3 km among females in Sweden ($\chi^2 = 44.01$, df = 1, $P < 0.001$; Fig. 4a), males in Sweden ($\chi^2 = 54.55$, df = 1, $P < 0.001$; Fig. 4b) and males in Finland ($\chi^2 = 18.87$, df = 1, $P < 0.001$; Fig. 4d),

Table 1. Characteristics of the breeding patches where Baltic Dunlins were sampled.

Location	Dist near	Dist all	Pairs	Size	Recruits	Disp prob
Sweden (mean):	12.39	32.62	–	83.6	12.6	–
1. Ödsmåls kile	55.80	71.13	0–4	35.9	5	0.00
2. Torkelstorp	3.50	24.61	0–7	18	4	0.50
3. Tjolöholm	2.50	22.52	0–3	98	3	1.00
4. Ölmevalla	2.50	22.41	0–3	30	2	1.00
5. Båtafjorden	6.80	25.75	2–13	188	47	0.23
6. Klosterfjorden	6.80	27.45	0–3	29	1	0.00
7. Getterön	8.80	34.45	2–15	186	26	0.23
Finland (mean):	7.13	15.72	–	64.7	18	–
1. Pökönnokka	13.92	20.38	1–4	20.6	4	0.50
2. Kuivasäikkä	5.24	14.51	1–2	21	3	0.67
3. Tömppä	2.12	11.35	5–12	70	26	0.77
4. Isomatala	2.12	11.49	0–3	16	1	1.00
5. Tauvo	13.92	19.57	2–7	65	16	0.88
6. Savilahti	2.42	12.63	0–2	21	0	–
7. Säärennokka	2.42	12.23	1–6	32	11	1.00
8. Pitkänokka	14.92	23.60	20–30	272	83	0.27

'Dist near' = distance to the nearest patch (km), 'Dist all' = mean distance to all other patches (km), 'Pairs' = range of observed number of breeding pairs, 'Size' = size of the patch (ha), 'Recruits' = the number of produced recruits, Disp prob' = the proportion of natal dispersers out of the recruits. The site numbers refer to the country-specific locations in Figure 1.

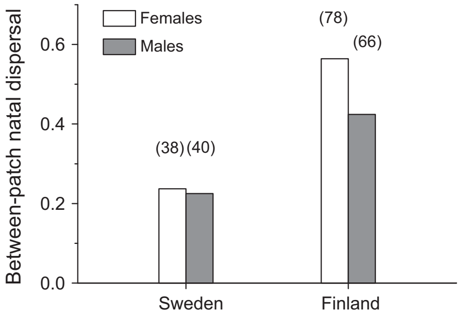

Figure 2. Natal dispersal probability of female and male Baltic Dunlins breeding in Finland and Sweden. Sample sizes are noted above bars.

but not among females in Finland ($\chi^2 = 3.195$, df = 1, $P = 0.074$; Fig. 4c).

When examining only distances of individuals that left their natal patch, there were no differences in natal dispersal distances between the sexes in Sweden (Table 3; $W = 32.5$, $P = 0.508$) or Finland ($W = 537$, $P = 0.364$), and these distances did not significantly differ between Swedish and Finnish males ($W = 176$, $P = 0.080$) or females ($W = 263$, $P = 0.127$). For individuals that returned to their natal patch, natal dispersal distance was similar between the sexes in both Finland and Sweden (Table 3, Fig. 5) but was clearly further in Finland than in Sweden in both males ($W = 951$, $P < 0.001$) and females ($W = 696$, $P = 0.005$; Fig. 5).

DISCUSSION

We identified strong natal philopatry in two patchy metapopulations of Dunlins. Individuals returned close to their natal patch more often than expected by chance. As predicted, the between-patch natal dispersal probability was higher and dispersing individuals tended to disperse further in the Finnish metapopulation than in the Swedish one. Females in Finland were the only group that followed the expected proportion of individuals returning within 3 km, but there were no sex-related differences in natal dispersal in either metapopulation. Strong philopatry in both sexes suggests a lack of inbreeding avoidance via dispersal, which is noteworthy given that it is considered to be one of the main drivers in the evolution of sex-biased dispersal (Gros *et al.* 2008). This result provides an explanation for the increased frequency of inbreeding, subsequent loss of fitness and decline of the Swedish population (Blomqvist *et al.* 2010).

Table 2. Analyses of between-patch natal dispersal probabilities (a, b) and dispersal distances (c) of Baltic Dunlins.

Parameter	Coefficient	se	*z*	*P*
(a)				
Intercept	−1.1112	0.3225	3.428	0.0006
Sex	−0.1894	0.3623	0.521	0.6025
Metapopulation	**1.2430**	**0.3601**	**3.434**	**0.0006**
Metapopulation : Sex	−0.0992	0.3463	0.285	0.7754
(b)				
Intercept	4.9013	1.3564	3.600	0.0003
Sex	−2.3902	1.7391	1.370	0.1705
Distance	**−0.1655**	**0.0591**	**2.791**	**0.0053**
Patch size	**−0.0689**	**0.0202**	**3.384**	**0.0007**
Distance : Sex	0.0790	0.0738	1.068	0.2857
(c)				
Intercept	2.755e–04	4.904e–05	5.588	< 0.0001
Sex	2.346e–05	4.481e–05	0.521	0.6023
Metapopulation	**−1.764e–04**	**4.944e–05**	**3.549**	**0.0004**
Sex : Metapopulation	3.188e–06	3.904e–05	0.081	0.9353

The table shows parameter coefficients and their significance levels ($P < 0.05$ in bold) derived from model averaging of most supported (ΔAICc ≤ 2) generalized linear models (a, b: binomial distribution, logit link; c: gamma errors, $n = 222$). (a) *A priori* models include only effects of sex (male vs. female), metapopulation (Finland vs. Sweden) and their interactions (:), and in (b) *a priori* models also include mean distance to other patches (Distance, km) and natal patch size (ha) and interactions (:). In (c) *a priori* models for natal dispersal distance (in metres) included effects of sex (male vs. female), metapopulation (Finland vs. Sweden) and their interactions (:). See model selection results for all *a priori* models in Supporting Information Tables S1–S3.

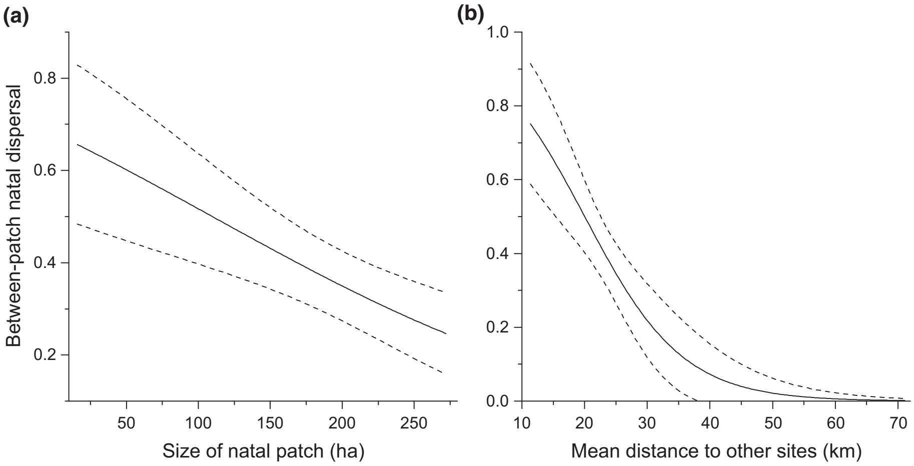

Figure 3. Predicted natal dispersal probability of the Baltic Dunlins in relation to (a) size of the natal patch (ha) and (b) the mean distance (km) from the natal patch to other patches (solid line) and two times standard error (dotted lines).

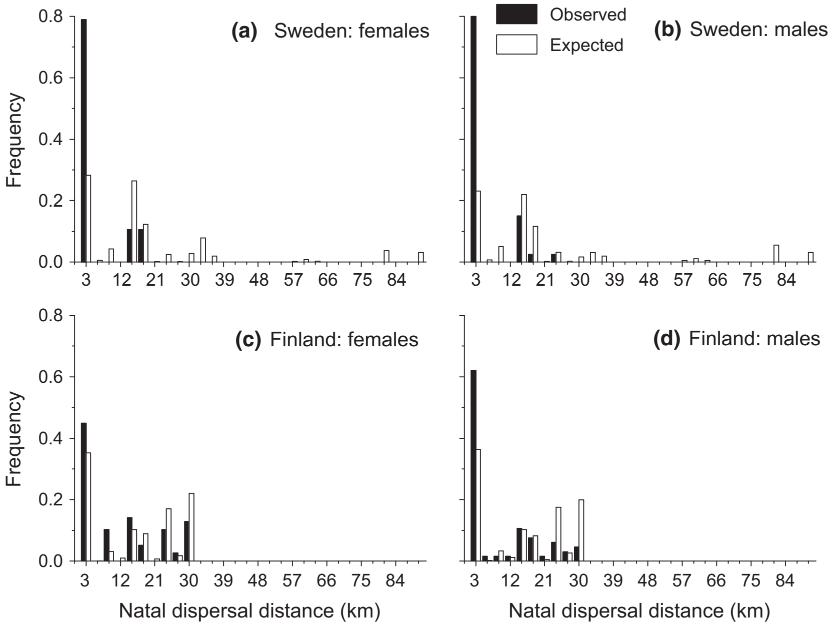

Figure 4. Observed (black bars) and expected (white bars) distributions of natal dispersal distances in 3-km classes for Baltic Dunlin for (a) females and (b) males born on the west coast of Sweden, and for (c) females and (d) males born on the coast of the Bothnian Bay in Finland.

The difference in natal dispersal between the metapopulations disappeared after considering natal patch-specific attributes (patch size and distance to other patches) that are the basis of metapopulation and landscape ecology (Hanski 1998, Calabrese & Fagan 2004). First, dispersal was more common from small natal patches. In Sweden, the majority of recruits (83%) originated from two large patches, inevitably leading to low between-patch movement. The patch size effect on the probability to disperse from a patch is well documented in insects and small mammals (Bowler & Benton 2005) but not specifically in birds. This pattern can, however, be related to carrying capacity, density, population size, demography or some other factor that correlates with patch size

Table 3. Sex-specific between-patch natal dispersal probabilities and dispersal distances (km) for all individuals, philopatric individuals, and dispersing individuals in the Swedish and the Finnish Dunlin metapopulations.

			Distances for all				Distances for philopatrics				Distances for dispersers			
Sex	Probability	se	Mean	se	Median	*n*	Mean	se	Median	*n*	Mean	se	Median	*n*
Sweden														
Female	0.237	0.069	3.64	1.00	0.46	38	0.50	0.09	0.39	29	13.75	1.65	13.51	9
Male	0.225	0.066	3.35	0.94	0.47	40	0.43	0.07	0.34	31	13.39	1.71	14.13	9
Finland														
Female	0.564	0.056	10.72	1.21	8.58	78	0.75	0.08	0.79	34	18.43	1.23	15.89	44
Male	0.424	0.061	7.36	1.14	1.18	66	0.82	0.06	0.80	38	16.26	1.41	14.97	28

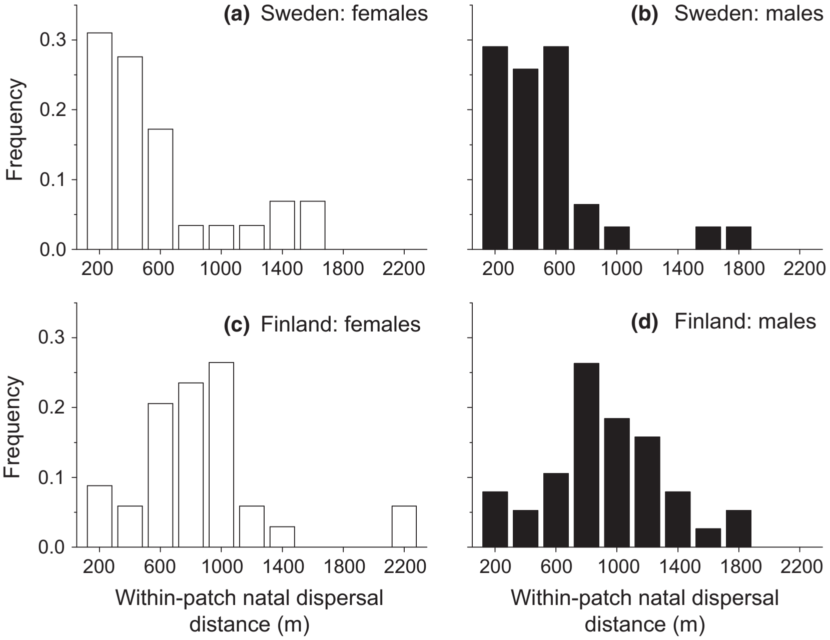

Figure 5. Within-patch natal dispersal distances in 200-m classes for Baltic Dunlins that returned to breed in their natal patch for (a) females and (b) males born on the west coast of Sweden, and for (c) females and (d) males born on the coast of the Bothnian Bay in Finland.

(Poethke & Hovestadt 2002, Serrano & Tella 2003, Doligez *et al.* 2004, Bowler & Benton 2005). Benefits from returning to small natal patches are probably low due to reduced mate availability, high risk of inbreeding and kin-competition (Gros *et al.* 2008, Massol & Débarre 2015).

Secondly, dispersal rates decreased with increasing isolation of the natal patch, suggesting that structural connectivity affects movement of the Dunlin. This is corroborated by molecular genetic data which reveal an isolation-by-distance pattern, i.e. increasing genetic differentiation with geographical distance, across the Baltic Sea (Rönkä 2016). Because these migratory birds are not constrained by movement within these landscapes, it is likely that their preference for philopatry and the potentially time-consuming search for other patches are the factors that reduce the likelihood of dispersing from isolated patches. By following marked birds, we thus demonstrate that reduced structural connectivity reduces functional landscape connectivity, which has rarely been shown in bird populations (Serrano & Tella 2003, Martín *et al.* 2008).

Our results give further support for the impact of reduced structural connectivity on movement of migratory bird species (Weatherhead & Forbes 1994, Hansson *et al.* 2002). Natal dispersal patterns found in our study are consistent with other populations of migratory species that have patchy distributions (e.g. Hansson *et al.* 2002, Ceresa *et al.* 2016). They contrast with the low philopatry observed in populations of ecologically similar migratory wader species such as Little Ringed Plover *Charadrius dubius*, Kentish Plover *Charadrius alexandrinus alexandrinus*, Snowy Plover *Charadrius alexandrinus nivosus*, Semipalmated Plover *Charadrius semipalmatus*, Semipalmated Sandpiper *Calidris pusilla* and even different sub-species of the Dunlin *Calidris alpina pacifica* that breed in more abundant networks of suitable habitat (Foppen *et al.* 2006, Stenzel *et al.* 2007, Pakanen *et al.* 2015, Saalfeld & Lanctot 2015).

Clearly, the spatial configuration of available habitat affects movement. In contrast to the previous claims that Dunlins mainly return to the close vicinity of their natal patch (Soikkeli 1970, Jackson 1994), our results show that up to 50% of the juvenile Dunlins can disperse relatively long distances. This illustrates how observed dispersal distributions may be biased towards shorter distances if they fail to consider movements beyond the study area (Koenig *et al.* 1996). This may apply to our results, as the Finnish study population is known to receive immigrants from Pori, over 400 km away, indicating that natal dispersal movements of Dunlins can be at least that (Pakanen *et al.* 2016, see also Soikkeli 1970). However, several facts suggest that if emigration of hundreds of kilometres from the Bothnian Bay to the south occurs, it concerns only a very small portion of individuals (Pakanen *et al.* 2016).

First, our juvenile survival estimates from hatching to age one are relatively high (20%; Pakanen *et al.* 2016) compared with estimates from other small calidrid species (6–9%; Sandercock & Gratto-Trevor 1997, Koivula *et al.* 2008), leaving little room for emigration. Secondly, molecular data indicate stronger gene flow from the south to Bothnian Bay than vice versa (Rönkä 2016). Phenological changes across such long distances may lead to directed northward dispersal (Edelaar *et al.* 2008, Burger *et al.* 2013). Assuming that arrival dates differ between the latitudes, and that laying dates are at least to some extent genetically determined, the south to the north immigration into the Bothnian Bay population may be facilitated by the favourable difference in phenology (e.g. Burger *et al.* 2013). In contrast, movement in the opposite direction may be more difficult: birds of northern origin (Bothnian Bay) will be too late for the phenology in southern breeding areas, such as in southern Finland or Estonia. Thirdly, the sex ratio in the Finnish sample was biased towards the commonly more dispersive sex (females 78; males 66), suggesting that we have sampled all or nearly all of the surviving young recruits and that females probably do not emigrate from the study area. Finally, the birds that have been ringed in our study populations have not been seen breeding elsewhere despite regular censuses and specific ringing schemes of this endangered subspecies. For example, colour-ringed Dunlins within the metapopulation on the Swedish west coast have never been observed breeding in another colour-ringed and well-monitored population in the far south of Sweden (only about 200 km away), and vice versa (Blomqvist *et al.* 2010). Moreover, in the Swedish population the relationship between the annual number of unringed birds and the number of previously ringed birds was as predicted from capture–recapture models for closed populations (Blomqvist *et al.* 2010 and references therein).

The observed low dispersal probabilities suggest that efforts should be made to increase long-distance dispersal and between-population gene flow through the creation of ‘stepping stones’ (Saura *et al.* 2014), thereby reducing the risk of inbreeding and genetic drift (Keller & Waller 2002). Based on our results, movement of individuals may be affected by focusing on patch size and distance between patches when forming networks of suitable habitat. Habitat patches should be close enough to each other to facilitate dispersal. In our study, the dispersal rate from an average-sized patch reached 50% when mean distance to other sites was on average 20 km. Creation of new habitats outside this range may have lower chances of colonization. Our results on patch size-dependent dispersal can be applied to the old debate on conservation of biodiversity in large vs. small reserve areas (Simberloff & Abele 1982). When a target population is small, philopatric and at risk of inbreeding, and when the aim is to increase between-patch movement, investing in few large patches (100–300 ha) may not be as good a strategy as investing in a network of patches of varying size that include multiple small patches (20–100 ha) in between the larger ones (see also Massol *et al.* 2011). However, the optimal patch size is also affected by the likelihood of colonization, immigration, the maximum number of pairs (patch extinction probability) and by possible edge-effects on life history (Hanski 1998, Doligez *et al.* 2004, Haddad *et al.* 2015). From a dispersal rate standpoint, increasing recruit production in small patches would be profitable.

Our study shows that natal dispersal patterns may differ markedly between populations of the same species due to the structure of the landscape. Given that dispersal was rare even between the closest patches in Sweden, some other mechanisms may also have played a role. Individuals may show different responses to environmental factors that trigger dispersal (Bowler & Benton 2005). The Swedish metapopulation appears to be closed and is not likely to have received any immigrants for some time (Blomqvist *et al.* 2010). Assuming that there is a genetic basis for dispersal (Doligez *et al.* 2012), non-dispersing genotypes may have accumulated in this population as a consequence of lacking gene flow from other breeding areas. Future studies should consider the genetic basis of dispersal and examine the cues that influence dispersal decisions in different environments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Model diagnostics for the global GLM (Sex + Metapopulation + Sex : Metapopulation) used for analysing dispersal distance (Gamma errors).

Table S1. Modelling results for analysing variation in between-patch natal dispersal probability in the Baltic Dunlin (*Calidris alpina schinzii*) in relation to sex, metapopulation (Finland and Sweden) and their interaction (:) using a GLM with binomial errors.

Table S2. Modelling results for analysing variation in between-patch natal dispersal probability in the Baltic Dunlin (*Calidris alpina schinzii*) in relation to sex, metapopulation (Finland and Sweden), mean distance to other patches (Distance), patch size and relevant interactions (:) using a GLM with binomial errors.

Table S3. Modelling results for analysing variation in natal dispersal distance in the Baltic Dunlin (*Calidris alpina schinzii*) in relation to sex, metapopulation (Finland and Sweden) and their interaction (:) using a GLM with a Gamma error structure.