

Lone male loser? Effects of spatial isolation on male pairing success in the Ortolan Bunting *Emberiza hortulana*

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Abstract

In small, isolated or fragmented bird populations, past studies have shown that there can be a high proportion of unpaired males. Low male pairing success is suggested to be the result of female-biased natal dispersal and low female recruitment. Indirect evidence indicates that such an effect operates among populations with different degrees of isolation, but little is known of how isolation affects male pairing success within populations. The Norwegian population of Ortolan Buntings (*Emberiza hortulana*) is distributed in about 50 discrete patches in an area of nearly 500 km². In this study, we examined whether patch isolation and individual male isolation affected male pairing success. The population has a strongly male-biased sex ratio, with almost half of all males being unpaired. We found that male pairing success was negatively related to isolation of patches and isolation of individual males in most analyses, and with significant effects in particular in some analyses of individual isolation. Patch population size was measured as the total number of males observed in a particular patch in a specific year and did not have an effect on male pairing success, and was not related to patch isolation. Even though some tests were statistically significant, the magnitude of effects were small and there was large variance in male pairing success. Variance in success suggests that other factors than isolation such as male age or experience may be just as important for male fitness within our study population. Furthermore, we suggest that small effects of isolation were due to the ability of Ortolan Buntings to move large distances within the breeding season, and that isolation effects on small spatial scales are more likely for species with restricted dispersal, such as resident species or species with high population density.

INTRODUCTION

Small, isolated or fragmented populations are exposed to a number of threats that can make them vulnerable to extinction, including the loss of genetic variation, demographic and environmental stochasticity, and natural catastrophes (Shaffer 1981, Young & Clarke 2000, Beissinger & McCullough 2002). In addition, population persistence depends on the balance between emigration and immigration. The effects of both processes on population viability are well documented theoretically and empirically, although the relative role of each process is often debated (Lande 1993, Allendorf

& Ryman 2002). The factors affecting recruitment of new individuals into the population are essential in understanding population dynamics of small and isolated populations. Insufficient recruitment is usually assumed to be the result of either poor reproductive success or high mortality rates, but a skewed operational sex ratio may be just as important (Dale 2001a, Steifetten & Dale 2006). A skewed operational sex ratio is equivalent, at least in socially monogamous species, to a high proportion of unpaired individuals of one sex. As a result, the reproductive output of the population will decrease, which again will reduce population size. Thus, knowledge of the patterns of pairing success in

small and isolated populations may help understand the proximate causes underlying population declines.

In small, isolated or fragmented bird populations, past studies have often shown that there can be a high proportion of unpaired males (reviewed by Dale 2001a, see also Walters et al. 1999, Dale 2001b, Bayne & Hobson 2001, Zanette 2001, Fraser & Stutchbury 2004, Steifetten & Dale 2006, Donald 2007, Dale 2011, Morrison et al. 2016). Dale (2001a) argued that small and isolated bird populations are particularly prone to skewed sex ratios due to female-biased natal dispersal. Sex-biased dispersal can have consequences for small populations that are restricted in range because females that emigrate during natal dispersal may be lost from the breeding pool (Dale 2001a). Moreover, population isolation may make it difficult for females to disperse among local populations, especially if large stretches of unsuitable habitat separate patches of suitable habitat. Habitat fragmentation can result in a high proportion of unpaired males, due to a lack of female immigration (Cooper & Walters 2002).

In natural populations, female mate search may be restricted because of energetic costs, time constraints, female-female competition or predation risk (Alatalo et al. 1988, Slagsvold et al. 1988, Dale et al. 1992, Milinski & Bakker 1992, Berglund 1993). In fragmented populations, females also face the problem of locating males distributed over a wide area which can reduce the probability of encountering a potential mate. As a result, the more isolated a habitat patch is, the less likely it is to be visited by a female. In addition, because female mate search is typically done by locating singing or displaying males (Eriksson & Wallin 1986), small habitat patches with few males are less likely to be heard by females than large habitat patches with more males. Thus, the probability of locating a mate should be higher in large and continuous populations, or in the centre of small or fragmented populations (Dale 2001a). Indirect evidence indicates that such an effect operates between populations with different degrees of isolation within a species' distributional range (Dale 2001a), but little is known of how isolation affects pairing success within populations, either among patches or individuals. Pairing success is a vital demographic parameter for population growth (Steifetten & Dale 2006), and it should be given more attention in studies trying to elucidate the proximate causes for population declines, especially for populations that are small, isolated or fragmented.

The Norwegian population of Ortolan Buntings (*Emberiza hortulana*) is highly isolated and fragmented. In addition, it is characterized by a strongly skewed operational sex ratio, with almost half of all males being unpaired (Steifetten & Dale 2006, Dale 2011). The population contains less than 150 singing males, with nearly all individuals distributed in an area of nearly 500 km². The birds occur in several well-defined habitat patches differing in the degree of isolation and patch population size. In this study, we examined whether

patch isolation or patch population size affected the probability of attracting females. We expected that males in larger and less isolated patches would have higher pairing success than males in smaller and more isolated patches. In addition, we tested whether the degree of isolation at an individual level affected male pairing success. Last, we examined whether patch isolation affected patch population size. Based on the above predictions, we expected that patch population size would decrease towards the edge of the study area as a negative effect of isolation.

METHODS

Study area and population

The Norwegian population of Ortolan Buntings is located in central Hedmark in Innlandet County (60°29'–60°53' N, 11°40'–12°18' E), but up until 2004 a minor sub-population was also found ~60 km further south in Akershus County. The population lies at the edge of the species' range, and the nearest neighbouring population is located around 250 km further east, in Sweden. The study area consists mainly of farmland habitat, with interspersed elements of forests and bogs. Breeding habitats include raised peat bogs, forest clear-cuts on poor sand, land being cleared for cultivation, and a forest burn and all of the habitats are patchily distributed (Figure 1; Dale & Christiansen 2010). Many patches were surrounded by farmland on most sides, or they were situated at the edge between farmland and continuous boreal forest, and were well-defined against surrounding matrix and easy to identify both on the ground and from the air. Males move frequently between patches during breeding dispersal, and movements occurred freely in relation to habitat type so that most males switched among habitat types one or more times during their lifespan (Dale & Christiansen 2010). A total of about 50 different patches have been used by Ortolan Buntings during the study period. All patches are located close to arable land due to the use of cereal fields during foraging by breeding birds (Dale 2000, Dale & Olsen 2002).

Data collection and procedures

Data on male pairing success were collected during the breeding seasons (May–June) of the 7-year period of 1999 to 2005. For individual identification, males were ringed with a unique combination of three colour-rings and one numbered metal ring, and in each year between 55–87% of all males had colour-rings. To record the spatial position of individual males, we performed regular visits of 1–3 days interval to all patches which have been used by Ortolan Buntings. In addition, we visited all other potentially suitable patches within the study area. Due to the possibility of counting unmarked males twice because of extensive within-breeding season and between-patch dispersal by adult males (Dale et al. 2005, 2006), only unmarked males that were observed

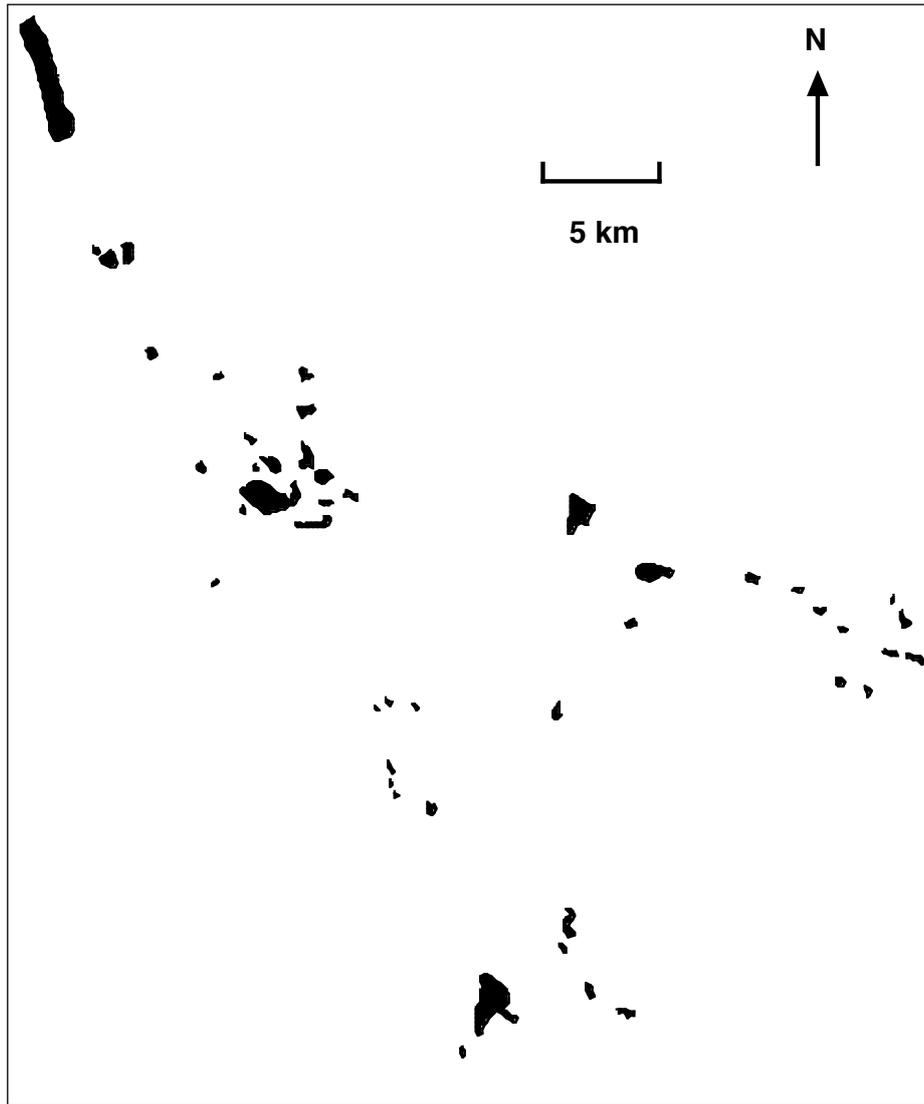


Figure 1. A schematic representation of the spatial configuration of the main study area showing all patches (dark areas) that were used by Ortolan Buntings at least once during 1999–2005. Outlying patches located more than 15 km from the nearest neighbouring patch in the main population are not shown.

five days or more in the same territory were included in our analyses (Steifetten & Dale 2006). Based on the position of males recorded every 1–3 days in the field, we used the centre of all positions as the location of territories. We plotted male territories on a digital map as a basis for calculating the degree of isolation between individuals and between patches (see below for details of how isolation was calculated). The pairing status of each male in the population was identified based on the presence of females together with the males, singing activity, and/or feeding behaviour (Steifetten & Dale 2006), and males were classified as either paired or unpaired. Males of uncertain status were excluded from analyses of pairing success, but were included in calculations of degrees of isolation.

Habitat patches were well-defined against the matrix of farmland or forest and some patches were close to each other. Thus, if male territories were less than 500 m apart, we defined them as belonging to the

same patch. Territories located more than 500 m away from the nearest neighbouring territory were classified as belonging to different patches. Distances between patches were measured as the shortest distance from one patch to another, measured as the distance from the outer boundaries of each male's territory, which is roughly 100 m in diameter (Cramp & Perrins 1994, personal observations). A threshold distance of 500 m was used because females searching for a mate within one patch are unlikely to hear the songs of other males beyond this distance (personal observations). The number of patches differed from year to year due to some patches lost due to clear-cuts becoming overgrown, or cultivation projects being completed so that disturbed habitats useful for Ortolan Buntings disappeared, but with creation and colonization of some new patches due to logging creating new clear-cuts. Thus, the number of patches used for analyses were based on the overall distribution of male territories for all years combined.

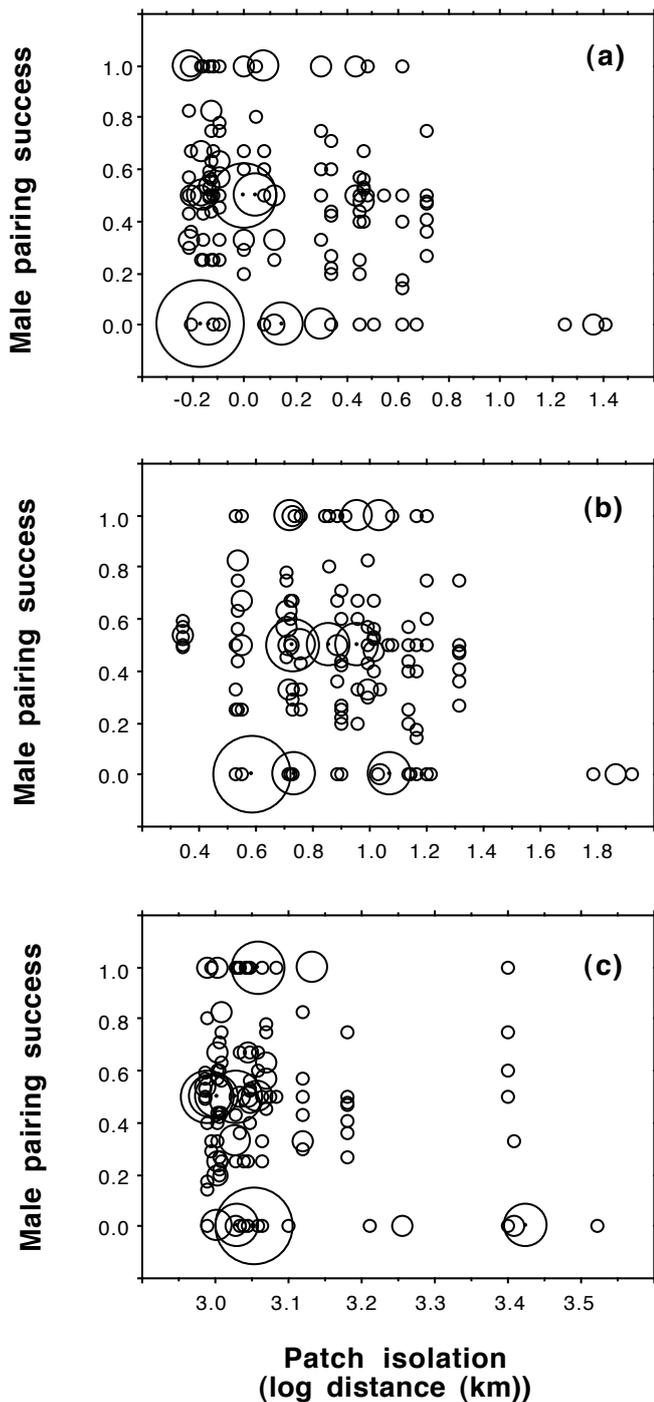


Figure 2. Relationship between male pairing success (unpaired = 0, paired = 1) and patch isolation measured as distances to: a) the nearest neighbouring patch, b) the three closest patches, and c) to all other patches in the population. Overlapping data points are indicated by larger symbols where the largest symbols represent 8, 7, 7 observations in a, b and c, respectively. Data shown are based on the entire dataset of 37 patches, 7 years, and 169 patch-years.

Total patches were used because they better reflected the general spatial distribution of Ortolan Buntings in the focal population, and are therefore likely to be a better indicator for patch isolation. Hence, the same patches were used for all years. A total of 37 patches were used, but they were included in analyses only in

years in which males were present (mean 4.6 years out of the study duration of 7 years). The number of males in occupied patches varied from 1 to 52 (mean = 7.2, median = 4, $n = 169$ patch-years).

We used three different measures of the degree of isolation among patches and among individual males to capture isolation at different spatial scales (from the scale of nearest neighbours up to the scale of the Norwegian population). At the patch level, we measured the distance from a specific patch to the nearest neighbouring patch, the distances to the three closest patches (including the nearest neighbouring patch), and also to all other patches in the population to capture variation at the landscape level up to the national level. At the individual level, we measured the distance from a specific male to the nearest neighbouring male, distances to the three closest males, and to the five closest males to capture variation in isolation at a more local level, both within patches for males inhabiting patches with several males, and among neighbouring patches for males that were alone or with few neighbours within patches. Distances among patches and males were measured based on the outer boundaries of patches and male territories. Summed distance values were used in analyses involving distances to several patches or males. Patch population size was measured as the total number of males observed in a particular patch during the breeding season in each year, whereas the pairing success within a patch was measured as the proportion of males which successfully attracted a female. At an individual level, pairing success of males was defined as either paired or unpaired.

Statistical analysis

Annual variation in male pairing success was initially analysed with non-parametric tests (Kruskal-Wallis rank sum test and Spearman rank correlation). To test whether patch isolation, individual male isolation or patch population size affected male pairing success, we used generalized linear mixed models (GLMM) to control for dependencies in the dataset. We included patch as a random variable to control for the effect of repeated measurements. The population of buntings was declining annually (Dale 2001b, Steifetten & Dale 2006), and isolation measures could change over time. Year was therefore included as a continuous variable. At the patch level, pairing success was measured as the proportion of the males present that became paired. Thus, the main models of how patch isolation affected pairing success included pairing success as the response variable, one measure of patch isolation as a fixed variable, year as a fixed variable, and patch ID as a random variable. In the analyses of individual male isolation, male pairing success was modelled with a binomial distribution (unpaired = 0, paired = 1). Male ID could not be included as a random factor in this analysis because 13–45% of the males were unmarked in each year. For the model analysing the effect of patch isolation on patch population size we assumed

Table 1. Generalized linear mixed models of the effect of patch isolation on pairing success of male Ortolan Buntings. Patch isolation was measured as the distance to the nearest neighbouring patch, the three closest patches, and to all other patches in the population. Analyses were based on the entire dataset (37 patches, 7 years, 169 patch-years), or a reduced dataset which excluded six spatially outlying patches (31 patches, 7 years, 153 patch-years). Patch was included as a random effect.

Data set/variables	Estimate	SE	p
<i>Isolation = distance to nearest patch</i>			
Full data set			
Patch isolation	-0.632	0.332	0.065
Year	-0.070	0.027	0.012
Reduced data set			
Patch isolation	-0.415	0.309	0.19
Year	-0.065	0.028	0.021
<i>Isolation = distance to three closest patches</i>			
Full data set			
Patch isolation	-0.750	0.370	0.050
Year	-0.070	0.027	0.012
Reduced data set			
Patch isolation	-0.544	0.334	0.11
Year	-0.066	0.028	0.020
<i>Isolation = distance to all patches</i>			
Full data set			
Patch isolation	-1.337	1.107	0.24
Year	-0.071	0.027	0.011
Reduced data set			
Patch isolation	1.413	2.027	0.49
Year	-0.066	0.028	0.020

a Poisson distribution. The dataset on patch isolation included six spatial outliers that were likely to bias the results: one patch 18 km to the northeast, one patch-year; one patch 23 km to the south, two patch-years; three patches 52 km to the southwest, twelve patch-years; and one patch 71 km to the south-southwest, one patch-year. Thus, our main conclusions are based on a reduced dataset excluding these outliers. However, we report results from both analyses with and without spatial outliers. We used cross-validation estimates to assess the predictive accuracy of models with binomial distribution (Maindonald & Braun 2007). Model assumptions and fit were evaluated using analysis of Pearson residuals versus fitted values and each of the predictor variables, and overdispersion was checked. We used the statistical software R version 4.2.2. (<http://www.R-project.org>). The lme4 package (Bates et al. 2015) was used for GLMM-analyses.

RESULTS

Mean yearly male pairing success was 52.4% (range = 45–63%). There was no difference among years (Kruskal-Wallis rank sum test, $\chi^2 = 6.00$, $df = 6$, $p = 0.42$), nor was there a trend that male pairing success changed during the study period (Spearman rank correlation, $r_s = 0.04$, $n = 7$, $p = 0.93$).

Male pairing success was significantly negatively affected by patch isolation in only one out of six analyses when measured as the distance to the three closest patches, but five out of six analyses indicated negative relationships (Table 1; Fig. 2). Patch isolation and year had a predictive accuracy of only 24–29%. At an individual level, isolation had significant negative effects on male pairing success in three out of six analyses when measured as the distance to the three closest males and five closest males (Table 2; Fig. 3). Individual isolation and year had a predictive accuracy

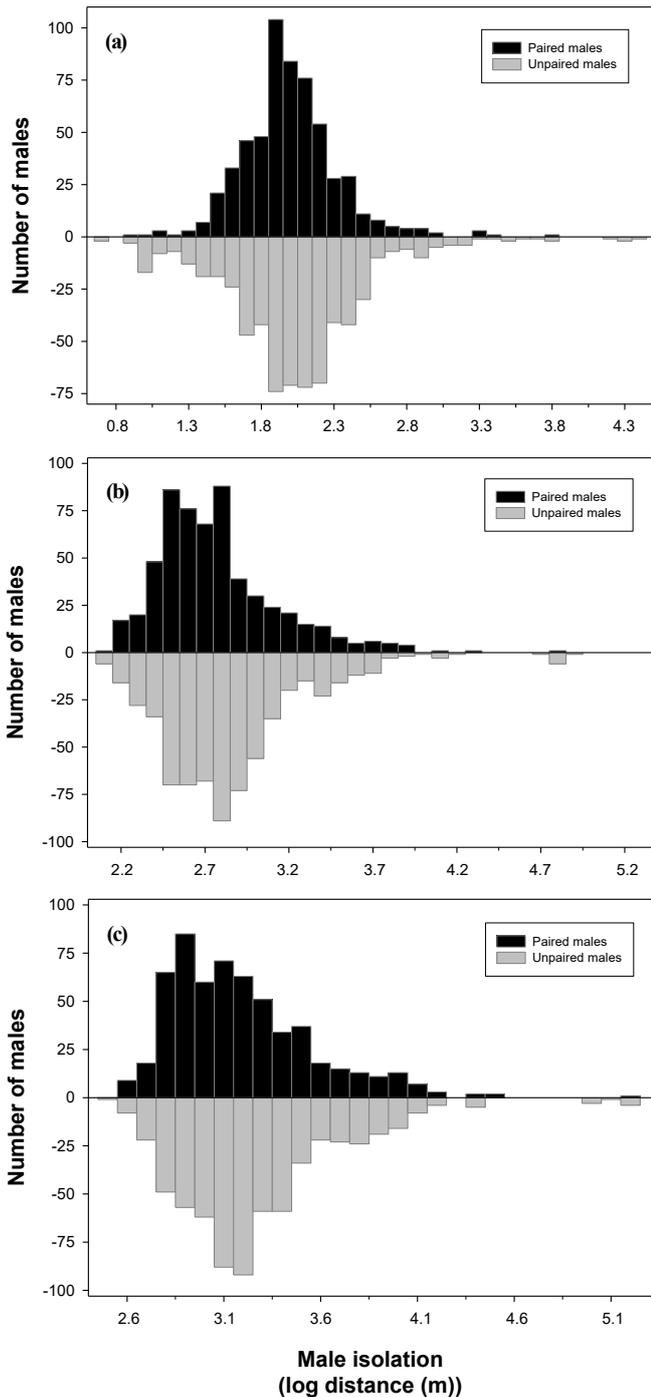


Figure 3. Distribution of paired and unpaired males in relation to male isolation measured as distances to: a) the nearest neighbouring male, b) the three closest males, and c) the five closest males. Data shown are based on the entire dataset of 37 patches, 7 years, and 1238 male-years.

of 53–57%.

Male pairing success was not related to patch population size (Table 3; Fig. 4). Moreover, patch isolation did not affect patch population size (Table 4; Fig. 5). For most analyses, year had a significant effect on male pairing success, suggesting that the annual declines in population size might increase the effects of isolation.

DISCUSSION

Limited effects of patch isolation

In the focal population of Ortolan Buntings, low male pairing success has been suggested to be the result of female-biased natal dispersal and low female recruitment (Dale 2001a, b). Females might be expected to have difficulties in locating males far apart because patches are distributed over wide areas. Moreover, it is reasonable to assume that patches that are small and isolated are harder to locate than patches that are larger and less isolated. There were statistically significant effects of isolation in some of the analyses, and it is possible that effects of isolation are scale-dependent. However, the observed distributions of pairing success suggest that the absolute magnitude of the changes in pairing success from low to high isolation were small. Furthermore, the proportion of variance in pairing success explained by the models was moderate, but higher in analyses of individual isolation than in analyses of patch isolation. Thus, although isolation had negative effects on pairing success, the combined effect of other factors may be just as important for male pairing success as isolation within the study population. The degree of patch isolation measured as the distance to all other patches in the population and patch population size had little or no effect on male pairing success, which was also consistent with a lack of a relationship between patch isolation and patch population size. Negative effects of isolation on male pairing success may therefore be more likely to operate at larger spatial scales between separate breeding populations with larger barriers to movements of females (Dale 2001a).

The analyses of patch isolation (Tables 1, 3 and 4) and individual male isolation (Table 2) gave relatively similar results. However, we could not include male ID as a random factor in the analyses of individual male isolation because some of the males were not colour-ringed. Thus, there could be some pseudoreplication in the analyses of male isolation if some unmarked males were included with data from several different years. Consistent individual variation in pairing success could arise if females returning one year select the same male as they were paired to in the previous year. However, for most males there is no between-years correlation in pairing success for the two first years of their lives because first-year males are often unpaired whereas older males have much higher pairing success (Dale 2011). Age-specific variation in pairing success was relevant for a large proportion of our repeated measures of individual males, thereby removing some of the potential effect of pseudoreplication. Furthermore, if individual differences in pairing success were related to patch quality, our use of patch ID as a random factor controlled for the effect. Thus, we do not believe our analyses of individual male isolation are affected by pseudoreplication to any substantial degree.

Table 2. Generalized linear mixed models of the effect of male isolation on pairing success of male Ortolan Buntings. Male isolation was measured as the distance to the nearest neighbouring male, the three closest males, and the five closest males. Analyses were based on the entire dataset (37 patches, 7 years, 1238 male-years), or a reduced dataset which excluded six spatially outlying patches (31 patches, 7 years, 1210 male-years). Patch was included as a random effect.

Data set/variables	Estimate	SE	p
<i>Isolation = distance to nearest male</i>			
Full data set			
Male isolation	-0.155	0.142	0.27
Year	-0.105	0.029	< 0.001
Reduced data set			
Male isolation	-0.014	0.152	0.93
Year	-0.100	0.029	0.001
<i>Isolation = distance to three closest males</i>			
Full data set			
Male isolation	-0.525	0.160	0.001
Year	-0.105	0.029	< 0.001
Reduced data set			
Male isolation	-0.443	0.174	0.011
Year	-0.103	0.029	< 0.001
<i>Isolation = distance to five closest males</i>			
Full data set			
Male isolation	-0.621	0.174	< 0.001
Year	-0.107	0.029	< 0.001
Reduced data set			
Male isolation	-0.025	0.164	0.88
Year	-0.015	0.029	0.61

Male strategies

Based on our findings that isolation had only a moderate effect on male pairing success, males should not pay too much attention to the degree of isolation in settlement decisions about where to establish a territory within the landscape. Thus, males should also use other cues to enhance individual fitness. For example, differences in habitat quality may differentially attract females to settle, subsequently leading to differences in male pairing success between patches. Habitat quality was not investigated in our field study, but does not seem to affect pairing success (S. Dale and Ø. Steifetten, unpublished data). Another possibility is that individual male perception of habitat suitability or the probability of attracting a female may be based on the presence of conspecifics (Danchin *et al.* 2001, Stamps 2001), a phenomenon which has been documented in Ortolan Buntings (Darrud 2006), but male age structure within a habitat patch might also be important. However, available data on dispersal and settlement decisions in Ortolan Buntings have shown that males did not base their decisions to settle on male

density or on male age structure, indicating that the number of males present within a patch are of minor importance for males' perception of the probability of acquiring a female (Steifetten & Dale 2012). Previous results support the findings in the current study in which we found no effect of patch population size or male density on male pairing success. In the focal population, several patches had small and intermediate population sizes that annually fluctuated with regard to male pairing success from 0 to 1. Patches with larger population sizes are more stable between years with male pairing success of around 0.5, but males should experience the same probability of acquiring a female in whichever patch regardless of population size. On the other hand, dispersing males have been shown to leave breeding sites with lower female density and a more male-biased sex ratio (Steifetten & Dale 2012), indicating that males evaluate the number of females present within a patch as the most important factor in order to increase the chances of pairing success. However, males that dispersed were less likely to acquire a female than males that were site faithful (Steifetten

Table 3. Generalized linear mixed models of the effect of patch population size on pairing success of male Ortolan Buntings. Patch population size was measured as the total number of males observed in a particular patch in a specific year. Analyses were based on the entire dataset (37 patches, 7 years, 169 patch-years), or a reduced dataset which excluded six spatially outlying patches (31 patches, 7 years, 153 patch-years). Patch was included as a random effect.

Data set/variables	Estimate	SE	p
Full data set			
Patch population size	-0.002	0.008	0.85
Year	-0.070	0.028	0.012
Reduced data set			
Patch population size	-0.003	0.008	0.70
Year	-0.066	0.028	0.019

Table 4. Generalized linear mixed models of the effect of patch isolation on patch population size of Ortolan Buntings. Patch population size was the total number of males observed in a particular patch in a specific years. Analyses were based on the entire dataset (37 patches, 7 years, 169 patch-years), or a reduced dataset which excluded six spatially outlying patches (31 patches, 7 years, 153 patch-years). Patch was included as a random effect.

Data set/variables	Estimate	SE	p
Full data set			
Patch isolation	-1.985	1.223	0.11
Year	-0.017	0.013	0.18
Reduced data set			
Patch isolation	0.026	3.870	0.99
Year	-0.015	0.013	0.25

& Dale 2012). Thus, the best strategy to increase the probability of acquiring a female would be to stay in the same area during the breeding season, which indirectly supports the conclusion that the degree of isolation does not affect male pairing success.

Female mate search

In the focal population, female mate search is expected to be restricted due to habitat fragmentation. Although the overall pairing success in the population was low, and there was some evidence that individual isolation affected male pairing success, even highly isolated males had some chance of attracting a female. Thus, it seems that females are able to locate potential mates despite the isolation of some males and some patches. We have little data on female movements within the focal population, but a substantial amount of data is available on male dispersal within the breeding season (Dale et al. 2005, 2006). The general pattern is that males are capable of moving extraordinary long distances of up to 45 km, and often in just a few days, and will then, in principle, also be able to cover the entire length of the main study area in whichever direction. In addition, males often visit several patches during dispersal before final settlement (Dale et al. 2006). If females have the same ability as males to move long distances in just a few days, and the same ability to locate several habitat

patches during dispersal, females are then likely to be part of an inter-connected patch system, and the effect of isolation on male pairing success should be low. Another possibility is that female mate search is limited to within patches or between patches in close proximity. A limited female mate search has been found in the Pied Flycatcher (Dale et al. 1992) and several other species (Gibson & Langen 1996). Tracking female movements is much more difficult than for males which establish territories and sing, and a better understanding of the spatial extent of female mate search in Ortolan Buntings would require use of radio telemetry or other tracking systems.

When may isolation effects be expected?

Several previous studies (see references in Introduction) have shown that pairing success is often low in small and isolated bird populations. Most of these studies were conducted at large spatial scales. In the present study, we found relatively small effects of isolation and fragmentation within a smaller-scale study area where most patches were within an area which at least males could cover within a few days. Thus, the relatively small effects of isolation can be interpreted as a consequence of a good ability of Ortolan Buntings to move among patches (Dale et al. 2006). We are not aware of any other detailed studies that have investigated pairing

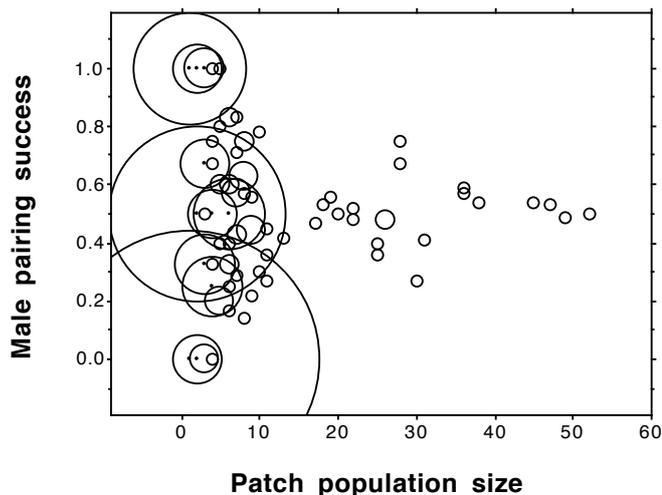


Figure 4. Relationship between patch population size measured as the total number of males observed in a particular patch in a specific year and male pairing success (unpaired = 0, paired = 1). Males of uncertain mating status are excluded in calculating male pairing success, but included in patch population size. Overlapping data points are indicated by larger symbols where the largest symbol represents 25 observations. Data shown are based on the entire dataset of 37 patches, 7 years, and 169 patch-years.

success in relation to isolation at small scales. The long breeding dispersal distances of males may be a consequence of the general lack of females in the Norwegian population of Ortolan Buntings, but may also be related to the species typically having a patchy distribution (Cramp & Perrins 1994, Dale *et al.* 2005, 2006). Thus, we predict that isolation effects at small spatial scales may be more common in species that have more restricted dispersal, such as resident species or species with high population density (Paradis *et al.* 1998). In general, isolation effects might be more likely if distances among patches are longer than the typical distances moved by individuals within breeding seasons.

Conclusions

In this study, we have shown that there were some effects of isolation at the patch level and at the individual level but the magnitude of effects were small. Moreover, patch population size was not related to pairing success or patch isolation. Our results suggest that within the study population there are probably other factors such as male age or experience that are just as important as isolation for determining male pairing success. However, the effect of isolation on male pairing success is likely to be important at a larger spatial scale. In particular, the extremely male-biased sex ratio observed in the declining and isolated population in Norway is likely to differ from a less biased sex ratio in stable populations of Ortolan Buntings in the core of the species' range (Dale 2001a, Donald 2007), but geographic variation in sex ratios has not been tested yet.

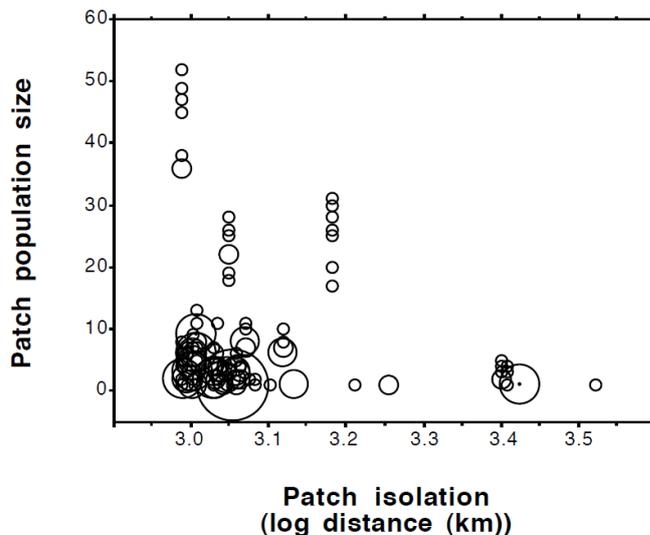


Figure 5. Relationship between patch isolation and patch population size measured as the total number of males observed in a particular patch in a specific year. Overlapping data points are indicated by larger symbols where the largest symbol represents 7 observations. Data shown are based on the entire dataset of 37 patches, 7 years, and 169 patch-years.

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REFERENCES

- Alatalo RV, Carlson A & Lundberg A. 1988. The search cost in mate choice of the Pied Flycatcher. *Animal Behaviour* **36**: 289–291.
- Allendorf FW & Ryman N. 2002. The role of genetics in population viability analysis. Pp. 50–85 in: Beissinger SR & McCullough DR (Eds.) *Population viability analysis*. University of Chicago Press, Chicago.
- Bates D, Mächler M, Bolker B & Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48.
- Bayne EM & Hobson KA. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: importance of male age and floater behaviour. *Auk* **118**: 380–388.
- Beissinger SR & McCullough DR. 2002. *Population viability analysis*. University of Chicago Press, Chicago.

- Berglund A. 1993. Risky sex: male pipefishes mate at random in the presence of a predator. *Animal Behaviour* **46**: 169–175.
- Cooper CB & Walters JR. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology* **16**: 471–478.
- Cramp S & Perrins CM. 1994. *The birds of the Western Palearctic. Volume IX: Buntings and New World Warblers*. Oxford University Press, Oxford.
- Dale S. 2000. The importance of farmland for Ortolan Buntings nesting on raised peat bogs. *Ornis Fennica* **77**: 17–25.
- Dale S. 2001a. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* **92**: 344–356.
- Dale S. 2001b. Causes of population decline of the Ortolan Bunting in Norway. Pp. 33–41 in: Tryjanowski P, Osiejuk TS & Kupczyk M (Eds.) *Bunting studies in Europe*. Bogucki Wydawnictwo Naukowe, Poznan, Poland.
- Dale S. 2011. Lifetime patterns of pairing success in male Ortolan Buntings *Emberiza hortulana*. *Ibis* **153**: 573–580.
- Dale S & Christiansen P. 2010. Individual flexibility in habitat selection in the Ortolan Bunting *Emberiza hortulana*. *Journal of Avian Biology* **41**: 266–272.
- Dale S & Olsen BFG. 2002. Use of farmland by Ortolan Buntings (*Emberiza hortulana*) nesting on a burned forest area. *Journal of Ornithology* **143**: 133–144.
- Dale S, Lunde A & Steifetten Ø. 2005. Longer breeding dispersal than natal dispersal in the Ortolan Bunting. *Behavioral Ecology* **16**: 20–24.
- Dale S, Rinden H & Slagsvold T. 1992. Competition for a mate restricts mate search of female Pied Flycatchers. *Behavioral Ecology and Sociobiology* **30**: 165–176.
- Dale S, Steifetten Ø, Osiejuk TS, Ratynska K & Cygan JP. 2006. How do birds search for breeding areas at the landscape level? Interpatch movements of male Ortolan Buntings. *Ecography* **29**: 886–898.
- Danchin E, Heg D & Doligez B. 2001. Public information and breeding habitat selection. Pp. 243–258 in: Clobert J, Danchin E, Dhondt AA & Nichols JD (Eds.) *Dispersal*. Oxford University Press, Oxford.
- Darrud AK. 2006. *The importance of conspecific attraction in settlement decisions for the ortolan bunting*. MSc thesis. Norwegian University of Life Sciences, Norway.
- Donald PF. 2007. Adult sex ratios in wild bird populations. *Ibis* **149**: 671–692.
- Eriksson D & Wallin L. 1986. Male bird song attracts females – a field experiment. *Behavioral Ecology and Sociobiology* **19**: 297–299.
- Fraser GS & Stutchbury BJM. 2004. Area-sensitive forest birds move extensively among forest patches. *Biological Conservation* **118**: 377–387.
- Gibson RM & Langen TA. 1996. How do animals choose their mates? *Trends in Ecology and Evolution* **11**: 468–470.
- Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**: 911–927.
- Maindonald J & Braun J. 2007. *Data analysis and graphics using R. An example-based approach*. Cambridge Series in Statistical and Probabilistic Mathematics. Cambridge University Press, Cambridge.
- Milinski M & Bakker TCM. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society of London, series. B* **250**: 229–233.
- Morrison CA, Robinson RA, Clark JA & Gill GA. 2016. Causes and consequences of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology* **85**: 1298–1306.
- Paradis E, Baillie SR, Sutherland WJ & Gregory RD. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67**: 518–536.
- Shaffer ML. 1981. Minimum population sizes for species conservation. *Bioscience* **31**: 131–134.
- Slagsvold T, Lifjeld JT, Stenmark G & Breiehagen T. 1988. On the cost of searching for a mate in female Pied Flycatchers *Ficedula hypoleuca*. *Animal Behaviour* **36**: 433–442.
- Stamps JA. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Pp. 230–242 in: Clobert J, Danchin E, Dhondt AA & Nichols JD (Eds.) *Dispersal*. Oxford University Press, Oxford.
- Steifetten Ø & Dale S. 2006. Viability of an endangered population of Ortolan Buntings: The effect of a skewed operational sex ratio. *Biological Conservation* **132**: 88–97.
- Steifetten Ø & Dale S. 2012. Dispersal of male Ortolan Buntings away from areas with low female density and a severely male-biased sex ratio. *Oecologia* **168**: 53–60.
- Walters JR, Ford HA & Cooper CB. 1999. The ecological basis of sensitivity of Brown Treecreepers to habitat fragmentation: a preliminary assessment. *Biological Conservation* **90**: 13–20.
- Young AG & Clarke GM. 2000. *Genetics, demography and viability of fragmented populations*. Cambridge University Press, Cambridge.
- Zanette L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* **32**: 38–46.



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