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Fitness Consequences of Intra-Island dispersal in a House Sparrow (*Passer domesticus*) Population

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Content

Abstract

Dispersing individuals have the ability to link fragmented populations to each other, and influence a wide range of ecological and evolutionary processes. Understanding the fitness differences between resident and dispersing individuals is important if we want to be able to understand how populations will response the on-going and future habitat fragmentation and climate change. Fitness consequences of natal intra-island dispersal was studied in a house sparrow (*Passer domesticus*) population on the island Hestmannøy. Hestmannøy is one of 18 islands in a house sparrow metapopulation study system in northern Norway (66°N, 13°E). Annual number of mates (in males), annual number of eggs (in females), annual number of fledglings and recruits, lifespan and lifetime reproductive success were used as fitness measures. There was an overall tendency for dispersing individuals to have a higher fitness than resident individuals. In analyses carried out for each sex separately the difference was however only significant for lifetime reproductive success in females. Residents and dispersers did not produce significantly different numbers of fledglings but dispersers produced significantly more recruits when the sexes were analysed together. The result contrast with fitness consequences of inter-island dispersal in the same insular house sparrow metapopulation (Pärn et al. 2009), indicating that dispersal scale (within or between populations) is an important factor affecting the fitness outcome of dispersing house sparrow in this metapopulation. I recommend future studies to focus on the differences between intra and inter-island dispersing individuals and the factors that causes the advantage offspring produced by a disperser has compared to offspring produced by a resident.

Norsk sammendrag

Individer som sprer seg har muligheten til å koble fragmenterte populasjoner sammen, og på den måten påvirke en rekke økologiske og evolusjonære prosesser. Kunnskap om fitness forskjeller mellom individer som forblir stedfaste og de som sprer seg er viktig dersom vi ønsker å forstå hvordan populasjoner vil reagere på dagens og fremtidige habitat fragmenteringer og klima forandringer. Fitness konsekvenser av innen-øys spredning ble studert i en gråspurv populasjon på Hestmannøy. Hestmannøy er en av 18 øyer i en gråspurv metapopulasjon i Nord-Norge (66°N, 13°E). Årlig antall partnere (for hanner), årlig antall egg (for hunner), årlig antall flyveklare unger, årlig antall rekrutter, levetid og reproduktiv suksess målt over levetiden ble brukt som mål på fitness. Det var en generell trend at individer som hadde spredt seg hadde høyere fitness enn de som forble stedfaste, men kun reproduktiv suksess målt over levetiden for hunner viste signifikant forskjell. Stedfaste og individer som hadde spredt seg hadde ikke signifikant forskjellig antall flyveklare unger, men individer som hadde spredt seg hadde signifikant flere rekrutter når kjønnene ble analysert sammen. Resultatene her er i kontrast med hva som ble funnet i en studie av fitness konsekvenser av mellom-øy spredning i den samme gråspurv metapopulasjonen (Pärn et al. 2009). Dette indikerer at spredningskala (innad eller mellom populasjoner) er en viktig faktor når det kommer til fitness konsekvenser av spredningen. Anbefaler fremtidige studer å fokusere på hvilke forskjeller det er mellom individer som sprer seg innad og mellom populasjoner, og hva som forårsaker fordelen det virker som avkom har av å være produsert av individer som sprer seg på Hestmannøy.

Introduction

Due to an increasing human population size, natural habitats are fragmented and lost at a much higher rate than before (Clobert 2001, Kokko and Lopez-Sepulcre 2006). Thus, populations of an increasing number of natural plant and animal species are converted to a metapopulation structure, where several local populations are connected by dispersing individuals (Hanski and Gaggiotti 2004). As patches of suitable habitat become smaller they may not be able to sustain viable populations. The reason is firstly that small populations are more likely to be influenced negatively by environmental and demographic stochasticity (Lande et al. 2003, Soule 1987). Secondly, population subdivision may have negative genetic consequences because it can lead to elevated levels of inbreeding and reduced effective population size of a species (Hanski and Gaggiotti 2004). In turn this may lead to an increase in the rate of genetic drift, an increase in the rate of accumulation of deleterious alleles, a decrease in the probability of fixation of beneficial alleles and lower levels of genetic variance at equilibrium (Hanski and Gaggiotti 2004, Whitlock 2001). Furthermore, the level of dispersal and gene flow between populations and the (re-)colonization rate of empty patches is expected to decrease when the geographic distance between populations becomes greater and habitat patches smaller (Hanski 2001) . In addition to habitat loss and fragmentation, climate change may alter currently suitable habitat to unsuitable habitat in the future. Populations then either have to adapt to the new environmental conditions or disperse to a new area (Travis and Dytham 2012). Habitat fragmentation and climate changes combined will represent even stronger threats to the long-term viability of a population than fragmentation or climate changes alone (Brook et al. 2008). To better understand how populations will cope with the ongoing and future environmental changes, it is important to have in depth knowledge about the consequences of dispersal both with respect to population and individual level because it is the dispersers that have the potential to link fragmented populations to each other.

Several ecological and evolutionary processes are affected by dispersing individuals and the genes they transfer between sub-populations (Bowler and Benton 2005, Ronce 2007). Dispersal may allow a species to occur in patches were local recruitment alone is too low to sustain long-term viability of the population (Hanski 2001). Such "sink-populations" may be rescued from extinction by immigration from surrounding "source-populations" (Sæther et

al. 1999). Another ecological consequence of dispersal to small populations is that it may counteract any Allee-effects, i.e. reduced population growth rate at low population sizes (Courchamp et al. 1999, Lande et al. 2003). If there are no Allee-effects, but a negatively density dependent growth rate dispersal will on the other hand likely lead to a reduction in population growth rate, for example through increased competition for resources (Benton and Bowler 2012).

For dispersal event to translate gene flow, the immigrant must have at least one successful mating and produce at least one recruits in the new population (Benton and Bowler 2012). Gene flow will counteract negative genetic consequences of population fragmentation mention above. If immigrants are genetically different from the local individuals in the sub-population, they may contribute with new genetic variation that may enable the population to adapt to any changes in the environment (Willi et al. 2006). On the other hand, if local adaption is important, then immigrants and their offspring are likely to be less fit, since they will be less adapted to the local conditions (Whitlock 2001).

Dispersal is a process that can be defined in many different ways. A general definition of dispersal is any movement between habitat patches, where habitat patches refer to any area of suitable habitat separated in space from other such patches (Bowler and Benton 2005). A more narrow and frequently used definition of dispersal refers to the permanent movement away from the birth patch to the patch of first breeding, also known as natal dispersal (Bowler and Benton 2005, Clobert 2001). The dispersal process can be divided into three different stages; emigration, inter-patch movement and immigration (or settling), were each stage may cause costs for the dispersing individuals (Bonte et al. 2012, Bowler and Benton 2005, Clobert 2001, Doligez and Pärt 2008, Ronce 2007). In the inter-patch movement stage the cost may be in terms of increase in energy expenditure and predation risk. Furthermore, in the immigration stage the dispersing individual may experience disadvantages due to a new and unfamiliar habitat, or because the immigrant individual may be less adapted to the new habitat (Clobert 2001, Doligez and Pärt 2008). There are several adaptive explanations for why some individuals disperse despite the costs it may impose. Avoidance of kin competition or inbreeding, or movement away from low-quality habitat might increase the fitness of dispersing individuals (Doligez and Pärt 2008, Lambin et al. 2001). It is the relative

importance of any individual costs and benefits of dispersal that will determine the dispersal rate of a population. To better understand the dispersal process in natural populations we therefore need to quantify such costs and benefits. In spite of the importance, such studies are rare.

Dispersal may affect both lifespan and reproductive output for an individual. A review of available data from different studies of effects on dispersal on and fitness showed that dispersal had positive effects on fitness as often as negative effects (Belichon et al. 1996). More recently, differences in fitness have been found for resident and dispersing individuals in a number of bird species, generally showing that dispersers have lower fitness than residents (Forero et al. 2002, Hansson et al. 2004, Tarwater and Beissinger 2012). Furthermore, it has been showed that individual characteristics such as sex or phenotype may influence whether dispersal has negative or positive effects on fitness. For example, in house sparrows (*Passer domesticus*) it was shown that males performing inter-island dispersal had a lower lifetime reproductive success than resident males, caused by a combination of shorter lifespan and lower mating success. This relationship was not found for females (Pärn et al. 2009). Tarwater and Beissinger (2012) found that green-rumped parrotlets (*Forpus passerines*) primarily dispersed in a way that increased their lifetime reproductive success. Dispersal distance (within and between populations) depended on the relative individual phenotype and on the natal environment conditions (Tarwater and Beissinger 2012).

Lifetime reproductive success (LRS) can be defined as the number of recruits to the following generation that the individual produces over its entire lifespan, and is the combined result of the two key fitness components, survival and breeding success (Newton 1989). LRS is assumed to be a good fitness estimate, mainly because lifetime measures are less affected by short-term changes in individual performance or environment that affect annual measures (Newton 1989). However, it has generally been difficult to measure LRS in natural populations, because it requires long-term studies of a sufficiently large number of individuals throughout their life (Newton 1989). To obtain this data knowledge of the genetic parents of the recruits is required. In addition, the study area needs to be large enough to minimize bias in LRS caused by dispersal out of the study system (Doligez and Pärt

2008, Pärn et al. 2009). A study system consisting of 18 insular house sparrow populations in northern Norway has the necessary characteristics that make measuring of LRS and its components possible. The study has been going on since 1993 and is based on extensive capture-recapture methods, where most the individuals are individually marked (Jensen et al. 2008, Pärn et al. 2009, Ringsby et al. 1998). Because the house sparrow is a very sedentary species (Anderson 2006, Kekkonen et al. 2011, Summers-Smith 1988, Tufto et al. 2005) all marked individuals (even natal dispersers) can be followed from hatching until their death (Jensen et al. 2004, Pärn et al. 2009). Furthermore, all marked individuals are sampled for blood, and can hence be genotyped so that genetic parents of each individual can be determined with use of DNA analyses (Jensen et al. 2003). Thus, we are able to record each adult individual's reproductive output every year until its death, and thereby determine LRS (Jensen et al. 2004, Pärn et al. 2009).

In this study my aim is to examine the fitness-differences between resident and dispersing individuals and in this way increase our knowledge about the consequences dispersal has at the individual level. Specifically, I will investigate whether dispersing individuals differ from residents with respect to annual mating success (in males), annual number of eggs (in females), annual number of fledglings and recruits, lifespan and lifetime reproductive success. By examining dispersal between suitable habitat-patches within an island population this study will provide further knowledge of the dispersal process and its demographic and genetic consequences. By comparing my results with results at the inter-island level in Pärn et al. (2009) this study will be important for identifying at which geographic scale (within or between populations) dispersal will have consequences for individual lifetime fitness and its components.

Methods

Study system

The study island, Hestmannøy, is one of 18 islands in a house sparrow metapopulation study system in northern Norway (66°N, 13°E). During the study period (1993-2010), there have been nine different house sparrow sub-populations on Hestmannøy. All the sub-populations were located at or near dairy farms. In the present study I will use data from seven of the sub-populations; two of the sub-populations were located on the southern part of the island, four on the northern part of the island and one sub-populations was located between the southern and northern part of the island (Figure 1). The area of the island is 13 km^2 and it consists of a mixture of agricultural land, heath-land and mountains (Sæther et al. 1999). The northern and southern parts of the island are connected by a road at the east of the island, which are surrendered by agricultural landscape. The area between the northern and southern sub-populations is also dominated by the two mountains Hestmannen (571 MASL) and Ambota (318 MASL) and heath-land.

Study species – House sparrow

The house sparrow is a small passerine bird about 14–16 cm long, with a global distribution (Anderson 2006, Svensson et al. 1999). The species is sexually dimorphic; the female is the less colourful sex with dull brown colour and whitish belly. The male is black around the eye and lores and has a black badge underneath the bill. The wings are chestnut with a broad white bar, and the crown of the head is dark grey (Summers-Smith 1988, Svensson et al. 1999). The species is highly sedentary, associated with human habitations and farms, and usually remain near the place of birth the whole life (Anderson 2006, Kekkonen et al. 2011, Pärn et al. 2009, Summers-Smith 1988, Tufto et al. 2005). Breeding dispersal is very rare, whereas natal dispersal is more frequent (Anderson 2006, Pärn et al. 2009, Pärn et al. 2012, Summers-Smith 1988). In my house sparrow study system the proportion of recruits that have carried out natal dispersal between islands is approximately 10% (Pärn et al. 2009).However, the dispersal distance is generally short and most individuals that disperse breed a few kilometres from their place of birth (Anderson 2006, Kekkonen et al. 2011, Tufto et al. 2005). The house sparrow is a social species also outside the breeding season, when they show communal roosting and feeding or dust and water bathing (Summers-Smith 1988). In the study area the breeding season lasts from early May to mid-August and the

birds can lay up to three clutches per season, with a mean clutch size of five eggs (Husby et al. 2006, Ringsby et al. 2002). The male house sparrow selects a potential nest pace before he starts to attract females. Females then select nest palace based on their response to vocalizing and displaying males (Anderson 2006). The house sparrow can reproduce and recruit into the breeding population in their second calendar year (Altwegg et al. 2000, Anderson 2006, Jensen et al. 2008, Pärn et al. 2009).

Field work

Individual information has been recorded for adults, fledged juveniles and nestlings each year since 1993 (Jensen et al. 2004, Ringsby et al. 2002).This was done during the breeding season (see above) and for approximately one month between the end of September and the beginning of November. The house sparrow and its nests are easily located on the island due to the fact that they live and breed in barns and nest boxes. The island was searched for active nests at least once a week during the breeding season and active nest were then visited 2-3 times during the incubation period to count eggs and determine day of hatching (Kvalnes et al. 2012). 25µL blood was collected from the nestlings' brachial vein when they were 8-12 days old (nestlings were then defined as fledglings), and they were banded with a numbered metal ring and a unique combination of plastic colour leg rings. Fledged juveniles and adult birds were captured during the summer and autumn, using mist nets. Any unmarked individuals were sampled for blood and marked (as described above) at first capture. The extensive capture and ringing protocol resulted in a very high proportion (> 90%) of birds being individually recognizable on the study island (Jensen et al. 2008, Pärn et al. 2009, Ringsby et al. 1998).

Dispersing individuals were in my study defined as those individuals that were marked as nestlings at one habitat patch and then performed intra island dispersal and recruited and produced at least one nestling at any of the other habitat patches. Similarly, resident individuals were marked ad nestlings at one habitat patch and then recruited and produced at least one nestling at the same habitat patch. A bird's lifespan was defined as the number of years from hatching to the last time it was recaptured or observed as this year is assumed to be the last it was alive.

Laboratory work

I used genotype of nestlings and potential parents on Hestmannøy during the years 1993-2008 to determine genetic parenthood. The information about genetic parenthood of nestlings was then used to determine individual mating success and reproductive success. The genetic parenthood analyses started with automated DNA extraction which was carried out on a Beckman Coulter NXp pipetting robot (Beckman Coulter, USA) using a Relia Prep Large Volume HT gDNA Isolation System (Promega, USA) procedure optimized for use with house sparrow blood samples. The DNA was then available for PCR-amplification, and individual genotypes was determined by using 15 microsatellite loci; Ase18 (Griffith et al. 2007), Pdoμ1, Pdoμ3(Neumann and Wetton 1996), Pdoμ5 (Griffith et al. 1999), Pdo10 (Griffith et al. 2007), Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo33, Pdo40, Pdo44, Pdo47 (Dawson et al. 2012).The PCR amplification was executed on Applied Biosystems GeneAmp PCR system 9700 PCR machines (Applied Biosystems, USA). Ase18, Pdoμ1, Pdoμ3, Pdoμ5, Pdo10, Pdo33, and Pdo40 was multiplexed with the avian sex-determination primers P2 and P8 (Griffith and Stewart 1998) in multiplex Panel1, whereas Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo44 and Pdu47 was multiplexed in multiplex Panel 2. Included in each reaction mixture (10μL) was 5μL 2x QIAGEN Multiplex PCR Master Mix (QIAGEN Inc, USA), 5μL MilliQ H2O, 0.09-0.26μM of each primer, and approximately 20ng of genomic DNA. For both multiplex panels PCR was carried out using a touchdown profile: first a denaturing step at 94^oC for 15 minutes followed by 12 cycles at 94^oC for 30 seconds, an annealing step initially at 62^oC for 30 seconds (successively reduced by 1^oC for each cycle); and an elongation step at 72^oC for 60 seconds. Following this there was 19 cycles with 94^oC for 30 seconds, 50^oC for 30 seconds and 72^oC for 60 seconds. Finally, the PCR machine was run for 5 minutes at 60^oC, and the PCR-product was kept at 4^oC. For each sample, 1μL of the PCR products in a multiplex panel was mixed with 0.5μL of a size ladder (GeneScan LIZ 600, Applied Biosystems, USA), and 10μL Hi-Di Formamide solution (Applied Biosystems, USA). Separation of PCR products was by electrophoresis in an automated 16 capillary electrophoretic analysis system: ABI Prism 3130xl Genetic Analyzer (Applied Biosystems, USA). Alleles were visualized by fluorescently labeling the forward primer, either with FAM (Pdoμ1, Pdoμ5, Pdo19, Pdo22, Pdo44), NED (P2P8, Pdoμ3, Pdo16, Pdo27, and Pdo33), VIC (Ase18, Pdo10, Pdo32, Pdo40 and Pdo47) or PET (Pdo17).

Genotypes of all individuals on the microsatellite loci were scored using the software package GENEMAPPER 4.0 (Applied Biosystems, USA). Then the software CERVUS 3.0 (Kalinowski et al. 2007, Marshall et al. 1998) was used to determine parenthood and constructing genetic pedigrees. Further information on the genotyping and pedigree construction procedures can be found in Billing et al. (2012), Jensen et al. (2003, 2004, 2007, 2008) and Engen et al. (2007).

After genetic parenthood of individual nestlings was determined the different individual fitness components were calculated. Male mating success was defined as the number of mates a male sired nestlings with in a given breeding season. The number of eggs produced by females was calculated as the sum of the clutch size of the clutches where a female was genetic mother. Annual reproductive success was measured as 1) the number of fledglings and 2) the number of recruits (i.e. the number of offspring that survived to their second calendar year). Lifetime reproductive success was defined as the total number of recruits an individual produced across its lifetime.

Statistical analyses

Data on residents and dispersers from cohort 1993 to 2008 and their genetic parenthood of nestlings from the breeding seasons 1994 to 2008 was used in analyses of reproductive success. Reproductive success was analysed by fitting generalized linear mixed-effects models using the lme4 package in R (Bates et al. 2012). Annual number of mates was analysed as a binomial variable: one mate vs. more than one mate, and analysed with a binomial error and a logit link. In models of annual number of eggs, fledglings, recruits and LRS (count data) a Poisson error and a log link function were used. The explanatory variables (coded as fixed factors) included in the model were sex and whether the individual was a resident or a disperser. Hatch year of each individual was included as a random factor to account for possible cohort effects affecting reproductive output. Because reproductive information was recorded for birds over several years, the individual identity number was also included as a random factor, to avoid any potential problems due to pseudoreplication.

To quantify the predictive ability of each model I calculated Pearson's correlation (r^2) between the predicted values derived from the model and the observed values (Pärn et al. 2012, Zheng and Agresti 2000).

In analyses of lifespan I used data on individuals from the cohorts 1993-2007, and their recapture and observation-information until (and including) 2010. Lifespan was analyzed by fitting a coxph proportional hazard model in the survival package in R (Therneau 2012). An individual that was recorded as alive in 2009-2010 was classified as censored, to account for the possibility that these individuals could still be alive after the end of the study period. One model was then fitted for each sex, with the dispersal category as an explanatory variable (coded as fixed factor). To test whether the dispersal category explained any significant variation in lifespan, I carried out a χ^2-test as explained above. After testing each sex separately, both sexes were analysed together to examine whether the effect of dispersal category on lifespan differed between the sexes.

Three individuals (two males and one female) were registered in 2009 and 2010. Because data on genetic parenthood were not available for these years these individuals were excluded from the analyses of LRS in order to avoid a potential downward bias in their LRS. Individuals that were breeding in 2008 but then not recaptured or observed in 2009 and 2010 were, considering the high recapture rate on the island, treated as dead (Jensen et al. 2004, Pärn et al. 2009, Ringsby et al. 1998). They were consequently included in the LRS analyses. To test for differences between resident and dispersing males and females with respect to different reproductive measures a χ^2-test was carried out between models with and without dispersal category as an explanatory variable. After testing the sexes separately I tested for an interaction between dispersal category and sex to examine whether the effect of dispersal category on annual production of fledglings and recruits differed between sexes. The LRS analyses were carried out in the same way, for each sex separately and then together with an interaction term.

All statistical analyses were conducted using the statistical software R, version 2.15.1 (R Core Team 2012) and the descriptive statistics of the various fitness component are presented as mean ± 1 standard deviation (SD).

Results

Of 116 individuals with known natal sub-population, and that were genetic parent of at least one offspring, 69 individuals (33 males, 36 females) had performed natal dispersal. 38 individuals (27 males and 11 females) were resident and bred on the same farm that they hatched. 9 individuals (5 males and 4 females) that dispersed to a new habitat patch but later returned to their natal patch were excluded from the analyses. There was significantly more dispersal among females than males (β=0.48± 0.14, z=3.45, p=0.022). Most (59.4 %) of the dispersing individuals remained within their natal part of the island (i.e. within the northern, southern or middle parts; Table 1). Among the individuals that dispersed to the other part of the island, 9 dispersed from north to south while 16 dispersed from south to north (Table 1). Furthermore, the three individuals that hatched at the middle sub-population dispersed to the northern part of Hestmannøy (Table 1). There were individuals emigrating from all sub-populations, and all sub-populations except 12 and 24 had individuals that remained resident (Table 1). Most of the immigration was to three of the sub-populations: 21 (27%), 23 (23.9%), and 26 (25.4%).

Annual reproductive success

In males the annual number of mates did not differ significantly between dispersers (1.30±0.94) and residents (1.05±0.22, Table 2). Annual production of fledglings tended to be higher for dispersing males (3.14± 2.69) than for resident males (2.27±1.52, Table 2). The mean annual production of recruits also appeared to be higher for dispersing males (0.58±1.02) than for resident males (0.37±0.77). The difference was however not statistically significant (Table 2).

Resident females produced on average 5.70 (±2.93) eggs annually while dispersing females produced on average 7.76 (±4.10) eggs per year. However, the difference was not statistically significant (Table 3). The annual production of fledglings for resident females (3.82 ±1.61) and dispersing females (4.27±2.32) was not significantly different (Table 3). On the other hand, dispersing females tended to produce more recruits (0.84±1.15) than resident females did (0.29±0.59, Table 3).

When analyzing the sexes together there was no significant interaction between the dispersal category and sex in annual production of fledglings (χ^2=1.74, df=1, p=0.187), suggesting the same general relationship within the two sexes. After removing the interaction from the model, the difference between resident and dispersing individuals with respect on annual production of fledglings was almost statistically significant (χ^2=2.89, df=1, p=0.089, Table 4, model r^2=0.26). Similarly, annual production of recruits showed no interaction between dispersal category and sex (χ^2=0.22, df=1 p=0.637). However, when the interaction was removed from the model the number of recruits differed significantly between resident and dispersing individuals (χ^2=5.06, df=1, p=0.024, Table 4; model r^2=0.70). Hence, when both sexes were analysed together the dispersing individuals showed significantly higher annual production of recruits (0.49± 0.99) compared to resident individuals (1.13±1.72, Table 4, Figure 2).

Lifespan

The lifespan of males ranged from one to nine years. The mean lifespan for resident and dispersing males was 1.89 (±1.12) and 2.30 (±1.49) years, respectively. The hazard for dispersing males seemed lower than for resident males, indicating higher survival, of dispersing males (β=-0.25±0.27, Figure 3).The difference in lifespan between resident and dispersing males was however not significant (p=0.354). In females the lifespan ranged from one to seven years. Mean lifespan for resident females was 1.90 (±0.83) years, while it for dispersing females was 2.22 (±1.84). The hazard for dispersing females was lower than for resident females (β=-0.16±0.35, Figure 4), but the difference was not significant (p=0.641).

Lifetime reproductive success

Among the 58 males included in the LRS analyses, LRS ranged from zero to four. Most males (34 of 58 males) did not produce any recruits during their lifespan. The mean LRS of resident males was 0.54 (±1.10), while it was 0.87 (±1.18) for dispersing males. The difference in LRS between resident and dispersing males was not significant (p= 0.186, Table 3). For the 46 females in the LRS analyses, LRS ranged from zero to eight. As for males, most of the females produced no recruits (24 of 46). The mean LRS of resident females was 0.36 (±0.67) while it was 1.37 (±2.09) for dispersing females. The difference between resident and dispersing females was significant (p=0.005; model r^2=0.60) and showed that dispersing females

performed better than resident females do when it comes to lifetime reproductive success (Table 4).

When males and females were analysed together the interaction between sex and dispersal on LRS was not significant (p=0.230), suggesting the same general relationship within the two sexes. When the interaction was removed from the model dispersing individuals performed significantly better when it comes to LRS than resident individuals (χ^2=8.38, df=1, p=0.004; model r^2=0.47, Figure 5).

Discussion

This study suggests that LRS is higher for dispersing individuals than for residents when the sexes are analysed together (Table 4, Figure 5). This result seems to be generated mainly by a relationship between LRS and dispersal within females rather than for males (Table 2 and 3). In analyses carried out for each sex separately the difference was however only significant for lifetime reproductive success in females (Table 3). The lack of statistically significant differences when the sexes were analysed separately may partly be explained by the smaller sample size compared with the analyses of the sexes together. Small sample size increases the probability for making both type I and type II errors (Walpole et al. 2012). When males and females were analysed together dispersers produced significantly more recruits both annually and across the individuals' total lifetime (Table 4, Figure 2 and 5).

Results from this study contrasts with what was found when Pärn et al. (2009) studied inter-island dispersal in house sparrows in the same insular metapopulation, where dispersing males was found to have a much lower fitness than resident males, while no such relationship was found for females. Based on this, it is likely that dispersal distance and scale (within or between populations) has an impact on the fitness consequences for dispersing individuals. Differences in LRS between individuals that have dispersed on different scales are also shown for other bird species (Forero et al. 2002, Hansson et al. 2004, Tarwater and Beissinger 2012). Great reed warblers (*Acrocephalus arundinaceus*) males that carried out between-populations dispersal had a lower LRS than both within-populations dispersing and resident males, while short-distance females recruited more offspring per year than both long-distance dispersing and resident females (Hansson et al. 2004). Black kites (*Milvus migrans*) females that dispersed different distances did not differ in LRS, while males that dispersed shorter distances had a higher LRS than resident and long-distance dispersing males (Forero et al. 2002). Long-distance dispersal is assumed to be more costly due to higher cost of locomotion and risks associated with hostile habitat, which may lack shelter and resources and contains predators (Matthysen 2012). The different pattern in LRS for intra and inter-island dispersal in house sparrow may then be caused by the exceeded costs of dispersing longer distances in hostile habitat. Another reason for this may be that land and sea are different kind of barriers for the house sparrow (MacArthur and Wilson 1967).

Even though the habitat between the sub-populations on Hestmannøy may be hostile for the dispersing individuals; it contains at least some sort of shelter and resources. Inter-island dispersing house sparrow on the other hand, do not have access to shelter or resources in the transfer stage of the dispersal process. Based on the relatively high proportion (Table 1) of house sparrow that disperse between northern and southern parts of Hestmannøy, the mountains and the distance between the sub-populations is less hostile for the birds than first assumed.

Higher fitness for dispersing individuals on Hestmannøy (Table 4) and the relatively high proportion of dispersing individuals (Table 1) may be explained by the short distance between the sub-populations on both northern and southern part of Hestmannøy. In the late summer and autumn the house sparrow tends to move more around and longer away from their sub-populations (Anderson 2006, Myhre 2012). The individuals, especially the juveniles, might then gather information on quality of neighboring habitat patches, in terms of food availability, nest places and population density. This information can be used to decide whether to stay resident or to disperse to a new sub-population in a way that will increase the individuals' fitness (Clobert et al. 2009). Green-rumped parrotlets was shown to disperse in a way that increased their fitness. The decision of dispersal scale, or not to disperse at all, was made based on the environment condition and their phenotype and competitive ability (Tarwater and Beissinger 2012). Early hatched individuals on Hestmannøy are showed to be those that are most likely to disperse compared with individuals born later in the season (Myhre 2012). Early born individuals have more time to search for a suitable sub-population and may hence choose to disperse and increase their fitness.

Dispersing males on Hestmannøy tend to have higher annual number of mates than resident males (Table 2), and this resulted in a tendency that dispersing males annually produced more fledglings and recruits. Male house sparrows select a potentially nest place before he start to attract females with repeated vocalisations and displays (Anderson 2006). Resident males are therefore normally assumed to have an advantage over dispersing males due to the familiar habitat and information about nest places and quality. Lower numbers of mates

for dispersing males have also been shown for great reed warbler (Hansson et al. 2004) and inter-island dispersing house sparrow males turned out to have lower mating success than resident males (Pärn et al. 2009). The house sparrows lives in loose colonies both in the breeding season and the rest of the year and there may be a dominant hierarchies in the flock (Solberg and Ringsby 1997). It has also been observed that house sparrows that nest closely tolerate neighbours but that strange birds are chased away (McGillivray 1980). The aggressiveness against dispersing individuals may then explain why inter-island dispersing individuals have lower number of mates (Pärn et al. 2009). Intra-island disperser may not be seen as strangers to resident individuals, due to the fact that the distances between most of the sub-populations are relatively short (Figure 1) and that the juveniles tend to move more around in the autumn before they settle down in one sub-population (Anderson 2006, Myhre 2012). If this is the case it may explain why dispersing males on Hestmannøy do not have fewer mates than resident males; however the positive trend for dispersing males cannot be explained exclusively from this argument without further study.

The most distinct difference in fitness between resident and dispersing individuals was found in the lifetime production of recruits (Figure 5). Because residents and dispersers did not produce significantly different numbers of fledglings but dispersers produced significantly more recruits, it may seem that a higher proportion of the fledglings that are produced by a parent that have carried out intra-island dispersal survive until recruitment than fledglings produced by resident parent. This result indicate that offspring produced by individuals that has dispersed has an advantage over offspring produced by resident individuals. One possible reason could be that offspring produced by dispersing individuals may be less inbred than those produced by resident individuals. Individuals from the same sub-populations are more likely to carry the same recessive deleterious alleles on any given loci than individuals from different sub-populations (Ingvarsson and Whitlock 2000). However, the high frequency of natal intra-island dispersal on Hestmannøy and the relatively high fitness of dispersing individuals of both sexes indicate high levels of gene flow in the population (Table 1). High levels of gene flow are associated with low levels of inbreeding. This is consistent with results from a study conducted by Jensen et al. (2007) on multilocus heterozygosity and inbreeding depression on Hestmannøy and four other islands in the

house sparrow metapopulation study system in northern Norway. The study used data from 1993 to 2002 and found that the mean level of inbreeding among fledglings on Hestmannøy was found to be nearly zero, with a mean inbreeding coefficient on 0.004 (Jensen et al. 2007). The advantages of been produced by a dispersing individual may be found elsewhere, and would be an interesting topic for future studies.

A possible explanation for the overall positive trend in LRS for dispersing individuals on Hestmannøy may be that only individuals that have produced at least one fledgling are included in the study. The exclusion of individuals that are not recorded as a genetic parent was done to make sure that the individuals were correctly defined as resident or dispersing individuals. This is a restrictive criterion for data selection, but the best way to make sure that no individuals are incorrectly defined as resident or disperser. The house sparrow is remarkably sedentary and even forages close to the breeding patch during most of the year, however in late summer and autumn the degree of movement and foraging distance increases (Anderson 2006). By including individuals that only are observed or recaptured at a habitat patch, but not known to breed at that patch, and thus wrongly defined as disperser, could have contributed to errors in the data. The restrictive data selection may have caused biased data as it is possible that the real picture includes a lot more individuals that produces zero eggs, fledglings and recruits, and do not mate successfully. Nevertheless, one conclusion can be drawn from this; among the individuals that do mate and breed successfully, dispersing individuals perform better than resident individuals.

The dispersal pattern of house sparrows between local sub-populations on Hestmannøy was consistent with other studies of house sparrow (Anderson 2006) as well as general results on dispersal in birds (Clarke et al. 1997); females were more likely to carry out natal dispersal than males. While approximately 10% of the individuals on this and neighboring islands performed inter-island dispersal (Pärn et al. 2009, Pärn et al. 2012), approximately 64% performed intra-island dispersal on Hestmannøy (Table 1). Consequently, there seems to be a considerable increase in dispersal rates within compared to between islands in the insular house sparrow metapopulation in northern Norway. Earlier results on dispersal in house

sparrow show that those individuals that disperse away from their natal habitat patch (i.e. natal sub-population), usually settle to breed within a few kilometers, and that long-distance dispersal is more uncommon (Anderson 2006, Kekkonen et al. 2011, Tufto et al. 2005). This corresponds well with the results from my study system where most dispersal occurs between sub-populations that are separated by only a few kilometers on the same island (Figure 1), but where dispersal between islands that are separated by the same or longer distances of sea is less common (Pärn et al. 2009, Pärn et al. 2012).

Comparison of the results from the inter-island dispersal study with the results of this study clearly indicates that the dispersal scale has an important effect on the individual fitness consequences of dispersal. The gene flow created by inter-island dispersing individuals turned out to be lower than expected based on the number of dispersing individuals because male dispersers had very low fitness (Pärn et al. 2009). Intra-island dispersal on the other hand turned out to result in more gene flow than expected based on the number of dispersing individuals because dispersers had higher recruit production than residents. Hence, individuals seem to benefit due to increased annual and lifetime number of recruits by dispersing between sub-populations on Hestmannøy, but perform equally good or worse than resident individuals when they disperse between different islands (depending on their sex). Inter and intra-island dispersal may hence have different ecological and evolutionary consequences in the house sparrow metapopulation. Intra-island dispersing individuals tend to contribute with gene flow and hence maintain the levels and distribution of genetic variation on Hestmannøy. Such genetic variation may be important when the population need to adapt to changes in the environment (Willi et al. 2006). The different consequences of within and between population dispersal is important knowledge if we want to understand how populations will cope with the ongoing and future habitat fragmentation and environmental changes, and should hence be an issue for future studies.

Acknowledgements

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Tables

Table 1: The number of resident (in the diagonal) and dispersing house sparrows between the different sub-populations on the island Hestmannøy; 11 and 12 are located at the southern end of the island, 21-23 and 26 are at the northern part, while 24 are located in between (see Figure 1).

Natal Patch	Breeding patch							Proportion disperser (%)
	11	12	21	22	23	34	26	
11	15	3	5	0	5	1	4	54.4
12	1	0	0	1	1	0	0	100
21	4	1	11	1	3	1	2	52.2
22	1	0	4	5	5	0	6	76.2
23	2	0	4	2	3	1	4	81.3
24	0	0	2	1	0	0	0	100
26	1	0	2	0	1	0	4	50

Table 2: Comparison of reproductive success for resident and dispersing male house sparrow on the island Hestmannøy. Reproductive success was measured as; annual number of mates, fledglings, recruits and as lifetime reproductive success. The fitness measures was analysed by fitting a glmm. Estimates ± SE for number of fledglings, recruits and LRS are on log scale, while estimates of number of mates are on logit scale.

	Resident	Disperser	
No. of mates	-2.97±0.74	1.28±0.82	X^2=2.99, df=1, p=0.084
No. of fledglings	0.73±0.14	1.04±0.12	X^2=3.36, df=1, p=0.067
No. of recruits	-1.33±0.33	-0.83±0.24	X^2= 1.76, df= 1, p=0.185
LRS	-0.67±0.32	-0.21±0.25	X^2=1.74, df=1, p=0.186

Table 3: Comparison of reproductive success for resident and dispersing female house sparrow on the island Hestmannøy. Reproductive success was measured as; annual number of eggs, fledglings, recruits and as lifetime reproductive success. The fitness measures was analysed by fitting a glmm,. The estimates ± SE are on log scale.

	Resident	Disperser	
No. of eggs	1.71±0.13	1.94±0.08	X^2=2.48, df=1, p=0.115
No. of fledglings	1.35±0.14	1.44±0.08	X^2=0.40, df=1, p=0.529
No. of recruits	-1.39±0.53	-0.47±0.21	X^2=3.28, df=1, p=0.070
LRS	-1.15±0.56	1.33±0.55	X^2=7.98, df=1, p=0.004

Table 4: Comparison of reproductive success for resident and dispersing house sparrow (sexes pooled together) on the island Hestmannøy. Reproductive success was measured as annual number of fledglings, recruits and as lifetime reproductive success. The fitness measures was analysed by fitting a glmm. There was no interaction between sex and dispersal category. The estimates ± SE for resident males and females and dispersing males and females (termed Disperser) are on log scale.

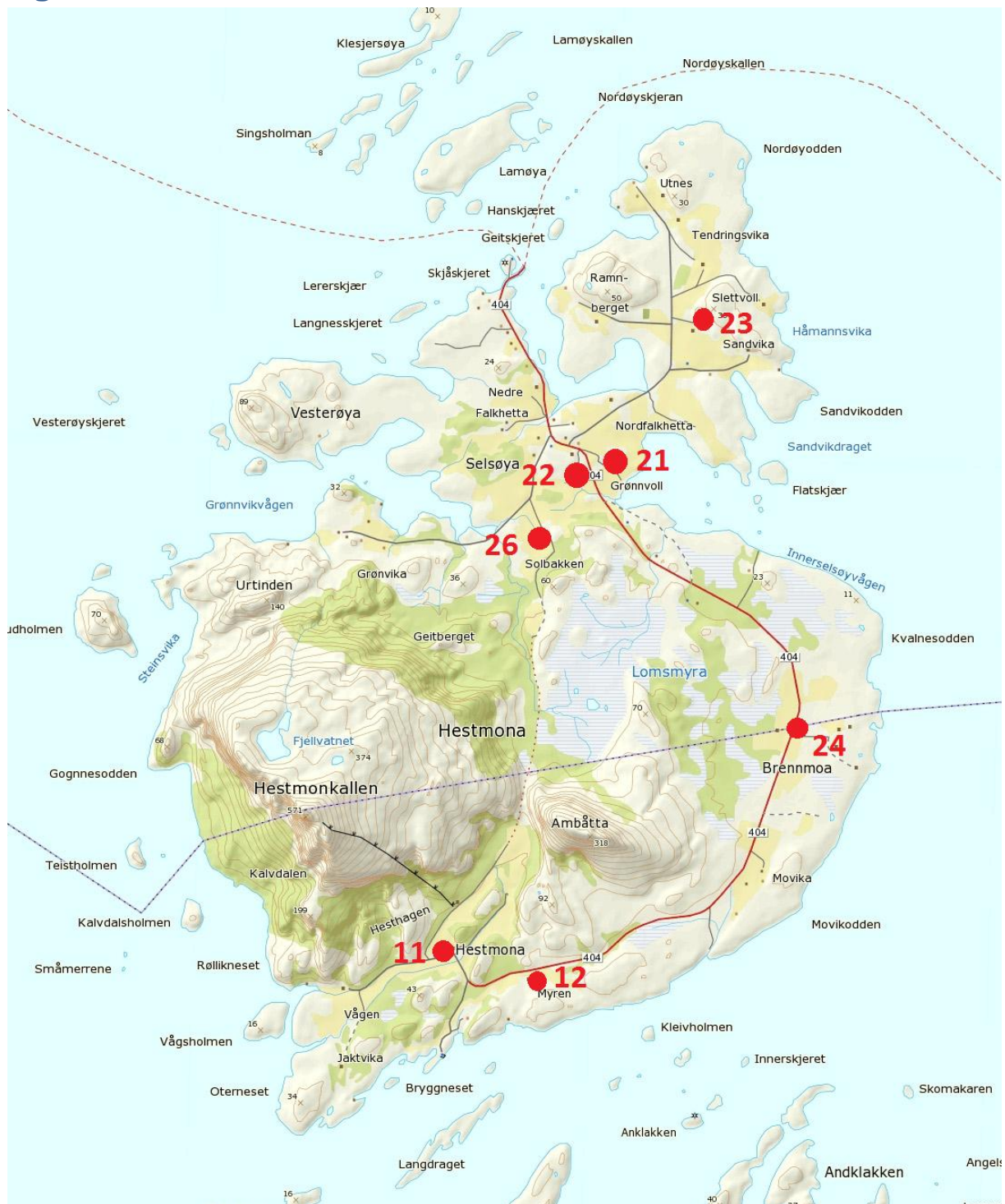|	Resident male	Resident female	Disperser	
No. of fledglings	0.944±0.077	1.329±0.076	0.197±0.114	χ^2=2.89, df=1, p=0.089
No. of recruits	-1.334±0.099	-1.100±0.338	0.658±0.308	χ^2=5.06, df=1, p=0.024
LRS	-0.957±0.303	0.404±0.224	-0.194±0.25	χ^2=8.38, df=1, p=0.004

Figures

Figure 1: The study island, Hestmannøy (13 km^2), in northern Norway (66°N, 13°E) with the seven different sub-populations of house sparrows. The habitat on the island is a mixture of agricultural land, heath-land and mountains.
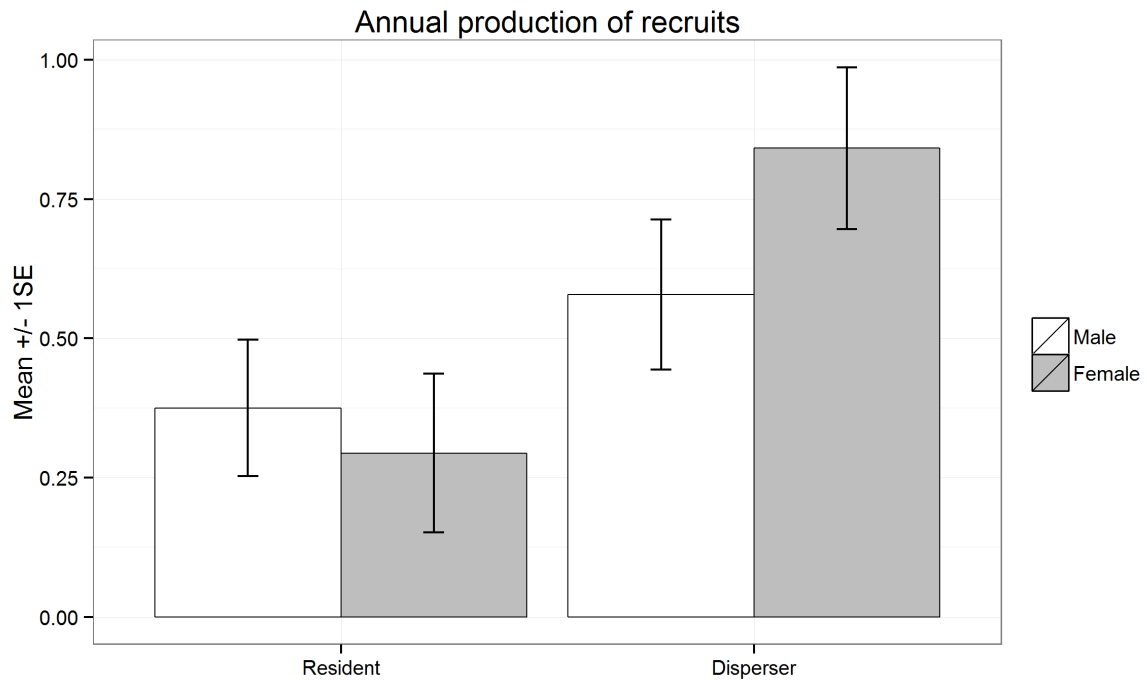
Figure 2: Annual production of recruits for dispersing and resident males and females on the island Hestmannøy.
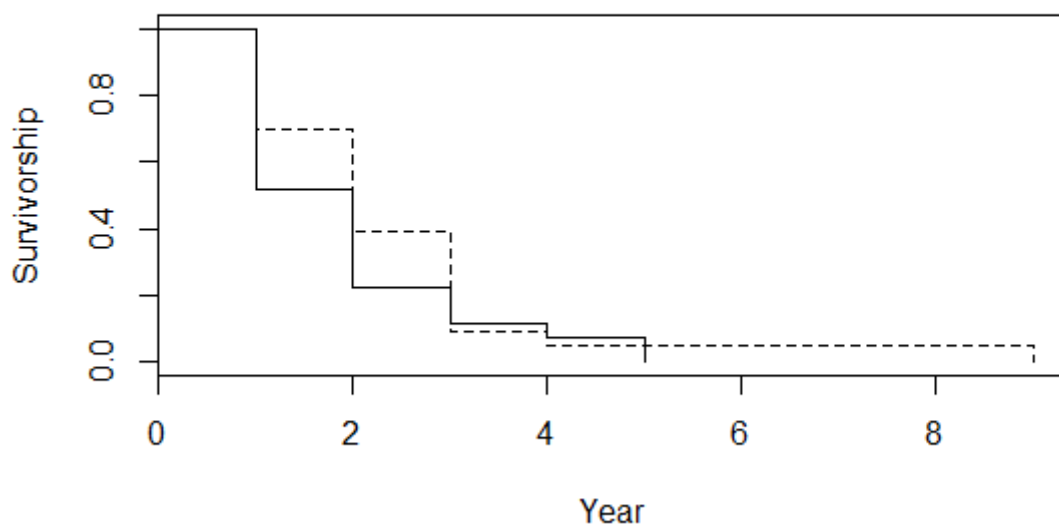
Figure 3: Lifespan for resident (solid line) and dispersing (dashed line) male house sparrows on the island Hestmannøy.
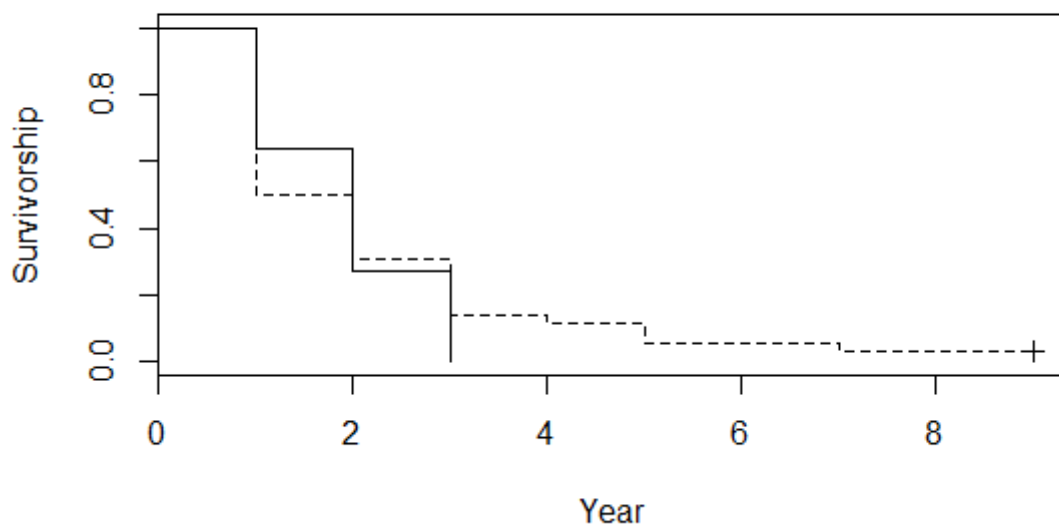

Figure 4: Lifespan for resident (solid line) and dispersing (dashed line) females on the island Hestmannøy
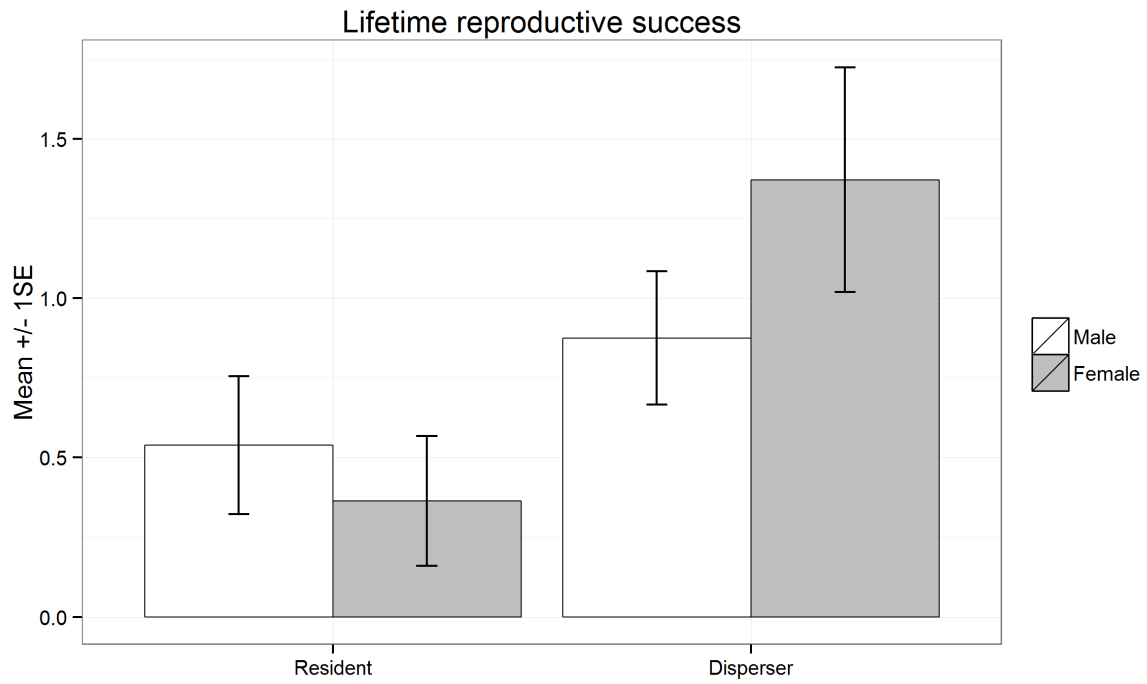
Figure 5: Lifetime reproductive success in resident and dispersing male and female house sparrows on the island Hestmannøy.