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Factors Affecting Juvenile Movement in a House Sparrow Metapopulation

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Abstract

Dispersal propensity can vary considerably between individuals in a population. Understanding which individuals disperse- and under what circumstances these individuals disperse is valuable for conservation. Factors influencing juvenile movement and natal dispersal were studied in individually marked house sparrows, *Passer domesticus*, in an archipelago off the coast of Helgeland, northern Norway. Sex, clutch size, body size and body mass did not significantly explain variation in movement. Movement rate was however negatively related to hatch date on one of the islands. Moreover, there was a decrease in movement rate with increasing patch isolation and hostility of the matrix habitat. This study suggests that habitat configuration is an important factor determining movement of juvenile house sparrows, and that the environment experienced early in life may be related to movement propensity. I strongly recommend incorporating landscape features in further analyses of movement and dispersal rate.

Key-words: dispersal, house sparrow, proximate causes, emigration, condition-dependent dispersal, patch isolation, matrix habitat, metapopulation

Sammendrag

Individer kan variere vesentlig i hvilken grad de er tilbøyelige til å spre seg. Kunnskap om hvilke individer som sprer seg, samt under hvilke forhold dette skjer er verdifull med hensyn til bevaring. I dette studiet ble faktorer som påvirker juvenil bevegelse og spredning studert hos gråspurv, *Passer domesticus*, i en øygruppe utenfor Helgeland i nord-Norge. Hverken kjønn, kull-størrelse, kroppsstørrelse eller kroppsvekt kunne forklare variasjon i spredning. Spredning var negativt relatert til klekke-dato på en av studieøyene. Videre gikk spredningsraten ned med økende grad av isolasjon og ugjestmildt habitat mellom patchene. I dette studiet foreslår jeg at habitat konfigurasjon er viktig for spredningsrate hos juvenile gråspurv. Jeg vil på det sterkeste anbefale å ta hensyn til landskapets konfigurasjon i videre studier av spredningsrate.

Introduction

Dispersal, the permanent movement between habitat patches, has important consequences for genetic variation and population dynamics (Hanski 1999; Bowler and Benton 2005; Hovestadt et al. 2011). Gene flow mediated by dispersing individuals may contribute to the local genetic variation necessary for adapting to environmental changes (Garant et al. 2007), and decrease genetic differentiation between populations. Furthermore, dispersal may regulate population size and immigration may allow populations to persist also when the recruitment rate alone is not sufficient (Hanski 2001). Dispersal is thus crucial for the distribution and persistence of populations facing environmental change, such as increasing habitat fragmentation and shifts in suitable habitat due to climate change (Bowler and Benton 2005). Dispersal behaviour of alien species will also to a large degree determine the rate at which they spread (Davis 2009). Thus, dispersal plays a central role in conservation biology and in the management of populations (Clobert et al. 2001). Despite this, dispersal remains one of the least understood processes in ecology and evolution (Bennett et al. 2001; Wiens 2001).

The dispersal process can be divided into three basic stages: (1) emigration, i.e. the departure from a patch, (2) transfer, i.e. the movement between patches, and (3) immigration, i.e. the settlement in a new patch (Bowler and Benton 2005). Costs and benefits during any of these stages may select for different dispersal behaviours. A number of empirical studies have shown that dispersal, and its costs and benefits, may depend on both the phenotype of the individual and external abiotic and biotic environmental cues (Ims and Hjermann 2001; Clobert et al. 2009), although dispersal also may partly be determined by genetic factors (Roff and Fairbairn 2001; Selonen and Hanski 2010).

One major force that selects for dispersal is to avoid local crowding and escape poor quality habitat (Enfjäll and Leimar 2009). Food is generally a limiting resource and the quality and abundance of food could thus affect emigration rate. For instance, with increased population density, the food availability often decreases, which could result in an increased emigration rate (Bowler and Benton 2005). In accordance with this, food availability has been shown to affect emigration in both insects (Kuussaari et al. 1996) and birds (Drent 1984; Kennedy and Ward 2003).

Another selective force acting for dispersal, though highly debated (see Perrin and Goudet 2001), is inbreeding avoidance (Pusey and Wolf 1996). Sex-biased dispersal may be one way

to avoid mating with close relatives (Perrin and Goudet 2001). The sex that should disperse depends on costs and benefits of dispersal, which often differ between the sexes (Greenwood 1980). In birds, males commonly defend resources that are needed to obtain a mate, such as territories or nest sites. Therefore, benefits from familiarity and prior residence of the breeding site may be higher for males than for females. Females, being the choosy sex, may benefit from dispersing through increased access to mates and resources. Accordingly, female biased dispersal is common in birds (Clarke et al. 1997).

Third, dispersal may be an ultimate means to avoid kin competition. Leaving the natal patch, where it is likely that competitors are relatives, will increase inclusive fitness (Hamilton and May 1977). Hence, dispersal may depend on the number of siblings (i.e. brood size) (Kisdi 2004), and this has been documented in several empirical studies (Lambin et al. 2001; Kisdi 2004). A relationship with brood size can also be expected if number of siblings affects nestling growth rate and thereby influences condition-dependent dispersal (see Shutler and Clark 2003). For instance, if individuals with reduced growth rate are more likely to originate from large broods, such individuals may become weaker and subordinate and more prone to emigrate. Effects of brood size on dispersal has for example been found in the marsh tit, *Parus palustris* (Nilsson 1989), and red-cockaded woodpecker, *Picoides borealis* (Pasinelli and Walters 2002), where dispersal probability was positively related to number of siblings.

The phenotype of an individual may affect costs and benefits during all three stages of dispersal and may influence the dispersal propensity between individuals (i.e. phenotype dependent dispersal). There is substantial empirical evidence indicating that dispersers and residents differ in various phenotypic traits, such as physiology, social status, aggressiveness, and morphology (Ims and Hjernmann 2001; Clobert et al. 2009; Cote et al. 2010). For example, initiation of dispersal may be dependent on a certain amount of metabolic reserves, or morphological specialization might be necessary to successfully perform the transience between patches (Clobert et al. 2009). This is true for many insect species where a particular body shape and strong wing muscles are needed for long-distance dispersal (Zera and Denno 1997). A large body size may also reduce the energetic costs and mortality during transfer between patches and enhance settlement success in the new patch (Clobert et al. 2009). Hence, larger body size and better body condition of dispersers have been reported in a wide range of species (e.g. Fleischer et al. 1984; Kuussaari et al. 1996; Gundersen et al. 2002; Barbraud et al. 2003). On the other hand, if philopatry is beneficial, weaker subordinate individuals in poor condition, or less aggressive individuals, may be forced to emigrate by

larger, more dominant individuals (Bonte and de la Pena 2009; Cote et al. 2010), or voluntarily emigrate by the recognition of low survival probability within their natal patch (Barbraud et al. 2003). Accordingly, smaller body size led to increased emigration rate in the Atlantic salmon, *Salmo salar* (Einum et al. 2012), and great tit, *Parus major* (Drent 1984).

The condition and behaviour of an individual - traits that may affect dispersal - may be influenced by environmental factors acting during early stages of the ontogeny (Massot et al. 2002; Cote et al. 2010). If there is a seasonal variation in environmental quality, such as food availability or temperature (Wiens 2001), time of birth will affect the natal environment experienced by an individual, which in turn may influence its dispersal propensity later in life (Verhulst et al. 1997; Ims and Hjermmann 2001; Bowler and Benton 2005). Natal environmental conditions may either function as a direct cue, or indirectly by causing some phenotypic change (Ims and Hjermmann 2001; Cote et al. 2010). Depending on how the phenotype is affected by time of birth, and how dispersal behaviour is affected by a particular phenotype (see above), different relationships between time of birth and dispersal are expected. For example, if environmental conditions early in the breeding season are poor, and staying in the natal patch is beneficial, then early born individuals in poor body condition may be forced to emigrate by later born individuals in better body condition, causing a negative relationship between dispersal and time of birth. Both positive (e.g. Dhondt and Huble 1968; Drent 1984; Nilsson 1989; Spear et al. 1998) and negative (e.g. Nilsson 1989; Verhulst et al. 1997; Altwegg et al. 2000) relationships between time of birth and dispersal have been found.

Age-dependent dispersal can also lead to a relationship between time of birth and dispersal. For example, late born (i.e. young) individuals may be subordinate and forced to disperse by older, more dominant individuals (Pocock et al. 2005), causing a positive relationship between time of birth and dispersal.

In addition to the factors above, landscape characteristics such as patch size, isolation and configuration, as well as the matrix habitat are major determinants of dispersal (Ims 1995; Wiens 2001). The fact that patch occupancy should decrease with increasing isolation and decreasing patch size are well known expectations from metapopulation theory (Hanski 1999). This is due to the expectation that immigration rate to a given patch decreases with patch isolation, while emigration rate increases with a decrease in patch size, possibly caused by a larger edge:area ratio in smaller patches (Ims 1995; Andreassen and Ims 2001). Furthermore, lower dispersal rate is expected when the matrix habitat is inhospitable (Ims and

Hjermann 2001; Wiens 2001). In addition to the wide theoretical support for the existence of such effects, empirical evidence for an effect of landscape characteristics on movement and occupancy is widespread (see Ims 1995; Hanski 1999). For example, forest bird movements were constrained in fragmented landscapes (Belisle and Desrochers 2002). Similarly, increased isolation decreased dispersal in the silver-spotted skipper butterfly, *Hesperia comma* (Hill et al. 1996), and decreased the likelihood of occupancy in the brown kiwi, *apteryx australis mantelli* (Potter 1990) and the koala, *Phascolarctos cinereus* (McAlpine et al. 2006). In the Glanville fritillary butterfly, *Melitaea cinxia*, emigration rates were higher from patches surrounded by an open landscape (Kuussaari et al. 1996). Landscape features may also interact with non-spatial factors in its influence on dispersal (Ims 1995). Thus, if for example emigration rate is expected to increase with population density, it may be reasonable to predict that this effect may be more pronounced in less isolated populations.

Here, I use data from an insular house sparrow, *Passer domesticus*, metapopulation. Due to the house sparrow's obligate commensalism with humans (Anderson 2006) they are easy to locate, catch and observe. This characteristic also makes it unproblematic to determine the distribution of inhabitable patches for the species. These characteristics make the species highly suitable for mark-resighting studies.

The purpose of this study was to investigate causes of- and factors influencing within-island juvenile movement using the house sparrow metapopulation as a study system. The study was conducted during the period when natal dispersal (i.e. permanent movement away from place of birth) is commonly initiated in the house sparrow. Thus, the data obtained can be related to the emigration phase of natal dispersal, and I was able to discuss my results with respect to this process.

A previous study on causes of dispersal in the same study area focused on dispersal between islands (Altwegg et al. 2000). However, there may be different forces acting on dispersal behaviour at different scales (Ronce et al. 2001; Bowler and Benton 2005). As a consequence, other factors may be important on the smaller geographic scale (i.e. within islands) which was the focus of study.

One major methodological problem in studies of dispersal, particularly in mark-recapture studies, is dispersal out of the study area leading to truncated and biased estimates of dispersal rate and distance (Noordwijk 1984; Turchin 1998; Doligez and Pärt 2008). In this study, I will avoid such problems by using data from a study area that is large compared to the dispersal

range (Tufto et al. 2005), minimizing the bias in dispersal rates. Furthermore, a high proportion of the individuals are marked and the resighting rate is equal between residents and immigrants. Hence, this study system is highly suitable for analysing dispersal- and movement patterns using a mark-recapture approach (see Altwegg et al. 2000; Pärn et al. 2009; 2012).

To investigate factors influencing juvenile movement during the dispersal phase, I examined the effect of several traits known to have affected natal dispersal: (1) *Sex*: In the study area, inbreeding level is relatively high and has negative fitness consequences (Jensen et al. 2007; Billing et al. 2012). Dispersal could therefore be an inbreeding avoidance mechanism in this system. In addition, the cost of dispersal seems to be high for male house sparrows (Pärn et al. 2009). Thus, I expect movement rate to be female-biased. (2) *Clutch size*: Although clutch size did not affect between-island dispersal in this study-system (Altwegg et al. 2000), it could be important at a smaller geographic scale. According to predictions from kin competition theory I expect individuals from large clutches to be more prone to move away from natal site. A similar prediction can be derived from the hypothesis of brood-size dependent growth and negative condition-dependent dispersal. (3) *Hatch day*: In the beginning of breeding season, the conditions for nestlings and fledglings can be energetically demanding due to low temperatures and low insect availability in the study area. Accordingly, a previous study suggested that early born individuals were smaller and in poorer condition, at least in some years (Ringsby et al. 1998). Under a hypothesis of negative condition-dependent dispersal, I thus expect early born individuals to move more. (4) *Morphology*: If subordinate individuals are forced to disperse, which is not unlikely in a sedentary species (suggesting great costs of dispersal), it follows that smaller and lighter individuals should have a higher probability to disperse. Thus, and in accordance with the prediction from negative condition-dependent dispersal, I expect a negative relationship between movement away from natal site and fledgling size and -mass. (5) *Landscape characteristics*: In the study area, two basic types of islands can be defined: Farm islands, and non-farm islands (see Methods section). On the former, juvenile sparrows have access to considerable amounts of food at their natal patch, while on the latter food is more evenly distributed throughout a homogenous habitat. Thus, if low food availability increases foraging distance, I expect more movement on non-farm islands. Furthermore, the islands differ in the degree of patch isolation and configuration of matrix habitat (see Methods section). Thus, I also expect more movement to occur between less isolated patches separated by hospitable matrix habitat.

This study will contribute to our knowledge about the factors affecting juvenile movement and natal dispersal. Understanding causes of variation in individual propensity to disperse as well as environmental dependence of dispersal is valuable in species conservation.

Materials and methods

STUDY SPECIES

The house sparrow is a small, sedentary passerine bird with a global distribution (Anderson 2006). It is a highly social species that breeds in small colonies, forages in flocks and forms large, communal roosts. In addition, it lives in close association with human habitations, and mainly nests in crevices on buildings and other man-made constructions, and nest boxes (Anderson 2006).

The adult house sparrow is sexually dimorphic where males have a more striking plumage than females. Males have a black throat patch (“badge”), a white postocular spot and a more colourful postocular stripe. The back and rump are grey-brown with black streaked scapulars. Females have a pale throat, no white postocular spot, a drab postocular stripe, and are dull brown above except for some darker streaking (Summers-Smith 1988; Anderson 2006). The plumage of fledglings resembles an adult female, though it tends to be paler. The juveniles can also be distinguished from adult females by the much more yellow and fleshy lobe at the base of the bill, a thicker and smoother tarsus, and a more “fluffy” plumage. About one month after fledging, the juvenile house sparrow undergoes a complete moult and begins to display a sexually dimorphic plumage (Anderson 2006).

During late summer and early autumn the juvenile house sparrows gather in large flocks and search the nearby area, resulting in some settling in a patch away from their natal patch, i.e. they perform natal dispersal (Fleischer et al. 1984; Anderson 2006). In general, the dispersal rate is low and the dispersal distances short in the species (Anderson 2006). In the study area about 10 % of the juveniles disperse between islands, and breeding dispersal between islands is virtually zero (Altwegg et al. 2000; Pärn et al. 2009) which agrees with previous studies elsewhere (Fleischer et al. 1984; Anderson 1994; Anderson 2006).

STUDY AREA

The data was collected from an insular house sparrow metapopulation at the coast of Helgeland in northern Norway (66°N, 13°E; Figure 1) during summer 2011. The study area consists of 18 small islands which can be divided into two major types that differ in the spatial configuration of breeding sites and in terms of food and shelter. On one set of islands, henceforth called farm islands, the house sparrows mainly live in small, discrete colonies at dairy farms, where they breed, forage and find shelter. A small number of the sparrows on one of these islands (Hestmannøy) breed in nest boxes on houses next to a feeding station in one specific area away from the farms. In contrast, on another set of islands, henceforth called non-farm islands, the sparrows do not breed in discrete colonies, but breed in nest boxes that are evenly distributed in small villages, and they forage at bird feeders and in gardens in a more or less continuous habitat in the villages. Due to some of the differences in properties between farm and non-farm islands, they may reflect high- and low quality habitat for the house sparrows, respectively (Pärn et al. 2012). In this study, individual within-island movement was closely monitored (see below) on two farm islands (Hestmannøy and Gjerøy; Figure 2 a,b) and two non-farm islands (Træna and Selvær; Figure 2 c,d). These four islands were chosen because a large proportion of the individuals are banded as nestlings, and thus their natal site is known with certainty. In addition, the islands differ in the spatial distribution of habitable patches. As mentioned above, on the two non-farm islands, the sparrow habitat is more or less homogenous and is not larger than for a sparrow to search the whole area during a day of foraging. On one of the farm-islands, Gjerøy, there are two dairy farms, separated by 2200 m, and a hostile matrix habitat. On the other farm-island, Hestmannøy, there are four dairy farms, in addition to the area around the feeding station. The mean distance between these patches is 1670 m (range: 308 m - 3820 m). However, one farm is highly isolated by distance (and matrix habitat) from the others, and the mean distance between the remaining patches is 785 m (range: 308 m - 1440).

FIELD WORK

Field work was carried out 1st May - 28th September 2011. In the study area, the breeding season lasts from early May to mid-August (Ringsby et al. 1998) and the house sparrow lays 1-3 clutches each season. In this study, I investigated movement of juveniles with known natal sites only, i.e. they had been followed from the nestling stage. During the breeding season, the study islands were searched for new nests and clutches at least once a week. On

the non-farm islands, the UTM-coordinates of each nest were determined to the nearest meter using the online map provided by “Statens kartverk” (UTM zone 33N). On the farm islands, coordinates of individual nests were not determined. Instead I used one coordinate for each colony as a position for the natal site.

During incubation, each nest was visited 2-3 times. Hatching day was estimated from nestling age at the first visit after hatching. Clutch size was estimated as the maximum number of offspring recorded for each clutch.

When nestlings were 8-12 days they were marked with a numbered metal ring (provided by Stavanger Museum, Norway) and a unique combination of three coloured plastic rings. A small (25 μ l) blood sample was taken (not used in this study), and fledgling morphology was measured. Tarsus length was measured with a slide calliper to the nearest 0.1 mm, wing length with a ruler to the nearest mm, and body mass to the nearest 0.1 g using a 50 g Pesola spring balance. All morphological measurements were standardized to the age of 11 days, by using the residuals from a quadratic regressions of the focal trait on age (see Ringsby et al. 1998).

Throughout the whole field period, sparrows were also captured using mist nets. Captured birds were measured (see above) and a faecal sample (not used in this study) and a blood sample (not used in this study) were collected.

Sex was recorded both for captured individuals and during observations (see below). However, sex determination of juveniles before onset of moult may be difficult (see above). Whenever sex differed between registrations, sex determined at capture was generally considered to be more reliable than sex determined during observations. However, sex determined during observations were considered more reliable when capture was done at a young age, and all subsequent observations (>2) suggested the other sex, and when the only capture was carried out by an inexperienced fieldworker and all other observations (>2) suggested the opposite sex. Furthermore, observations at an older age were generally considered to be more reliable than those at a younger age. However, if the sex registered at the last observation differed from the preceding observations, the last observation was considered to be incorrect.

Observations of colour-ringed individuals using telescope were performed twice a week on each of the four study islands, and on the same weekdays (Mondays and Fridays). On each

observation day, one person visited the two non-farm islands and one person visited the two farm islands. The time of the day of observations on a particular island was alternated before and after noon to avoid bias in observation rates due to diurnal variation in activity patterns of the sparrow (Summers-Smith 1963). On the farm islands the observation effort on each colony was 1.5 - 2 hours. On one of the islands, Hestmannøy, the total population size was larger than on the other islands. Therefore, to ensure approximately the same observation effort in relation to population size on each island, one additional day per week was spent on observations on Hestmannøy. The UTM-coordinates of each observation were determined to the nearest 100 m using maps (see above). For the two farm islands, this corresponds to one coordinate for each colony (i.e. farm).

CALCULATION OF NET DISPLACEMENT

Net displacement (ND) was defined as the Euclidian distance between the natal site of an individual (i.e. the nest on non-farm islands and the colony on farm islands; see above) and the site of the last observation during the study period.

DATA SELECTION

On the four study islands, 289 individuals were followed from the nestling stage and then observed at least once after fledging (1339 observations). Natal dispersal in the house sparrow generally takes place from late summer and onwards (see above). Thus, there is a trade-off when determining a minimum date of last observation. On one hand, this date should be as late as possible to ensure that individuals actually have entered the natal dispersal period. On the other hand, the number of individuals excluded because they were not observed after a certain date should be minimized. In this study, I included only individuals with their last observation between 1st August and the end of the study period, 28th September, in my main set of analyses (but see Result section), which resulted in 248 juveniles (1279 observations, median: 5 observations per individual, range: 1-20).

On one of the farm islands, Gjerøy, none of the juveniles followed from nestling stage and observed at least once after fledging were observed away from their natal site ($n = 86$). Thus, individuals on Gjerøy were not included in any further analyses.

STATISTICAL ANALYSES

All statistical analyses were performed in the software R, version 2.14.2 (R Development Core Team 2012). At the non-farm islands, the relationship between net displacement and the different predictor variables (see below) was analyzed using linear models (LM), fitted with the `lm` function in the `stats` package. When inspecting the distribution of net displacement at the farm island, Hestmannøy, a large proportion of the juveniles did not disperse from their natal site (i.e. a large number of individuals with zero net displacement) and the distribution was strongly right-skewed. Consequently, inspection of residual plots after fitting linear models on the data from Hestmannøy clearly revealed that such models were not appropriate. Instead, the originally continuous response variable (net displacement), was transformed to a binary variable: either an individual had remained in its natal colony (0), or it had moved to another colony (1). This binary response variable was then analyzed using generalized linear models (GLM) with a binomial family and logit link, fitted with the `glm` function in the `stats` package. Because I used different response variables on non-farm islands and farm islands (continuous vs binary), a direct test of the effect of island type on displacement was not possible.

The following predictor variables were used in models of net displacement and probability of displacement: sex, clutch size, hatch day, tarsus length, body mass, and wing length. Because dispersal is often found to be sex-specific, I tested if the influence of the predictor variables differed between sexes by including the interaction term between sex and the other predictors in the models. If the interaction term was not statistically significant it was removed from the model. Then, if the main effect of sex was not significant (after removing the interaction-term), it was also removed from the model. In order to avoid problems with overfitting (i.e. trying to estimate too many parameters from the sample), I used the rules of thumb for sample size suggested by Harrell (2006) of a minimum of 10 events for the least frequent of the two response values in the binary regression model of probability of displacement, and a sample size of 10 per candidate predictor for the continuous response net displacement. In this study, this corresponded to models with a maximum of three candidate predictors for the binary regression model. That is, I included two main effects and the interaction between them in the full model. In the linear models of net displacement for the two non-farm islands the main effect of island was also included in the model in addition to the other predictors.

Coefficients for the interaction terms including sex were always calculated relative to an intercept representing females. In models where sex was included as an explanatory variable, individuals with unknown sex were excluded.

Evaluation of the fit of the logistic models was performed by graphical inspection of the relationship between the response variable and the fitted values of the models. The assumptions of the linear models were evaluated using residual plots.

Results

THE FARM ISLAND - HESTMANNØY

On the farm island, Hestmannøy, of the 192 individuals marked as fledglings in 2011, 71 individuals (28 males, 39 females, 4 of unknown sex) were observed at least once after 1st August. Of these, 28 individuals (39 %; 15 females, 12 males, 1 unknown) were at the last registration observed away from their natal patch, whereas the remaining 43 (61 %; 24 females, 16 males, 3 unknown) were observed at their natal site. Three individuals had performed movement to the most isolated southern farm (2 males and 1 female), while no individuals had moved away from this farm. The probability for a male to leave the natal patch did not differ significantly from the females' probability ($\beta = 0.18 \pm 0.50$, $z = 0.36$, $P = 0.718$). Thus, in the subsequent analyses for the farm island, sex was removed from the models unless a significant interaction between sex and the other predictor was found. The distribution of net displacement was highly right-skewed (median = 0.0 m, mean = 424 m, range: 0.0 - 3843 m; Figure 3a).

In a logistic regression model the probability of displacement tended to be negatively related to hatch day ($\beta = -0.03 \pm 0.01$, $z = -1.96$, $P = 0.051$, Figure 4a). The predictions from the model can be illustrated in the following way: individuals born 1 SD earlier (= 20 days) than the mean (= day 181) had a 12.6 % higher probability of displacement than the predicted mean of 38.7 % (i.e. 51.3 % probability of displacement). On the other hand, individuals that hatched 1 SD later than mean had a decreased probability of displacement of 11.3% compared to the predicted mean (i.e. 27.4 % probability of displacement). The relationship between hatch day and probability of displacement did not differ significantly between the sexes

(interaction sex \times hatch day: $\beta = 0.01 \pm 0.03$, $z = 0.45$, $P = 0.651$). There are at least two possible non-mutually exclusive explanations for the negative relationship between probability of displacement and hatch day. First, early born individuals may experience environmental conditions that affect their phenotype so that they later become more prone to disperse. Second, the fact that I used the last registration after 1st August to determine whether inter-patch movement had occurred means that early hatched individuals were on average older when movement was determined. If juvenile movement increases with age during the summer and autumn, this may also lead to a negative relationship between probability of displacement and hatch day of the juveniles. One way to disentangle these alternative explanations is to investigate the influence of hatch day for juveniles of a similar age. Thus, instead of using the registrations during a certain period (1st August - 28th September) to determine if displacement had occurred, I instead used the observations for individuals of similar age. The maximum age reached by the latest hatched individuals on each island during the study period was 9-10 weeks. I therefore chose registrations at this age when I re-analyzed the relationship between probability of displacement and hatch day. However, all individuals were not observed at the age of 9-10 weeks. Thus, this sample size was smaller. In addition, the observation (if an individual was observed more than once during that age) that *maximized* net displacement was used. This was done because choosing the last observation in this analysis would have resulted in a higher chance of underestimating the displacement probabilities or -distances possible at that given age. Analyzing this data gave a similar, though not significant, relationship between the probability of displacement and hatch day ($\beta = -0.03 \pm 0.02$, $z = -1.57$, $P = 0.115$, $n = 41$). One early born individual (hatch date = 2011.05.25) that did not leave its natal site and reached the age of 9-10 weeks in July, but then disappeared before the 1st of August, was the main reason for the increase in P-value (i.e. it was not included in the previous analyses when using data from the last registration after 1st August). When excluding this individual the influence of hatch day on probability of displacement agrees with the result obtained when using the last observation ($\beta = -0.04 \pm 0.02$, $z = -1.86$, $P = 0.063$, $n = 40$). As previously, the relationship between hatch day and probability of displacement did not differ significantly between the sexes, neither when including the early born individual (interaction sex \times hatch day: $\beta = 0.03 \pm 0.04$, $z = 0.62$, $P = 0.532$), nor when excluding it (interaction sex \times hatch day: $\beta = 0.06 \pm 0.05$, $z = 1.13$, $P = 0.257$). Although an effect of age cannot be excluded, these results suggest that early born individuals are more likely to leave their natal patch on the farm island Hestmannøy.

Using the data on individuals observed at least once between 1st August and 28th September (as previously), the probability of displacement was not significantly related to clutch size ($\beta = 0.11 \pm 0.23$, $z = 0.46$, $P = 0.644$). The influence of clutch size on probability of displacement did not differ between the sexes (interaction sex \times clutch size: $\beta = 0.56 \pm 0.62$, $z = 0.90$, $P = 0.369$).

Variation in dispersal propensity between the individuals could be due to morphological differences. I investigated possible effects of tarsus length, nestling body mass and wing length. There was no significant relationship between probability of displacement and tarsus length on the farm island ($\beta = -0.24 \pm 0.22$, $z = -1.08$, $P = 0.281$), neither did nestling body mass influence the probability of displacement ($\beta = -0.01 \pm 0.07$, $z = -0.18$, $P = 0.861$). Similarly, the probability of displacement was not affected by wing length ($\beta = -0.03 \pm 0.05$, $z = -0.64$, $P = 0.523$). The influence of the morphological traits did not differ between the sexes (interaction sex \times tarsus length: $\beta = 0.23 \pm 0.44$, $z = 0.51$, $P = 0.609$; interaction sex \times body mass: $\beta = 0.02 \pm 0.14$, $z = 0.16$, $P = 0.876$; interaction sex \times wing length: $\beta = 0.11 \pm 0.10$, $z = 1.10$, $P = 0.271$).

Although no relationship between the probability of displacement and morphological traits *per se* was found, an indirect relationship through seasonal effects on these traits could be present. To investigate the mechanisms behind the effect of season on displacement, I therefore analyzed the relationship between nestling morphology (tarsus length, body mass and wing length) and hatch day by fitting linear regression models to the data on individuals observed after 1st August. I found a significant, positive effect of hatch day on both tarsus length ($\beta = 0.02 \pm 0.01$, $z = 2.64$, $P = 0.011$, $R^2 = 0.10$; Figure 5a), body mass ($\beta = 0.05 \pm 0.02$, $z = 2.21$, $P = 0.031$, $R^2 = 0.07$; Figure 5b) and wing length ($\beta = 0.09 \pm 0.03$, $z = 2.94$, $P = 0.005$, $R^2 = 0.12$; Figure 5c). Together, these results suggest that individuals hatched early in the season both are smaller and have a higher probability of displacement than individuals hatched later in the season.

NON-FARM ISLANDS

On the non-farm islands, Træna and Selvær, of the 254 individuals marked as fledglings in 2011, 100 individuals (47 males, 50 females, 3 of unknown sex) were observed at least once after 1st August. All individuals were observed away from their natal site on these islands (note that direct comparison with the lower fraction of dispersers on the farm island is not

possible due to the scale differences). Net displacement was slightly right-skewed and the between-individual variation in net displacement distances was large on both islands (Træna: mean \pm SD = 250 m \pm 151 m, median = 205 m, n = 54; Selvær: mean \pm SD = 315 m \pm 221 m, median = 279 m, n = 46; Figure 3b). In a model including sex and island as predictor variables, there was no difference in net displacement between the sexes ($\beta = 35.64 \pm 38.8$, $t = 0.92$, $P = 0.361$, ND males = mean \pm SD = 296 \pm 177 m (n = 47); ND females = mean \pm SD = 270 \pm 203 m (n = 50)). Thus, as for the farm island, sex was removed from the subsequent models unless a significant interaction between sex and the other predictor variables was found. However, island (Træna/Selvær) was included in all subsequent models to account for the difference in possible net displacement distances.

Net displacement was not significantly related to hatch day ($\beta = -1.52 \pm 0.91$, $t = -1.66$, $P = 0.100$, $R^2 = 0.05$, n = 100; Figure 4b), although the relationship tended to be negative as on Hestmannøy. Similarly, when using data on individuals of similar age (9-10 weeks; see above), there was still not any significant relationship between net displacement and hatch day ($\beta = 0.27 \pm 1.23$, $t = 0.22$, $P = 0.828$, $R^2 = 0.04$, n = 48). The relationship between net displacement and hatch day did not differ significantly between the sexes (interaction sex \times hatch day: $\beta = 0.29 \pm 1.75$, $t = 0.17$, $P = 0.870$). This suggests that the relationship between net displacement and hatch day on the non-farm islands was mediated through age-dependent movements rather than an effect of early hatching itself on juvenile phenotype and subsequent movement decisions.

Net displacement was not significantly related to clutch size ($\beta = -2.60 \pm 18.17$, $t = -0.14$, $P = 0.886$). The influence of clutch size on net displacement did not differ between the sexes (interaction sex \times clutch size: $\beta = -26.33 \pm 37.77$, $t = -0.70$, $P = 0.487$).

In agreement with the results on the farm island, there was no relationship between net displacement and tarsus length ($\beta = -2.24 \pm 19.19$, $t = -0.12$, $P = 0.907$), body mass ($\beta = -2.08 \pm 5.61$, $t = -0.37$, $P = 0.712$), or wing length ($\beta = -4.10 \pm 3.59$, $t = -1.15$, $P = 0.256$). These results on morphology did not differ between sexes (interaction sex \times tarsus length: $\beta = 42.12 \pm 36.70$, $t = 1.15$, $P = 0.254$; interaction sex \times body mass: $\beta = 8.79 \pm 11.90$, $t = 0.74$, $P = 0.462$; interaction sex \times wing length: $\beta = 7.98 \pm 7.30$, $t = 1.09$, $P = 0.277$).

In summary, my results indicate that juvenile movement may be influenced by time of birth. On the farm island, Hestmannøy, there was some support that the effect of hatch date on probability of movement was mediated by seasonal effects, rather than the fact that early hatched individuals were older. On the other hand, on the non-farm islands, distance moved away from the natal site seemed to be related to age, where older juveniles move further. Movement did not differ between the sexes. Neither did the influence of the various predictors differ between the sexes.

Discussion

This study found that juvenile movement is higher for early born individuals in an insular house sparrow metapopulation. On one island, where the sparrows breed in colonies on farms, the environment experienced during early life may influence phenotype, which in turn may generate a negative relationship between movement and hatch day. However, although early born individuals were smaller and lighter, none of the morphological traits influenced movement directly. On the non-farm islands, movement distance seemed to increase slightly with age. The lack of movement between the two colonies on the second farm-island suggests that the hostility of the matrix habitat influence movement. I found no evidence for sex-biased juvenile movement, which may suggest that dispersal is not an important mechanism for inbreeding avoidance.

Juvenile movement was negatively related to hatch day on the farm island, Hestmannøy (Figure 4a) and slightly so on the two non-farm islands (Figure 4b). A negative relationship between dispersal and hatch day could be explained in at least two ways, both of which relates early environment to phenotypic variation, which in turn may affect dispersal behaviour. First, in birds, there are often large benefits of early natal dispersal to gain access to high-quality territories (Dufty and Belthoff 2001). If environmental conditions are more favourable early in the season and if dispersal is related to the ability to acquire sufficient resources and attain certain body size or condition, then early born (i.e. older) individuals may be more prone to disperse. This is both because they experience a better environment than later born individuals, and because older individuals often are more competitive, or more dominant than younger individuals (e.g. Arcese and Smith 1985). Similarly, mortality during transfer and

competitive ability in the new patch may depend on body condition. In addition, early laid clutches may have higher concentrations of testosterone (Schwabl 1996), which may affect competitive abilities and in turn dispersal (Clobert et al. 2009). Thus, more dispersal by early born birds is expected when early environment is benign, and dispersal is positively dependent on body condition.

On the other hand, if the benefits of remaining at the natal site are high and the cost of dispersal is high, individuals in the worst body condition or subordinate individuals may be forced to emigrate from the natal population (Bonte and de la Pena 2009; Clobert et al. 2009; Cote et al. 2010). Given that the house sparrow has a high fidelity to its natal site (Anderson 2006), it can be expected that benefits of philopatry, such as familiarity with nest sites and food, and social status in groups, are high. Indeed, males that disperse to another island have much lower fitness than resident males in the study area (Pärn et al. 2009). Thus, it is more likely that high-quality individuals remain at their natal site whereas low-quality individuals disperse (i.e. negative condition-dependent dispersal), than the other way around.

Furthermore, early in the breeding season the weather can be very cold and insect abundance low in the study area, which reduces the growth and body condition of early born nestlings, as shown in this study and previously in the same study area (Ringsby et al. 1998). However, although all parameter estimates were negative there was no significant relationship between movement and any of the morphological traits measured (body mass, wing and tarsus length; Figure 5a,b,c), which agrees with some other studies on natal dispersal (Wright and Mauck 1998; Dingemanse et al. 2003). In contrast, some studies have found that smaller individuals, or individuals in poor condition were more likely to disperse (see Clobert et al. (2009) and references therein). In some instances this effect is only detectable within broods (Altwegg et al. 2000; Pasinelli and Walters 2002). Despite highly variable and often cold weather early in the breeding season, early fledged house sparrows that survive have the benefit of experiencing a summer abundant with food and relatively high temperatures. Thus, their relatively small fledgling size could be compensated for by better conditions during the post-fledging period, and their decision to leave the natal site could thus be voluntary. Indeed, it can be beneficial to explore the nearby area (i.e. nearby farms) before making the final decision whether to stay philopatric or disperse (Ims and Hjermann 2001).

Nevertheless, a lack of influence of body size on juvenile movement in the house sparrow suggests that there are other aspects of the phenotype, not measured in this study, that may correlate with time of birth and movement rate. There may for example be behavioural or

physiological differences between early and late born individuals which in turn could affect their movement and dispersal behaviour (Dingemanse et al. 2003; Clobert et al. 2009; Cote et al. 2010). For instance, it has been shown in other species that unpredictable food supply during early life may affect exploration and boldness (Chapman et al. 2010), traits that have been shown to correlate with dispersal (see Cote et al. (2010) and references therein). Accordingly, post fledging movement was highly correlated with natal dispersal in a population of great tits (Dingemanse et al. 2003). Furthermore, low parental provisioning rates has been hypothesized to increase corticosterone levels, which in turn increases dispersal (Belthoff and Dufty 1998). In my study area this may be an explanation for increased movement of juveniles born early as it has been shown that feeding frequencies are lower early in the breeding season (Ringsby et al. 2009). Finally, early born individuals may be subordinate due to an effect of harsh conditions on phenotype and forced to disperse by dominant individuals (Bekoff 1977; Cote et al. 2010). Forced dispersal of subordinate individuals has been suggested for several species (e.g. Red-Cockaded woodpeckers: Pasinelli and Walters 2002; cichlid fish: Schradin and Lamprecht 2002; house mice, *Mus musculus*: Pocock et al. 2005). On the farm island, Hestmannøy, the negative relationship between movement and hatch date was present both when the last registered patch was used in the analysis, as well as when the patch registered for individuals at a given, similar age was used (see Results section). This suggests that a hatch date dependent environmental effect on phenotype, together with phenotype-dependent dispersal may generate the observed pattern in this part of the study area.

Evidence for a relationship between time of birth, phenotype and dispersal exists in a population of the highly philopatric western gull, *Larus occidentalis* (Spear et al. 1998). In this population, more philopatric males hatched earlier in the season displayed traits related to higher dominance and had higher post-fledging survival probabilities than did less philopatric males (Spear and Nur 1994; Spear et al. 1998). Thus, for western gull males, hatch date could relate to natal dispersal through dominance: early born individuals are dominant over later born individuals which, in turn, are forced to disperse.

In this study area, dispersal at a larger scale (i.e. between islands) was negatively related to hatch date in house sparrow males, but not in females (Altwegg et al. 2000). It was suggested that this could be due to competitive superiority by early born individuals, leading to a higher establishment success in between-island dispersal by these. However, the dispersing individuals were also the smallest within the brood, and so the authors further suggested that

dispersal could be a means to increase the chances of future survival. This might indicate subordination of dispersing individuals. There was no relationship between natal dispersal rate and hatch date in a house sparrow population in eastern Kansas (Fleischer et al. 1984).

Together with the results found in this study, this suggests that the relationship could vary spatially in the house sparrow, even within the small spatial scale focused on here.

Indeed, the relationship between dispersal and hatch date can differ between populations within the same species: in the great tit, Verhulst et al. (1997) compared dispersal from high- and low-quality areas and found that early hatched individuals in high-quality areas had a higher probability of dispersing to the surrounding, low-quality area, while no such relationship was present for juveniles hatched in the low-quality area. However, they argued that these findings were due to spatial variation in time of hatching in the high quality area, rather than an effect of hatch date *per se*. In contrast, Dhondt and Hubble (1968) and Drent (1984) found that great tits born late disperse more frequently, whereas no relationship between time of birth and dispersal was detected in other studies of the same species (Greenwood et al. 1979; Smith et al. 1989; Dingemanse et al. 2003). Verhulst et al. (1997) suggested that spatial variation between study sites in the number of clutches within one season could explain the contradictory results regarding this relationship in the great tit.

Several studies have failed to find a relationship between natal dispersal and hatch date, or time of fledging (e.g. sparrowhawk, *Accipiter nisus*: Newton and Marquiss 1983; Tengmalm's owl, *Aegolius funereus*: Korpimäki and Lagerstrom 1988; Savannah sparrow, *Passerculus sandwichensis*: Wright and Mauck 1998; tree swallow, *Tachycineta bicolor*: Winkler et al. 2005).

The fact that the relationship between dispersal and hatch day varies a lot, also within species, suggest a complex relationship between temporal variation in the environment, the effect of early environment on phenotype, and the relationship between phenotype and dispersal behaviour. The latter is in turn determined by costs and benefits during departure from the natal site, movement, and settlement at a new site.

On the two non-farm islands, the weak tendency of early born individuals to move longer distances disappeared when analyzing individuals of similar age. This suggests that movement increases with age in this habitat. The fact that all juveniles moved on the non-farm islands, but not on the farm-islands could be due to differences in habitat configuration and distribution of food. On the farm islands, the house sparrow nest on the farm, and the

juveniles do not have to leave their natal patch (i.e. dairy farm) to find food and shelter. On the non-farm islands on the other hand, the nest sites are evenly distributed in the human settlements, whereas there are only a limited number of bird feeders in people's gardens. This means that basically all individuals have to move from their natal site to forage in small patches, which due to the small area of suitable habitat on these islands, are all accessible during a day of foraging. Thus, on Træna and Selvær, the observed movement could be part of a daily routine associated with foraging, where this type of movement is age-dependent, i.e. movement away from natal site increases with age during the post-fledging and juvenile period. In addition, the bird-feeders on the non-farm islands are spatially more concentrated food sources than the cow sheds and barns on the farm islands. This could lead to higher densities of foraging sparrows on the non-farm islands compared to the farm islands which in turn may contribute to differences in aggressive encounters, and thereby movement, in the two different habitats (Pärn et al. 2012).

There was a large difference in movement rate on the two farm islands. While there were no records of movements between the colonies on Gjerøy, 39 % of the individuals on Hestmannøy were last observed away from their natal colony. The distance between the two farms on Gjerøy (2.2 km) is larger than the mean distance between the farms on Hestmannøy (1.7 km). Perhaps more importantly than the distance *per se* is however the fact that the matrix habitat between the farms differs on the two islands. On Hestmannøy, the matrix habitat between the colonies consists of a more or less continuous open agricultural landscape, with fields, meadows and pastures. In contrast, on Gjerøy, the matrix habitat partly consists of small mountains and rocky areas, small forests and areas without human settlements (see maps in Figure 2a,b). These areas are barriers for house sparrow movement - and increase the isolation of the farms on Gjerøy. Similarly, on Hestmannøy, most movements occurred between farms on the northern part of the island, where the distance between the farms are smaller and the matrix habitat more suitable. Only three individuals moved between any of the northern colonies and the colony on the southern part of the island. This farm is both isolated by distance and by configuration of the matrix habitat. It might be worth mentioning that this data cannot separate between whether or not a lower proportion of the juveniles *tried* to move to or from the isolated colonies. Finding another suitable patch, when in effect there is only one, is probably not an easy task when the size of the matrix habitat is way larger than the size of the suitable patches themselves. Thus, an unknown number, not detected due to mortality, could have initiated movement from (or towards) these

isolated colonies. Nevertheless, these observations suggest that matrix habitat and patch isolation (Wiens 2001; Bowler and Benton 2005) is an important determinant to at least successfully perform movements between colonies in the house sparrow. Accordingly, Kekkonen et al. (2011) found in a large scale study that house sparrow populations separated by land (without geographical barriers) were more genetically similar than populations separated by sea despite longer inter-population distances between many of the land-separated populations. Thus, they suggested that open sea is a (large-scale) barrier for the species, and, in accordance with this study, that landscape structure is important for dispersal in the species.

The importance of matrix habitat and patch isolation on movement and dispersal has been stressed for species in several taxa (e.g. Glanville Fritillary Butterfly: Kuussaari et al. 1996; woodpeckers and passerines: Belisle and Desrochers 2002; koala: McAlpine et al. 2006), as well as been theoretically supported (e.g. Gustafson and Gardner 1996). For instance, both landscape matrix and patch isolation affected the occurrence of the Dupond's lark, *Chersophilus duponti*, an endangered step passerine (Vogeli et al. 2010).

This study provides information about juvenile movement in a house sparrow metapopulation. Although the study was conducted during the dispersal phase of the house sparrow, I recommend further study of juvenile movement before- and during their first breeding season. This would add to the results of this study, and together this would give valuable information about the mechanisms behind natal dispersal decisions in both the emigration phase and the immigration phase. For instance, differences in the properties of the new patch compared to the natal patch are of particular interest. In the great tit, juveniles tended to disperse more from high-density patches, while differences in sex-ratio between the local patches influenced the probability of settlement at each given patch (Nicolaus et al. 2012). Such in-depth knowledge would add to the understanding of the complex process of dispersal and is thus valuable for species conservation in a world facing the challenge of increased fragmentation and rapid climate change.

In conclusion, this study suggests that habitat configuration could be an important factor determining movement rate of juvenile house sparrows. The distribution of inhabitable patches seems to affect movement, where increased hostility of the matrix habitat decreases the movement rate. Based on the results in this study, I would recommend more in depth studies to further quantify the relative importance of patch isolation, patch size and matrix habitat for dispersal rate. For instance, experimental studies to quantify the costs of dispersing

through heterogenic landscape, in addition to assessing the fitness consequences of dispersal in different types of habitats would give valuable information about the dispersal process. Further studies should not ignore the impact that these landscape features may pose on movement- and dispersal rate.

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Figure labels

Figure 1. Map showing the house sparrow metapopulation study system at the coast of Norway (66°N, 13°E). The main study islands are Hestmannøy and Gjerøy (farm islands), and Træna and Selvær (non-farm islands).

Figure 2. Maps showing the four main study islands. (a) Hestmannøy. The black dots represent the colonies (i.e. location of the farms and the feeding station). (b) Gjerøy. The black dots represent the colonies (i.e. location of farms). (c) Træna. The inhabited area represents the suitable breeding habitat for the sparrows. (d) Selvær. The inhabited areas represent the suitable breeding habitat for the sparrows.

Figure 3. The distribution of net displacement distance (m) for juvenile house sparrows at (a) the farm island, Hestmannøy (n = 71) and (b) the non-farm islands, Træna and Selvær (n = 100) in northern Norway. Net displacement was calculated as the distance between the natal site and the site of last observation for individuals that were observed at least once between 1st August 2011 and the end of the study period 28th September 2011.

Figure 4. Movement of juvenile house sparrows away from the natal site. Movement is determined from the last observation for individuals that were observed at least once between 1st August 2011 and the end of the study period 28th September 2011 (day 140 = 2011.05.20). (a) Movement (0 = resident, 1 = dispersed) on the farm island Hestmannøy as a function of hatch day (n = 71). The regression line shows predicted values from a generalized linear model with binomial error and logit link function. (b) Net displacement distance away from natal site (m) of juvenile house sparrows on the non-farm islands Træna and Selvær as a function of hatch day (n = 100). The regression line shows the predicted values from a linear regression model with normal errors.

Figure 5. Nestling morphology of house sparrow juveniles as a function of hatch day on the farm island Hestmannøy. The morphological measures were standardized to the age of 11 days (see Methods). The regression lines give the predicted values from a linear regression model with normal errors. (a) Tarsus length (mm) as a function of hatch day. (b) Body mass (g) as a function of hatch day. (c) Wing length (mm) as a function of hatch day.

Figures

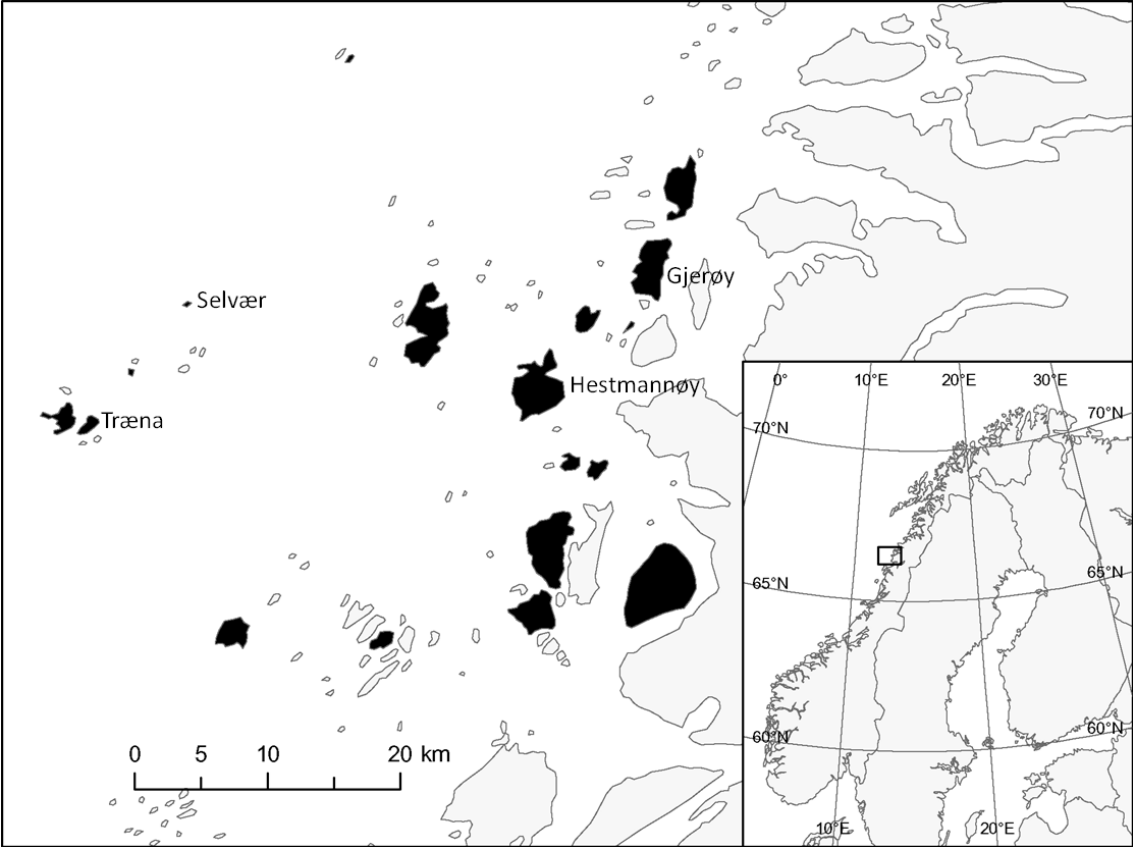


Figure 1

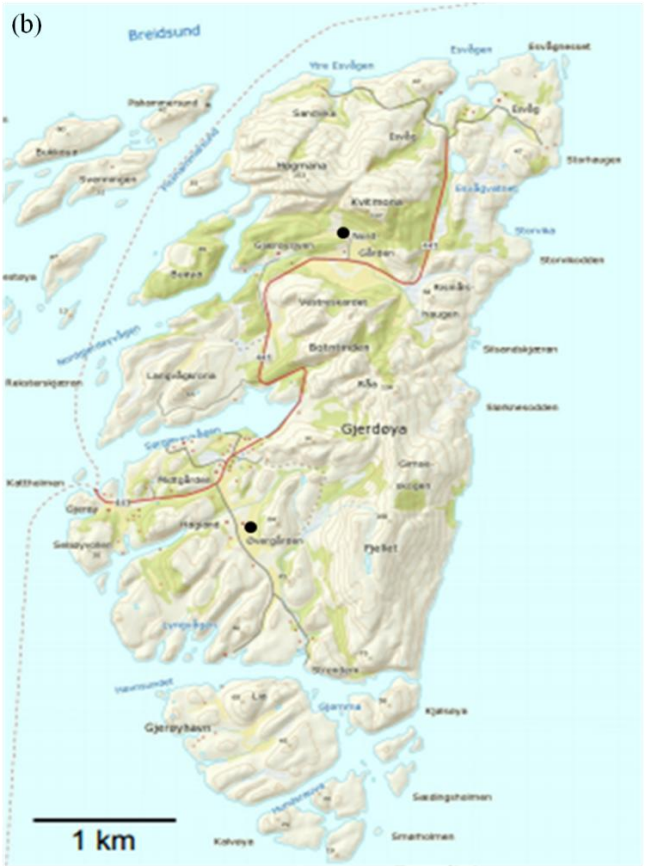


Figure 2

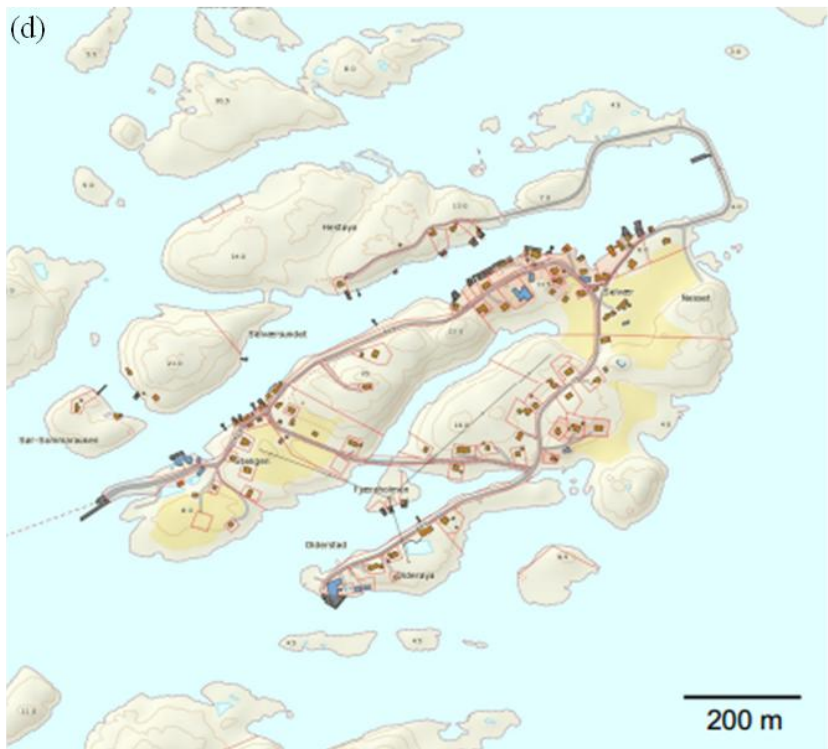
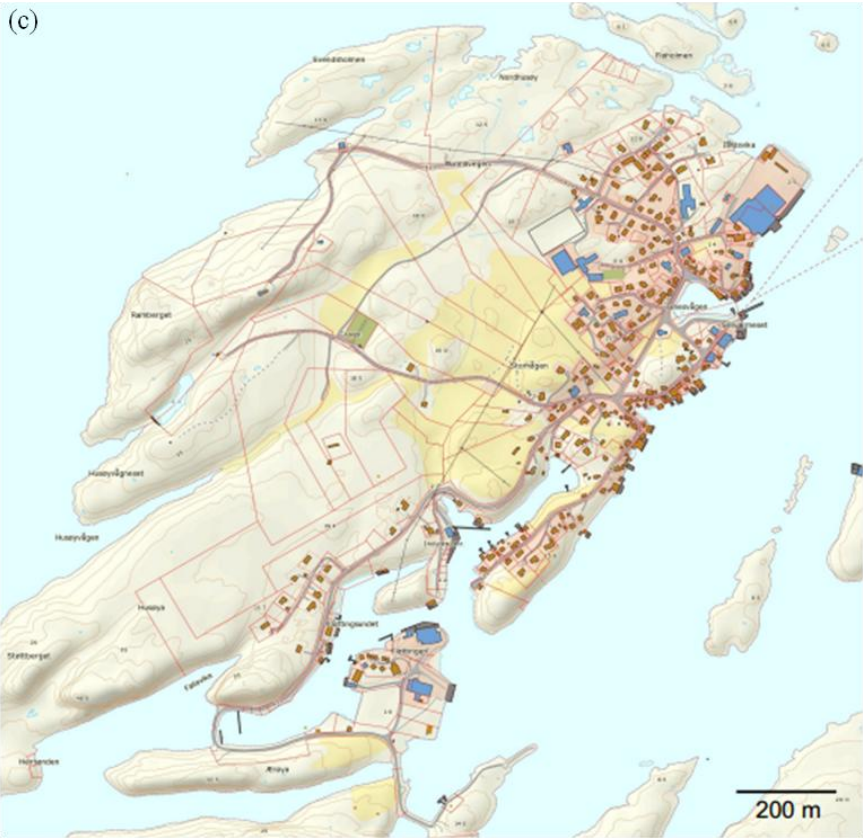


Figure 2

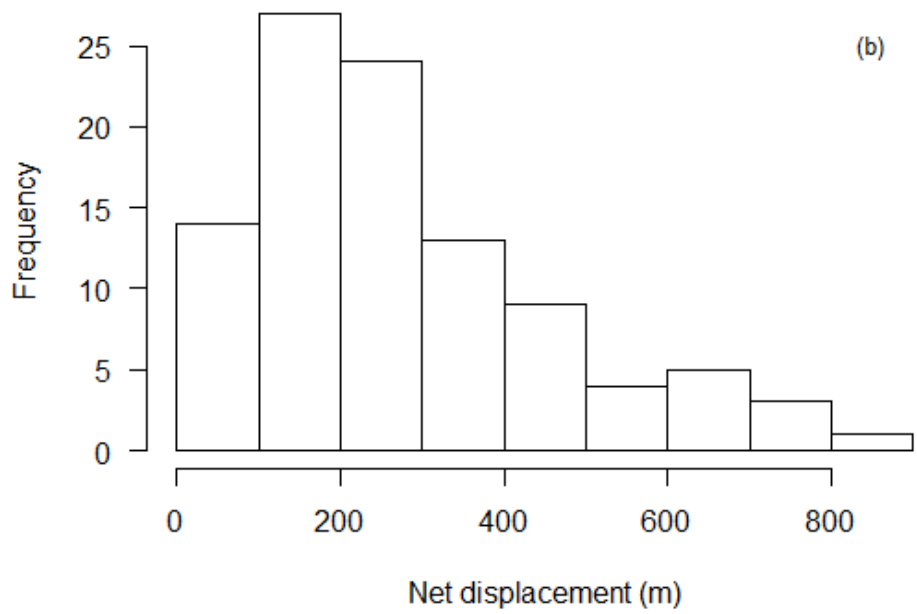
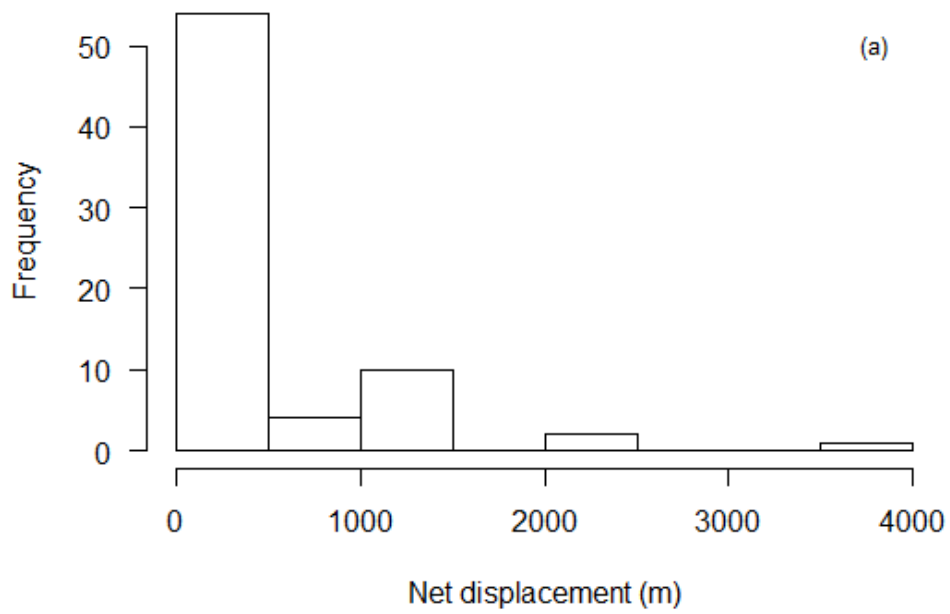


Figure 3

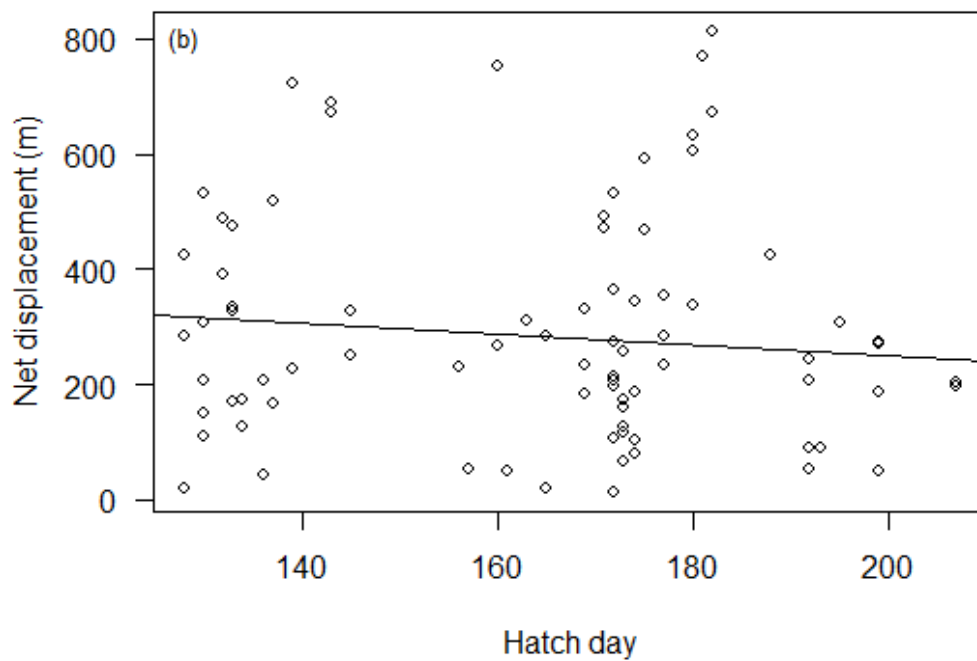
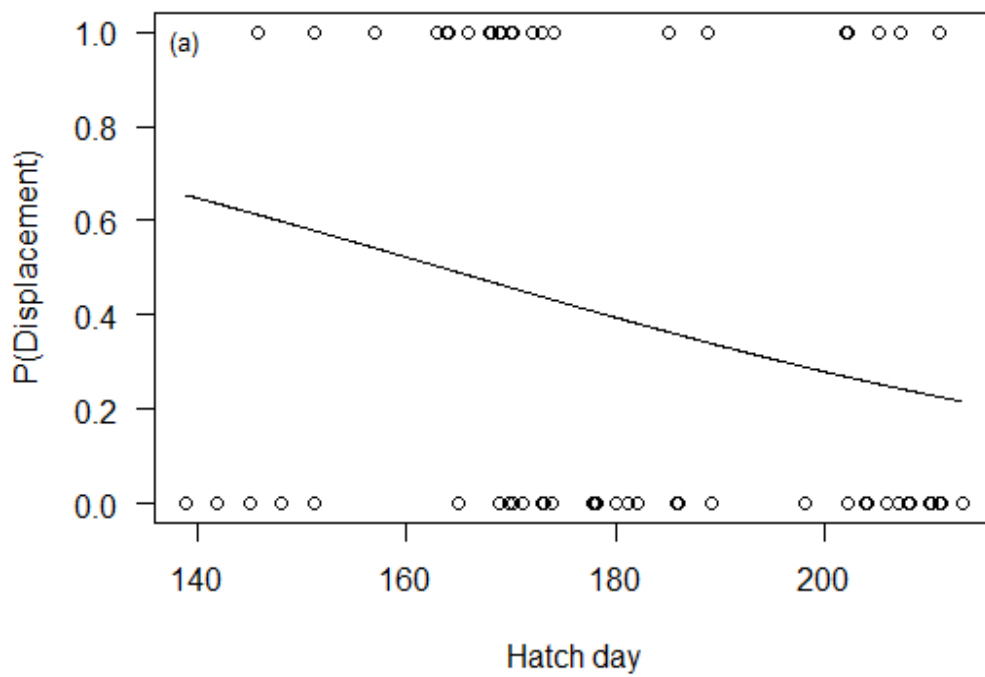


Figure 4

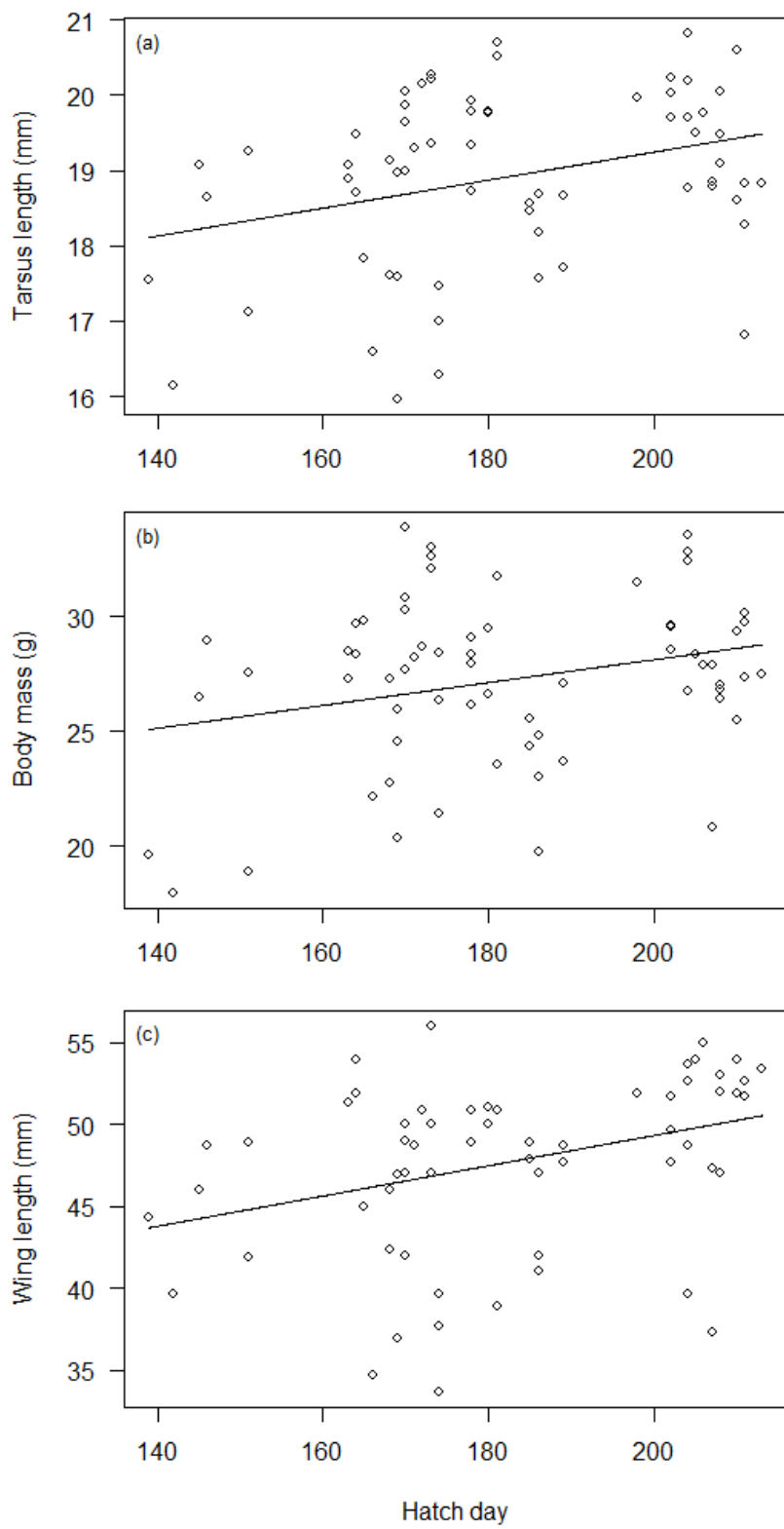


Figure 5