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Peter Sjolte Ranke

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Department of Biology

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Preface & acknowledgements

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Trondheim
November 2018 *Peter Sjolte Ranke*

Contents

Papers I-IV

Summary

The key role of dispersal in population dynamics is widely acknowledged. Important questions are to what extent dispersers contribute to local population growth and to genetic composition, and whether the contributions depend on specific habitat characteristics or phenotypic traits. The main aim of this thesis was to study consequences of dispersal within and among populations by examining natural dispersers within a metapopulation as well as individuals translocated into a recipient population.

In the first paper (I) we focus on dispersal dynamics within a natural metapopulation. By examining long-term data on individually marked house sparrows we studied the influence of variation in population size and density on emigration and immigration across two habitat types. Results show that dispersal dynamics may differ within a rather small geographic area, due to differences in habitat type. In one habitat with harsh environmental conditions, we found higher numbers and rates of dispersal. However, in this habitat, dispersal rates were unaffected by population size, i.e. the number of emigrants was proportional to the population size. In contrast, in a more benign (farm) habitat, emigration decreased and immigration increased with larger mean population size across years. Moreover, the influence of variation in population density (i.e. annual population size relative to the mean across years) on emigration and immigration revealed large heterogeneity among islands, independent of habitat type. Interestingly, the effect of population density on male dispersal differed between the habitat types with males dispersing more in the harsh environment, but less in the benign habitat at high densities. Female dispersal, were unaffected by population density.

In small and isolated populations, translocation of conspecifics into an existing population (i.e. reinforcement) might increase local population growth. In the second paper (II), we examine how translocated individuals, after successful establishment in the recipient population, contribute to the long-run growth rate. Results showed that reproductive success of translocated males depended more strongly on a fitness-related trait (badge size) than for resident individuals. This contributed to a skewed fledgling production favouring resident males. However, offspring from parents of mixed origin experienced higher survival rates i.e. hybrid vigour, resulting in overall similar recruitment rates for translocated and resident individuals. Adult survival was not different between origins. Due to no differences in fitness (reproduction and survival) and equal contributions

to the demographic variance in the recipient population, we suggest that resident and translocated individuals contributed equally to population long-run growth rate in the first breeding season following the translocation.

Small and isolated populations are often subject to increased levels of inbreeding and decreased genetic variation making them vulnerable to extinction. To counteract these negative genetic effects, translocating individuals from less inbred populations into such populations may result in increased genetic variation. Important for the long-term improvement of genetic composition is the genetic contribution from translocated individuals. In paper (III), we examined allele frequency changes, levels of heterozygosity and genetic differentiation in a recipient population over multiple generations following a translocation. Although the reinforcement contributed to a short-term increase in the levels of heterozygosity, the recipient population experienced a decrease in the mean number of alleles across loci and a slow genetic differentiation. However, there were still a few alleles originating from the translocated individuals present at the end of the study period. We suggest that low establishment and mating success led to little contribution from translocated individuals, and together with increased genetic drift, resulting in an overall decrease in allelic diversity. Additionally, the individuals selected for translocation originated from an isolated source population (often less genetically diverse), and therefore the individuals offered few novel alleles, limiting the potential for impact on the recipient population. Our findings give valuable insights on how to select individuals for translocation, and highlight the importance of selection and genetic drift as forces that may decrease the genetic contribution of reinforcement.

In the last paper of the thesis (IV), we aimed to examine the role of male badge size on dispersal in a metapopulation. Both badge size and the propensity to emigrate are known to be negatively related to hatch date in house sparrows. Therefore we expected badge sizes of dispersers to be larger. In addition, we accounted for the influence of habitat type, due to its ecological differences in dispersal dynamics. Dispersers into non-farm habitat had larger badge size than resident recruits. This might indicate larger dependence of badge size in this habitat type, which would have consequences for the phenotypic distribution and metapopulation dynamics.

This thesis contributes to the knowledge of the underlying mechanisms of dispersal and how it is influenced by phenotype and habitat characteristics. Awareness of such effects might also be important for successful management of small and isolated populations.

List of papers

I **Ranke, P. S.**, Araya-Ajoy, Y. G., Ringsby, T. H., Pärn, H., Rønning, B., Jensen, H., Wright, J., Sæther, B.-E. 2018. Spatio-temporal variation in dispersal in a house sparrow metapopulation: population size, density and habitat quality. Journal of Animal Ecology (Submitted).[1]

II **Ranke, P. S.**, Skjelseth, S., Pärn, H., Herfindal, I., Pedersen, Å. A. B., Stokke, B. G., Kvalnes, T., Ringsby, T. H., Sæther B.-E., Jensen, H. 2017. Demographic influences of translocated individuals on a resident population of house sparrows. Oikos 126:1410–1418.[2]

III **Ranke, P. S.**, Skjelseth, S., Hagen, I. J., Billing, A. M., Pedersen, Å. A. B., Pärn, H., Ringsby, T. H., Sæther, B.-E., Jensen, H. 2018. Multi-generational genetic consequences of reinforcement in a bird metapopulation. Journal of Applied Ecology (Submitted).[3]

IV **Ranke, P. S.**, Araya-Ajoy, Y. G., Pärn, H., Rønning, B., Saatoglu, D., Holand, H., Kvalnes, T., Myhre, A. M., Wright, J., Jensen, H., Ringsby, T. H., Sæther, B.-E. 2018. Habitat-specific effects of a sexually selected trait on successful dispersal. Proceedings of the Royal Society of Sciences B (Submitted).[4]

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[1] B.-E.S., T.H.R., H.J. and H.P. conceived the initial idea. P.S.R and Y.G.A.-A. further developed hypotheses, performed the statistical analysis, interpreted the results and wrote the draft, with critical input from all authors. All authors contributed to the data collection.

[2] B.-E.S., H.J. and T.H.R. conceived and designed the experiments. B.G.S., H.J. and T.H.R. performed the experiments. H.J., S.S. and Å.A.B.P. carried out the genetic parentage analyses. H.P., I.H., P.S.R., S.S. and T.K. analysed the data. H.P., P.S.R. and S.S. wrote the manuscript with input from the other authors.

[3] T.H.R, H.J. and B.-E.S. conceived the study. The experiment was carried out by T.H.R. and H.J. with the help of field workers. Laboratory analyses were carried out by S.S., A.M.B. and Å.A.B.P., and was supervised by H.J. Data analyses were carried out by I.J.H., P.S.R. and S.S., with support from H.J. and H.P. Writing of the manuscript was led by P.S.R, with input from all co-authors. All authors contributed to manuscript editing and revisions.

[4] All authors contributed to fieldwork. P.S.R. and Y.G.A.-A. analysed the data. P.S.R. wrote the manuscript, with inputs from all co-authors.

Introduction

Increased habitat fragmentation, climate change and biological invasions cause rapid changes to natural habitats (Pimm et al., 2006; Butchart et al., 2010; Haddad et al., 2015). Thus, there is an increasing demand for understanding the underlying mechanisms of dispersal (Kokko and López-Sepulcre, 2006; Ronce, 2007). Dispersal may substantially affect population size (Pulliam, 1988; McPeek and Holt, 1992) and at the same time also be affected by variation in population size (Travis et al., 1999; Pärn et al., 2012), creating an eco-evolutionary feedback loop where ecological causes of dispersal have impacts on population dynamics (Sæther et al., 1999; Hanski, 2011; Legrand et al., 2017).

Dispersal consists of three main processes e.g. emigration, transit, and immigration (Bowler and Benton, 2005; Ronce, 2007). These processes may respond rather differently to variation in population density, e.g. due to competition or attraction (Matthysen, 2005). Dispersal rate may be positively related to density, resulting in more emigration from high-density populations due to competition, whereas low-density populations receive more immigration. This is known as source-sink dynamics (Pulliam, 1988, 1996). In such systems, a sink population would have negative growth rates and go extinct if not continuously supplied with immigrants originating from a source population. An extension of this pattern was made by including "pseudo-sinks" (Watkinson and Sutherland, 1995). These populations would appear as sinks (i.e. based on negative growth rate without immigration), but in such populations growth rate may in fact be suppressed by the immigration (e.g. fewer local individuals are able to breed), and thus, not dependent on immigration for its persistence. Negative density dependent dispersal may emerge when dispersers have the ability to assess different cues in other sites, e.g. conspecific aggregations (Stamps, 1988) or breeding success (Doligez et al., 2002). This type of dispersal would lead to a more even number of individuals dispersing between sites within a system, therefore called "balanced dispersal" (McPeek and Holt, 1992). Presence of this type of dynamics has been found in e.g. collared flycatcher (*Ficedula albicollis*) (Doncaster et al., 1997) and small mammals (Diffendorfer, 1998). Of importance for local populations is that dispersal may increase the synchrony in population size (Lande et al., 1999) and may reduce the strength of density-dependent regulation (Engen et al., 2002).

Increased population size due to immigrants might have important effects on population growth rate. For instance, the demographic contributions of immigrants to local populations may decrease the risk of local extinction (Brown and Kodric-Brown, 1977; Stacey and Taper, 1992). In five great tit (*Parus major*) populations in the Netherlands, immigration rates contributed substantially to annual fluctuations in population size (Grøtan et al., 2009). Contribution from immigrants to the local population growth rate rely on small fitness differences between immigrants and residents. In some metapopulation models, dispersers and residents are regarded equivalents in their population contribution. However, demographic contributions to local populations from dispersers and resident individuals might differ. For example, in a population of great reed warblers (*Acrocephalus arundinaceus*) in Sweden immigrants had lower lifetime reproductive success than philopatric individuals (Bensch et al., 1998; Hansson et al., 2004). Also in black kite (*Milvus migrans*) (Forero et al., 2002), male dispersal distance was negatively related to fitness, likely due to low quality individuals unable to compete for high quality habitat. To make unbiased estimates of contribution from immigrants to population growth rate, reliable estimates of disperser's and residents' fitness are important. Estimation of dispersers' fitness may be challenging due to its heritable characteristics (Doligez et al., 2009), which could lead to a bias in the detection of offspring, thus leading to underestimation of lifetime reproduction (Doligez and Pärt, 2008). Thus, large study areas relative to dispersal capacity or utilisation of an experimental setup are needed. Contribution to local populations can be evaluated by estimating individual contribution to the deterministic growth rate, and its variance, i.e. demographic variance (Lande et al., 2003; Engen et al., 2007).

In conservation, a powerful tool to augment small and isolated populations is by the intentional translocation of conspecific individuals i.e. “reinforcement” (IUCN/SSC, 2014), to boost population numbers, and thereby enhance local population growth rate. Griffith et al. (1989) evaluated the success of translocations in various taxonomic groups based on those leading to self-sustaining populations. However, essential for the success of reinforcements, is the contribution to local population dynamics. Some examples demonstrate population recovery after reinforcement (Westemeier et al., 1998; Madsen et al., 1999, 2004). These demonstrations of increased growth rate by reinforcements are important examples of demographic consequences of novel individuals into local populations. What has often been challenging in reinforcements is to link population growth and recovery to specific contributions due to inadequate control populations (Pinter-Wollman et al., 2009; Roe et al., 2010).

Small and isolated population are also subject to adverse negative genetic effects, e.g. increased inbreeding (Keller and Waller, 2002). Increased inbreeding, may negatively affect individual fitness i.e. inbreeding depression (Charlesworth and Charlesworth, 1999). In addition, small and isolated populations experience a gradual loss of genetic variation, due to the negative effects of stochasticity, e.g. increased levels of genetic drift and Mendelian segregation. These effects may lead to a reduced potential for adaptation

(Willi et al. 2006) increasing the risk of population extinction (Saccheri et al., 1998; Frankham et al., 2011). Counteracting these negative effects are immigration and mutations (Allendorf and Luikart, 2007). Due to generally low mutation rates in vertebrates (Lynch et al., 2016), immigration is the primary source for gene flow into natural vertebrate populations. For example, in a population of song sparrow (*Melospiza melodia*), Keller et al. (2001) revealed that, due to immigration, the population genetic variation recovered from a critically low level within only 2-3 years after a rather severe bottleneck. Positive effects of heterosis were found in the F1-generation, however, subsequent negative effects in the F2-generation were also found (Marr et al., 2002). Furthermore, in an inbred population of Scandinavian wolf (*Canis lupus*), pairing and breeding success were substantially increased for immigrant offspring versus native, resulting in genetic rescue (Vilà et al., 2003; Åkesson et al., 2016). However, studies of long-term genetic impact from immigrants into wild population are still rare (Åkesson et al., 2016).

Reinforcement may also improve genetic composition of genetically depleted populations, i.e. genetic rescue (Tallmon et al., 2004; Frankham, 2015; Whiteley et al., 2015). For instance, Hogg et al. (2006) and Johnson et al. (2010) provided thorough evidence of the underlying genetic effects resulting from recovery of severely inbred populations, in respectively big-horn sheep (*Ovis canadensis*) and Florida pather (*Puma concolor coryi*). However, also in the reinforcement literature, examinations of long-term genetic impact are still few.

Phenotype- and condition-dependent dispersal has been increasingly recognised (Bowler and Benton, 2005; Clobert et al., 2009) i.e. that certain phenotypic traits show higher dispersal propensity, and that dispersal depends on various interactions between phenotypes and habitat (Edelaar et al., 2008; Edelaar and Bolnick, 2012). Phenotypes with increased dispersal propensity may also evolve into dispersal morphs (O'Riain et al., 1996). In a water vole (*Arvicola amphibius*) metapopulation in Sweden, morphological differences between dispersers and residents was apparent, and phenotypic characteristics increasing dispersal ability (e.g. longer feet) were positively related to the degree of isolation (Forsman et al., 2011). A study of western bluebirds (*Sialia mexicana*) revealed that increased immigration success for males showing more aggression was dependent on habitat (Duckworth, 2006), i.e. phenotype-habitat dependent immigration. Moreover, in green-rumped parrotlets (*Forpus passerinus*) in Venezuela, environmental conditions in early development had large impact on dispersal decisions, and later reproductive output, thus, affecting fitness (Tarwater and Beissinger, 2012). Such phenotype and habitat interactions with regard to dispersal can cause variation in the fitness consequences of dispersers and residents.

Dispersal has long been assumed to have a consistent homogenising effect on population genetics, decreasing local adaptation through gene flow. For example, in a great tit population on Vlieland, immigration prevented local adaptation in one subpopulation, whereas the more isolated subpopulation allowed for adaptation to a smaller clutch size (Postma and van Noordwijk, 2005). However, individuals may as well maximise their fitness by selecting a suitable habitat matching their phenotype, i.e. "habitat matching" (Edelaar et al., 2008; Edelaar and Bolnick, 2012). Bonte et al. (2014) demonstrated fitness maximisation in populations of two-spotted spider mites (*Tetranychus urticae*), where dispersers could substantially increase their fitness, by choosing the most suitable habitat for their phenotype. A prerequisite for habitat matching is the ability to sample neighbouring populations, or at least receive information in terms of reliable cues e.g. from immigrants (Doligez et al., 2002, 2004; Enfjäll and Leimar, 2009; Clobert et al., 2009). Non-random dispersal may also in fact cause genetic divergence within metapopulations, e.g. between habitats. In great tits, Garant et al. (2005) revealed that heterogeneity in fledgling weights between high and low density habitats, was caused by non-random immigration of individuals having larger fledgling weight, and thereby also better accustomed to compete for a territory in high density (and high quality) habitat. Also, in pied flycatcher (*Ficedula hypoleuca*), non-random dispersal into two distinct habitat types resulted in phenotypic divergence in body size (Camacho et al., 2013).

Knowledge of the mechanisms in natural dispersal is important to the management and conservation of endangered populations. This knowledge might be best derived from a combination of studies of natural populations and controlled translocation experiments.

Aim

The overall aim of the thesis is to add to current understanding of demographic and genetic consequences off dispersal among populations. In paper I, the aim is to disentangle the influence of temporal and spatial variation in population size and density, on emigration and immigration between populations, both in terms of the absolute number, as well as in terms of the proportion of recruits that disperse. In paper II and III the aim is to study the impact of "assisted dispersal" by examining the contribution of translocated individuals (i.e. assisted immigrants) into a recipient population. In paper II we examine the demographic contribution from translocated individuals to a recipient population long-run growth rate, while in paper III we examine the genetic consequences for the recipient population over multiple generations following the translocation. In paper IV we examine differences in badge size (a fitness-related trait) for dispersers and residents across two different habitat types. We adressed these research questions evaluating empirical data from two study systems of free-living house sparrow populations, one natural metapopulation and one experimental translocation.

1. Separate the effect of spatial and temporal variation in population size on dispersal across two habitat types (Paper I)

2. Examine the sex-specific demographic contribution from translocated individuals to a recipient population in terms of reproductive success and survival. Thus, the contribution to the long-run population growth of the recipient population (Paper II)

3. Examine the genetic contribution from translocated individuals to a recipient population in terms of changes in allele frequencies, levels of heterozygosity and genetic differentiation (Paper III)

4. Investigate badge size variation between dispersers and residents across differing habitat types within a metapopulation (Paper IV)

General methods

The study species

The house sparrow (*Passer domesticus*) (Fig. 1) is a small bird in the family Passeridae, sexually dimorphic differing in plumage and slightly in size, males having brighter colours and are somewhat larger (Summers-Smith, 1988; Svensson, 1992; Anderson, 2006). The house sparrow is among the most numerous and widely distributed bird species in the world (Summers-Smith, 1988; Anderson, 2006). Over the last 10 000 years, house sparrows have been living in close association with humans (Sætre et al., 2012). In most parts of the world, the house sparrow is sedentary undertaking only small movements, however, one migratory subspecies (*P. d. bactrianus*) is found east of the Caspian sea (Anderson, 2006), assumed to be a relict of the ancestral house sparrow (Sætre et al., 2012).

Figure 1: A male house sparrow *Passer domesticus*. Photo: Peter S. Ranke.

In Norway, the house sparrow breeds and forages all year round in urban areas, and in rural areas closely attached to human settlements (Summers-Smith, 1988; Bjordal, 1994; Anderson, 2006). Despite still being numerous, the house sparrow is sensitive to agricultural and anthropogenic change, and has experienced population declines in many parts of western Europe (Hole et al., 2002). Therefore, we are able to observe and study similar processes as in populations of endangered species, e.g. population extinction (Ringsby et al., 2006). Dispersal rates are generally low (<10 % in juveniles and <2 ‰ in adults, Altwegg et al., 2000; Pärn et al., 2009, 2012) and dispersal distances are short (Finnish data: 90 % < 16 km, Kekkonen et al., 2011) (see also, Tufto et al., 2005). This may contribute to locally high levels of inbreeding (Billing et al., 2012) and population differentiation at small scale (Jensen et al., 2013).

Helgeland metapopulation

The study system consists of 18 main island populations covering a large area (ca. 1600 km^2) outside the coast of Helgeland (66.30-66.80°N, 12.00-13.10°E; Fig. 2). Fieldwork was initiated in 1992/1993, and individual and population data are still being collected annually (see e.g. Sæther et al., 1999; Ringsby et al., 2002; Jensen et al., 2006, 2008). Dispersal records including the years 1993-2014 were used in this thesis. Due to some populations having discontinuous time series (mostly resulting from population extinctions) only 11 out the total number of populations were included.

The islands within the study system consists of two different types of habitat. One with farms situated in the inner parts of the archipelago, where the exposure to environmental conditions is low due shelter within farm buildings. Moreover, populations restricted to farm buildings leads to nest sites being more aggregated in this habitat. The other set of islands are situated further from the coast in absence of farms. Therefore, in this habitat house sparrows are experiencing harsher environmental conditions by being more exposed to the environment. Moreover, in contrast to the benign habitat, sparrows in this habitat are breeding exclusively in outdoor nest boxes. Hence the breeding sites are less aggregated. The two habitat types are presented on the map in Fig. 2.

Translocation experiment

In another house sparrow study system further south, 35 % of the individuals in a local population at one island (Vikna; 64.91°N, 10.90°E, Fig. 3) were removed in late winter 2002. These individuals were translocated to a distant habitable location (Steinkjer; 64.01°N, 11.29°E, 110 km to the southeast), confident that they would not return, thus the removal mimicked a severe population decline. Immediately after removal, a large number of conspecifics (n = 126) i.e. half the adult population from Vega (65.65°N,

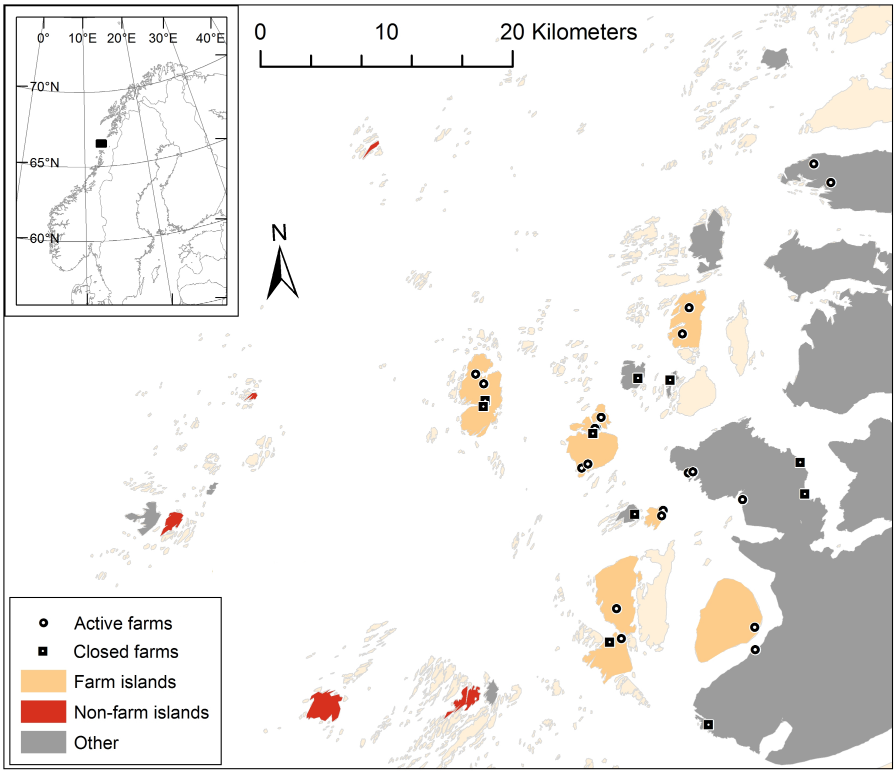

Figure 2: The natural metapopulation at the Helgeland coast in northern Norway. Dark red depict islands without farms, where individuals are more exposed to harsh environmental conditions throughout the year. Pale orange depict islands with farms. Farm location is indicated with a black circle, and with a black square if closed down. Dark grey depict area regularly visited, but not a part of the focal islands in this thesis.

11.90°E), were at the same time captured, translocated, and released at Vikna. Thus, these translocations initiated a large-scaled experimental reinforcement (Skjelseth et al., 2007; Ranke et al., 2017).

Field procedures

The field work in both study systems were carried out from the start of May to mid August, and for a month during the period September-October. Individuals were caught using mist nets, and ringed using a unique combination of a metal ring (supplied by the Bird Ringing Centre at Museum Stavanger), and three plastic colour leg bands (A. C. Hughes, UK) making it possible to identify individuals using binoculars and telescopes.

By intensively capturing and observing individuals throughout the field season, we obtain high annual recapture rates (> 80 %). For all captured individuals, we measured tarsus length, bill length, bill depth, (all ± 0.05 mm) with a digital caliper (Mutitoyo, USA), wing length (± 0.5 mm) with a metal ruler with stopper, and body mass (± 0.05) with a Pesola Light-Line Scale (Pesola AG, Switzerland). Wing length was measured as maximum length following the method described in Svensson (1992). To correct for different fieldworkers, adjustments of measurements were done by adding mean difference if significantly different from T. H. Ringsby (paired t-tests; using a comparison sample of 30 birds). In addition, the length (L) and width (B) of male badge size was measured with a digital caliper (± 0.5 mm), and the badge size area in mm^2 was calculated following Møller (1987); badge size = 166.7 + (0.45 * L * B). In the analyses using badge size, consistent observer differences in badge size measurements was accounted for by adding random intercepts for observer.

During the breeding season, nests were searched for in both study systems. All nests found were visited regularly to determine the age of the chicks. At 11 (8-13) days of age, they were banded and measured following the same procedure as for the fledged juveniles and adults (see above).

Population sizes

Population size were estimated using individual level capture-mark-recapture methods. Due to a higher rate of marked individuals in populations in the benign habitat (and in the translocation experiment), we could use the total number of adults present throughout the breeding season as a reliable estimate for the adult population size, adding a few individuals observed the year before and the year after, assuming presence also in the given year. In the harsh habitat, population estimates rely on spring counts of adult individuals, estimating the population size prior to breeding following a specific procedure.

Genetic data

In the translocation experiment, genetic data for parentage and population genetic analyses were collected. A blood sample was extracted from the brachial vein using a 25 μL capillar tube, and stored in pure ethanol, in a freezer at -25°C. This enabled us to estimate individual parentages, and relate offspring survival to parent origin. Moreover, the blood samples were also analysed using a set of microsatellites, to perform population genetic analyses. See paper III for more details on genotypic procedures, and paper II for parentage analyses.

Figure 3: Map of source (Vega; dark orange) and recipient population (Vikna; pale orange) in a large-scaled experimental reinforcement. Farms (subpopulations) in the recipient depicted with circles (active) or squares (closed by the end of the study period).

General statistical procedures

A disperser was defined as an individual recruiting to a non-natal population prior to its first breeding season, separated by at least 1 km of open sea. Residents were on the other hand recruits to their respective natal populations.

The long-term dispersal data from a natural free-living house sparrow metapopulation (Fig. 2) used in this thesis contains multiple years, populations, and individuals, where each individual were measured multiple times. This hierarchical structuring of the levels of variation requires the use of generilized linear mixed-effects models (Gelman and Hill, 2007). We utilised the package "lme4" (Bates et al., 2015) in R (R Core Team, 2018) to fit all the mixed-effect models. In paper I, the response variables were counts and proportions of inter-island dispersers in each population. Counts are generally Poisson distributed, whereas proportions usually follow a binomial distribution, thus, requiring generalised linear mixed-effects models (GLMMs, Bolker et al., 2009). In paper IV the response variables under examination were morphological traits, which follows a normal distribution, thus, this facilitated the use of general linear mixed models (LMMs; Gaussian error distribution). In order to assess statistical significance, we estimated posterior distributions of parameter estimates using the arm package and we treated estimates which 95% credible intervals did not overlap zero as statistically significant (Gelman and Hill, 2007).

In paper II we quantified the demographic contribution to the long-run growth rate. Using data on reproduction the first breeding season following the translocation and survival to the next year, we examined whether there were any fitness differences between resident and translocated individuals. First, we examined several parameters associated with the reproductive component of fitness (number of mates (for males), eggs (for females), fledglings, and recruits), and analysed them separately with generalized linear models (GLMs). Annual individual fitness was estimated from the number of recruits plus itself if surviving to the next breeding season (Engen et al., 1998; Sæther et al., 1998; Sæther and Engen, 2015). Individual survival was determined by observation, whereas the sex-specific survival rates for the two groups (resident and translocated individuals) and offspring survival were estimated using capture-mark-recapture models in "jags" (Kéry and Schaub, 2012), using the R-package "r-jags" (Plummer, 2016). Thereafter, the sex-specific contribution to the demographic variance was estimated using the formula developed by Engen et al. (2007), using information from individual reproduction (recruits produced) and survival, and the covariance between reproduction and survival:

$$\sigma_{df}^2 = b_f q(1-q) + \sigma_f^2 q^2 + s_f(1-s_f) + 2qc_f \tag{1}$$

where the b_f is the breeding success for females (i.e. number of recruits), q is the sex-ratio,

σ_f^2 is the variation in breeding success, s_f is the survival of a female from one breeding season to the next, and c_f is the individual covariation between breeding success and survival.

In paper III several genetic metrics were used to examine the multi-generational influence of translocated individuals on genetic changes in the recipient population (see map of source and recipient populations, Fig. 3). The allele frequencies were quantified using the software HP-Rare 1.0 (Kalinowski, 2005), which enabled assessment of temporal changes in genetic diversity and tracking of specific alleles with known origin (i.e. private to either source or recipient population; Kalinowski (2004)). In that way we could assign changes in certain allele frequencies to influences from individuals with specific genetic background (i.e. most reliable in the first cohorts following translocation before too much mixing). Moreover, we also examined the genetic influence of the translocated individuals on the recipient population in terms of changes in levels of heterozygosity. Furthermore, the changes in genetic differentiation relative to both the source and recipient populations could be monitored based on pairwise F_{ST} (fixation index; Holsinger and Weir (2009)). Levels of heterozygosity and genetic differentiation were estimated using the R-package HIERFSTAT (Goudet, 2005).

Main results and discussion

In paper I we examined dispersal dynamics within a free-living population of house sparrows (Fig. 2). We revealed considerable spatial heterogeneity in emigration and immigration within the metapopulation, differing between two habitat types. Populations residing in “harsh habitat” (also termed: “non-farm islands”; assumed to have harsher environmental conditions, due to the lack of shelter from farms) had consistently higher numbers and proportions of dispersers compared with populations residing in “benign habitat” (also termed “farm islands”; assumed to have more benign environmental conditions, due to shelter from farms). Within the “benign habitat” the proportions of recruits emigrating from the populations was negatively related to mean population size, whereas the number of immigrants was positively related to mean population size. In contrast, within the “harsh habitat”, the number of emigrants was related proportionally to the mean population size, and there was no effect of mean population size on immigration (Fig. 4). Thus, the dispersal pattern we found in the “benign habitat” resembles a balancing dispersal pattern (McPeek and Holt, 1992; Doncaster et al., 1997). When examining the within-island temporal variation in population density (i.e. annual deviation from the mean population size), we found large heterogeneity among islands, but these differences were not associated to habitat type. Therefore, neither of the habitats seemed to follow a source-sink dynamics (Pulliam, 1988, 1996). Interestingly, we found opposing effects of population density between the habitat types for males, but not for females. For males in the benign habitat, we found a negative relationship between population density and dispersal. This indicates increased costs of dispersal for males when populations are dense (Pärt, 1995; Bonte et al., 2012). In contrast, for males in the harsh habitat dispersal was positively related to population density, perhaps due to stronger density-dependence and a lower cost of dispersal (Rodrigues and Johnstone, 2014).

Populations threatened by extinction may be recovered by reinforcement (Tallmon et al., 2004; IUCN/SSC, 2014). Such populations are often small and isolated and are therefore dependent on assisted dispersal in order to boost population numbers and increase population growth. In paper II we examine demographic influences of translocated individuals after a reinforcement. We quantify several demographic parameters, and estimate mean individual fitness for both translocated and resident individuals. We found that after the translocated individuals had successfully established, they contributed to

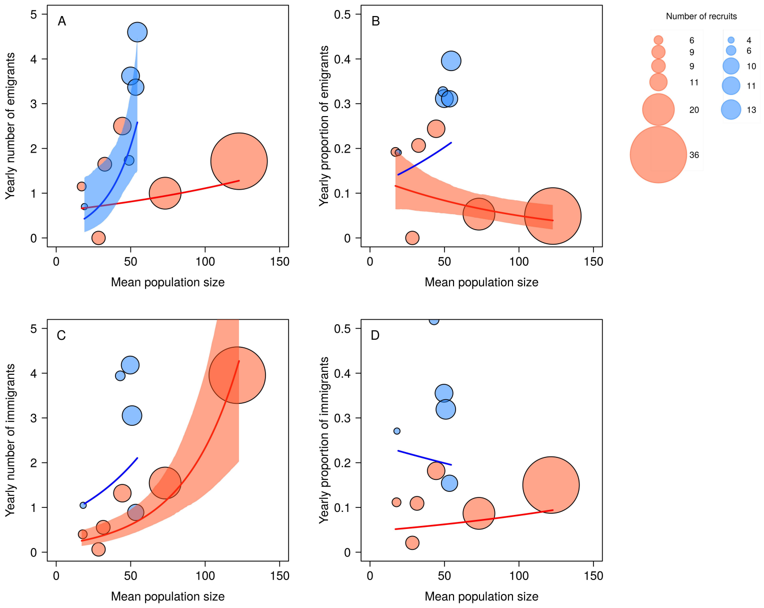

Figure 4: The relationship between mean population size and the number and proportions of emigration and immigration across two habitats within a metapopulation. Blue represents the harsh habitat/non-farm islands where individuals are more exposed to harsh weather. Red represents benign habitat/farm islands, considered as a more benign habitat type.

the long-run growth rate of the recipient population. Although we revealed assortative mating among individuals based on origin (i.e. fewer parentages between mixed pairs than expected), positive influences of hybrid vigour on juvenile survival contributed to similar recruitment rates from the two origins. Thus, resident and translocated individuals had similar fitness, and contributed equally to the long-run growth rate of the recipient population. Additionally, we examined the influence of several phenotypic traits on fitness related traits for individuals from the two origins (translocated versus resident). We found that production of fledglings by translocated males depended more heavily on badge size (a sexually selected trait) than resident males (Fig. 5). This suggests that the importance of badges of status might be of larger importance for individuals new to populations, than for resident individuals already familiar to each other. This has earlier been found in great tits (Lemel and Wallin, 1993). A similar effect was also found in golden-crowned sparrows (*Zonotrichia atricapilla*), where experimental enlargement of badge size affected the dominance of strangers, but not familiar individuals (Chaine et al., 2018). Moreover, this effect was supported by our findings in paper IV, emphasising the importance of status signalling in environments with increased encounters with unfamiliar individuals.

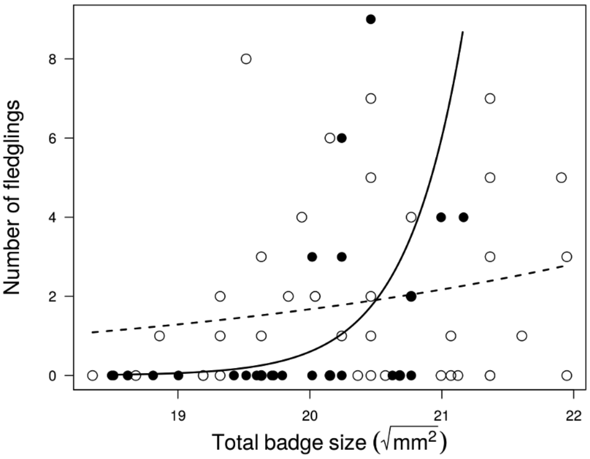

Figure 5: The effect of badge size on fledgling production in resident (open circles) and translocated (filled circles) male house sparrows.

In paper III we investigated the long-term genetic influence of the translocated individuals on the recipient population following a reinforcement. We found a rather small long-term genetic contribution from the translocated individuals. Despite a similar demographic contribution in the first breeding season (paper II), few alleles entered the recipient population, and genetic differentiation in the recipient population was slow and seemed unaffected by the translocation action. The fact that the recipient population was not genetically depauperate, and that the source population was more genetically (and geographically) isolated, contributed to a small potential for genetic contribution from translocated individuals. Moreover, increased genetic drift, resulting from several subpopulation extinctions due to farm closures, further decreased genetic variation. Despite increased offspring survival from hybrid vigour (paper II), lower establishment and mating success for translocated individuals may have limited the long-term genetic contribution. Although we found no long-term genetic contribution, a significant short-term increase in heterozogozity was observed. This supports the findings of Heber et al. (2013), that even individuals originating from inbred populations might increase levels of heterozygosity. This highlights how individuals with similar heterozygosity levels might increase heterozygosity in the admixed population, likely due to sufficient genetic differentiation. However, long-term increase in levels of heterozygosity seems to depend on recipient population being inbred (Johnson et al., 2010). In contrast, our recipient population did not show low levels of heterozygosity.

An important consequence of dispersal is that it may affect the phenotypic distribution in a metapopulation. Spatial distribution of phenotypes may depend on habitat characteristics. In paper IV we examine the metapopulation in northern Norway, where we aimed to test the influence of badge size on the dispersal dynamics. On non-farm islands dispersers had larger badge sizes than residents on islands into which they dispersed, in contrast to farm islands, where there were no differences (Fig. 6). These habitat-specific differences between dispersers and residents could not be explained by variation in body size or population size. Habitat-specific variation in a fitness-related trait associated with dispersal may cause differences in fitness for dispersers across habitats. Moreover, such differences may have important consequences for the eco-evolutionary dynamics in the metapopulation. For conservation management, these results highlight the importance of status signalling for individuals in a novel environment (see also paper II), and traits expected to increase establishment success and/or breeding success should be taken into careful consideration when selecting individuals for use in reinforcement.

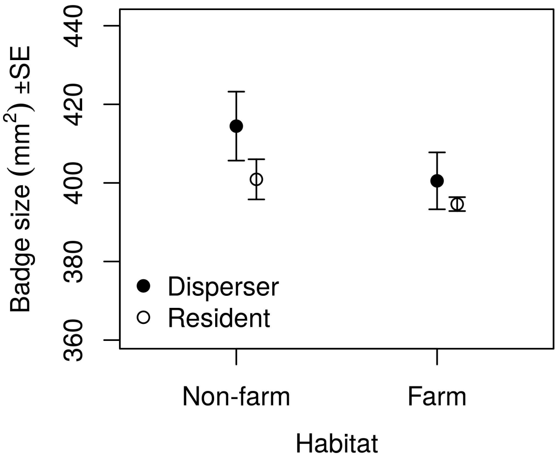

Figure 6: Differences in badge size between disperser and resident second calendar year old house sparrows, across two different habitat types in a metapopulation in northern Norway.

Future prospects

An important step for further examinations of dispersal dynamics within the metapopulation would be to obtain island-specific demographic rates (Diffendorfer 1998). A detailed comparison of demographic data; growth rates, recruit production and survival, together with dispersal, could give valuable information on the importance of dispersal for the growth of local populations. Moreover, a more detailed analysis on the impact of density would be beneficial, and therefore effort should be focused into examining processes that are most sensitive to variation in population density, e.g. competition for territories and mates (reproduction), or competition for food resources (annual survival).

We found that translocated and resident individuals contributed equally to the long-run growth rate. Moreover, we found hybrid vigour in terms of increased recruitment rate for hybrid offspring (paper II). A very interesting next step would be to examine demographic contribution from the two origins to the next generation (F2). In song sparrows, negative consequences in F2-generation of immigrants were found (Marr et al., 2002), and these potential negative effects might be one cause of the small genetic impact from translocated individuals. However, in the song sparrow population, the negative consequences of hybrid vigour in generation F2 seem to have little impact on the long-term population genetic contribution from immigrants (Keller et al., 2001). In order to better direct conservation efforts, each of the processes affecting translocated individuals e.g. establishment success, assortative mating, and recruitment rates should be quantified.

Our findings demonstrate differences in badge size between residents and dispersers that successfully immigrated into the new population. An interesting approach in future studies would be to examine the badge sizes of individuals that emigrated, but failed to immigrate. A prediction could be that successful immigrants would have larger badge sizes, and that it is the difference in immigration success within the habitat that causes this difference.

Furthermore, with the knowledge from paper I and IV that impact of population density and the importance of badge size for immigration differ across habitat types, it would be very interesting to examine the fitness-consequences of the dispersal dynamics, across the two habitats in this metapopulation.

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Paper I

Paper II

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Demographic influences of translocated individuals on a resident population of house sparrows

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Translocation of individuals from source populations to augment small populations facing risk of extinction is an important conservation tool. Here we examine sex-specific differences between resident and translocated house sparrows *Passer domesticus* in reproductive success and survival, and the contribution of translocated individuals to the growth of a local population. We found evidence for assortative mating based on origin revealed by fewer parentages between translocated males and resident females than expected, and the total number of fledglings produced by such pairs was lower. The reproductive success of translocated males was positively related to the size of the throat badge (a sexual ornament), such that only translocated males with a large badge size were as successful as resident males. However, offspring with parents of different origin had higher survival than offspring with parents of the same origin, which suggests hybrid vigour. The contribution of resident and translocated individuals to the stochastic component of the long-run growth rate of the population was similar; neither the mean individual contributions in fitness nor the demographic variance differed between the two groups. Thus, this experiment shows that translocated individuals may have a similar demographic influence on the growth of local populations as resident individuals. Still, the intermixing of translocated and resident individuals was low, and fitness differed according to origin in relation to individual differences in a sexually selected trait. In addition, hybrid vigour with respect to offspring recruitment seemed to partially decrease the negative fitness consequences of the assortative mating based on origin.

Translocation is a widely used conservation tool to increase viability of threatened populations (Griffith et al. 1989, Fischer and Lindenmayer 2000, Armstrong and Seddon 2008). Translocated individuals may increase population genetic variation, alleviating negative impacts from inbreeding depression and genetic drift in small populations (Westemeier et al. 1998, Madsen et al. 1999). However, this relies on that the contribution of translocated individuals to population growth, matches that of the resident individuals, but few studies have experimentally examined the demographic contribution of translocated individuals to a local population. There is therefore a need for studies comparing the reproductive success and survival of resident and translocated individuals, using either data before the translocation or the resident individuals after translocation as reference baseline (Pinter-Wollman et al. 2009, Roe et al. 2010). Such studies may provide insights to the specific demographic and ecological drivers affecting the success of a translocation (Armstrong and Seddon 2008).

Fitness advantages for translocated individuals over residents have been reported in a few translocation experiments, i.e. through increased mating success for translocated males (Jones et al. 1995) and indirectly through hybrid vigour in offspring from parents of mixed origin in inbred populations (Ebert et al. 2002). However, translocated individuals may be subject to adverse effects, both directly through transportation and stress, and indirectly through lack of acclimatisation and familiarity with the environment or other individuals (Letty et al. 2007). This can for instance result in increased dispersal rates of translocated individuals (Skjelseth et al. 2007, Roe et al. 2010). Therefor, the impact of translocated individuals on local population dynamics depends on how well individuals cope with their new environmental conditions, and how successful these individuals are, both with respect to fecundity and survival. Thus, an important part of individual contribution to the next generation is through reproduction, which depends on a wide range of circumstances, including mating success (Emlen and Oring 1977). Therefore, if mating success among translocated individuals differs from that of resident individuals (Sigg et al. 2005, Lewis et al. 2012), it might affect their contribution to the next year's breeding population, and in the long-run the population growth (Lande et al. 2003).

Increased variation in mating success between resident and translocated individuals could potentially decrease genetic diversity, especially in small populations (Miller et al. 2009). In translocations, such differences may result from assortative mating, e.g. where individuals pair assort with respect to origin (Bradley et al. 2014). Assortative mating could cause increased variation in mating success, where the total population may suffer a decrease in effective population size (Wright 1931, Anthony and Blumstein 2000, Bradley et al. 2014) and may have consequences for demographic variance and viability of small populations (Lande 1988, Lee et al. 2011).

Population augmentation as a conservation tool aims to improve growth and viability of local populations, and reduce the risk of extinction. In the absence of negative density dependence this means to increase the long-run growth rate of the population (Lande et al. 2003), which is reduced by demographic and environmental stochasticity. Thus, examining the demographic consequences of translocations requires estimates of the expected contributions of an individual to the next generation as well as its variance. Although translocation of individuals may strongly affect the vital rates of a population, few empirical studies of vertebrates have examined how translocated individuals affect the demographic variation in population growth of a local population (Fischer and Lindenmayer 2000, Goossens et al. 2002, Sigg et al. 2005, Seddon et al. 2007). Here we will partition the contribution of individuals with different sources of origin to the population growth into deterministic and stochastic components, following the approach of Engen et al. (1998), Sæther et al. (1998) and Engen and Sæther (2014). The annual mean individual fitness can be partitioned into components caused by mean differences in fecundity and survival, as well as components due to random variation among individuals generating demographic variance (Engen et al. 1998, Engen and Sæther 2014). This allows us to compare the contribution of individuals of different origin to key population properties affecting population dynamics and viability.

In this experiment we translocated house sparrows *Passer domesticus* from a distant population, into a metapopulation to investigate how translocated individuals influenced the demography of the population they were introduced to. The resident individuals served as a reference to the performance of translocated individuals (Pinter-Wollman et al. 2009, Roe et al. 2010). We used an experimental design that kept sex-ratios equal in all subpopulations. In addition, the selected populations (receipt and donor) had only minor differences in population density and size, and had experienced similar environmental conditions. With its sedentary nature, preference for urban and agricultural areas, and easily accessible nests (Anderson 2006), the house sparrow is a suitable model species for investigating fitness consequences of translocation. Our first objective was to compare sex-specific fitness differences between resident and translocated individuals to predict the annual demographic contribution from the two groups of origin. We recorded the following fitness components; number of mates, eggs, fledglings and recruits in addition to whether the individual survived to the next breeding season or later. Second, because several morphological traits have been shown to influence reproductive success (Jensen et al. 2008), we examined whether there were any sex-specific relationships between phenotypic characteristics and fitness that differed between resident and translocated individuals. Third, we examined whether translocated and resident individuals mated assortatively. Fourth, we investigated whether offspring recruitment probability depended on the origin of parents, to test for hybrid vigour. Finally, we estimated the contributions of resident and translocated individuals to the demographic variance and hence how they affected the long-run population growth rate.

Methods

Experimental design and field procedures

In February–March 2002, before the translocation, two house sparrow populations were visited, one at the island Vega (65°65′N, 11°90′E) and the other in the Vikna archipelago (64°91′N, 10°90′E) located approximately 95 km south along the Norwegian coast (Supplementary material Appendix 1 Fig. A1). House sparrows were captured with mist nets, and banded with a numbered aluminium ring and plastic colour rings of unique individual combinations. At capture we measured body mass (± 0.05 g), wing length (± 0.5 mm; maximum length, Svensson 1992), tarsus length (± 0.05 mm), bill depth (± 0.05 mm), bill length (± 0.05 mm), and badge size (males only). The badge size was defined as the total area covered with black pigmented feathers including feathers with black bases and grey tips on the throat and the chest when the bird was held with its head in a perpendicular angle to its body (Jensen et al. 2006). The area of the badge were calculated according to Møller (1987):

$$\textit{total badge size}\,(mm^2) = 166.7 + (0.45 \times h \times w)$$

where h denotes the height (± 0.5 mm) of the badge and w the width (± 0.5 mm). Except for the measure of badge size, we adjusted each trait for differences between fieldworkers due to variation in measurement techniques. Paired *t*-test comparisons for each phenotypic trait were made with samples of birds measured by each fieldworker together with T. H. Ringsby. Except for eight birds, all morphological measurements were taken at the beginning of the translocation experiment (i.e. in February–March 2002). Thus, we avoided any inter-individual variation owing to different abrasion of feathers or bills, or differences in body mass due to seasonal variation (Anderson 2006). Mean adjustments of wing length were 0.84 mm, bill depth 0.25 mm and bill length 0.38 mm. However, the measurements of tarsus length did not differ significantly between any of the fieldworkers, and were thus not adjusted. A small sample of blood (approximately 25 μl) for parentage analyses was drawn for each individual from its brachial vein.

In March 2002, we translocated 126 (63 male and 63 female) house sparrows from the population at Vega to the population at Vikna. The two locations have similar topography: hills, lakes and fjords, sparsely populated with small beef- or dairy-farms, where the house sparrows breed in small subpopulations (defined by individuals residing on a farm separated by at least 1 km from a neighbouring farm). The two populations had minor differences in size and structure, Vega being the largest in total (population size = 246, number of subpopulations = 24, mean size of subpopulations = 10.3 individuals, range size of subpopulations = 2–34 individuals) compared to the total population at Vikna (population size = 192, number of subpopulations = 17, mean size of subpopulations = 11.3 individuals, range size of subpopulations = 1–29 individuals). Removal of individuals on Vega due to a selection experiment (Kvalnes 2016), created an opportunity to perform this translocation experiment. Within each sex all individuals with a tarsus length longer than the mean minus 0.3 standard deviations were translocated from Vega to Vikna. Because tarsus length does not increase with age after their first winter, the selection should create an unbiased translocation propagule with respect to age. Moreover, since the subpopulations were rather stable in size during several years before the experiment (local farmers, pers. comm.) the age-distribution of both resident and translocated individuals of the population should be similar. Possible age-dependent fitness effects, such as actuarial senescence (Holand et al. 2016) could therefore be assumed to be similar between the two groups. The translocated individuals only differed from residents having deeper bills in both sexes (males: $t = 6.00$, $df = 120$, $p < 0.001$, females: $t = 4.36$, $df = 122$, $p < 0.001$) and larger badge size in males ($t = 3.76$, $df = 119$, $p < 0.001$). Hence, for other measured traits there were no significant differences between resident and translocated individuals (all $p \geq 0.109$, Supplementary material Appendix 2 Table A1).

Immediately before the translocation, the Vikna population was reduced to 120 individuals, adjusting the size of the resident population to match the number of translocated individuals. Experience from former translocations reveals heavy loss during the establishment phase (Krogstad et al. 1996, Letty et al. 2007). Hence, the subpopulation sizes were increased to some extent (on average by 3.18 individuals) to account for some of this loss, and therefore the densities were increased slightly for both groups at the initiation of the experiment. Resident individuals were randomly removed for each sex (within each subpopulation, when all local birds were caught) and transported to a distant location (Steinkjer; 64°01′N, 11°29′E) approximately 110 km to the southeast. None of the individuals that were removed returned to Vikna, but two individuals translocated from Vega to Vikna returned to their origin at Vega. All individuals included in the experiment (resident and translocated) went through the same experimental treatment, though differed only in the transportation (95 km) and time between capture and release (approximately one additional week for translocated individuals). House sparrows seem to cope with captivity well based on previous experiments (Krogstad et al. 1996), hence they were conveniently kept in aviaries and provided with food and water ad libitum for logistical reasons. The experimentally merged population at Vikna (population size = 246, number of subpopulations = 17, mean size of subpopulations = 14.5 individuals, range size of subpopulations = 5–33 individuals) was thus larger in size than the original Vikna population and the sex-ratios were adjusted to 0.5 ± 0.1 in all subpopulations.

We started the monitoring of the subpopulations in the Vikna archipelago on 15 April 2002 (approximately one month after the translocation), which corresponds to the normal onset of breeding in the area. Only individuals present at Vikna after this date were considered established and included in the analyses. From the 246 individuals which were released, 120 (59 males and 61 females) originated from Vikna ('resident'), whereas 126 (63 males and 63 females) had been translocated from Vega ('translocated'). Additionally, 27 adult individuals (17 males and 10 females) were captured by use of mist nets and banded at Vikna within the breeding season of 2002. These 27 individuals were thus not a part of the translocation experiment, but 9 of these individuals produced offspring that were included in the offspring survival analysis. Of the 246 individuals released in March 2002, 161 (65%) were present at Vikna in the 2002 breeding season, i.e. they were captured or observed at Vikna after 15 April 2002, or were genetic parent of nestlings or juveniles hatched at Vikna in 2002. The majority of these were captured or observed during the field season ($n = 146$): 82 individuals (42 males and 40 females) were resident, and 64 individuals (30 males and 34 females) were translocated. Moreover, 15 individuals were identified as present only through genetic parentage analyses (i.e. they had offspring assigned to them), but these individuals were excluded from the analyses of fitness differences between resident and translocated individuals, to ensure an unbiased sampling method.

Within the 2002 breeding season all available nests were visited and monitored closely during the breeding season. At the age of 7–13 days we banded fledglings in all nests individually with a numbered aluminium ring and a unique combination of colour rings. Even though all farms were very thoroughly searched for nests, a few inaccessible and/or undiscovered nests were present. Therefore, any unmarked fledged juvenile was captured with mist nets, either during the breeding season, or when the Vikna population were revisited in the end of September and beginning of October 2002. During the breeding season 2002 we recorded 232 fledglings and fledged juveniles in the Vikna archipelago. Of these, 210 were banded as fledglings and 22 were captured as newly fledged juveniles within the breeding season. All fledglings and juveniles were included in the genetic parentage analyses.

Genetic parentage analyses

The procedure for determining the genetic parentage of fledglings and fledged juveniles is described in the supplementary material (Supplementary material Appendix 5). We used 11 polymorphic microsatellite markers in the parentage analyses, and had a total non-exclusion probability of $p = 6.68 \times 10^{-6}$ and $p = 4.00 \times 10^{-8}$ for first and second parents respectively. All individuals released in the Vikna archipelago were included as candidate parents, except for one male and one female. In addition, the 17 adult males and 10 adult females that were captured in the population within the 2002 breeding season were included as candidate parents, giving a total of 138 males and 133 females as candidate parents in the parentage analyses. For parentage determination, we used the software CERVUS 3.0 (Kalinowski et al. 2007). Based on observations of unbanded individuals in the Vikna archipelago, the average proportion of potential mothers and fathers sampled was estimated to be 0.850, i.e. we assumed that 15% of the adult population was not sampled and genotyped. To account for any inbreeding and resulting close relatedness among candidate parents in the Vikna archipelago, we assumed that 1% of the candidate mothers and fathers were related by a factor of 0.25 to other potential parents of the same sex. Thus, we assumed a similar level of relatedness among candidate parents as the average level of inbreeding found in a house sparrow archipelago of similar size approximately 200 km north along the coast (Jensen et al. 2007; excluding data from one highly inbred population). The genetic fathers were assigned after genetic mothers were identified. For both maternity and paternity analyses the average proportion of loci typed was 0.892. In order to minimize potential erroneous assignments of parentage, the proportion mistyped loci was estimated to 0.01. The level of confidence in our parentage analyses was set to 95%. Hence, less than 5% of the genetically assigned mothers or fathers should be incorrectly assigned (Kalinowski et al. 2007).

Successful assignment of both parents was achieved for 168 (72.4%) offspring, whereas 46 (19.8%) offspring were only assigned a mother, one (0.4%) was only assigned a father, and 17 (7.3%) offspring had unknown genetic parents. One male was recorded having sired fledglings at two different, but closely situated farms. Except for this male, each adult individual had reproduced on one single farm (i.e. subpopulation). Offspring with unknown genetic parents were assigned to the population clusters to control for bias in assignment in relation to origin of parents (Supplementary material Appendix 6 Table A4). Examining how the 232 offspring were distributed among clutches, 210 fledglings was assigned to 66 clutches (154 assigned to 49 clutches with known parents, 39 of these with pairs consisting of experimental adults (n = 120 offspring)), and the 22 offspring captured as fledged juveniles (14 was assigned to 11 clutches with known parents, 7 of these pairs consisting of experimental (resident or translocated) adults (n = 8 offspring)).

Statistical analyses

Resident and translocated individuals were compared with respect to several fitness components. For each reproductive component, we used the total annual production: number of mates (for males; measured by the number of females with shared parentage), number of eggs produced (for females), and number of fledglings and recruits produced. It should be noted that these components stem from parentage analyses of fledglings, and thus depend on the success of the incubation and early nestling stage of the breeding. The annual individual fitness was calculated as the sum of an adult individual's own survival (0 or 1) and its fecundity; the number of recruits (surviving offspring) to the breeding population the year after (Sæther and Engen 2015). The differences between translocated and resident individuals ('origin') for the different fitness components (except survival) were analysed using generalized linear models (GLM; Crawley 2013). Based on an evaluation of model fit, we used Poisson family with log link when analysing number of mates (males), quasi-Poisson family with log link when analysing number of eggs produced (females), and negative-binomial family with log link when analysing number of fledglings and recruits produced, whereas annual individual fitness was analysed using Poisson family and log link. The error distributions were selected to fit the variable's error structure in order to avoid over-dispersion. The house sparrow is a sexually selected species, with sexual dimorphism in size, morphology and behaviour (Anderson 2006). The fitness effects of the translocation may thus differ between sexes. We therefore included the main effect of sex and the interaction between origin and sex in our GLM analyses, and analysed survival and demographic variance separately for the sexes. Furthermore, because individual fitness in both male and female house sparrows is related to adult morphology (Jensen et al. 2004, 2008) we included morphological traits (body mass, tarsus length, wing length, bill length, and bill depth for both sexes, and badge size in addition for males) as covariates that potentially could explain variation in fitness among individuals (for summary statistics of the morphological traits see Supplementary material Appendix 3 Table A2). The significance of the interactions was tested with likelihood-ratio tests. Badge size area was square root transformed and body mass was log transformed prior to the statistical analyses in order to operate on the same scale for morphological measurements.

To investigate whether individuals mated assortatively based on their origin, we compared the expected parentage combinations under random mating with the distribution of parentage combinations from our parentage analysis. We also compared the expected distribution of fledgling and recruit production among pair combinations (in relation to origin) to the outcome in our study population. To compare whether the distributions differed we performed Pearson's χ^2-contingency tests (Crawley 2013). In these analyses we also included some newly fledged juveniles banded within the breeding season at Vikna (n = 8), and their respective parents, since they were identified as adults (from the 246 individuals) that were released in March 2002.

To examine whether adult survival probability differed between residents and translocated individuals we used information on whether an individual was observed or captured in the Vikna archipelago after 15 April 2003 (the start of the breeding season one year after the translocation experiment). Because annual re-capture rates for the individuals banded in 2002 were somewhat lower than one, additional capture and observation data in the years 2004–2007 were also used when performing a capture–mark–recapture analysis. Adult survival was analysed with a multi-event Bayesian model following Kéry and Schaub (2012), run with 3 chains each with 10 000 iterations and a thinning rate of 4; the first 6000 iterations were discarded ('burn in'). We assessed the chain mixing and convergence to a stationary distribution by visual inspection of trace-plots and the Brooks–Gelman–Rubin criterion (R-hat, Brooks and Gelman 1998). Origin and sex were added as additive covariates in our analysis. Significance was determined from whether the Bayesian 95% credible interval of the posterior distribution of the difference between groups (Delta) included zero. A similar model was applied to analyse whether survival differed between offspring with parents with similar origin (either two resident parents or two translocated parents), and offspring with a mixed parent pair (a resident and a translocated parent). Thus, in analyses of offspring survival pair combination was added as a covariate. To increase statistical power, additional offspring (n = 34) from pairs involving nine adults banded in the Vikna archipelago within the breeding season shortly after release (and thus regarded as residents), were included. This analysis examined the existence of any hybrid vigour, evident if offspring from mixed parent pairs had higher recruitment probability than offspring from single origin pairs (Ebert et al. 2002). In this analysis we included 154 offspring from 80 parents distributed among 49 pair combinations, from which only four pairs had more than one recruit. Accounting for similar background of siblings was not possible in our capture–mark–recapture model.

Finally, we calculated the demographic variance separately for resident and translocated, males and females. Demographic variance is the expected variance in the individual fitness in a given year (Lande et al. 2003). Following Engen et al. (1998), Sæther et al. (1998) and Engen and Sæther (2014) the relationship between adult survival and the number of recruits produced (fecundity) enabled us to partition the deterministic and stochastic components of the contribution to future population growth. We could then estimate the contribution from each group of origin (resident and translocated) to the total population demographic variance, by using the equation for females (used for both sexes separately) from Engen et al. (2007):

$$\sigma^2_{df} = b_f q(1-q) + \sigma^2_f q^2 + s_f(1-s_f) + 2qc_f$$

where σ^2_{df} denotes the demographic variance, and b_f, σ^2_f, s_f and c_f denotes the parameters for individual level data for the respective number of recruits, variance in recruit production, survival and the covariance between recruit production and survival. Assuming an equal sex-ratio among offspring q is set to 0.5. In order to estimate the sampling error of our estimates, mean estimates and standard error of the demographic variance were estimated from separate samples consisting of 10 000 bootstrap replicates drawn randomly from our data dependent on sex and origin.

All statistical analyses were performed in R ver. 3.3.0 (<www.r-project.org>). For the capture–mark–recapture analyses we used the 'r-jags'-package ver. 4-6 (Plummer 2016).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b4q6q> (Ranke et al. 2017).

Results

From the breeding season in 2002, parentage analyses revealed that 40.5% (17) of resident males remained unmated, 42.9% (18) had one mate, and 16.7% (7) had two mates. Among the translocated males 69.0% (20) remained unmated, 27.6% (8) had one mate, and only 3.4% (1) had two mates.

Resident males acquired more mates than translocated males (Table 1). However, there were no statistically significant differences between resident and translocated individuals in the other fitness components, or in the measure of annual individual fitness (Table 1). The effect of origin on number of fledglings, number of recruits and the annual individual fitness did not differ between males and females, as indicated by the non-significant sex × origin interactions (number of fledglings: $\chi^2_1 = 1.52$, n = 144, p = 0.217; number of recruits: $\chi^2_1 = 0.85$, n = 144, p = 0.358, annual individual fitness: $\chi^2_1 = 0.57$, n = 144, p = 0.451).

There seemed to be a positive interaction between male badge size and origin on the number of mates (badge size × origin interaction: $\beta = 1.03 \pm 0.55$, $\chi^2_1 = 3.90$, n = 71, p = 0.048), however this was not significant after controlling for multiple tests. The positive relationship between badge size and the number of fledglings was stronger in translocated males than in resident males (badge size × origin interaction: $\beta = 2.04 \pm 0.70$, $\chi^2_1 = 8.25$, n = 71, p = 0.004, Fig. 1). The difference in effect of resident and translocated males on the negative relationship between bill length and both the number of fledglings and recruits did not remain significant after controlling for multiple tests. There were no other differences between resident and translocated individuals in the relationship between fitness components and the remaining morphological traits measured (males: all $\chi^2_1 \leq 2.38$, n = 72, $p \geq 0.123$; females: all $\chi^2_1 \leq 3.51$, n = 74, $p \geq 0.061$, Supplementary material Appendix 3 Table A2).

Table 1. Means and parameter estimates for tests of difference in fitness components between resident and translocated house sparrows in the Vikna archipelago in Norway the breeding season 2002. Analyses of the number of mates were carried out with Poisson error distribution, the number of eggs with quasi-Poisson error distribution, the number of fledglings and recruits with negative binomial error distribution, and analyses of annual individual fitness (Ann. fitness) was carried out with a Poisson error distribution. e^{β}-values represents the difference between resident and translocated individuals retransformed from the link-scale, with corresponding standard errors retransformed with the delta method. The degrees of freedom = 1 for all tests, and significant p-values are depicted in bold.

	Resident mean ± SD	Translocated mean ± SD	e^{β} ± SE	z	p
Males (n = 71)					
Mates	0.76 ± 0.73	0.35 ± 0.55	2.20 ± 0.80	2.19	**0.029**
Fledglings	1.88 ± 2.29	1.07 ± 2.22	1.76 ± 0.74	1.34	0.181
Recruits	0.29 ± 0.81	0.21 ± 0.49	1.38 ± 0.92	0.49	0.627
Ann. fitness	0.79 ± 1.05	0.59 ± 0.68	1.34 ± 0.40	0.98	0.327
Females (n = 73)					
Eggs	2.35 ± 3.43	2.58 ± 3.78	0.91 ± 0.31	–0.27	0.790
Fledglings	1.65 ± 2.54	2.09 ± 3.05	0.79 ± 0.39	–0.48	0.632
Recruits	0.23 ± 0.58	0.36 ± 0.82	0.62 ± 0.36	–0.83	0.407
Ann. fitness	0.75 ± 0.74	0.76 ± 1.03	0.99 ± 0.27	–0.04	0.970

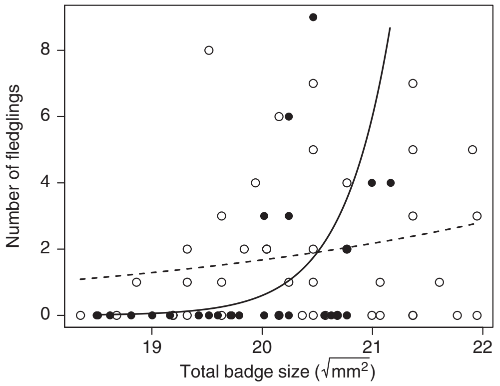

Figure 1. The relationship between a sexually selected trait, the badge size, and the number of fledglings produced by translocated (n = 29; filled circles and solid line) and resident (n = 42; open circles and dashed line) male house sparrows.

The overall observed mating pattern (see the expected and observed distributions in Supplementary material Appendix 4 Table A3), i.e. whether the genetic fathers and mothers in a pair had the same or different origin, deviated from what was expected from random mating. The overall pattern suggested that mating was assortative based on origin ($\chi^2_1 = 11.64$, n = 46 pairs, $p < 0.001$; Fig. 2), where in particular translocated males were very unlikely to mate with resident females. The mating pattern was subsequently apparent with a significant deviation in the production of fledglings compared to what is expected from a random fledgling production among parent pair types ($\chi^2_1 = 43.36$, n = 128 fledglings, $p < 0.001$; Fig. 2). The distribution in production of recruits among the pair types however, did not deviate from the expected distribution ($\chi^2_1 = 2.24$, n = 19 recruits, p = 0.135).

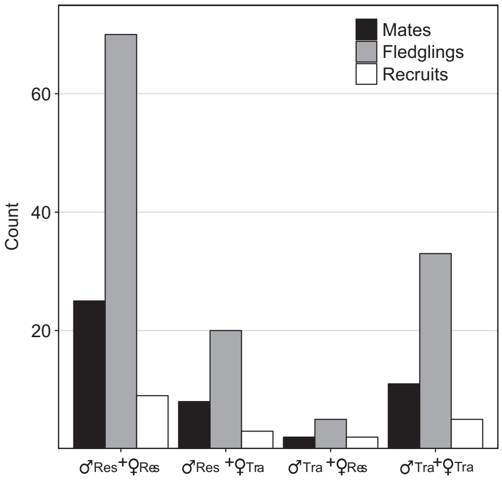

Figure 2. Number of parentage pairs, fledgling- and recruit production based on genetic parentage in resident and translocated house sparrows. Dark bars represents the number of pairs (mates, n = 46), grey bars represents the number of fledglings (n = 128) and the white bars represents the number of recruits (n = 19). Res = resident, and Tra = translocated.

Table 2. Estimates of mean survival probability for established adults and for offspring from different composition of parent pairs based on source of origin. Estimates of mean survival rate (survival) and 95% credible intervals (CI) were obtained from capture–mark–recapture models. Mean resighting probability (and corresponding credibility intervals) for adults and offspring, 0.65 (CRI: 0.52, 0.77) and 0.65 (CRI: 0.51, 0.77) respectively.

Origin	Survival	CRI
Adult (n = 146)		
Resident males	0.56	(0.44, 0.70)
Resident females	0.59	(0.46, 0.73)
Translocated males	0.55	(0.40, 0.70)
Translocated females	0.48	(0.33, 0.64)
Offspring (n = 154)		
Parents of similar origin	0.29	(0.20, 0.38)
Parents of different origin	0.54	(0.40, 0.68)

The adult survival probability from the breeding season to the next year was similar for resident and translocated individuals in both sexes (Table 2). The analysis of offspring survival revealed however that the survival probability was significantly higher for offspring produced by parents of different origin than for offspring produced by parents of similar origin ($\text{Delta}_{S(\text{different})-S(\text{similar})} = 0.25 \pm 0.08$, CRI = (0.10, 0.41), n = 154, Table 2). The Brooks–Gelman–Rubin statistic for convergence was less than or equal to 1.008 and 1.004 respectively, for all parameters in the two simulations.

Finally, we examined the variance in individual fitness to estimate the contribution from each origin to the demographic variance in the population. Estimates of the sex-specific demographic variance ranged from $\sigma^2_d = 0.33 \pm 0.06$ SE in translocated males to $\sigma^2_d = 0.60 \pm 0.16$ SE in translocated females (Table 3). The sex-specific demographic variance did not differ consistently between resident and translocated individuals in either sex, indicating that individuals from both origins contribute to the demographic variance of the population.

Discussion

We found a stronger positive relationship between badge size and the production of fledglings among translocated

Table 3. Comparison of demographic variance (σ_d^2) and its components for resident and translocated, male and female, house sparrows: individual rate of production of recruits to the next year breeding population (b), survival rate (s) and covariance between recruitment rate and survival rate (cov(b, s)). Standard errors represents the sampling error of the estimates.

Origin	b	s	cov(b, s)	$\sigma_d^2 \pm$ SE
Male				
Resident	0.29	0.50	0.10	0.58 ± 0.20
Translocated	0.21	0.38	–0.02	0.33 ± 0.06
Female				
Resident	0.23	0.53	–0.01	0.38 ± 0.06
Translocated	0.36	0.39	0.09	0.60 ± 0.16

males than among resident males (Fig. 1). This may have contributed to an assortative mating based on origin, causing unexpectedly few number of parentages and number of fledglings from pairs of parents with mixed origin, especially pairs consisting of translocated males and resident females (Fig. 2). The effects on individual fitness by a low total number of fledglings from pairs of mixed origin seem to have been partially counteracted by an increased recruitment probability in offspring from pairs of parents with mixed origin (Table 2, Fig. 2), suggesting hybrid vigour.

The comparison of fitness components between resident and translocated individuals revealed that resident males acquired more mates than translocated males (Table 1), however, this did not result in higher reproductive success. Due to morphological differences between resident and translocated individuals (Supplementary material Appendix 1 Table A1), and a positive relationship between badge size and lifetime reproductive success (Jensen et al. 2004), one should also expect a difference in reproductive success between resident and translocated males. Neither of the other fitness components, nor a measure of annual individual fitness in either sex differed between resident and translocated individuals. Even though few translocation studies compare fitness components with a reference baseline, some bird translocations among rather similar populations and habitats indicate small differences in fitness between resident and translocated individuals after establishment (Krogstad et al. 1996, Kaler et al. 2010), often apparent only in components of fitness measured early in the breeding cycle (Kaler et al. 2010). In contrast, fitness of translocated individuals may also exceed that of the resident individuals e.g. if the translocated individuals have increased mating success compared to the resident (Jones et al. 1995).

In house sparrows, the size of the black throat badge is important for the dominance structure in sparrow flocks (Møller 1987, Solberg and Ringsby 1997) and badge size is often positively related to reproductive success (Jensen et al. 2004, Nakagawa et al. 2007, Jensen et al. 2008). Interestingly, we found a stronger positive relationship between badge size and number of fledglings in translocated males compared to resident males (Fig. 1). This implies that only the larger badged translocated males (with badge size in the upper 27%) produced equally many or more fledglings as resident males, while translocated males with smaller badge size (the remaining 73%) on average produced fewer fledglings compared to resident males with equal badge size. The weaker effect of badge size on the number of fledglings for resident males may be an effect of living in small populations where individuals know each other's fighting ability from previous encounters (the individual recognition hypothesis; Shields 1977, Solberg and Ringsby 1997). Hence, the translocated males may experience increased costs in terms of aggressive interference encounters because resident males test the reliability of their badge signal. Accordingly, the only morphological trait that affected fitness of translocated and resident individual differently was related to sexual selection and male–male competition for mates.

Although the two groups of origin performed equally well with respect to fitness components and annual individual fitness (Table 1), further examination of parentage showed an assortative mating based on origin (Fig. 2). Only 6.7% of resident mothers produced offspring with a translocated father, emphasizing the reduced mating success for translocated males with respect to resident females. Reproductive skew caused by assortative mating has previously been found in translocation studies, e.g. related to male body mass (Sigg et al. 2005) and male song affected by source of origin (Bradley et al. 2014). The low success for translocated males to mate with resident females (and partly also translocated females with resident males) limited the intermixing of the translocated individuals into the local population (Fig 2).

In our analyses of adult survival, we found no differences between resident and translocated individuals in either sex. Unlike the similar adult survival rates, our results for the fledgling survival probability until recruitment showed an effect of hybrid vigour, as the recruitment probability was significantly higher for offspring with parents of mixed origin than for offspring with parents of similar origin. In the present experiment hybrid vigour seem to have been important for alleviating the observed skew in the distribution of parentage and fledglings for pairs of mixed origin (Fig. 2), and might have enhanced gene flow between the resident and the translocated individuals of the population (Ebert et al. 2002). Similarly, Marr et al. (2002) found increased performance e.g. offspring survival, in offspring from immigrant-resident pairs in song sparrows *Melospiza melodia* on Mandarte Island, Canada.

Our results did not indicate any differences between resident and translocated individuals in the sex-specific estimates of demographic variance, and the estimates were within the range of what has been reported for temperate passerines (Sæther et al. 2004). The contribution to the demographic variance from the two groups of origin (Table 3) might be according to what was expected due to the lack of significant differences between residents and translocated individuals in most fitness components (Table 1, 2). A potential bias estimating demographic variance in this population was related to an underestimation of vital rates. The CMR-analysis predicted a slightly higher adult survival rate compared to our individual data (Table 3), which could potentially overestimate the demographic variance to some extent. However, this bias should be independent of source of origin, thus not influence the difference in the contribution to the demographic variance. Additionally, the integration of survival rates from the CMR-analysis had only marginal effects on the estimates of contribution to demographic variance. Although we lack demographic data to estimate demographic variance in the period before the translocation, our estimates are within the variation in a neighbouring population of house sparrows (Sæther et al. 1999, Ringsby et al. 2006, Engen et al. 2007), indicating that our estimates seem reliable.

The present study has experimentally demonstrated that translocated individuals of both sexes contribute to the future population dynamics, since there were no differences in either the individual contributions nor the demographic variance between resident and translocated individuals. Moreover, the experiment revealed that the success of translocated individuals may depend on their sex-specific phenotypic characteristics, and furthermore, that the contributions to the local population might also be affected by the recruitment probability of offspring. Our findings have substantial implications for conservation programs and the understanding of individual ecology of translocated individuals in recipient populations.

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Permits – Guidelines for the care and use of animals were followed. The study was approved by the Norwegian Environment Agency (permit 2001/6427-ARTS/VI/ARE), the Norwegian Animal Research Authority (permit S-2603-01), and the Bird Ringing Centre at Museum Stavanger, Norway.
Author contribution statement – BES, HJ and THR conceived and designed the experiments. BGS, HJ and THR performed the experiments. HJ, SS and ÅAB carried out the genetic parentage analyses. HP, IH, PSR, SS and TK analysed the data. HP, PSR and SS wrote the manuscript with input from the other authors.
Conflict of interest – All the authors declare that they have no conflict of interest.

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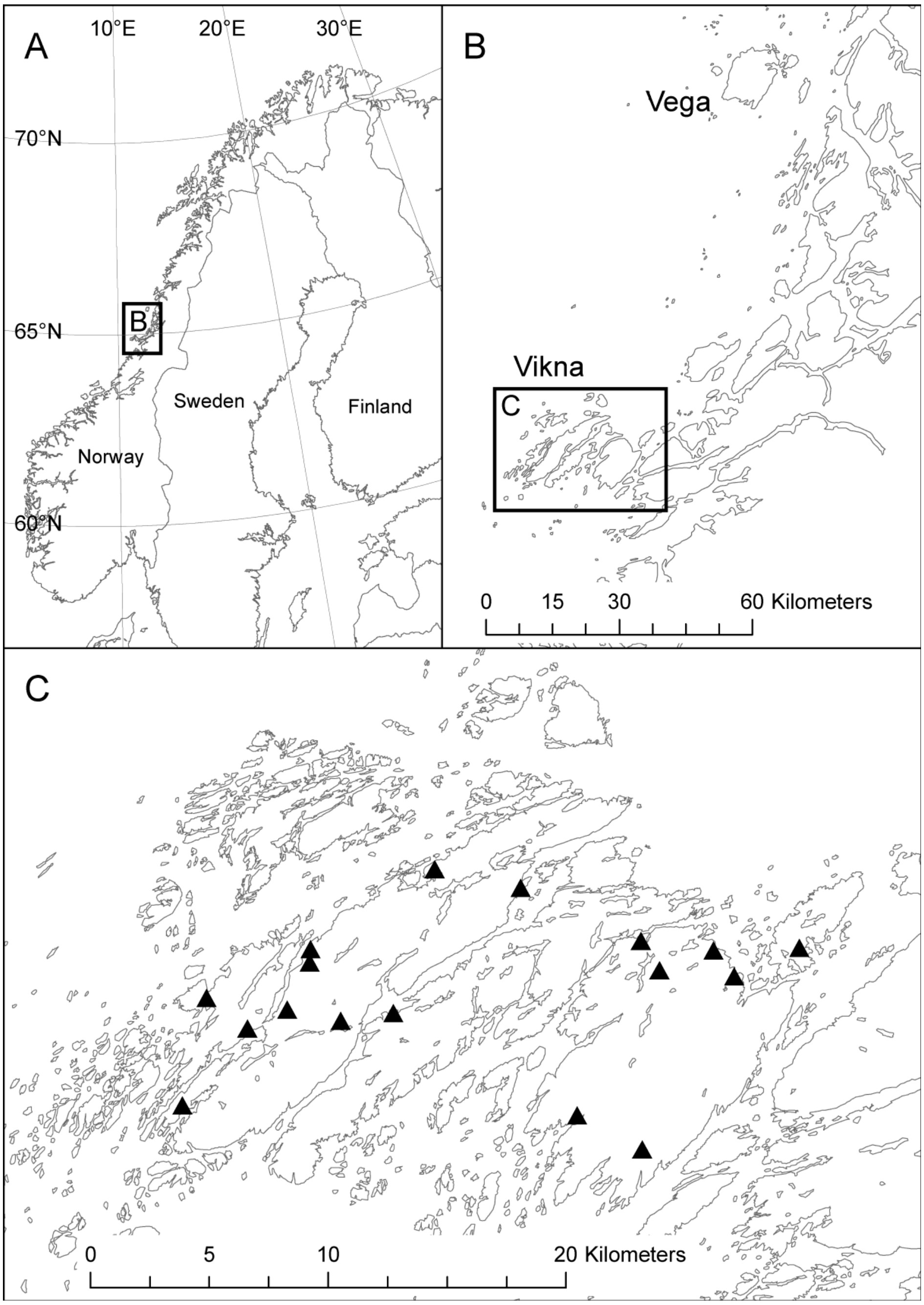
Supplementary material (available online as Appendix oik-04065 at <www.oikosjournal.org/appendix/oik-04065>). Appendix 1–6.

Appendix 1

The study site and location at the Norwegian coast.

Fig. A1 Fennoscandia (A), with the two areas included in the experiment (B) involving the island Vega were the translocated population of house sparrows in 2002 were residing, and the study area, Vikna (C), where birds were translocated. The local subpopulations (*n* = 17) that were included in the experiment are indicated as black triangles.

Figure A1


A
10°E
20°E
30°E
70°N
65°N
60°N
B
Norway
Sweden
Finland
B
Vega
Vikna
C
0
15
30
60 Kilometers
C
0
5
10
20 Kilometers

Appendix 2

Morphological differences between the resident and translocated individuals

Table A1. Differences in mean morphological characters between resident and translocated individuals before released into the Vikna archipelago. Resident refer to the local birds, and translocated to the birds moved from Vega. Male n = 122 individuals (59 resident and 63 translocated), female n = 124 (61 resident and 63 translocated), or given from degrees of freedom for each test.

	Resident mean ±SD	**Translocated mean ±SD**	**t**	**df**	**p**
Males					
Body mass (log g)	3.428 ±0.060	3.439 ±0.064	1.009	120	0.315
Wing length (mm)	82.147 ±1.555	81.668 ±1.709	-1.616	120	0.109
Tarsus length (mm)	19.811 ±0.686	19.917 ±0.527	0.958	119	0.340
Bill depth (mm)	7.975 ±0.260	8.247 ±0.241	5.997	120	**<0.001**
Bill length (mm)	13.601 ±0.531	13.723 ±0.518	1.270	119	0.206
Total badge size ($\sqrt{mm^2}$)	20.417 ±0.849	19.853 ±0.801	-3.758	119	**<0.001**
Females					
Body mass (log g)	3.441 ±0.074	3.443 ±0.057	0.212	122	0.833
Wing length (mm)	79.293 ±1.829	79.036 ±1.939	-0.759	122	0.449
Tarsus length (mm)	19.645 ±0.714	19.728 ±0.413	0.797	122	0.427
Bill depth (mm)	7.993 ±0.260	8.193 ±0.249	4.356	122	**<0.001**
Bill length (mm)	13.589 ±0.499	13.703 ±0.494	1.272	121	0.206

Appendix 3

Model outputs from GLMs testing differences in fitness components between resident and translocated individuals with interactions of morphological traits

Table A2. Generalized linear model outputs for the relationship between the given response and origin, and differences between resident and translocated individuals for the interactions from each of the morphological traits (BM = body mass, TL = tarsus length, WL = wing length, BD = bill depth, BL = bill length and BS = badge size). Males n = 71 in all tests (70 in test of BL). Females n = 73 in all tests (72 in test of BL). Each model separated by line break. P-values written in bold depicts that tests are still significant after controlling for multiple testing, following the procedure by Holm (1979) for sequential Bonferroni correction.

Response: Number of mates (males)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	-28.76	13.63		
origintransloc	5.21	22.57		
log(BM)	8.25	3.94		
origintransloc:log(BM)	-1.74	6.51	0.07	0.789

origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	-2.78	5.35		
origintransloc	8.09	14.44		
TL	0.13	0.27		
origintransloc:TL	-0.45	0.73	0.38	0.537

origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	-6.02	9.95		
origintransloc	-4.00	16.62		
WL	0.07	0.12		
origintransloc:WL	0.04	0.20	0.04	0.846

origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	-0.47	5.16		
origintransloc	18.88	12.74		
BD	0.03	0.65		
origintransloc:BD	-2.41	1.58	2.38	0.123

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	1.22	5.51		
origintransloc	10.18	10.29		
BL	-0.11	0.41		
origintransloc:BL	-0.81	0.76	1.11	0.291

origin + sqrt(BS) + origin:sqrt(BS)	Intercept	SE	χ^2_1	p
(Intercept)	-1.72	3.99		
origintransloc	-21.41	11.31		
sqrt(BS)	0.07	0.20		
origintransloc:sqrt(BS)	1.03	0.55	3.90	0.048[1]

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[1] Not statistically significant after controlling for multiple testing

Response: Number of eggs (females)				
origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	3.80	12.45		
origintransloc	-2.48	20.17		
log(BM)	-0.86	3.63		
origintransloc:log(BM)	0.75	5.87	0.02	0.899
origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	5.12	5.63		
origintransloc	24.15	16.87		
TL	-0.22	0.29		
origintransloc:TL	-1.23	0.86	2.19	0.139
origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	-1.97	9.28		
origintransloc	-17.80	13.65		
WL	0.04	0.12		
origintransloc:WL	0.23	0.17	1.71	0.192
origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	9.52	6.73		
origintransloc	-4.75	11.28		
BD	-1.09	0.85		
origintransloc:BD	0.62	1.40	0.20	0.655

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	5.60	6.36		
origintransloc	3.85	9.62		
BL	-0.35	0.47		
origintransloc:BL	-0.27	0.71	0.15	0.699

Response: Number of fledglings (males)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	-35.94	17.53		
origintransloc	-27.15	27.35		
log(BM)	10.58	5.08		
origintransloc:log(BM)	7.60	7.89	0.78	0.376

origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	4.74	7.58		
origintransloc	-9.40	15.90		
TL	-0.21	0.38		
origintransloc:TL	0.45	0.80	0.37	0.541

origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	4.99	14.52		
origintransloc	4.30	20.16		
WL	-0.05	0.18		
origintransloc:WL	-0.06	0.25	0.05	0.829

origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	9.12	7.41		
origintransloc	10.90	14.46		
BD	-1.07	0.94		
origintransloc:BD	-1.37	1.78	0.46	0.500

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	3.17	7.41		
origintransloc	37.90	13.85		
BL	-0.19	0.55		
origintransloc:BL	-2.85	1.03	5.47	0.019[1]

origin + sqrt(BS) + origin:sqrt(BS)	Intercept	SE	χ^2_1	p
(Intercept)	-4.69	5.22		
origintransloc	-41.89	14.31		
sqrt(BS)	0.26	0.26		
origintransloc:sqrt(BS)	2.04	0.70	8.25	**0.004**

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[1] Not statistically significant after controlling for multiple testing

Response: Number of fledglings (females)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	11.48	17.35		
origintransloc	-6.80	28.56		
log(BM)	-3.20	5.05		
origintransloc:log(BM)	2.06	8.30	0.05	0.824
origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	5.26	8.03		
origintransloc	32.08	22.26		
TL	-0.24	0.41		
origintransloc:TL	-1.62	1.13	1.85	0.174
origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	2.58	13.46		
origintransloc	-23.77	21.63		
WL	-0.03	0.17		
origintransloc:WL	0.30	0.27	1.19	0.276
origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	13.10	9.55		
origintransloc	-7.82	16.32		
BD	-1.59	1.20		
origintransloc:BD	1.03	2.01	0.30	0.586

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	4.91	8.65		
origintransloc	14.60	13.46		
BL	-0.33	0.64		
origintransloc:BL	-1.05	0.99	0.86	0.355

Response: Number of recruits (males)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	-87.76	35.96		
origintransloc	49.36	47.06		
log(BM)	24.96	10.35		
origintransloc:log(BM)	-14.33	13.55	0.89	0.345

origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	1.04	11.67		
origintransloc	-15.94	25.52		
TL	-0.12	0.59		
origintransloc:TL	0.78	1.28	0.33	0.567

origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	-6.99	22.59		
origintransloc	0.26	31.63		
WL	0.07	0.28		
origintransloc:WL	-0.01	0.39	0.00	0.987

origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	-1.59	11.53		
origintransloc	24.44	23.61		
BD	0.04	1.45		
origintransloc:BD	-3.03	2.92	0.86	0.354

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	-17.45	12.46		
origintransloc	53.14	22.01		
BL	1.18	0.91		
origintransloc:BL	-3.95	1.63	4.43	0.035[1]

origin + sqrt(BS) + origin:sqrt(BS)	Intercept	SE	χ^2_1	p
(Intercept)	-22.09	10.32		
origintransloc	-15.73	22.60		
sqrt(BS)	1.01	0.50		
origintransloc:sqrt(BS)	0.79	1.10	0.45	0.503

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[1] Not statistically significant after controlling for multiple testing

Response: Number of recruits (females)				
origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	15.76	21.50		
origintransloc	-52.04	33.00		
log(BM)	-5.04	6.29		
origintransloc:log(BM)	15.24	9.58	2.11	0.147
origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	4.36	9.69		
origintransloc	51.44	29.99		
TL	-0.30	0.50		
origintransloc:TL	-2.60	1.54	2.94	0.086
origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	0.95	16.25		
origintransloc	-42.62	24.02		
WL	-0.03	0.21		
origintransloc:WL	0.54	0.30	3.06	0.080
origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	0.87	11.63		
origintransloc	-17.15	19.57		
BD	-0.30	1.45		
origintransloc:BD	2.15	2.40	0.87	0.352

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	-7.80	10.61		
origintransloc	24.49	15.67		
BL	0.46	0.77		
origintransloc:BL	-1.76	1.15	2.28	0.131

Response: Annual individual fitness (males)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	-30.00	13.46		
origintransloc	-1.57	19.48		
log(BM)	8.61	3.88		
origintransloc:log(BM)	0.35	5.61	0.00	0.950

origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	3.71	4.97		
origintransloc	-2.72	11.36		
TL	-0.20	0.25		
origintransloc:TL	0.12	0.57	0.05	0.830

origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	4.14	9.79		
origintransloc	-16.83	14.18		
WL	-0.05	0.12		
origintransloc:WL	0.20	0.17	1.37	0.242

origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	0.20	5.08		
origintransloc	2.90	10.18		
BD	-0.06	0.64		
origintransloc:BD	-0.39	1.25	0.10	0.757

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	-1.74	5.34		
origintransloc	10.95	8.57		
BL	0.11	0.39		
origintransloc:BL	-0.82	0.63	1.70	0.192

origin + sqrt(BS) + origin:sqrt(BS)	Intercept	SE	χ^2_1	p
(Intercept)	-4.33	4.01		
origintransloc	0.90	7.58		
sqrt(BS)	0.20	0.20		
origintransloc:sqrt(BS)	-0.05	0.38	0.02	0.885

Response: Annual individual fitness (females)

origin + log(BM) + origin:log(BM)	Intercept	SE	χ^2_1	p
(Intercept)	0.14	9.48		
origintransloc	-28.04	15.31		
log(BM)	-0.12	2.76		
origintransloc:log(BM)	8.12	4.43	3.33	0.068

origin + TL + origin:TL	Intercept	SE	χ^2_1	p
(Intercept)	-0.52	4.60		
origintransloc	13.69	12.69		
TL	0.01	0.23		
origintransloc:TL	-0.70	0.65	1.21	0.272

origin + WL + origin:WL	Intercept	SE	χ^2_1	p
(Intercept)	8.43	7.72		
origintransloc	-21.96	11.61		
WL	-0.11	0.10		
origintransloc:WL	0.28	0.15	3.51	0.061

origin + BD + origin:BD	Intercept	SE	χ^2_1	p
(Intercept)	0.87	5.18		
origintransloc	-8.46	9.27		
BD	-0.15	0.65		
origintransloc:BD	1.04	1.14	0.84	0.361

origin + BL + origin:BL	Intercept	SE	χ^2_1	p
(Intercept)	-0.28	4.74		
origintransloc	6.59	7.31		
BL	0.00	0.35		
origintransloc:BL	-0.48	0.54	0.81	0.368

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Appendix 4

The observed and expected distributions for the χ^2 tests of contingency

Table A3. Observed and expected mating-, fledgling- and recruit distribution among pairs with parents of different combinations of origin (resident or translocated (transloc)).

Number of matings	**Observed**	Transloc ♂	Resident ♂
(n = 46)	Transloc ♀	11	8
	Resident ♀	2	25
	Expected	Transloc ♂	Resident ♂
	Transloc ♀	5	14
	Resident ♀	8	19
Number of fledglings	**Observed**	Transloc ♂	Resident ♂
(n = 128)	Transloc ♀	33	20
	Resident ♀	5	70
	Expected	Transloc ♂	Resident ♂
	Transloc ♀	16	37
	Resident ♀	22	53

Number of recruits	**Observed**	Transloc ♂	Resident ♂
(n = 19)	Transloc ♀	5	3
	Resident ♀	2	9
	Expected	Transloc ♂	Resident ♂
	Transloc ♀	3	5
	Resident ♀	4	7

Appendix 5

DNA-analysis procedure and parentage determination

DNA was extracted from the blood samples by using a Chelex (BioRad, USA) resin based extraction method (Walsh et al. 1991). The genetic parentage of nestlings and fledged juveniles was determined by using Polymerase Chain Reaction (PCR) to amplify 19 polymorphic microsatellite regions with the primers Pdoµ1, Pdoµ3 (Neumann and Wetton 1996), Pdoµ4, Pdoµ5, Pdoµ6 (Griffith et al. 1999), Pdo10 (Griffith et al. 2007), Mcyµ4 (Double et al. 1997), Fhuµ2, Indigoµ41 (Sefc et al. 2001), Aseµ18 (Richardson et al. 2000), Hruµ5 (Primmer et al. 1995), and Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo44, Pdo47 (Dawson et al. 2012). The PCR reactions were carried out on a GeneAmp PCR system 9700 (Applied Biosystems, USA) with 2 µL genomic DNA in addition to 8 µL PCR-solution, containing 0.5 units GoTaq DNA Polymerase (Promega, USA), 0.14 mM dNTP`s (Promega, USA), 0.6 µM of each primer and a PCR-buffer containing 20 mM $(NH_4)_2SO_4$, 75mM TrisHCl pH 8.8, 0.15 mg/mL-1 DNAse free BSA, 10 mM β-mercaptoethanol for the primers Pdoµ1, Pdoµ3, Pdoµ4, Pdoµ5, Pdoµ6, Pdo10, Mcyµ4, Fhuµ2, Indigoµ41, Aseµ18 and Hruµ5. The PCR products obtained using the primers Pdoµ, Pdoµ5, Pdoµ6, Pdo10, Aseµ18 and Hruµ5 were pooled after PCR in a mix hereafter referred to as Mix1, and a mix of the PCR products from primers Pdoµ3, Pdoµ4, Mcyµ4, Fhuµ2, Indigoµ41 is referred to as Mix 2. For the primers Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo44, Pdo47, hereafter referred to as Mix 3, 2 µL genomic DNA was added to 8 µL PCR-solution, containing 0.5 units GoTaq DNA Polymerase (Promega, USA), 0.14 mM dNTP`s (Promega, USA), 0.6 µM of each primer and 2.8 µL 5x GoTaq Flexi Buffer (Promega). For a given individual the PCR-products from each mix was added to a solution containing 0.5

µL size ladder (GeneScan LIZ 500 for Mix 1 and 2, and GeneScan LIZ 600 for Mix 3, Applied Biosystems, USA) in addition to 10 µL Hi-Di Formamide (Applied Biosystems, USA).

The reverse primers were fluorescence marked to be detectable in a 16-capillary ABI Prism 3100 Genetic Analyser (Applied Biosystems) before the genotypes were analyzed by Genotyper 3.7 (Applied Biosystems) for markers in Mix1 and 2. The genotypes from markers in Mix3 were run on an ABI Prism 3130xl and analyzed in GeneMapper 4.0 (Applied Biosystems, USA).

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Appendix 6

Assignment of offspring with unknown genetic parents

Table A4. Output of source population assignment in ONCOR (Kalinowski S. T. et al. 2007) of offspring with unknown parentage. The number of offspring assigned to each source population, the percentage, and the distribution in percent of known parentage in the population for comparison.

Source	**No. assigned**	**Percent**	**Distribution of offspring with known source**
Vega	21	38 %	36 %
Vikna	34	62 %	64 %

References

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Paper III

Paper IV

Catalogue

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
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1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal

			Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on Arabidopsis thaliana
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits