NTNU – Trondheim
Norwegian University of
Science and Technology

Sensitivity Analysis of Effective Population Size to Demographic Parameters in House Sparrow Populations

Marlene Wæge Stubberud

Natural Resources Management
Submission date: May 2015
Supervisor: Henrik Jensen, IBI
Co-supervisor: Ane Marlene Myhre, IBI
                        Bernt-Erik Sæther, IBI

Norwegian University of Science and Technology
Department of Biology

Abstract

In population management, the effective population size, N_e, can be viewed in tandem with actual population size, N, as the main factors determining a population's long-term viability and sustainability. N_e is the number of individuals in an observed population that would lose genetic variation at the same rate as an ideal population. Understanding which demographic factors that affect N_e/N, will make resource allocation and decision making more effective, either if the management goal is to maximise, maintain or minimize N_e/N. The goal of this thesis was to calculate the demographic parameters that determine N_e/N, following the method of Engen *et al.* (2010), and then determine which of these parameters N_e/N is most sensitive to. In other words, determine which parameters that contribute most to the total variation in N_e/N. This was done, using data on 13 Norwegian populations of house sparrows (*Passer domesticus*), including more than 4000 individuals, and spanning up to 20 years. To find which of the demographic parameters (demographic variance, generation time, stable age distribution, reproductive values, individual fecundity and survival) that affect N_e/N most, sensitivity analyses were carried out. Using the global variance-based Sobol' method, it was found that demographic variance, especially of older individuals, was the parameter that N_e/N was most sensitive to. Generation time was found to be less important than demographic variance, which includes all the other parameters. The demographic variance of a population is determined by fecundity and survival on the individual level. The individual reproductive values were found to be most sensitive to fecundity, followed by survival. In contrast, the stable sex-age distributions, and the sex-age specific reproductive values, were found to be of little importance. For population management purposes, the results from this study show that resources should be focused on the manipulation of demographic variance in older individuals, more specifically their fecundity and survival. Even though these results are from insular populations of house sparrows, they may also apply to fragmented populations of other species with similar life histories and demography.

Sammendrag

Innen populasjonsforvaltning er effektiv populasjonsstørrelse, N_e, sammen med observert populasjonsstørrelse, N, hovedfaktorene som avgjør overlevelse og hvor bærekraftig en populasjon er på sikt. N_e er antallet individer i en observert populasjon som ville miste genetisk variasjon med samme rate som i en ideell populasion. Å forstå hvilken faktorer som er med på å påvirke N_e/N, vil gjøre både ressursallokering og avgjørelser innen forvaltning mer effektive. Dette gjelder både for mål om å maksimere, opprettholde eller minimalisere N_e/N. Formålet med denne oppgaven var å beregne de demografiske parameterne som inngår i N_e/N, ved å følge metoden i Engen *et al.* (2010), for deretter å finne hvilke av disse parameterne N_e/N er mest sensitiv til. Det vil si at man identifiserer hvilke parametere som bidrar mest til den total variasjonen i N_e/N. Dette ble utført ved å bruke opptil 20 år med data på over 4000 individer fra 13 norske populasjoner med gråspurv (*Passer domesticus*). For å finne hvilke av de demografiske parameterne (demografisk varians, generasjonstid, stabil alderstruktur, reproduktiv verdi, individuell fekunditet og overlevelse) som påvirker N_e/N mest, ble det utført sensitivitetsanalyser. Ved å bruke den globale, varians-baserte Sobol'-metoden, ble det funnet at den demografiske variansen, nærmere bestemt variansen hos eldre individer, var parameteren som N_e/N var mest sensitiv til. Generasjonstid var mindre viktig enn den demografisk variansen som inkluderer alle de resterende parameterne. Den demografiske variansen til en populasjon, bestemmes av individuell fekunditet og overlevelse. Den individuelle reproduktive verdien var mest sensitiv til fekunditet, etterfulgt av overlevelse. Hverken den stabile kjønns-alderstrukturen eller de kjønns-aldersspesifikke reproduktive verdiene, ble funnet å være viktige parametere. Resultatene fra dette studiet viser at ressurser innen forvaltning burde bli fokusert på å manipulere demografisk varians hos eldre individer, mer spesifikt deres fekunditet og overlevelse. Selv om disse resultatene kommer fra øypopulasjoner av gråspurv, vil de kanskje også være gjeldende for andre fragmenterte populasjoner hos arter med liknende livssykluser og demografi.

Contents

List of Figures

List of Tables

1 Introduction

Today, there is a growing number of threats to natural populations, and many
are due to anthropological activities. The threats come in several forms: over-
exploitation, pollution, pathogens, climate change and habitat fragmentation, de-
gradation and destruction (Primack 2010), which in turn might lead to isolated
and small populations (Frankham *et al.* 2010). Small populations, and populations
with large variation in number of individuals, are known to have a higher risk of ex-
tinction (Legendre *et al.* 2008), due to both stochastic and deterministic ecological
and evolutionary processes (Lande *et al.* 2003). Population size is positively corre-
lated with genetic variation, and smaller populations therefore tend to have lower
genetic diversity, which may make them vulnerable to environmental changes and
selectional pressures such as diseases (Frankham 1996). For population managers,
it is important to focus on the maintenance of genetic variation. Small populations
are more susceptible to genetic drift, which are random changes in allele frequencies
from one generation to the next. Founder events, where a handful of individuals
are the basis of a new population, are often followed by increased rates of inbreed-
ing. Migration between local populations in a metapopulation is crucial to reduce
inbreeding (Allendorf *et al.* 2012), but also to maintain the metapopulation by
recolonizing locally extinct populations, as was found in the extensive metapopula-
tion study of the butterfly Glanville fritillary (*Melitaea Cinxia*) in Finland (Hanski
et al. 1994). Mating of related individuals, i.e. inbreeding, leads to further loss
of genetic variation and reduced fitness by increased homozygosity, or inbreeding
depression. Expression of deleterious recessive alleles are thought to be the main
mechanism behind this process (Allendorf *et al.* 2012). For example, traits such
as reproductive success, survival, immune response, and even male's song reper-
toire was negatively affected by severe inbreeding in a population of song sparrows
(*Melospiza melodia*) on Mandarte Island in Canada (Smith 2006). Furthermore,
historically small population sizes affect populations and species in the long-run.
An example is the endemic Tasmanian devil (*Sarcophilus harrisii*) that experienced
a founder event more than 12,000 years ago, when a small group of individuals was
separated from the now extinct mainland population in Australia. This founder
event, and the genetic drift and inbreeding that followed, left the species with low
genetic diversity, especially at the genes in the major histocompability complex
(MHC), which is important for immune recognition of foreign cells. The low ge-
netic variation in the MHC has allowed for a contagious cancer, known as devil
facial tumour, to spread across the island for the last 20 years, resulting in a 84%
population decline and the Tasmanian devil is now threatened by extinction (Miller
et al. 2011; Cheng *et al.* 2012).

A population is affected by both demographic and environmental stochasticity,
which are defined as the differences in survival and fecundity of individuals within
a year, and as the mean difference between years, respectively. Demographic vari-
ance have a larger effect in small populations, as the individual differences in large
populations are averaged out. While stochasticity increases probability of extinc-
tion, most documented extinctions follows a steady decline in population size over

time (Lande *et al.* 2003). One example is the Californian condor (*Gymnogyps californianus*), that went extinct in the wild in 1987, after decades of steadily declining population sizes. The main reasons of the decline was found to be loss of habitat, and lead poisoning from eating carcasses killed by hunters (Dennis *et al.* 1991). Several processes on the individual level in a population influence population size; birth, growth, development, maturation, migration, reproduction and death (Tuljapurkar and Caswell 1997). These processes depend on both genes and the environment, and they describe an individual's movement throughout the life cycle, either empirically or theoretically. It is these processes that ultimately determine whether the population increases, declines, fluctuates, or is stable (Caswell 2001).

In many ecological and evolutionary models, it is actually the effective population size, N_e, and not the actual population size, N, that is used. To be able to manage populations, and make predictions on how the aforementioned threats might affect populations in both long- and short-term perspective, one must understand the importance of N_e, as it includes both ecological and genetic factors (Shaffer 1981; Nunney and Elam 1994; Palstra and Fraser 2012). Wright (1984) defined the effective population size as the number of individuals in a population that substitutes the population size, N, in his formula for genetic drift in an ideal population:

$$H_t = H_0 \left(1 - \frac{1}{2N} \right)^t, \tag{1}$$

where H_t is the expected heterozygosity in the population in generation t, and H_0 is the original heterozygosity in the first or present generation. In other words, N_e is a theoretical number of individuals in an observed population that lose heterozygosity at the same rate as an ideal population (Freeman and Herron 2007; Frankham *et al.* 2010). An ideal population is a conceptual infinitely large panmictic population with constant size, consisting of monoecious diploid individuals that have discrete generations, Poisson distributed family sizes ($\mu = \sigma^2$) and no selection or mutations in autosomal loci. For the population size to remain constant, the mean and variance in family size must equal 2 (Nunney and Baker 1993; Caballero 1994; Wang and Caballero 1999; Kalinowski and Waples 2002; Frankham *et al.* 2010). If a population fulfils all of these conditions, the effective and observed size will be the same, $N_e = N$. Natural populations violate the conditions of an ideal population in one or several ways, by being finite, under selection, and so on (Harris and Allendorf 1989; Wang and Caballero 1999; Frankham *et al.* 2010). Due to these deviations from ideal population characteristics, most populations behave as if they were a lot smaller than their census size, N (Halliburton 2003; Freeman and Herron 2007; Frankham *et al.* 2010). In stable populations, N_e/N is expected to be between 0.5-1 (Nunney and Elam 1994; Nunney 1995), while in fluctuating, wild populations it has been found to be 0.10 on average (Frankham 1995; Palstra and Ruzzante 2008). N_e/N vary a lot between different taxa, e.g. marine species tend to have a very low average values ($N_e/N = 0.0001$), compared to many terrestrial species ($N_e/N = 0.14$) (Palstra and Ruzzante 2008). The

extremely low values of many marine species, such as fish and shellfish, is due to high fecundity and juvenile mortality. This means that only a few of the millions of individuals in the observed population contribute to the following generations (Hedrick 2005). In tandem with severe exploitation that leads to bottleneck events, the N_e/N is reduced even further as inbreeding and genetic drift increases, as found in populations of the commercially exploited Australasian snapper (*Pagrus auratus*) (Hauser *et al.* 2002). By maximising the effective, as well as the observed population size, the genetic variation and resilience to change is expected to increase in the population, and the risk of extinction will decrease (Frankham *et al.* 2010; Allendorf *et al.* 2012).

Of all deviations from the ideal population, variation in population size have been shown to be the factor that often reduce N_e most, relative to N (Kalinowski and Waples 2002; Engen 2005; Frankham *et al.* 2010). Furthermore, variation in family size, and skewed sex ratios might also be important (Caballero 1994; Frankham 1995; Frankham *et al.* 2010). In medium ground finches (*Geospiza fortis*) on Galapagos, there is a large variance in family size, which results in a reduced N_e/N compared to other species of finch on the islands (Grant and Grant 1992). Examples of skewed sex-ratios may be harem mating systems, such as in red deer (*Cervus elaphus*), where there are more females than males due to both natural selection and differential hunting (Van Dyke 2008). Other factors that affect N_e include overlapping generations and age structure (Engen 2005), generation time (Nunney and Baker 1993), population density, mating potential, birth and death rates, survival, and reproductive success (Lebreton *et al.* 1992; Frankham *et al.* 2010). All these factors may consequently be important to include, or account for, when estimating N_e.

In population management, it is of great importance to determine which factor(s) that affect N_e. This applies to all management strategies that aim to decrease, maintain or increase population sizes, e.g. pest species, fish stocks or threatened species (Tuljapurkar and Caswell 1997; Caswell 2001). Implementation of management actions can be challenging and, sometimes, give unexpected results, such as in supplementary feeding of females to stimulate production of offspring and hence increase N_e in the endemic and threatened kakapo (*Strigops habroptilus*) on New Zealand. The plan worked *per se*, by increasing reproduction, but the well-fed kakapo females only produced male offspring, as good quality males are more costly to produce, and the species have evolved a reproductive strategy to produce mainly males under good conditions. Instead of increasing N_e, the supplementary feeding reduced N_e even more, by increasing the already male biased sex-ratio. They solved the problem by feeding the females just enough to start breeding, but not so much that they only produced males (Robertson *et al.* 2006).

There are different ways to estimate N_e, and the appropriate approach depends on point of interest, knowledge of the biological processes of the population, or species in question, and available data. Since fluctuations in N are expected to have a large influence on N_e, the harmonic (Equation (2)), and not the arithmetic mean should be used when calculating N_e based on N. Small N's will affect N_e more

strongly, which is accounted for in the harmonic mean (Wright 1931; Halliburton 2003):

$$N_e = n^{-1} \sum_{t=1}^{n} \frac{1}{N_t},$$

(2)

where t is years, and $t = 1, 2, ..., n$. Extreme reductions in N are called bottleneck events, such as the hunting induced bottleneck of the northern elephant seal (*Mirounga angustirostris*) at the end of the nineteenth century. The population was reduced from tens of thousands to less than 20 individuals. This has reduced N_e drastically, and even though N now has been estimated to be back to pre-bottleneck levels (Hoelzel *et al.* 2002), it is still at risk of succumbing to environmental changes or diseases (Miller *et al.* 2011). Another important factor that affect N_e is variation in mean family sizes, and the effect of this variation on N_e is given by (Frankham *et al.* 2010):

$$N_e = \frac{4N - 2}{var(k) + 2},$$

(3)

where k is the mean family size. An ideal population will have $var(k) = 2$, which gives $N_e \approx N$. If there is no variation at all, $var(k) = 0$, then $N_e \approx 2N$, which shows that N_e is indeed a theoretical population size. The issue of variation in family size, is a well-known problem in breeding of captive, and often threatened species (Frankham *et al.* 2000). Equalization of family sizes have been found to successfully increase the effective number of breeders in captive breeding of coaster brook trout (*Salvelinus fontinalis*) in Lake Superior in North America (Cooper *et al.* 2010). This method of culling offspring of the most successive breeders has been shown to only be effective in species with high fecundity and short generation time, two characteristics that are not found in many threatened species currently being managed, such as larger mammals (Williams and Hoffman 2009). Variation in sex-ratio is also an important factor affecting N_e (Crow and Kimura 1970):

$$N_e = \frac{4N_{ef}N_{em}}{N_{ef} + N_{em}},$$

(4)

where N_{ef} and N_{em} is the effective population size of females and males, respectively. A skewed sex-ratio will reduce N_e significantly (Equation (4)), e.g. a breeding program with 1 male fertilizing 100 females, will lead to an effective population size of only four individuals, $N_e = (4 \times 100)/101 \approx 4$.

Some of the first models to estimate N_e were simplistic and purely theoretical (Wright 1931), but over time they have become increasingly complex and realistic for natural populations (Crow and Kimura 1970; Nei and Tajima 1981; Caballero and Hill 1992; Wang 2005; Engen *et al.* 2007). The challenge is to settle for a solution that is simple enough to be applicable, but at the same time complex enough

to give estimates of value. Short-term management often requires general and simple models, while more complex and specific models are needed for long-term goals. In general, more parameters add precision and realism to the model, but it might reduce the interpretability (Tuljapurkar and Caswell 1997). There are both genetic and demographic methods for estimating N_e, with different advantages and drawbacks depending on the situation. While genetic methods require data on DNA sequences or genetic markers (Wang 2005), demographic methods require data from successive years on population sizes, individuals sex and age, and individual reproductive success (Harris and Allendorf 1989; Nunney and Elam 1994). Genetic methods can estimate current, past, and even ancient effective population sizes (Wang 2005), while the demographic models in tandem with ecological information, have the possibility of predicting future changes in effective population size (Nunney and Elam 1994). This element of prediction can make demographic models the preferred choice, e.g., when several management options are considered. For example, it is possible to do a simulation of how wolf (*Canis lupus*) reintroduction will reduce Roosevelt elk populations (*Cervus elaphus rooseveltii*) (Fieberg and Jenkins 2005). When evaluating management strategies, it is preferable to get robust results quickly, and with minimal effort and costs. While demographic models can give solid and accurate estimates, a drawback is the extensive amount of data needed to execute the analyses (Caswell 2001). Since it is known that N_e in general is strongly correlated with N (Kalinowski and Waples 2002; Engen 2005; Frankham *et al.* 2010), it is in many cases more interesting to look at their ratio, N_e/N. The relative value of N_e/N can, at least in theory, be used to assess population persistence, based on the influence of demographical, environmental and genetic factors (Palstra and Fraser 2012). Because N_e/N can give insight into ecological factors that affect N_e, it might lead to more effective conservation and management decisions (Kalinowski and Waples 2002). The idea that species have a specific ratio between N_e and N (Frankham 1995), could ease the assessment of a population, but no studies have found evidence of such a simple relationship, because other factors than N also determine N_e (Palstra and Fraser 2012).

To make robust decisions in population management, knowledge about factors that influence the variance of effective population size is crucial. Or in other words: it is important to determine the parameters to which effective population size is most sensitive (Caswell 2001; Saltelli *et al.* 2004). This can be achieved with sensitivity analysis; by apportioning the output variance to the specific input variances, and determine which inputs that contribute most (and least) to the total variation in the output (Chan *et al.* 1997; Saltelli *et al.* 2009). By identifying the demographic parameter(s), or the stage(s) in the life cycle, that N_e is most sensitive to, the population size can be controlled through manipulation of said parameter(s). A famous example of how sensitivity analysis have been used in practice, is in the management of the declining populations of loggerhead turtles (*Caretta caretta*) (Crouse *et al.* 1987; Crowder *et al.* 1994). For many years, management effort was put into hatchling survival, but this had no effect, and the populations continued to decline. A sensitivity analysis showed that the population growth rate of the loggerhead turtle was most sensitive to juvenile survival, and very little to egg

and hatchling survival. Introduction of turtle excluder devices in trawl fisheries was therefore a logical management strategy, since by-catch is the main reason for juvenile mortality. The results of this strategy seems to be positive, but are so far inconclusive due to long generation times and poor implementation in some areas (Crowder *et al.* 1995; Lewison *et al.* 2003; Finkbeiner *et al.* 2011). Sensitivity analysis is recognized as an important tool in management, and has become part of governmental guidelines, such as the U.S. Environmental Protection Agency guideline for environmental model development, evaluation and application (EPA Council for Regulatory Environmental Modeling 2009), and the European Commissions guideline for impact assessments (European Commission 2009).

In this study, Norwegian populations of house sparrows (*Passer domesticus*) with data on more than 4000 individuals spanning up to 20 years, was used to calculate all parameters needed to estimate the demographic N_e and the effective to census population size ratio, N_e/N, as outlined in Engen *et al.* (2010). The demographic parameters include generation time and the demographic variance, which is given by the sex-age class specific variance, and the stable sex-age distribution. The sex-age class variance is given by the reproductive values, and the individual fecundity and survival. A sample-based Sobol' method will be used for a global variance-based sensitivity analysis, to determine which demographic parameters N_e/N is sensitive to. The principle of global analyses is that all inputs are varied simultaneously, the entire parameter space is explored, and any interactions between input parameters are accounted for (Sobol' 2001). Based on previous studies, all the included parameters are expected to have an effect on N_e/N, especially demographic variance since it includes all other parameters, except generation time. By identifying demographic parameters N_e/N is most sensitive to, one can infer where management efforts to regulate populations should be put. The house sparrow is used as a model species because it has a life history and demography that is similar to many other species, making it likely that my results will be relevant for other populations and species as well.

2 Materials and methods

2.1 Study populations

The 13 populations used in this study are spread out along the Norwegian coast, from near Trondheim in the south, to near Mo i Rana in the north (Figure 1). 6 of the northernmost populations were located in a long-term study system consisting of an insular metapopulation at Helgeland off the coast of Northern Norway, positioned at the Arctic Circle (66°N, 13°E). The remaining 7 populations were located on the mainland, and on islands to the south of this insular metapopulation. See Pärn *et al.* (2012) for more details about the study area. The dataset includes 4,074 unique individuals, and the number of years of data per population ranges from 2-20, with an average of 7 years. The mean population size over all years of data in a population varies from 19-170 individuals (Table 1). Annual population sizes for all populations can be found in Appendix A (Table A.1).
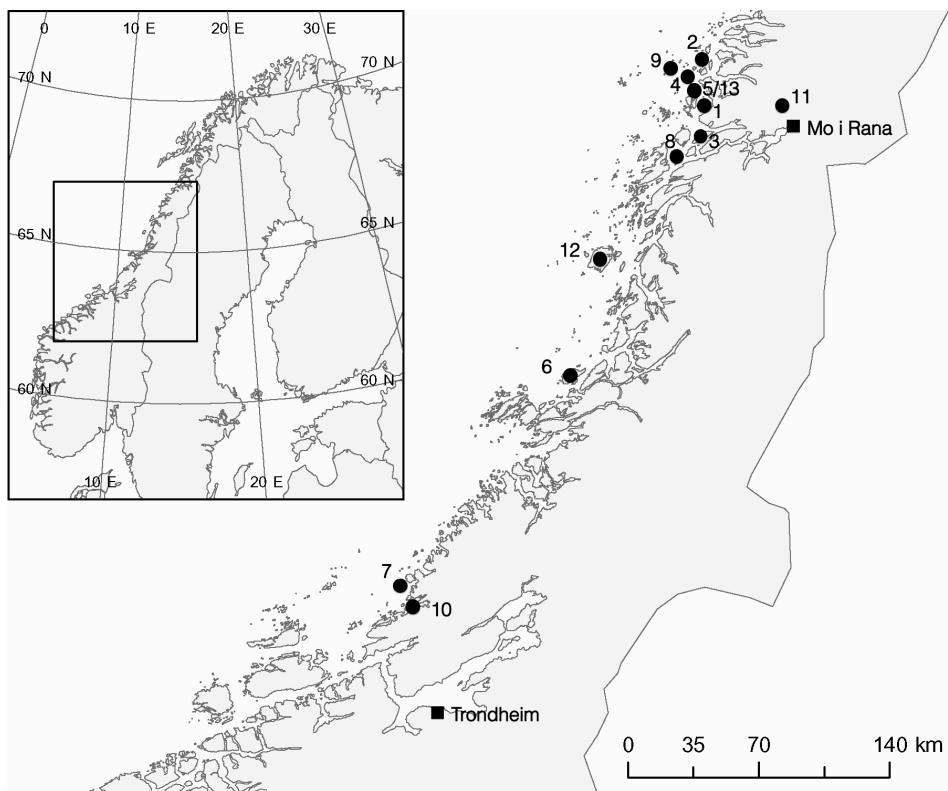
Figure 1: The populations in the dataset are spread out along the Norwegian coast, from an area outside of Trondheim (63°N, 10°E) in the south, to the coast outside Mo i Rana (66°N, 13°E) in the north (also see Table 1).

Table 1: Overview of study populations, their number on the map in Figure 1, years of data per population, n, and their mean population size over these years.

Number[a]	Population	Years of data	n[b]	Mean N
1	Aldra[c]	1998-2007	10	29
2	Gjerøy	1993-2002	10	45
3	Handnesøy	2011-2013	3	66
4	Hestmannøy	1993-2012	20	128
5	Indre Kvarøy	1993-2002	10	38
6	Leka[d]	2002-2009	8	127
7	Linesøya	2012-2013	2	73
8	Løkta	2011-2013	3	34
9	Nesøy	1993-2002	10	19
10	Rånes	2012-2013	2	46
11	Røvass	2011-2013	3	20
12	Vega[d]	2002-2009	8	170
13	Ytre Kvarøy[e]	1993-1998	6	25

[a] Numbers on map in Figure 1
[b] Total number of years of data for each population
[c] Founded in 1998, by four individuals (Billing *et al.* 2012)
[d] Was part of a selection experiment (2002-2005) (Kvalnes *et al.* in prep.)
[e] Went extinct in 2000 (Ringsby *et al.* 2006)

The locations of the 13 populations differ in quality of nesting sites, food availability and shelter (Pärn *et al.* 2012; Jensen *et al.* 2013), which is likely to have resulted in differences between the populations, e.g. mean population sizes (Table 1). One of the populations, on the island Aldra (population 1 in Figure 1), was founded in 1998 by one female and three males (Billing *et al.* 2012), while the population at Ytre Kvarøy (population 13 in Figure 1) went extinct in 2000 (Ringsby *et al.* 2006). Two other populations, Leka and Vega (population 6 and 12 in Figure 1), were part of a selection experiment in 2002-2005. On both islands, approximately 60 % of the population was removed based on their size measured by tarsus length. Small and large individuals were removed on Leka and Vega, respectively (Kvalnes *et al.* in prep.). These four islands are included to increase the range of variation, within natural limits, in the dataset.

2.2 Study species

The house sparrow is a small, sedentary passerine bird and is found around the globe in proximity to human settlements (Anderson 2006). In the study populations, it is often found at dairy farms, where there are nesting places, shelter and food. The house sparrow is sexually dimorphic with a brown-grey plumage. Females have a relatively light plumage, light coloured beaks, and a bright eyebrow stripe. Males have a generally darker plumage with chestnut brown heads, grey crowns, dark beaks, and black feathers around the beak and eyes, and on the throat and chest (Anderson 2006). The house sparrow is a socially monogamous species,

with some extra-pair mating (Jensen *et al.* 2008), where both parents contribute to brooding and feeding of chicks (Ringsby *et al.* 2009). In the study area, the breeding season is from May-August, and each pair produce 1-3 clutches with an average of five eggs per clutch during this time (Ringsby *et al.* 2002; Husby *et al.* 2006). Of all fledglings, only 15-20 % survive their first winter (i.e. still alive after 1 February) to become recruits in the next years breeding population (Ringsby *et al.* 2002). The average generation time, T, is 2 years in this system (Jensen *et al.* 2008), and an annual adult survival rate at approximately 50 % (Ringsby *et al.* 1999). There are quite low dispersal rates within the system; around 10 % of the new recruits are dispersers (Altwegg *et al.* 2000; Pärn *et al.* 2009, 2012), and 60 % of them travel distances shorter than 13 km (Tufto *et al.* 2005). The house sparrow has a life history that is typical for many small birds, with high mortality rates the first autumn and winter, and a relatively constant annual adult mortality rate (Botkin and Miller 1974). For a schematic overview of the house sparrow life cycle that is used in this thesis, see Figure 2.

2.3 Data collection and handling

The breeding season is the main field season, where most of the data was collected. Adults and fledged juveniles were caught in mist nets, while chicks were gathered directly from the nests. All birds were marked with a unique numbered metal ring, and three coloured plastic rings for identification (Ringsby *et al.* 2002; Jensen *et al.* 2004). A blood sample of approximately 25 µl were drawn from the brachial vein underneath the wing, which provide DNA necessary to genotype individuals on microsatellite markers needed to carry out genetic parentage analyses, and construct genetic pedigrees (Jensen *et al.* 2003). For details on the genotyping analyses, see Jensen *et al.* (2008, 2013), Billing *et al.* (2012) and Hagen *et al.* (2013). Most of the islands in my dataset had complete pedigrees, but for Handnesøy, Linesøya, Løkta, Rånes and Røvass, it had to be established. See Appendix B for method
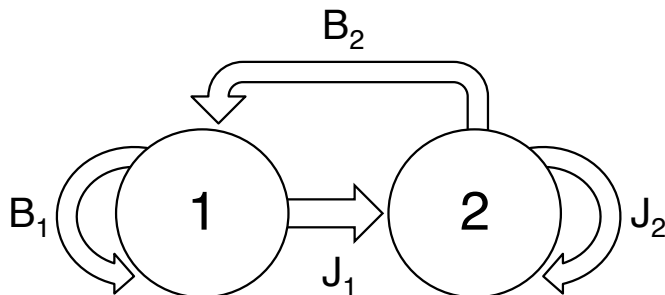
Figure 2: Life cycle of the house sparrow with two age classes, 1 and 2. J_1 is the probabilty of surviving from age class 1 to age class 2, J_2 is the probability of surviving and staying in age class 2. B_1 and B_2 is the number of recruits age class 1 and 2 respectively contributes with to age class 1

and results. The pedigrees in tandem with capture and observation, provides data on annual survival, fecundity and census population size. The birds are counted before, or during the first part of the breeding season, so only recruits and older adult birds are included in the census populations size, N. The females and males in the dataset were split into two age classes each; the first consisted of yearlings, and the second a terminal age class that included all individuals of age two years or older. In total there are four groups, hereafter addressed as sex-age classes, denoted by $i = (f_1, f_2, m_1, m_2)$ for females and males in age class 1 and 2, respectively. Since the survival rate for adult birds in the study system is approximately 50 % (Ringsby *et al.* 1999), the same number of individuals are included in each age class, which makes them directly comparable. The pooling of individuals into a terminal age class is done to exclude the effect of small sample sizes of older individuals (Appendix A, Figure A.3). This approach is justified, and has little effect on estimates of N_e, because the vital rates vary little with age (Engen *et al.* 2010). The sex-ratio at birth, q, given as the proportion of females, is assumed to be known, and set at 0.5 (Husby *et al.* 2006). Since q is known, the total number of recruits can be used for the calculations, instead of assigning the recruits by sex (Engen *et al.* 2010). In accordance with Engen *et al.* (2007, 2009), it is assumed that the population dynamics are density-independent, and that all parameters, except survival, can be evaluated as continuous due to the high number of individuals and the large timespan of the dataset. All data handling and statistical analyses were done in the software R version 3.1.2 and 3.1.3 (R Core Team 2014).

2.4   Demographic parameters

Demography describes the dynamics and structure of the population, and in age-structured populations demographic variation contribute to fluctuations in both the age structure, as well as the population size, N (Lande *et al.* 2003; Engen *et al.* 2005). Since it is already known that N is the most influential factor for determining N_e (Engen 2005; Frankham *et al.* 2010), the effective to census population size ratio, N_e/N, will be used, and I will start by examining how this ratio is affected by the input parameters demographic variance, σ_{dg}^2, and generation time, T (Equation (5)). For all populations, N_e/N was estimated following the method for age-structured populations with two sexes in Engen *et al.* (2010), with $k = 2$ age classes.

$$\frac{N_e}{N} = \frac{1}{\sigma_{dg}^2 T} \tag{5}$$

The data on individual survival and fecundity, were used to calculate the expected population projection matrix, l, for each population:

$$l = \begin{bmatrix} \frac{1}{2}q\bar{B}_{f_1} & \frac{1}{2}q\bar{B}_{f_2} & \frac{1}{2}q\bar{B}_{m_1} & \frac{1}{2}q\bar{B}_{m_2} \\[2ex] \bar{J}_{f_1} & \bar{J}_{f_2} & 0 & 0 \\[2ex] \frac{1}{2}(1-q)\,\bar{B}_{f_1} & \frac{1}{2}(1-q)\,\bar{B}_{f_2} & \frac{1}{2}(1-q)\,\bar{B}_{m_1} & \frac{1}{2}(1-q)\,\bar{B}_{m_2} \\[2ex] 0 & 0 & \bar{J}_{m_1} & \bar{J}_{m_2} \end{bmatrix} \qquad (6)$$

The matrix includes the mean number of total recruits produced in all sex-age classes, $\bar{B}_i$, and their mean specific survival probabilities, $\bar{J}_i$, where i signifies the four different sex-age classes. It also includes q for proportion of females, and $(1-q)$ for proportion of males at birth, which in this study was assumed to be the same ($q = 0.5$). The population growth rate, λ, is calculated as the real dominant eigenvalue of l. The left and right eigenvectors of l, u_i and v_i, are scaled so that $\sum u_i = 1$, and $\sum u_i v_i = 1$, are the stable sex-age distribution and reproductive values of each sex-age class i, respectively. The scaling is done so that the values of u_i represent proportions of the total population (Caswell 2001). Both u and v are conceptual values for a population in equilibrium, and if the population is in its stable sex-age distribution, the number of individuals equals the total reproductive value of the population (Engen et $al.$ 2010). The R-package lmf, version 1.2 (Kvalnes 2013) was used to calculate λ, u and v.

To estimate the population specific demographic variance, σ^2_{dg}, in Equation (5), data on annual fecundity, B_{ij}, and annual survival, J_{ij}, for all individuals, j, in each sex-age class, i, is needed. On the individual level, the sex-age specific individual reproductive value, W_{ij} can be calculated:

$$W_{ij} = J_{ij}v_{i+1} + \frac{1}{2}B_{ij}v_1 + \frac{1}{2}B_{ij}v_3 \qquad (7)$$

W_{ij} is defined as the annual individual contribution to the total reproductive value of the population the following year, and depends on v from the projection matrix l (Engen et $al.$ 2010). The first part is the individual's own survival, J, and the expected contribution of said individual to the next age class, v_{i+1}. The second and third part concerns the number of recruits, B, produced by the individual, and the expected contribution the recruits will make to their age class, v_1 and v_3 for females and males in age class 1, respectively. Remember that v is a vector of length four, representing each sex-age class, $i = (f_1, f_2, m_1, m_2)$. There is half a B per sex because half of the recruits are expected to be female and the other half male, since $q = 0.5$. The value v_{i+1}, can due to the number of $k = 2$ age classes in this case, maximally take the value v_2 for females, and v_4 for males. Since W_{ij} is calculated from observed and not estimated data on viability and fecundity, the annual demographic variance for each sex-age class, $\sigma^2_{dgi}(Z)$, is:

$$\sigma^2_{dgi}(Z) = var\left(W_{ij}|Z\right), \tag{8}$$

where Z is a vector that describes the environment a given year, and $var(W_{ij}|Z)$ is the variation in individual reproductive value for a given year. The subscript g denotes that the demographic variance has a genetic component, as explained in Engen (2005). $\sigma^2_{dgi}(Z)$ in Equation (8) can be estimated as the sum of squares (Engen *et al.* 2009):

$$\hat{\sigma}^2_{dgi}(Z) = \frac{1}{m_{ti}-1}\sum_{j=1}^{m_{ti}}\left(W_{ij}-\bar{W}_{ti}\right)^2, \tag{9}$$

where i is the sex-age class. The number of individuals, j, takes the value from 1 to m_{ti}, where m_{ti} is the total number of individuals in sex-age class i in year t. W_{ij} are the individual W's in year t, and $\bar{W}_{ti}$ is their mean value. The sex-age class specific demographic variance, σ^2_{dgi}, is the weighted mean of $\hat{\sigma}^2_{dgi}(Z)$ over all years with $m_{ti} - 1$ as weights:

$$\sigma^2_{dgi} = \frac{\sum \hat{\sigma}^2_{dgi}(Z)(m_{ti}-1)}{\sum m_{ti}-1} \tag{10}$$

The total demographic variance of the population, σ^2_{dg}, is the weighted mean of σ^2_{dgi} with weights u (remember that u sums up to 1 due to scaling):

$$\sigma^2_{dg} = \sum \sigma^2_{dgi}u_i \tag{11}$$

Finally, N_e/N was calculated for each of the 13 populations, by setting the values of σ^2_{dg} into Equation (5). The population specific generation time, T, was calculated as the mean age of all adults with recruits in each population (Lande *et al.* 2003). The N_e/N ratios of all populations were calculated with both the population specific generation time, and the average generation time for the entire study system ($T = 1.97$) (Jensen *et al.* 2008).

2.5 Sensitivity analysis

A global variance-based method was used in the sensitivity analysis of N_e/N, because it provides quantitative measures of how important the different demographic input parameters are for the variance in the model output, N_e/N. It is also model independent, and there are no assumptions about linearity, monotonicity or independence of inputs (Saltelli and Annoni 2010). This model independent approach suits biological data well, as parameters often are dependent (Caswell 2001), and it reduces the number of assumptions in the data. The variance-based method can be illustrated with a general model: $Y = f(X)$, where Y is the output with an

unconditional variance $var(Y)$, f is the function, and $X = (x_1, x_2...x_n)$ are the inputs. The importance of the input x_p is defined as: the smaller the conditional variance $var(Y|x_p)$ is, but the larger influence it has on $var(Y)$, the more important is x_p. The global variance-based method encompass the entire parameter space, and detect interaction effects between inputs (Saltelli *et al.* 2008). Even though variance-based methods can be computationally costly (Yang 2011), a good method is not only evaluated based on computational costs, it is also important that the multidimensional parameter space of the input parameters is explored sufficiently. A lot of the data is distributed away from the centre of the space, so there is a natural trade-off between computational cost and the degree of exploration of the parameter space (Saltelli *et al.* 2010). For more information on sensitivity analysis, and the chosen method, see Appendix C.

2.5.1   Sobol's method

Sobol's method (Sobol' 1990, 1993) is based on variance decomposition of the total output variance, $V = var(Y)$, into the partial, or conditional, variance, $V_p = var(Y|x_p)$, of input parameter, p. It has been shown to be a robust method, and used as a benchmark to compare other methods to (Tang *et al.* 2007; Yang 2011). The method use Sobol' indices, or sensitivity indices, to quantitatively measure the importance of inputs. This is done by looking at the ratio of each input's partial variance to the total variance in the output (Sobol' 1993, 1990):

$$S_p = \frac{V_p}{V},$$
(12)

where the first order index, S_p, is the main effect of input parameter p. S_p is normalized, and varies between 0 and the partial variance of the input in question. The partial variances have an additive effect on the output, and sum up to one, since they are based on ratios of the total variance. The input(s) the output is most sensitive to, are those with the largest Sobol' indices (Sobol' 2001). Ranking of inputs is most easily done by estimating the first order indices (Equation (12)), but these indices do not include possible interactions among inputs, and might lead to an erroneous ranking. To account for the effect of possible interactions, it is preferable to use the total-order index, S_{Tp}, which is calculated as:

$$S_{Tp} = 1 - \frac{V_{\sim p}}{V} = 1 - S_{\sim p},$$
(13)

where $\sim p$ is all input parameters, except p (Homma and Saltelli 1996; Chan *et al.* 1997). The interaction effect of a parameter, ΔS, is given as the difference between the total and first order index of the parameter (Nossent and Bauwens 2012). In Chu-Agor *et al.* (2011), they only focus on interactions ≥ 0.05, and the same limit is used in this thesis. 95% confidence intervals (CI) were used to establish if two (or more) input parameters were significantly different (Yang 2011). The input

parameters for the analysis were sampled from their respective distributions with a Sobol' quasi-random sampling scheme (Saltelli *et al.* 2010). Such sequences are characterized by having enhanced convergence of parameter values (Sobol' 2001), which is preferable, as it reduces the total number of model runs. To monitor the convergence, and estimate confidence intervals of the indices, one can use bootstrapping. Here, the sensitivity index for each re-sample is calculated, and the sampling distribution of all indices is used to construct the confidence intervals (Yang 2011). Saltelli (2002) used a bootstrap dimension of 10,000, and Yang (2011) found that the Sobol' method converges at $n \approx 3000$. Based on this, each parameter was sampled $n = 5000$ times, and bootstrapped 10,000 times to ensure convergence of the indices.

2.5.2 Parameter distributions

In practice, input parameters are associated with uncertainty, but there often exist some knowledge about their range of variation, e.g. through measurements, observations, expert opinions, biological or physical limits (Saltelli *et al.* 2004). Due to this uncertainty, it is convenient to view inputs as random variables with probability density functions (PDF). The R-package *fitdistrplus* (Delignette-Muller and Dutang 2015) was used to evaluate the parameters and fit the density functions. Due to few data points (13) for most parameters, their most likely distribution was not always clear, but in tandem with biological assumptions, a distribution was chosen (Table 2). To evaluate the distribution of the data, Shapiro-Wilk tests of normality was performed. This test have a H_0 that states that values are sampled from a normal distribution, and use p-values to decide if H_0 should be accepted or not (see Table 2 for the p-values). Also the symmetry of the distributions were assessed, and parameters that looked symmetric, and had a $p > 0.05$ in the Shapiro-Wilk test, were assumed to be normally distributed. There were two exceptions (σ^2_{dgf1}, σ^2_{dgm1}), where the $p > 0.05$ in the Shapiro-Wilk test, but the parameters were fitted to log-normal distributions. There were also one exception (v_{f1}) that had $p < 0.05$ in the Shapiro-Wilk test, but it was fitted to a normal distribution regardless. These three exceptions were all close to 0.05, and given the relatively few numbers of values, they were not fitted based solely on their p-values (Table 2), but also evaluated according to the shape of their density plots (Appendix D, Figure D.3 and D.5). They were also compared to the distributions of the other sex-age classes for the parameter in question, as all four were assumed to have the same distribution. To evaluate the distributions visually, I plotted the empirical distribution in form of a histogram together with the density function and the fitted distribution. In cases where there was a positive tail to the distribution, a log-normal distribution was assumed. When there was a positive tail, and zero values in the negative tail, a gamma distribution which is closely related to the log-normal, was assumed. For survival there are only two possibilities, to live or die, and a binomial distribution was fitted. The package *fitdistrplus* also calculated the distributions, and the respective estimates, such as mean and standard deviation for the normal and log-normal distributions, the probability of success for the

Table 2: Description and notation of all parameters included in the sensitivity analyses. For each parameter, the number of values used to fit the distribution, n, the sex-age class, i, the chosen distribution and the estimates of its shape parameters in parentheses, and p-values from Shapiro-Wilk tests of normality is given. N is the normal distribution with shape parameters mean and standard deviation, lnN is the log-normal distribution with shape parameters log-mean and log-standard deviation, B is the binomial distribution with probability of success, and Γ is the gamma distribution with shape and rate parameters.

Parameter	Notation	n^{a}	i	Distribution	Shapiro-Wilk (p-value)
Generation time	T	13	-	$N(1.718, 0.399)$	0.296
Population demographic variance	σ^2_{dg}	13	-	$lnN(0.283, 0.451)$	0.013
Sex-age class demographic variance	σ^2_{dgi}	13	f_1	$lnN(0.226, 0.411)$	0.078
		13	f_2	$lnN(0.373, 0.479)$	0.021
		13	m_1	$lnN(0.166, 0.470)$	0.064
		13	m_2	$lnN(0.238, 0.694)$	0.005
Stable sex-age distribution	u_i	13	f_1	$N(0.209, 0.054)$	0.277
		13	f_2	$N(0.269, 0.087)$	0.449
		13	m_1	$N(0.209, 0.054)$	0.277
		13	m_2	$N(0.312, 0.069)$	0.677
Sex-age class specific reproductive value	v_i	13	f_1	$N(0.924, 0.245)$	0.035
		13	f_2	$N(1.058, 0.225)$	0.131
		13	m_1	$N(0.890, 0.097)$	0.887
		13	m_2	$N(1.066, 0.287)$	0.202
Survival (0,1)	J_{ij}	1 982	f_1	$B(1, 0.467)$	$2.20x10^{-16}$
		1 428	f_2	$B(1, 0.487)$	$2.20x10^{-16}$
		2 001	m_1	$B(1, 0.493)$	$2.20x10^{-16}$
		1 585	m_2	$B(1, 0.503)$	$2.20x10^{-16}$
Fecundity	B_{ij}	1 982	f_1	$\Gamma(0.399, 0.479)$	$2.20x10^{-16}$
		1 428	f_2	$\Gamma(0.448, 0.475)$	$2.20x10^{-16}$
		2 001	m_1	$\Gamma(0.325, 0.474)$	$2.20x10^{-16}$
		1 585	m_2	$\Gamma(0.430, 0.487)$	$2.20x10^{-16}$

$^{\mathrm{a}}$ Number of values the distributions were fitted to

binomial, and the shape and rate in the case of the gamma distributions (Table 2).

2.5.3   Estimation of indices

To estimate the sensitivity indices, the R-package *sensitivity* version 1.11 (Pujol and Janon 2015) was used. The inputs for the estimation of the indices were sampled from the parameter distributions identified above, and presented in Table

2. The *sensitivity* package includes several of the most common methods for global sensitivity analysis. For this thesis, the *soboljansen* estimator was chosen, as it has been shown to be a efficient estimator (Saltelli *et al.* 2010), and is good both for large first-order indices, and both large and small total indices (Pujol and Janon 2015). Due to restrictions of the *sensitivity* package and the *soboljansen* estimator, and the input and output requirements, N_e/N (Equation (5)) was first evaluated by T and σ_{dg}^2. Then generation time was fixed at the average generation time in the study system ($T = 1.97$), and σ_{dg}^2 was replaced by σ_{dgi}^2 and u_i (Equation (11)). Since the scope of this thesis does not include investigation of the effect of number of years in a dataset, and a stochastic annual function is too complex for the chosen sensitivity estimator, the annual input parameter $\sigma_{dgi}^2(Z)$ was not included in the sensitivity analysis. Instead, the sensitivity analysis started at the population level in step one and two, and then continued at the individual level in step three (Equation (7)), where W_{ij} given by J_{ij}, B_{ij} and v_i, was evaluated. From Equation (8-11), we see that W_{ij} can be regarded as the basic demographic level for N_e/N.

3 Results

3.1 Demographic parameters

All the demographic parameters needed to estimate N_e/N were calculated using Equations (5-11) (Tables 3-4 and Appendix E, Table E.1). The population specific T ranged from 1.20-2.39 years, and had a mean of 1.72 years. T was highest (> 2.1 years) for Aldra, Gjerøy and Nesøy, intermediate and approximately equal to the mean $T = 1.97$ in the study system, on Hestmannøy and Indre Kvarøy, and lowest (< 1.5 years) for Handnesøy, Linesøya, Løkta, Rånes and Røvass (Table 3). The low T in these populations, could be due to the fact that they all had $n < 4$ years of data (Table 1). The population specific demographic variance, σ_{dg}^2, ranged from 0.69-2.98, with a mean at 1.48. Four of the populations known to have special demographic histories, had a higher σ_{dg}^2 than the other populations. The four populations are the recently founded population on Aldra ($\sigma_{dg}^2 = 1.40$), the population that went extinct on Ytre Kvarøy ($\sigma_{dg}^2 = 1.63$) and the two populations Leka ($\sigma_{dg}^2 = 2.56$) and Vega ($\sigma_{dg}^2 = 2.98$) that were subject to strong artificial selection (Table 3, see also Appendix A, Table A.1 and Figure A.1). All four, except Aldra, had a higher σ_{dg}^2 than the overall mean ($\sigma_{dg}^2 = 1.48$). The reasons for why these four populations had a higher σ_{dg}^2, might be due to several reasons.

Table 3: Population level parameters for each of the populations. Both the ratio N_e/N calculated with a fixed $T = 1.97$ (N_e/N, fix. T), and with the population specific T (N_e/N, pop. T) are listed. The population specific demographic variance, σ_{dg}^2 is also listed, as well as the population growth rate, λ, from the projection matrix l (Equation (6)).

Population	N_e/N (fix. T)[a]	N_e/N (pop. T)	T	σ_{dg}^2	λ
Aldra	0.36	0.30	2.35	1.40	1.08
Gjerøy	0.39	0.35	2.19	1.29	0.89
Handnesøy	0.56	0.74	1.49	0.91	0.81
Hestmannøy	0.42	0.42	1.95	1.22	0.80
Indre Kvarøy	0.47	0.48	1.94	1.08	0.76
Leka	0.20	0.22	1.75	2.56	1.06
Linesøya	0.54	0.89	1.20	0.93	0.90
Løkta	0.74	1.18	1.23	0.69	0.58
Nesøy	0.53	0.44	2.39	0.96	0.85
Rånes	0.19	0.30	1.25	2.67	1.26
Røvass	0.58	0.79	1.44	0.88	0.71
Vega	0.17	0.22	1.55	2.98	1.10
Ytre Kvarøy	0.31	0.38	1.63	1.63	0.70
Mean values	0.42	0.55	1.72	1.48	0.88

[a] T in Equation (5) is fixed at the average generation time in the study system ($T = 1.97$) (Jensen *et al.* 2008).

There was high and skewed fecundity the first years in the case of Aldra (Appendix A, Table A.1), while for Ytre Kvarøy there was decreasing fecundity and skewed sex ratios (e.g. in 1996, see Appendix A, Table A.1). For Leka and Vega, that went through artificial selection experiments, there was high mortality during the years of selection, followed by high fecundity (Appendix A, Table A.1). Rånes also had a high σ^2_{dg} ($\sigma^2_{dg} = 2.67$), but this may be due to chance, as there were only 2 years of data (Table 1). In contrast, for Handnesøy, Linesøya, Løkta, Nesøy and Røvass, σ^2_{dg} was low (< 1), and they all have few years of data, except for Nesøy which seem to be a small, but stable population (Appendix A, Figure A.1). For the population growth rate, λ, only four populations (Aldra, Leka, Rånes and Vega) have a $\lambda > 1$, while all others have $\lambda < 1$. For the sex-age specific parameters, the mean, variance and the minimum and maximum values are presented in Table 4 (all parameters can be found in Appendix E, Table E.1). For the sex-age class specific demographic variance, σ^2_{dgi}, both the mean and the variance is highest in the two oldest sex-age classes (Table 4). For the two populations included in the artificial selection experiment, Leka and Vega, σ^2_{dgi} was exceptionally high for both

Table 4: Sex-age class specific parameters averaged across all islands; their specific demographic variance, σ^2_{dgi}, stable sex-age distribution, u_i, reproductive values, v_i, survival, J_{ij}, and fecundity, B_{ij}. The mean, variance, minimum and maximum values are listed instead of empirical data, to ease interpretation.

Parameter	i	Values			
		Min	Mean	Max	Var
σ^2_{dgi}	f_1	0.57	1.37	2.81	0.38
	f_2	0.69	1.63	3.19	0.74
	m_1	0.47	1.32	2.91	0.46
	m_2	0.38	1.64	5.03	1.81
u_i	f_1	0.13	0.21	0.30	$3.15 x 10^{-3}$
	f_2	0.14	0.27	0.49	$8.27 x 10^{-3}$
	m_1	0.13	0.21	0.30	$3.15 x 10^{-3}$
	m_2	0.20	0.31	0.44	$5.11 x 10^{-3}$
v_i	f_1	0.45	0.92	1.20	$6.52 x 10^{-2}$
	f_2	0.46	1.06	1.49	$5.50 x 10^{-2}$
	m_1	0.70	0.89	1.06	$1.02 x 10^{-2}$
	m_2	0.70	1.07	1.76	$8.95 x 10^{-2}$
J_{ij}	f_1	0	0.47	1	0.25
	f_2	0	0.49	1	0.25
	m_1	0	0.49	1	0.25
	m_2	0	0.50	1	0.25
B_{ij}	f_1	0	0.83	14	1.74
	f_2	0	0.94	8	1.99
	m_1	0	0.69	11	1.44
	m_2	0	0.88	9	1.81

age class 2 ($\sigma_{dgi}^2 > 3$) and age class 1 ($\sigma_{dgi}^2 \approx 2$) (Appendix E, Table E.1). The most extreme value of σ_{dgi}^2 was found for older males on Rånes ($\sigma_{dgi}^2 = 5.034$), which might explain why Rånes had a large demographic variance ($\sigma_{dg}^2 = 2.67$) (Table 3). For both the stable sex-age distribution, u_i, and for the sex-age class specific reproductive values, v_i, the mean was highest in age class 2 for both sexes (Table 4). Moreover, the variance was very low (< 0.1) for all classes (Table 4). There was a tendency for m_2 to have the highest values of u (9/13 populations), and in general (10/13 populations) age class 2 had larger u values than age class 1 (Table 4 and Appendix E, Table E.1). Exceptions were Leka, Rånes, and Vega, where age class 1 had the highest values. Leka and Vega both experienced increased population sizes after their bottleneck events, which is consistent with the expectation of more young than old individuals in a growing population, while Rånes most likely has such a distribution due to chance. For v, there was a tendency for age class 2 to have higher values than age class 1 for one or both sexes (11/13 populations). When it comes to survival, J, the mean was approximately the same (≈ 0.50) for all sex-age classes, and the difference between the highest and lowest mean value was small ($\Delta J = 0.03$, Table 4). Furthermore, the variance was the same for all age classes (Table 4). For the fecundity, B, the highest mean value is found in older females ($f_2 = 0.94$), while it was lowest for young males. Age class 2 had the highest mean values for both sexes, but the difference between age classes was smaller for females ($\Delta B = 0.11$), than for males ($\Delta B = 0.19$). Finally, the highest variance in B was found in older females, whereas the lowest was found in young males.

3.2 N_e/N

The ratio, N_e/N, calculated with $T = 1.97$ ranged from 0.17-0.58, with a mean of 0.42. For N_e/N calculated with the population specific T, it ranged from 0.22-1.18, with a mean of 0.55. N_e/N calculated with $T = 1.97$ tends to be smaller than the ratio calculated with the population specific T (Table 3). This is true for all populations, except Aldra, Gjerøy and Nesøy where it is the opposite, and Hestmannøy where the two ratios are the same. For Indre Kvarøy, the two ratios are approximately the same.

Table 5: The results ($\pm$ standard error of the indices) from the variance-based sensitivity analysis of N_e/N, with demographic variance, σ_{dg}^2, and generation time, T, as input parameters. The parameters are ranked based on their total sensitivity indices, S_{Tp}. The parameter interactions, ΔS, are given as the difference between the total and the first order index of each parameter.

| Parameters	Rank	S_p	S_{Tp}	ΔS
σ_{dg}^2	1	0.69 ± 0.02	0.72 ± 0.03	0.03
T	2	0.30 ± 0.04	0.31 ± 0.01	0.01

3.3   Sensitivity analysis

In the first sensitivity analysis of N_e/N with input parameters being the population specific estimates of σ^2_{dg} and T, the demographic variance was found to be the most important parameter (Table 5, Figure 3). The 95% CI in Figure 3 for the total order indices of the two parameters, do not overlap, meaning that N_e/N is significantly more sensitive to σ^2_{dg} than to T. Because $\Delta S < 0.05$, the effect on the output seems to be due to the main effect of the input parameters, and not through interactions (Table 5). Since T was found to be the least important of the two inputs in the first analysis, it was fixed at the average value of the study system ($T = 1.97$), and in order to examine which components of σ^2_{dg} N_e/N was most sensitive to, σ^2_{dg} was replaced by the parameters in Equation (11). For the second sensitivity analysis of N_e/N with input parameters σ^2_{dgi} and u_i, I found that the demographic variance of age class 2 was most important. Most of the effects of the parameters on the output were due to the main effects of the input parameters, although two parameters had $\Delta S \geq 0.05$ (Table 6). From the results (Figure 4), it was also quite clear that N_e/N was not sensitive to u_i, and that it was most sensitive to the demographic variance of males in age class 2 followed by females in the same age class. These two input parameters, σ^2_{dgm2} and σ^2_{dgf2}, had clearly non-overlapping 95% CI's, which means that they were significantly different. The total order index for males in age class 1 was only slightly larger than for females in the same age class, but their 95% CI did not overlap (f_1: 95% CI $[0.101, 0.116]$, m_1: 95% CI $[0.119, 0.137]$), which means that they are also significantly different. In the third sensitivity analysis, the output parameter was the individual reproductive value W_{ij}. W_{ij} can be regarded as the basic demographic level for N_e/N, through σ^2_{dgi} (Equation (8-11)). The W_{ij}'s for all four sex-age classes were analysed with J_{ij}, B_{ij} and v_i as input parameters. In all four analyses, fecundity, B, was identified as the most important input, followed by survival J, and as none of the 95% CI's overlapped, these differences were significant (Figure 5). Furthermore, the effect

Table 6: The results ($\pm$ standard error of the indices) from the variance-based sensitivity analysis of N_e/N, with sex-age class specific demographic variance, σ^2_{dgi}, and the stable sex-age distribution, u_i, as input parameters. The parameters are ranked based on their total sensitivity indices, S_{Tp}, and the parameter interactions, ΔS, are given as the difference between the total and the first order index of each parameter.

Parameters	Rank	S_p	S_{Tp}	ΔS
$\sigma^2_{dgf_1}$	4	0.08 ± 0.02	0.11 ± 0.00	0.03
$\sigma^2_{dgf_2}$	2	0.23 ± 0.02	0.27 ± 0.01	0.05
$\sigma^2_{dgm_1}$	3	0.12 ± 0.02	0.13 ± 0.00	0.01
$\sigma^2_{dgm_2}$	1	0.47 ± 0.02	0.53 ± 0.01	0.06
u_{f_1}	6	-0.01 ± 0.02	0.01 ± 0.00	0.02
u_{f_2}	5	0.00 ± 0.02	0.02 ± 0.00	0.02
u_{m_1}	6	-0.01 ± 0.02	0.01 ± 0.00	0.02
u_{m_2}	6	-0.01 ± 0.02	0.01 ± 0.00	0.02
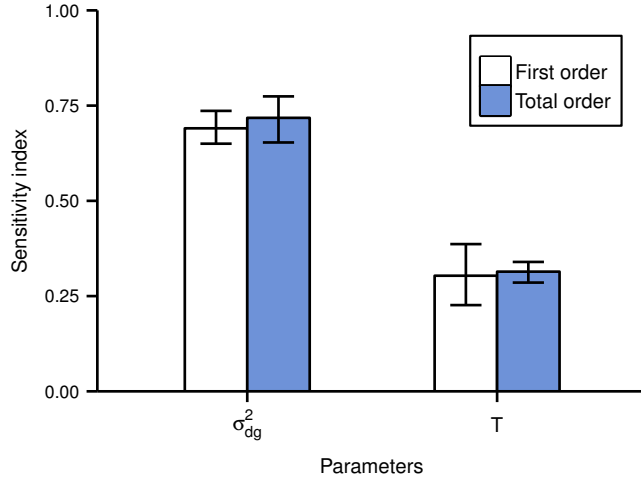
Figure 3: The first, S_p, and total order, S_{Tp}, sensitivity indices from the variance-based sensitivity analysis of N_e/N, with the demographic variance, σ^2_{dg}, and the generation time, T, as input parameters. The error bars are the 95% confidence intervals of the indicies.
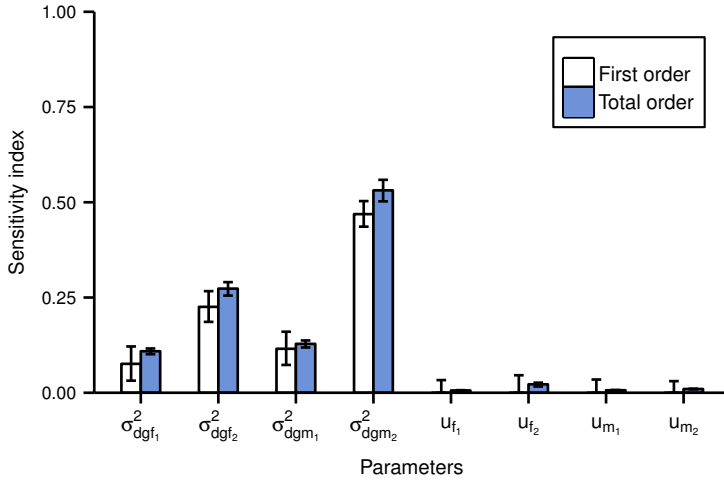

Figure 4: The first, S_p, and total order, S_{Tp}, sensitivity indices from the variance-based sensitivity analysis of N_e/N, where $T = 1.97$ and the sex-age class specific demographic variance, σ^2_{dgi}, and the stable sex-age distribution, u_i, as input parameters. The error bars are the 95% confidence intervals of the indicies.

on the outputs are due to the main effect of the input parameters, and not through interactions ($\Delta S < 0.05$). It was not possible to rank the v_i's, as they were all close to zero and each other (Table 7), and it is clear that none of the W_{ij}'s are sensitive to v_i (Figure 5). Note that there are only three v's in each analysis, due to the fact that no females contribute directly to m_2, just as no male contribute directly to f_2 (Equation (7)).

To investigate whether the extreme value of sex-age specific demographic value of older males on Rånes (Table Appendix E, E.1) was likely to affect the analysis

(a)

(b)

(c)

(d)
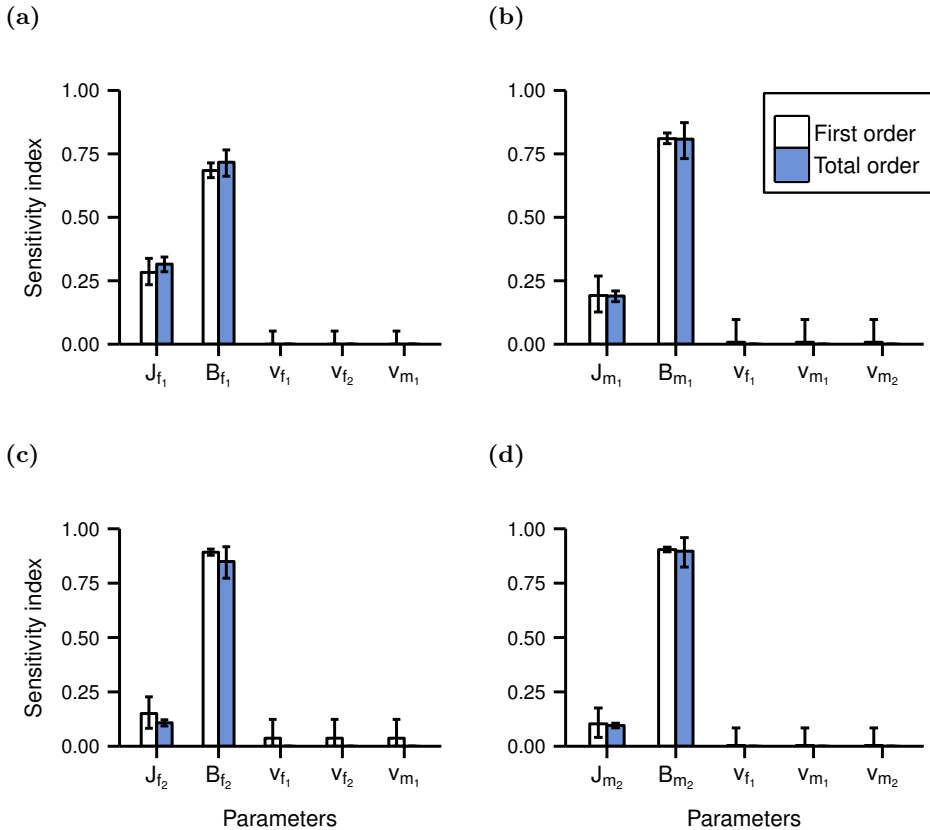
Figure 5: The result from the four variance-based sensitivity analyses of individual reproductive value, W_{ij}, with fecundity, B, survival, J, and the sex-age specific reproductive values v_i, as input parameters. The panels (a) and (b) show the results from females and males in age class 1, respectively, while panels (c) and (d) show the results from females and males in age class 2, respectively. Both the first, S_p, and total order, S_{Tp}, sensitivity indices are given. The error bars are the 95% confidence intervals of the indices. Note that there are only three v's in each panel, due to the fact that no females contribute directly to m_2, just as no male contribute directly to f_2 (Equation (7)).

and the fitted distribution (Table 2), it was removed. After removing the Rånes value, the p-value in the Shapiro-Wilk test was still low ($p = 0.009$), and the new distribution parameters ($lnN(0.123, 0.592)$), did not have an effect on the outcome of the sensitivity analysis (results not shown), so the value was not removed from the dataset.

Table 7: The results ($\pm$ standard error of the indices) from the four variance-based sensitivity analysis of individual reproductive value, W_{ij}, with survival, Jij, fecundity, Bij, and the class specific reproductive value, v_i, as input parameters. The parameters are ranked based on their total sensitivity indices, S_{Tp}, and the parameter interactions, ΔS, are given as the difference between the total and the first order index of each parameter. The v_i's are not ranked, as they are all close to zero, and there is no difference between them within a sex-age class.

Output	Parameters	Rank	S_p	S_{Tp}	ΔS^{a}
	J_{f_1}	2	0.28 ± 0.03	0.32 ± 0.01	0.03
	B_{f_1}	1	0.68 ± 0.01	0.72 ± 0.03	0.03
W_{f_1}	v_{f_1}	-	-0.02 ± 0.03	0 ± 0.00	0.02
	v_{f_2}	-	-0.02 ± 0.03	0 ± 0.00	0.02
	v_{m_1}	-	-0.02 ± 0.03	0 ± 0.00	0.02
	J_{f_2}	2	0.15 ± 0.04	0.11 ± 0.01	-0.04
	B_{f_2}	1	0.89 ± 0.01	0.85 ± 0.04	-0.04
W_{f_2}	v_{f_1}	-	0.04 ± 0.04	0 ± 0.00	-0.04
	v_{f_2}	-	0.04 ± 0.04	0 ± 0.00	-0.04
	v_{m_1}	-	0.04 ± 0.04	0 ± 0.00	-0.04
	J_{m_1}	2	0.19 ± 0.04	0.19 ± 0.01	0
	B_{m_1}	1	0.81 ± 0.01	0.81 ± 0.04	0
W_{m_1}	v_{f_1}	-	0.01 ± 0.04	0 ± 0.00	-0.01
	v_{m_1}	-	0.01 ± 0.04	0 ± 0.00	-0.01
	v_{m_2}	-	0.01 ± 0.04	0 ± 0.00	-0.01
	J_{m_2}	2	0.10 ± 0.03	0.10 ± 0.01	-0.01
	B_{m_2}	1	0.90 ± 0.01	0.90 ± 0.03	-0.01
W_{m_2}	v_{f_1}	-	0 ± 0.04	0 ± 0.00	0
	v_{m_1}	-	0 ± 0.04	0 ± 0.00	0
	v_{m_2}	-	0 ± 0.04	0 ± 0.00	0

$^{\mathrm{a}}$ $S_{Tp} - S_p$

4 Discussion

First, N_e/N was analysed with the demographic variance, σ_{dg}^2, and the generation time, T, as input parameters. From this sensitivity analysis, σ_{dg}^2 was found to be the parameter N_e/N was most sensitive to (Figure 3). This is not so surprising, as σ_{dg}^2 include all the other demographic parameters; σ_{di}^2, u, v, B and J, which ultimately determines the population dynamics and N_e. Second, to see which of the parameter(s) in σ_{dg}^2 that N_e/N was sensitive to, the generation time was fixed at the average value for the study system ($T = 1.97$), and σ_{dg}^2 was replaced by σ_{di}^2 and u (Equation 11). From this second analysis, it was clear that N_e/N was most sensitive to the demographic variance in older males, followed by the demographic variance in older females, and that N_e/N was not sensitive to u (Figure 4). Finally, to investigate which parameter(s) in σ_{dgi}^2 that N_e/N was most sensitive to, the sensitivity analysis was carried out at the individual level, since σ_{dgi}^2 can be decomposed into survival and fecundity by looking at the variance components of the individual reproductive value, W_{ij} (Engen *et al.* 2010). In this third sensitivity analysis, the four W_{ij}'s were analysed with v, B and J as input parameters. For all four sex-age classes B was found to the input parameter W_{ij} was most sensitive to, followed by J, while it was not sensitive to v (Figure 5). These results are consistent with previous findings, that variance in family size is important for N_e (Frankham *et al.* 2010).

4.1 Demographic parameters

When using N_e/N, it is important that estimates of N_e and N are correctly linked, as in properly matched, both temporally and methodologically, i.e. using either genetic or demographic estimates (Waples 2005). In a review by Palstra and Fraser (2012), it was found that only a third (31%) of the studies with N_e/N, linked N_e and N correctly. In this thesis, demographic estimates were used for both parameters, and the two parameters were calculated annually for all populations. The observed number of individuals in the populations was included in the annual estimate of $\sigma_{dgi}^2(Z)$ (Equation (9)), and as weights for σ_{dgi}^2 (Equation (10)). Since N and N_e are related, they will affect each other, but so far little is known on how. For example, Newton (1995) found that in seven different bird species, only a few breeders (16–32%) produced 50% of the next generation. Thus, a large increase in N might improve population viability, but it is often a result of highly skewed individual contributions, which reduce N_e (Lee *et al.* 2011). Furthermore, which N that has been used, is of particular importance when considering N_e/N. Some studies have used all individuals, both juveniles and adults, others only adults, while others again only include the breeders (Frankham 1995). Palstra and Fraser (2012) argues that it is important to use the individuals assumed to be part of the active breeding population, as done in this thesis, since these are the individuals that ultimately determine N_e.

The generation time, T, was calculated as the mean age of all individuals that had produced a recruit (Lande *et al.* 2003). T was calculated for each population, with a mean for all 13 populations of 1.72 years (Table 3). For the 5 populations with less than 4 years of data, the mean was 1.32 years, while for the 8 populations with more than 4 years of data, the mean was 1.97 years, which is the same value found by Jensen *et al.* (2008). The limit at 4 years was set because this includes two generation times, and populations with less than 4 years of data are expected to have a lower T (Table 1 and 3). When new house sparrow populations are included in the study system, all adult individuals are assumed to be 1 year old the first time they are caught and marked (see Appendix A, Table A.1). This is an assumption which is most likely false, but reasonable, as adult house sparrows lack age specific traits. Given the 50% annual adult survival, the true age of most individuals ($\approx 94\%$) will be known after 4 years. Due to the relation between N_e/N and T (Equation (5)), populations with a short estimated generation time will have a higher N_e/N compared to populations with longer generation times (but which are otherwise similar), which was also found in this study (Table 3).

Demographic variance, σ^2_{dg}, is the variation among individuals in their contribution to future breeding populations, both directly through survival, and indirectly through recruits (Lande *et al.* 2003). Sæther *et al.* (2004) found that the majority of 52 populations of 31 bird species, had a mean female $\sigma^2_{dg} = 0.358$. This is considerably lower than what I found in this study where both sexes are accounted for (see Table 3), but the study of Sæther *et al.* (2004) included only females, and long-lived birds with very different life cycles from the house sparrow, e.g. wandering albatross (*Diomedea exulans*). Bird species with more similar life cycles to the house sparrow, such as blue tit (*Parus caeruleus*) and great tit (*Parus major*), have higher σ^2_{dg}'s than the average found by Sæther *et al.* (2004). Blue tits have a $\sigma^2_{dg} = 0.85$ for females, or 1.70 for both sexes (Sæther *et al.* 2004), and great tits have $\sigma^2_{dg} = 0.57$ for females, or 1.14 for both sexes (Engen *et al.* 2003). The 13 populations in this study, have a mean $\sigma^2_{dg} = 1.48$ (Table 3), which fall within the range of σ^2_{dg} found in other passerines.

The mean values of N_e/N calculated with $T = 1.97$ ($N_e/N = 0.42$), and population specific T ($N_e/N = 0.55$) (Table 3), are slightly larger than the mean values of the sampled ratios from the sensitivity analyses, both for $T = 1.97$ ($N_e/N = 0.37$), and for sampled T ($N_e/N = 0.51$). The sampled values are the means of 50,000 and 20,000 model runs for fixed and sampled T, respectively. The differences between calculated and sampled ratios ($\Delta N_e/N = 0.05$ and $\Delta N_e/N = 0.04$) might be due to sampling error, or that the calculated ratios are slightly higher due to few data points or simply by chance. All of the ratios, both calculated and sampled, are within the range of N_e/N values found in other studies on several different passerines: from 0.09-0.80, and with an average of 0.49 (see Table 2 in O'Connor *et al.* (2006)). The values in this study are also similar to the mean values ($N_e/N = 0.37$ and $N_e/N = 0.50$, $\lambda = 1$) found by Engen *et al.* (2007) in six populations in the same house sparrow study system. As several different methods are used to estimate N_e/N, it is not always possible to compare the results of

different studies. For example, in a study of the common frog (*Rana temporaria*), they used different methods to estimate N_e/N from the same dataset, and they got values spanning a range of 0.23-1.67 (Schmeller and Merilä 2007). Furthermore, different taxa tend to have different ranges, e.g. a tropical dioecious tree species (*Triplaris americana*) on Costa Rica, have a N_e/N close to 1 (Melampy and Howe 1977), while many marine species such as fish and shellfish have values of N_e/N in the area of 0.0001 (Hauser *et al.* 2002).

Three of the calculated parameters are from the population projection matrix, l (Equation 6); the population growth rate, λ, the stable sex-age distribution, u, and the reproductive values of the sex-age classes, v. The population growth rate, λ, is not used in the analysis, but will be discussed briefly. For most populations $\lambda < 1$ (Table 3), which is unexpected as some seems to be increasing (Appendix A, Figure A.1), but it might be explained by migration. Migration of juveniles happens mostly in autumn (Altwegg *et al.* 2000), and they are therefore gone by the time population census is done the following year. Emigrants from a local population are not included among the recruits in this population, but assumed dead, and immigrants are not counted as recruits as they are produced in another population. This affects λ, which is calculated from l with mean fecundity based on local parents and their recruits. The stable sex-age distributions of age class 1 is the same for both sexes (Appendix E, Table E.1), due to the assumption of $q = 0.5$, and the use of total number of offspring in l (Equation (6)). Since u is scaled so that $\sum u_i = 1$, the values of u_i represent ratios. Based on the mean values of u_i, the house sparrow populations on Helgeland will consist of approximately 40% recruits, and 60% older individuals, if they reach their stable population structure (Table 4). Age class 2 also had the highest mean v_i values (Table 4), and v_i reflect the expected future contribution from an individual in a sex-age class to the long-term population growth (Caswell and Keyfitz 2005). Neither u_i nor v_i were found to be important parameters in the sensitivity analyses. This might be because they are non-important, or because they are (in contrast to all the other observed values) conceptual values for a population in equilibrium, calculated as the eigenvectors of l (Equation (6)).

The mean survival was found to be approximately equal (50%) for all sex-age classes, and they also had the same variance (0.25) (Table 4). This is consistent with the assumption of constant adult survival rates in this study system (Ringsby *et al.* 1999). The mean fecundity, or the mean number of recruits produced, was highest for females in both age classes. This means that females have produced more recruits than males (in the dataset, 2,997 and 2,770 recruits were produced by females and males, respectively), which cannot be true, as all recruits must have two parents. In the dataset, there are in general more males than females in both age classes (f_1: 1,982, f_2: 1,428, m_1: 2,001, m_2: 1,585). Based on the data from the five populations in Appendix B, it seems like mothers and fathers are similarly related, and at the same proportions. This suggests that some fathers have avoided capture, and/or that the assignment of recruits are lower to fathers than to mothers due to the procedures in genetic parentage analyses (Jensen *et al.*

2008; Billing *et al.* 2012). Within sexes, age class 2 had the highest mean values of B_{ij} ($f_2 = 0.94$, $m_2 = 0.88$), and the highest variance ($f_2 = 1.99$, $m_2 = 1.81$) (Table 4). In females there was a smaller difference in mean B_{ij} between age class 2 and 1 ($\Delta B_{ij} = 0.11$) than for males ($\Delta B_{ij} = 0.19$). This is consistent with studies of other passerines, where it has been found that males increase their reproductive success most with age (Green 2001; Geslin *et al.* 2004). The importance of age on reproductive output in males, might contribute to the explanation of why older males were found to be the input parameter N_e/N is most sensitive to. Also J_{ij} was identified as an important factor, especially in age class 1 (Figure 5), which might be explained by the importance of surviving to age class 2 to increase lifetime reproductive success, as mean fecundity increase from age class 1 to 2 for both sexes (Table 4).

4.2 Sensitivity analysis

Distributions of the calculated parameters were fitted for sampling in the sensitivity analyses (Table 2). Sources of error might be that the wrong distributions were fitted, or wrong distribution parameters were estimated. Even though some of the parameters had quite few data points (Table 2), it is reasonable to assume that the chosen distributions were good approximations of the data. To be able to fit a distribution to raw data, some compromises and generalisations when it comes to assumptions about the distribution must be allowed. The dataset used in this study is large, encompassed thousands of unique individuals and included populations with up to 20 years of data. It also included both a founder, an extinct, and two manipulated populations, so the range of the parameters was expected to be quite large, but biologically reasonable. By including these four populations, the analyses probably reflect the sensitivity of N_e/N to various demographic parameters both in isolated populations, and in a dynamic metapopulation with strong selection events, local extinctions and recolonizations. The dataset may therefore be assumed to represent trends not only found in house sparrow populations, but also in other species with similar life cycles, e.g. great tits, common starlings (*Sturnus vulgaris*), red squirrels (*Sciurius vulgaris*) or tri-coloured bats (*Pipistrellus subflavus*) (Gurnell 1983; Sibly *et al.* 1997).

It is important to keep in mind that variance-based sensitivity analyses can be used to see how inputs impact the variance of the output (Da Veiga 2014). Therefore, in this study, conclusions can be drawn based on how the variance of W_{ij}, and finally the variance of N_e/N was affected by the different demographic parameters. It is a common misconception that it is the input parameters with large variance the output is most sensitive to. Some of the parameters the output is most sensitive to can have little variation, and strong regulatory mechanisms, which makes evolutionary sense (Tuljapurkar and Caswell 1997). To account for possible interactions between input parameters, Sobol' total index (Equation 13) was used to rank the different parameters (Tables 5-7). In this study, very little of the effect was explained by interactions, and only two input parameters, the sex-age demographic

variances in age class 2, had $\Delta S \geq 0.05$ (Table 6). This interaction might be explained by the fact that production of recruits require both sexes. The effect input parameters have on output variation, tend to be asymmetrically distributed, in the way that only a few parameters are found to be important, while the rest have a negligible effect (Saltelli *et al.* 2008). This is true for two of the analyses, where u and v was found to be non-important (Figure 4 and 5). For the analysis of N_e/N with only two input parameters, σ_{dg}^2 and T, both were found to be important, σ_{dg}^2 significantly more so than T (Figure 3). N_e is known to be dependent on T (Nunney and Baker 1993), but as generation time depends on the average age of parents with recruits, it was not possible to analyse T further in this study, as only two age classes were used for the sensitivity analysis. σ_{dg}^2, on the other hand, was investigated further as it includes all the other demographic parameters; σ_{dgi}^2, u, v, B and J. Sensitivity analyses of N_e/N and W_{ij} was therefore done, with these parameters as inputs, as they ultimately determine N_e and N_e/N. The sensitivity estimator chosen for this study, *soboljansen*, is a good estimator for large first order indices, and both large and small total order indices (Pujol and Janon 2015), which was suitable for the value-ranges of the total order indices found here (Tables 5-7). To ensure that the input parameters were significantly different from each other, 95% confidence intervals based on 10,000 bootstraps were used. For all analyses, none of the CI's for the total indices overlapped, meaning they were significantly different, except for u and v which were found to be non-important (Figures 3-5).

There are several possible explanations to why N_e/N is more sensitive to age class 2, and why older males seem to be more important than females. In birds, it has been established by many studies that reproductive success tend to increase with age (Forslund and Pärt 1995). The effect of age on reproductive success has also been found in mammals, e.g. in European badgers (*Meles meles*), where lower reproductive rates was found in younger, compared to middle aged individuals of both sexes (Dugdale *et al.* 2011). The three main hypotheses for why reproductive success increases with age are; (i) the selection hypothesis, (ii) the restraint-hypothesis and (iii) the constraint-hypothesis (Curio 1983; Forslund and Pärt 1995). The first is based on the idea that reproductive success is higher in older birds because the poor breeders are selected against, and implicitly have higher mortality. The second hypothesis states that young breeders restrain themselves, and save investment for later breeding attempts. The third hypothesis states that young breeders are constrained by their lack of breeding skills, and/or their physiological condition. The effect of age on reproductive success in birds has mainly been looked at in long-lived species, such as lesser snow geese (*Chen caerulescens caerulescens*) (Rockwell *et al.* 1993) or mute swans (*Cygnus olor*) (McCleery *et al.* 2008). Many of the studies only include the female segment of the population. However, there are some studies on short-lived bird species, where both the effect of male and female age on reproductive performance have been compared. Examples are studies done on the Australian brown thornbill (*Acanthiza pusilla*) (Green 2001), French bluethroats (*Luscinia svecica*) (Geslin *et al.* 2004), and North-American house sparrows (Hatch and Westneat 2007). Both brown thornbills and bluethroats are small and short-lived passerines, socially monogamous, and have biparental care, just as

the house sparrow. For the house sparrows, the increase in reproductive success with age was due to earlier onset of breeding in older individuals, which could be explained by both the restraint- and the constraint-hypotheses. In brown thornbills and bluethroats it was found that yearlings lacked skills and experience that influenced their breeding performance, supporting the constraint-hypothesis. Some of the breeding skills important for reproductive success differ between sexes, while others are common for both sexes. Examples might be timing of egg-laying, nest location, predation avoidance, foraging skills and feeding rate (Green 2001; Geslin *et al.* 2004). Both in bluethroats (Geslin *et al.* 2004) and in blackbirds (*Turdus merula*) (Desrochers 1992), it has been found that younger birds are less good at foraging, but this tendency was not found in the brown thornbill (Green 2001). In all these species, including house sparrows (Ringsby *et al.* 2009), the female feed the chicks more than the male. In the study system used in this thesis, it has been found that badge size increase with age (Jensen *et al.* 2004), and that there is a positive relationship between badge size and feeding rates in males (Ringsby *et al.* 2009). Higher feeding rate by older males, especially in the first days after hatching, when the female must eat after brooding, is believed to be the main reason for why males have the highest increase in reproductive success with age in brown thornbills and bluethroats (Green 2001; Geslin *et al.* 2004). This tendency is found not only in passerines, but also in birds of prey, e.g. Tengmalm's owls (*Aegolius funereus*) (Laaksonen *et al.* 2002). In the brown thornbill, only males had a significant improvement in reproductive success with age (Green 2001), in the bluethroats both sexes improved with age, but males improved most (Geslin *et al.* 2004), while in house sparrows, both sexes improved with age (Hatch and Westneat 2007). This is consistent with the findings of this study, where mean fecundity increased to age class 2, and males had the largest increase in mean fecundity between age classes (Table 4). This might contribute to explain why N_e/N was most sensitive to older individuals, especially males (Figure 4).

Since older individuals, especially males, were found to be what N_e/N was most sensitive to, this is where management action on house sparrows, and species with a similar life history, should be focused. Either if the goal is to increase, maintain or decrease the N_e or N_e/N of a population, manipulation of the fecundity and survival in the oldest age class is assumed to be the quickest way to the desired outcome. How the manipulation is done is another question, and it depends on the hypothesis, or reason, for why older individuals are better at producing recruits. If poor quality breeders are selected against and die as yearlings, which implicate that parenting skills and survival are linked, it will not help to increase survival of yearlings, as they will still be "bad" breeders when they are older. But if they either save up resources to later breeding seasons, or they actually learn to be better parents and improve their breeding skills in subsequent breeding seasons, then it will help to increase survival. This will of course have to be tested before any management action is implemented, to assure that the desired outcome is achieved. There are several examples of management efforts being ineffective, or even having an opposite effect, often due the widespread usage of knowledge-based, instead of evidence-based data. Around 60% of decisions in conservation management have

been found to be based on experience, and not on empirical studies or reviews of the effects of the management actions (Cook *et al.* 2010). An example of an expensive, but ineffective management effort is from Australia, where the endemic ground-dwelling malleefowl (*Leipoa ocellata*) is listed as a vulnerable species. It faces several threats, i.e. habitat loss, grazing competition, frequent fires, and as so many other species in Australia: predation by the introduced European red fox (*Vulpes vulpes*). Fox baiting has been, and still is, widely used in malleefowl conservation, despite both the lack of empirical evidence, and studies that suggest fox baiting have little impact on increasing recruitment rates (Walsh *et al.* 2012). Sometimes management actions have the opposite effect of what was intended, e.g. the culling of the Eurasian badger in the United Kingdom, to prevent outbreaks of bovine tuberculosis. The disease is transferred from badgers to cattle, and the logic behind culling badgers is simple; fewer badgers near farms means less disease carriers, and less infected cattle. But the result of the extensive culling was actually increased number of infected badgers and cattle. This was due to the territorial nature of badgers, and the influx of individuals to areas where they had been culled. The increased ranging and mixing of healthy and infected badgers, resulted in more outbreaks of bovine tuberculosis on nearby farms (Carter *et al.* 2007). These examples emphasizes the importance of evaluating empirical data, and to quantify the effect of management implementations, both before and after implementation. This new way of thinking, and the incorporation of empirical data together with traditional knowledge-based management (Cook *et al.* 2010), will most likely be important for conservation and management of N_e and N_e/N in the future, and this is where sensitivity analyses can be especially useful.

For a manager, sensitivity analyses indicates the critical parameters in a model (Tuljapurkar and Caswell 1997), and this insight can contribute to more effective and better decisions, as there is never enough time or resources to be one-hundred percent certain when a decision has to be made (Cook *et al.* 2010). There are several examples of how sensitivity analysis have been applied to management issues; e.g. investigation of population growth in the desert tortoise (*Gopherus agassizii*) (Reed *et al.* 2009) and lesser prairie-chicken (*Tympanuchus pallidicinctus*) (Hagen *et al.* 2009), or to determine equilibrium population size in short-tailed shearwaters (*Puffinus tenuirostris*) (Yearsley *et al.* 2003). There are also examples of management predictions, e.g. how wolf reintroduction might affect the Roosevelt elk in Olympic National Park (Fieberg and Jenkins 2005), the effect of domestic cat (*Felis catus*) predation on birds (Maclean *et al.* 2008), future population trends in swamp wallabies (*Wallabia bicolor*) (Ben-Ami *et al.* 2006), or determine the invasive speed of species (Neubert and Caswell 2000; Caswell *et al.* 2010). Even though demography, models and analyses have a key role in conservation and management, there are also other factors that need to be considered. This includes both direct issues regarding habitat and genetic variation, and indirect issues such as economy, legal, politics, and ethics (Caswell 2001). The method used in this study is based on annual, demographic data, which is a short-term perspective affected by demographic variance. From a sustainable management perspective it is also important to consider that in the long-term, N_e/N will be affected by environmental variance

(Engen *et al.* 2010). It is important to keep in mind that N_e/N is affected not only by the species life history (Lee *et al.* 2011) and mating system (Engen *et al.* 2003), but also external factors such as anthropogenic activities (Therkildsen *et al.* 2010). Based on this study, it might be recommended to use the average species generation time for the calculation of N_e/N, especially if there are few years of data available, as a low T might lead to an overly optimistic N_e/N. It is known that T affects N_e/N (Nunney and Baker 1993), but if there is no, or poor data available, the average T of the study system or species might be appropriate. In absence of data or resources to collect data, one can also use samples to estimate demographic parameters, as was done for Siberian jay (*Perisoreus infaustus*) in Engen *et al.* (2010). The importance of number of years of data in a dataset was not evaluated here, but it is quite interesting to be able to maximize the output of management effort, and should be further studied. Through studies of a common and well-known species, such as the ubiquitous house sparrow, knowledge may be inferred to other species with similar life histories and demography. Due relatively extensive range of demographic characteristics of the populations in this study, it may be used a model for other isolated, fragmented and perhaps threatened populations and species with similar life histories. As a result, the findings from this study on sensitivity of N_e/N to demographic parameters, might assist to identify where efforts and resources in management and conservation should be focused in similar species.

Acknowledgements

References

Allendorf F W, Luikart G H and Aitken S N (2012). *Conservation and the Genetics of Populations*, John Wiley & Sons.

Altwegg R, Ringsby T H and Sæther B E (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows Passer domesticus, *Journal of Animal Ecology* **69**(5), 762–770.

Anderson T R (2006). *Biology of the Ubiquitous House Sparrow: From Genes to Populations*, Oxford University Press.

Ben-Ami D, Ramp D and Croft D B (2006). Population viability assessment and sensitivity analysis as a management tool for the peri-urban environment, *Urban Ecosystems* **9**(3), 227–241.

Billing A M, Lee A M, Skjelseth S, Borg Å A, Hale M C, Slate J, Pärn H, Ringsby T H, Sæther B E and Jensen H (2012). Evidence of inbreeding depression but not inbreeding avoidance in a natural house sparrow population, *Molecular Ecology* **21**(6), 1487–1499.

Botkin D B and Miller R S (1974). Mortality-Rates and Survival of Birds, *The American Naturalist* **108**(960), 181–192.

Caballero A (1994). Developments in the prediction of effective population size, *Heredity* **73**(6), 657–679.

Caballero A and Hill W G (1992). Effective size of nonrandom mating populations, *Genetics* **130**(4), 909–916.

Carter S P, Delahay R J, Smith G C, Macdonald D W, Riordan P, Etherington T R, Pimley E R, Walker N J and Cheeseman C L (2007). Culling-induced social perturbation in Eurasian badgers Meles meles and the management of TB in cattle: an analysis of a critical problem in applied ecology, *Proceedings of the Royal Society B: Biological Sciences* **274**(1626), 2769–2777.

Caswell H (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, Sinauer Associates Incorporated.

Caswell H and Keyfitz N (2005). *Applied Mathematical Demography*, Vol. 47 of *Statistics for Biology and Health*, 3rd edn, Springer New York.

Caswell H, Neubert M G and Hunter C M (2010). Demography and dispersal: invasion speeds and sensitivity analysis in periodic and stochastic environments, *Theoretical Ecology* **4**(4), 407–421.

Chan K, Saltelli A and Tarantola S (1997). Sensitivity Analysis of Model Output: Variance-Based Methods Make the Difference, *in Proceedings of the 29th conference on Winter simulation*, IEEE Computer Society.

Cheng Y, Sanderson C, Jones M and Belov K (2012). Low MHC class II diversity in the Tasmanian devil (Sarcophilus harrisii), *Immunogenetics* **64**(7), 525–533.

Chu-Agor M L, Muñoz-Carpena R, Kiker G, Emanuelsson A and Linkov I (2011). Exploring vulnerability of coastal habitats to sea level rise through global sensitivity and uncertainty analyses, *Environmental Modelling & Software* **26**(5), 593–604.

Cook C N, Hockings M and Carter R B (2010). Conservation in the dark? The information used to support management decisions, *Frontiers in Ecology and the Environment* **8**(4), 181–186.

Cooper A M, Miller L M and Kapuscinski A R (2010). Conservation of population structure and genetic diversity under captive breeding of remnant coaster brook trout (Salvelinus fontinalis) populations, *Conservation Genetics* **11**(3), 1087–1093.

Crouse D T, Crowder L B and Caswell H (1987). A Stage-Based Population-Model for Loggerhead Sea-Turtles and Implications for Conservation, *Ecology* **68**(5), 1412–1423.

Crow J F and Kimura M (1970). *An introduction to population genetics theory*, Harper & Row Publishers, New York.

Crowder L B, Crouse D T, Heppell S S and Martin T H (1994). Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Populations, *Ecological Applications* **4**(3), 437–445.

Crowder L B, Hopkins-Murphy S R and Royle J A (1995). Effects of turtle excluder devices (TEDs) on loggerhead sea turtle strandings with implications for conservation, *Copeia* **1995**(4), 773–779.

Cukier R I, Fortuin C M, Shuler K E, Petschek A G and Schaibly J H (1973). Study of the sensitivity of coupled reaction systems to uncertainties in rate coefficients. I Theory, *The Journal of Chemical Physics* **59**(8), 3873–3878.

Curio E (1983). Why Do Young Birds Reproduce Less Well, *Ibis* **125**(3), 400–404.

Da Veiga S (2014). Global sensitivity analysis with dependence measures, *Journal of Statistical Computation and Simulation* **85**(7), 1283–1305.

Delignette-Muller M L and Dutang C (2015). fitdistrplus: An R Package for Fitting Distributions, *Journal of Statistical Software* **64**(4), 1–34.

Dennis B, Munholland P L and Scott J M (1991). Estimation of Growth and Extinction Parameters for Endangered Species, *Ecological monographs* **61**(2), 115–143.

Desrochers A (1992). Age and Foraging Success in European Blackbirds: Variation Between and Within Individuals, *Animal Behaviour* **43**(6), 885–894.

Dugdale H L, Pope L C, Newman C, Macdonald D W and Burke T (2011). Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence, *Molecular Ecology* **20**(15), 3261–3274.

Engen S (2005). Effective Size of a Fluctuating Age-Structured Population, *Genetics* **170**(2), 941–954.

Engen S, Lande R and Sæther B E (2003). Demographic Stochasticity and Allee Effects in Populations with Two Sexes, *Ecology* **84**(9), 2378–2386.

Engen S, Lande R, Sæther B E and Dobson F S (2009). Reproductive Value and the Stochastic Demography of Age-Structured Populations, *The American Naturalist* **174**(6), 795–804.

Engen S, Lande R, Sæther B E and Gienapp P (2010). Estimating the ratio of effective to actual size of an age-structured population from individual demographic data, *Journal of Evolutionary Biology* **23**(6), 1148–1158.

Engen S, Lande R, Sæther B E and Weimerskirch H (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models, *Mathematical Biosciences* **195**(2), 210–227.

Engen S, Ringsby T H, Sæther B E, Lande R, Jensen H, Lillegård M and Ellegren H (2007). Effective size of fluctuating populations with two sexes and overlapping generations, *Evolution* **61**(8), 1873–1885.

EPA Council for Regulatory Environmental Modeling (2009). Guidance on the Development, Evaluation, and Application of Environmental Models, *Federal Register* **74**(60).

European Commission (2009). Impact Assessment Guidelines, **SEC (2009)**(92).

Fieberg J and Jenkins K J (2005). Assessing uncertainty in ecological systems using global sensitivity analyses: a case example of simulated wolf reintroduction effects on elk, *Ecological Modelling* **187**(2-3), 259–280.

Finkbeiner E M, Wallace B P, Moore J E, Lewison R L, Crowder L B and Read A J (2011). Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007, *Biological Conservation* **144**(11), 2719–2727.

Forslund P and Pärt T (1995). Age and reproduction in birds - hypotheses and tests, *Trends in ecology & evolution* **10**(9), 374–378.

Frankham R (1995). Effective population size/adult population size ratios in wildlife: a review, *Genetical Research* **66**(02), 95–107.

Frankham R (1996). Relationship of genetic variation to population size in wildlife, *Conservation Biology* **10**(6), 1500–1508.

Frankham R, Ballou J D and Briscoe D A (2010). *Introduction to Conservation Genetics*, 2nd edn, Cambridge University Press.

Frankham R, Manning H, Margan S H and Briscoe D A (2000). Does equalization of family sizes reduce genetic adaptation to captivity?, *Animal Conservation* **3**(4), 357–363.

Frasier T, Pew J, Wang J and Muir P (2014), 'Package related'.
  URL: *https://frasierlab.files.wordpress.com/2013/08/related.pdf*

Freeman S and Herron J C (2007). *Evolutionary Analysis*, Pearson International Edition, 4th edn, Pearson Prentice Hall.

Geslin T, Questiau S and Eybert M C (2004). Age-related improvement of reproductive success in Bluethroats Luscinia svecica, *Bird Study* **51**(2), 178–184.

Grant P R and Grant B R (1992). Demography and the Genetically Effective sizes of Two Populations of Darwin's Finches, *Ecology* **73**(3), 766–784.

Green D J (2001). The influence of age on reproductive performance in the Brown Thornbill, *Journal of Avian Biology* **32**(1), 6–14.

Gurnell J (1983). Squirrel numbers and the abundance of tree seeds, *Mammal Review* **13**(2-4), 133–148.

Hagen C A, Sandercock B K, Pitman J C, Robel R J and Applegate R D (2009). Spatial Variation in Lesser Prairie-Chicken Demography: A Sensitivity Analysis of Population Dynamics and Management Alternatives, *Journal of Wildlife Management* **73**(8), 1325–1332.

Hagen I J, Billing A M, Rønning B, Pedersen S A, Pärn H, Slate J and Jensen H (2013). The easy road to genome-wide medium density SNP screening in a non-model species: development and application of a 10 K SNP-chip for the house sparrow (Passer domesticus), *Molecular Ecology Resources* **13**(3), 429–439.

Halliburton R (2003). *Introduction to population genetics*, 1st edn, Pearson Prentice Hall.

Hanski I, Kuussaari M and Nieminen M (1994). Metapopulation Structure and Migration in the Butterfly Melitaea Cinxia, *Ecology* **75**(3), 747–762.

Harris R B and Allendorf F W (1989). Genetically effective population size of large mammals: an assessment of estimators, *Conservation Biology* **3**(2), 181–191.

Hatch M I and Westneat D F (2007). Age-related patterns of reproductive success in house sparrows Passer domesticus, *Journal of Avian Biology* **38**(5), 603–611.

Hauser L, Adcock G J, Smith P J, Ramírez J H B and Carvalho G R (2002). Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (Pagrus auratus), *PNAS* **99**(18), 11742–11747.

Hedrick P (2005). Large variance in reproductive success and the Ne/N ratio, *Evolution* **59**(7), 1596–1599.

Hoelzel A R, Fleischer R C, Campagna C, Le Boeuf B J and Alvord G (2002). Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal, *Journal of Evolutionary Biology* **15**(4), 567–575.

Homma T and Saltelli A (1996). Importance measures in global sensitivity analysis of nonlinear models, *Reliability Engineering & System Safety* **52**(1), 1–17.

Husby A, Sæther B E, Jensen H and Ringsby T H (2006). Causes and consequences of adaptive seasonal sex ratio variation in house sparrows, *Journal of Animal Ecology* **75**(5), 1128–1139.

Jansen M J W (1999). Analysis of variance designs for model output, *Computer Physics Communications* **117**(1-2), 35–43.

Jansen M J W, Rossing W A H and Daamen R A (1994). Monte Carlo Estimation of Uncertainty Contributions from Several Independent Multivariate Sources, *in Predictability and Nonlinear Modelling in Natural Sciences and Economics*, Springer Netherlands, Dordrecht, pp. 334–343.

Jensen H, Moe R, Hagen I J, Holand A M, Kekkonen J, Tufto J and Sæther B E (2013). Genetic variation and structure of house sparrow populations: is there an island effect?, *Molecular Ecology* **22**(7), 1792–1805.

Jensen H, Sæther B E, Ringsby T H, Tufto J, Griffith S C and Ellegren H (2003). Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (Passer domesticus), *Journal of Evolutionary Biology* **16**(6), 1296–1307.

Jensen H, Sæther B E, Ringsby T H, Tufto J, Griffith S C and Ellegren H (2004). Lifetime reproductive success in relation to morphology in the house sparrow Passer domesticus, *Journal of Animal Ecology* **73**(4), 599–611.

Jensen H, Steinsland I, Ringsby T H and Sæther B E (2008). Evolutionary dynamics of a sexual ornament in the house sparrow (Passer domesticus): the role of indirect selection within and between sexes, *Evolution* **62**(6), 1275–1293.

Kalinowski S T, Taper M L and Marshall T C (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment, *Molecular Ecology* **16**(5), 1099–1106.

Kalinowski S T and Waples R S (2002). Relationship of effective to census size in fluctuating populations, *Conservation Biology* **16**(1), 129–136.

Kvalnes T (2013). *lmf: Functions for estimation and inference of selection in age-structured populations.*

Laaksonen T, Korpimaki E and Hakkarainen H (2002). Interactive Effects of Parental Age and Environmental Variation on the Breeding Performance of Tengmalm's Owls, *Journal of Animal Ecology* **71**(1), 23–31.

Lagerwall G, Kiker G, Muñoz-Carpena R and Wang N (2014). Global uncertainty and sensitivity analysis of a spatially distributed ecological model, *Ecological Modelling* **275**, 22–30.

Lande R, Engen S and Sæther B E (2003). *Stochastic Population Dynamics in Ecology and Conservation*, Oxford University Press.

Lebreton J D, Burnham K P, Clobert J and Anderson D R (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies, *Ecological monographs* **62**(1), 67–118.

Lee A M, Engen S and Sæther B E (2011). The influence of persistent individual differences and age at maturity on effective population size, *Proceedings of the Royal Society B: Biological Sciences* **278**(1722), 3303–3312.

Legendre S, Schoener T W, Clobert J and Spiller D A (2008). How Is Extinction Risk Related to Population-Size Variability over Time? A Family of Models for Species with Repeated Extinction and Immigration, *The American Naturalist* **172**(2), 282–298.

Lewison R L, Crowder L B and Shaver D J (2003). The Impact of Turtle Excluder Devices and Fisheries Closures on Loggerhead and Kemp's Ridley Strandings in the Western Gulf of Mexico, *Conservation Biology* **17**(4), 1089–1097.

Maclean M M, Carslake D J, Evans M R, Townley S and Hodgson D J (2008). The usefulness of sensitivity analysis for predicting the effects of cat predation on the population dynamics of their avian prey, *Ibis* **150**(Suppl. 1), 100–113.

McCleery R H, Perrins C M, Sheldon B C and Charmantier A (2008). Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality, *Proceedings of the Royal Society B: Biological Sciences* **275**(1637), 963–970.

Melampy M N and Howe H F (1977). Sex Ratio in the Tropical Tree Triplaris americana (Polygonaceae), *Evolution* **31**(4), 867–872.

Miller W, Hayes V M, Ratan A, Petersen D C, Wittekindt N E, Miller J, Walenz B, Knight J, Qi J, Zhao F, Wang Q, Bedoya-Reina O C, Katiyar N, Tomsho L P, Kasson L M, Hardie R A, Woodbridge P, Tindall E A, Bertelsen M F, Dixon D, Pyecroft S, Helgen K M, Lesk A M, Pringle T H, Patterson N, Zhang Y, Kreiss A, Woods G M, Jones M E and Schuster S C (2011). Genetic diversity and population structure of the endangered marsupial Sarcophilus harrisii (Tasmanian devil), *PNAS* **108**(30), 12348–12353.

Nei M and Tajima F (1981). Genetic drift and estimation of effective population size, *Genetics* **98**(3), 625–640.

Neubert M G and Caswell H (2000). Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations, *Ecology* **81**(6), 1613–1628.

Newton I (1995). The contribution of some recent research on birds to ecological understanding, *Journal of Animal Ecology* **64**(6), 675–695.

Nossent J and Bauwens W (2012). Optimising the convergence of a Sobol' sensitivity analysis for an environmental model: application of an appropriate estimate for the square of the expectation value and the total variance, *in Proceedings*

of the sixth biannial meeting of the International Environmental Modelling and Software Society, Leipzig, Germany, July 1-5, 2012.

Nunney L (1995). Measuring the Ratio of Effective Population-Size to Adult Numbers Using Genetic and Ecological Data, *Evolution* **49**(2), 389–392.

Nunney L and Baker A E M (1993). The Influence of Mating System and Overlapping Generations on Effective Population Size, *Evolution* **47**(5), 1342–1359.

Nunney L and Elam D R (1994). Estimating the effective population size of conserved populations, *Conservation Biology* **8**(1), 175–184.

O'Connor K D, Marr A B, Arcese P, Keller L F, Jeffery K J and Bruford M W (2006). Extra-pair fertilization and effective population size in the song sparrow Melospiza melodia, *Journal of Avian Biology* **37**(6), 572–578.

Palstra F P and Fraser D J (2012). Effective/census population size ratio estimation: a compendium and appraisal, *Ecology and Evolution* **2**(9), 2357–2365.

Palstra F P and Ruzzante D E (2008). Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence?, *Molecular Ecology* **17**(15), 3428–3447.

Pärn H, Jensen H, Ringsby T H and Sæther B E (2009). Sex-specific fitness correlates of dispersal in a house sparrow metapopulation, *Journal of Animal Ecology* **78**(6), 1216–1225.

Pärn H, Ringsby T H, Jensen H and Sæther B E (2012). Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation, *Proceedings of the Royal Society B: Biological Sciences* **279**(1726), 144–152.

Pew J, Muir P, Wang J and Frasier T R (2014). related: an R package for analysing pairwise relatedness from codominant molecular markers, *Molecular Ecology Resources* **15**(3), 557–561.

Primack R B (2010). *Essentials of Conservation Biology*, 5th edn, Sinauer Associates.

Pujol G and Janon A (2015). *sensitivity: Functions for sensitivity analysis.*

R Core Team (2014). *R: A language and environment for statistical computing*, Vienna, Austria. http://www.R-project.org/.

Reed J M, Fefferman N H and Averill-Murray R C (2009). Vital rate sensitivity analysis as a tool for assessing management actions for the desert tortoise, *Biological Conservation* **142**(11), 2710–2717.

Ringsby T H, Berge T, Sæther B E and Jensen H (2009). Reproductive success and individual variation in feeding frequency of House Sparrows (Passer domesticus), *Journal of Ornithology* **150**(2), 469–481.

Ringsby T H, Sæther B E, Altwegg R and Solberg E J (1999). Temporal and spatial variation in survival rates of a house sparrow, Passer domesticus, metapopulation, *Oikos* **85**(3), 419–425.

Ringsby T H, Sæther B E, Jensen H and Engen S (2006). Demographic Characteristics of Extinction in a Small, Insular Population of House Sparrows in Northern Norway, *Conservation Biology* **20**(6), 1761–1767.

Ringsby T H, Sæther B E, Tufto J, Jensen H and Solberg E J (2002). Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment, *Ecology* **83**(2), 561–569.

Robertson B C, Elliott G P, Eason D K, Clout M N and Gemmell N J (2006). Sex allocation theory aids species conservation, *Biology Letters* **2**(2), 229–231.

Rockwell R F, Cooch E G, Thompson C B and Cooke F (1993). Age and Reproductive Success in Female Lesser Snow Geese: Experience, Senescence and the Cost of Philopatry, *The Journal of Animal Ecology* **62**(2), 323.

Sæther B E, Engen S, Moller A P, Weimerskirch H, Visser M E, Fiedler W, Matthysen E, Lambrechts M M, Badyaev A, Becker P H, Brommer J E, Bukacinski D, Bukacinska M, Christensen H, Dickinson J, du Feu C, Gehlbach F R, Heg D, Hotker H, Merilä J, Nielsen J T, Rendell W, Robertson R J, Thomson D L, Torok J and Van Hecke P (2004). Life-history variation predicts the effects of demographic stochasticity on avian population dynamics, *The American Naturalist* **164**(6), 793–802.

Saltelli A (2002). Making best use of model evaluations to compute sensitivity indices, *Computer Physics Communications* **145**(2), 280–297.

Saltelli A and Annoni P (2010). How to avoid a perfunctory sensitivity analysis, *Environmental Modelling & Software* **25**(12), 1508–1517.

Saltelli A, Annoni P, Azzini I, Campolongo F, Ratto M and Tarantola S (2010). Variance based sensitivity analysis of model output. Design and estimator for the total sensitivity index, *Computer Physics Communications* **181**(2), 259–270.

Saltelli A, Chan K and Scott E M (2009). *Sensitivity Analysis*, 1st edn, Wiley.

Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M and Tarantola S (2008). *Global Sensitivity Analysis: The Primer*, 1st edn, Wiley.

Saltelli A, Tarantola S, Campolongo F and Ratto M (2004). *Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models*, 1st edn, John Wiley & Sons.

Saltelli A, Tarantola S and Chan K (1999). A Quantitative Model-Independent Method for Global Sensitivity Analysis of Model Output, *Technometrics* **41**(1), 39–56.

Schmeller D S and Merilä J (2007). Demographic and Genetic Estimates of Effective Population and Breeding Size in the Amphibian Rana temporaria, *Conservation Biology* **21**(1), 142–151.

Shaffer M L (1981). Minimum population sizes for species conservation, *BioScience* **31**(2), 131–134.

Sibly R M, Collett D, Promislow D E L, Peacock D J and Harvey P H (1997). Mortality rates of mammals, *Journal of Zoology* **243**(1), 1–12.

Smith J N M (2006). *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island*, Oxford University Press.

Sobol' I M (1990). Sensitivity estimates for nonlinear mathematical models, *Matematicheskoe Modelirovanie* **2**, 112–118.

Sobol' I M (1993). Sensitivity estimates for nonlinear mathematical models (English Translation), *Mathematics and Computers in Simulation* **1**, 407–414.

Sobol' I M (2001). Global sensitivity indices for nonlinear mathematical models and their Monte Carlo estimates, *Mathematics and Computers in Simulation* **55**(1-3), 271–280.

Sobol' I M, Tarantola S, Gatelli D, Kucherenko S S and Mauntz W (2007). Estimating the approximation error when fixing unessential factors in global sensitivity analysis, *Reliability Engineering & System Safety* **92**(7), 957–960.

Speed D and Balding D J (2014). Relatedness in the post-genomic era: is it still useful?, *Nature Reviews Genetics* **16**(1), 33–44.

Tang Y, Reed P, Wagener T and Van Werkhoven K (2007). Comparing sensitivity analysis methods to advance lumped watershed model identification and evaluation, *Hydrology and Earth System Sciences Discussions* **11**(2), 793–817.

Therkildsen N O, Nielsen E E, Swain D P and Pedersen J S (2010). Large effective population size and temporal genetic stability in Atlantic cod (Gadus morhua) in the southern Gulf of St. Lawrence, *Canadian Journal of Fisheries and Aquatic Sciences* **67**(10), 1585–1595.

Tufto J, Ringsby T H, Dhondt A A, Adriaensen F and Matthysen E (2005). A Parametric Model for Estimation of Dispersal Patterns Applied to Five Passerine Spatially Structured Populations, *The American Naturalist* **165**(1), E13–E26.

Tuljapurkar S and Caswell H (1997). *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems*, Population and Community Biology Series, Springer Science & Business Media.

Van Dyke F (2008). *Conservation Biology: Foundations, Concepts, Applications*, Springer Science & Business Media.

Walsh J C, Wilson K A, Benshemesh J and Possingham H P (2012). Unexpected outcomes of invasive predator control: the importance of evaluating conservation management actions, *Animal Conservation* **15**(4), 319–328.

Wang J (2005). Estimation of effective population sizes from data on genetic

markers, *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **360**(1459), 1395–1409.

Wang J (2007). Triadic IBD coefficients and applications to estimating pairwise relatedness, *Genetical Research* **89**(3), 135–153.

Wang J (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients, *Molecular Ecology Resources* **11**(1), 141–145.

Wang J and Caballero A (1999). Review article: Developments in predicting the effective size of subdivided populations, *Heredity* **82**(2), 212–226.

Waples R S (2005). Genetic estimates of contemporary effective population size: to what time periods do the estimates apply?, *Molecular Ecology* **14**(11), 3335–3352.

Williams S E and Hoffman E A (2009). Minimizing genetic adaptation in captive breeding programs: A review, *Biological Conservation* **142**(11), 2388–2400.

Wright S (1931). Evolution in Mendelian Populations, *Genetics* **16**(2), 97–159.

Wright S (1984). *Evolution and the Genetics of Populations, Volume 2: Theory of Gene Frequencies*, University of Chicago Press.

Yang J (2011). Convergence and uncertainty analyses in Monte-Carlo based sensitivity analysis, *Environmental Modelling & Software* **26**(4), 444–457.

Yearsley J M, Fletcher D and Hunter C M (2003). Sensitivity analysis of equilibrium population size in a density-dependent model for Short-tailed Shearwaters, *Ecological Modelling* **163**(1-2), 119–129.

Appendix A   Dataset

Table A.1: All populations, their annual observed population sizes, N, their effective population sizes, N_e, calculated with $T = 1.97$, and the number of individuals in each sex-age class.

| Population | Year | N | N_e | Sex-age classes | | | |
				f_1	f_2	m_1	m_2
Aldra	1998	4	1	1	0	3	0
Aldra	1999	7	3	1	1	3	2
Aldra	2000	17	6	7	1	5	4
Aldra	2001	28	10	9	4	10	5
Aldra	2002	31	11	7	10	4	10
Aldra	2003	33	12	9	9	5	10
Aldra	2004	45	16	10	13	13	9
Aldra	2005	52	19	13	13	9	17
Aldra	2006	36	13	5	15	2	14
Aldra	2007	37	13	5	10	6	16
Gjerøy	1993	27	11	9	0	18	0
Gjerøy	1994	49	19	18	7	14	10
Gjerøy	1995	35	14	7	10	7	11
Gjerøy	1996	40	16	3	14	9	14
Gjerøy	1997	34	13	9	6	3	16
Gjerøy	1998	52	20	16	13	15	8
Gjerøy	1999	61	24	13	18	14	16
Gjerøy	2000	60	24	9	17	11	23
Gjerøy	2001	51	20	13	13	9	16
Gjerøy	2002	38	15	7	11	7	13
Handnesøy	2011	86	48	45	0	41	0
Handnesøy	2012	57	32	15	12	19	11
Handnesøy	2013	56	31	11	16	13	16
Hestmannøy	1993	96	40	46	0	50	0
Hestmannøy	1994	97	40	19	31	18	29
Hestmannøy	1995	92	38	19	23	28	22
Hestmannøy	1996	71	30	9	25	8	29
Hestmannøy	1997	73	30	23	17	18	15
Hestmannøy	1998	98	41	29	17	37	15
Hestmannøy	1999	134	56	48	16	42	28
Hestmannøy	2000	120	50	33	30	23	34
Hestmannøy	2001	119	50	33	31	29	26
Hestmannøy	2002	74	31	12	23	11	28
Hestmannøy	2003	95	40	30	15	30	20
Hestmannøy	2004	95	40	27	18	25	25

Table A.1: Continued from previous page

Population	Year	N	N_e	Sex-age classes f_1	f_2	m_1	m_2
Hestmannøy	2005	130	54	34	28	39	29
Hestmannøy	2006	137	57	37	32	31	37
Hestmannøy	2007	180	75	45	45	42	48
Hestmannøy	2008	162	68	42	43	36	41
Hestmannøy	2009	169	71	41	44	43	41
Hestmannøy	2010	225	94	74	43	59	49
Hestmannøy	2011	254	106	45	77	53	79
Hestmannøy	2012	142	59	36	34	31	41
Indre Kvarøy	1993	23	11	7	0	16	0
Indre Kvarøy	1994	46	22	14	4	18	10
Indre Kvarøy	1995	54	25	9	12	16	17
Indre Kvarøy	1996	49	23	8	16	7	18
Indre Kvarøy	1997	44	21	7	13	11	13
Indre Kvarøy	1998	38	18	7	9	8	14
Indre Kvarøy	1999	44	21	10	8	15	11
Indre Kvarøy	2000	20	9	7	3	3	7
Indre Kvarøy	2001	29	14	7	4	11	7
Indre Kvarøy	2002	32	15	8	7	5	12
Leka	2002	117	23	32	20	45	20
Leka	2003	125	25	46	11	41	27
Leka	2004	119	24	19	27	40	33
Leka	2005	109	22	25	25	27	32
Leka	2006	98	19	27	21	27	23
Leka	2007	161	32	56	29	48	28
Leka	2008	137	27	46	30	33	28
Leka	2009	147	29	45	30	52	20
Linesøya	2012	68	37	34	0	34	0
Linesøya	2013	78	42	26	13	25	14
Løkta	2011	24	18	11	0	13	0
Løkta	2012	18	13	3	5	5	5
Løkta	2013	61	45	23	6	25	7
Nesøy	1993	13	7	5	0	8	0
Nesøy	1994	16	8	7	3	2	4
Nesøy	1995	14	7	3	5	3	3
Nesøy	1996	16	8	3	6	5	5
Nesøy	1997	19	10	6	4	4	8
Nesøy	1998	21	11	1	4	3	8
Nesøy	1999	18	10	0	7	0	10

Table A.1: Continued from previous page

| Population	Year	N	N_e	Sex-age classes			
				f_1	f_2	m_1	m_2
Nesøy	2000	28	15	5	8	9	6
Nesøy	2001	25	13	3	8	3	11
Nesøy	2002	21	11	1	6	4	10
Rånes	2012	39	7	23	0	16	0
Rånes	2013	53	10	21	8	19	5
Røvass	2011	26	15	13	0	13	0
Røvass	2012	19	11	6	4	3	6
Røvass	2013	16	9	3	3	6	4
Vega	2002	123	21	38	17	51	17
Vega	2003	171	29	64	24	56	27
Vega	2004	163	28	56	39	41	27
Vega	2005	78	13	17	22	18	21
Vega	2006	145	25	51	22	49	23
Vega	2007	124	21	31	26	41	26
Vega	2008	223	38	81	31	75	36
Vega	2009	336	57	107	56	110	63
Ytre Kvarøy	1993	27	8	12	0	14	1
Ytre Kvarøy	1994	38	12	9	7	12	10
Ytre Kvarøy	1995	33	10	6	7	10	10
Ytre Kvarøy	1996	26	8	5	4	4	13
Ytre Kvarøy	1997	14	4	1	6	0	7
Ytre Kvarøy	1998	11	3	3	3	4	1

(a)
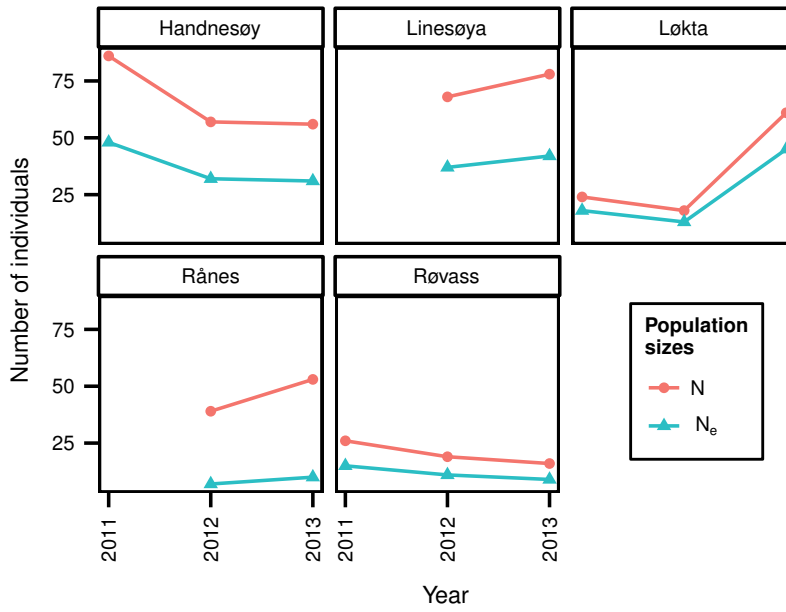
(b)
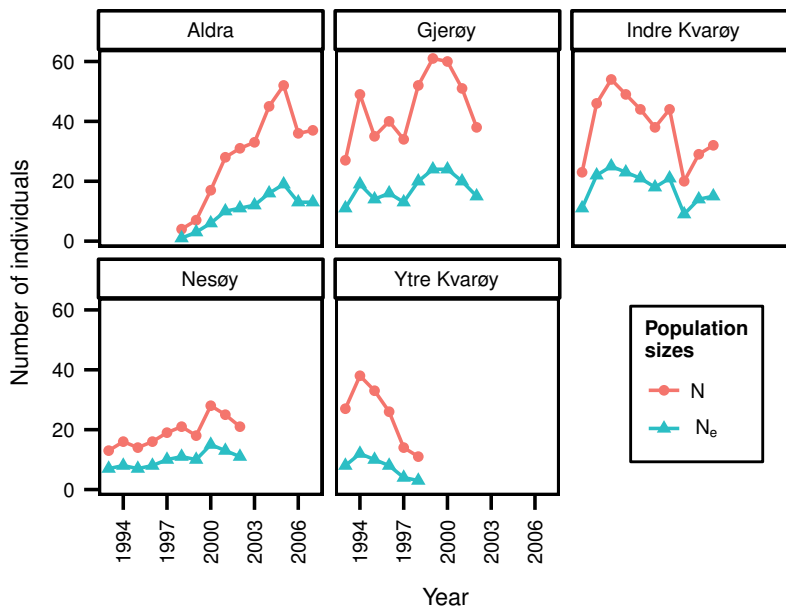
(c)
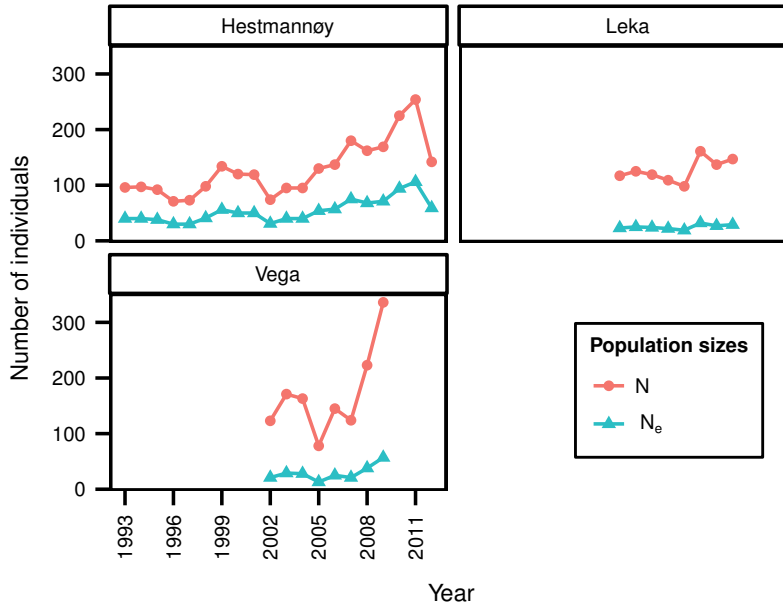
Figure A.1: Annual observed population sizes, N, and the annual effective population sizes, N_e, calculated with $T = 1.97$. The 13 populations have been split into three groups to ease interpretation: (a) few years of data, (b) medium sized populations and (c) large populations.
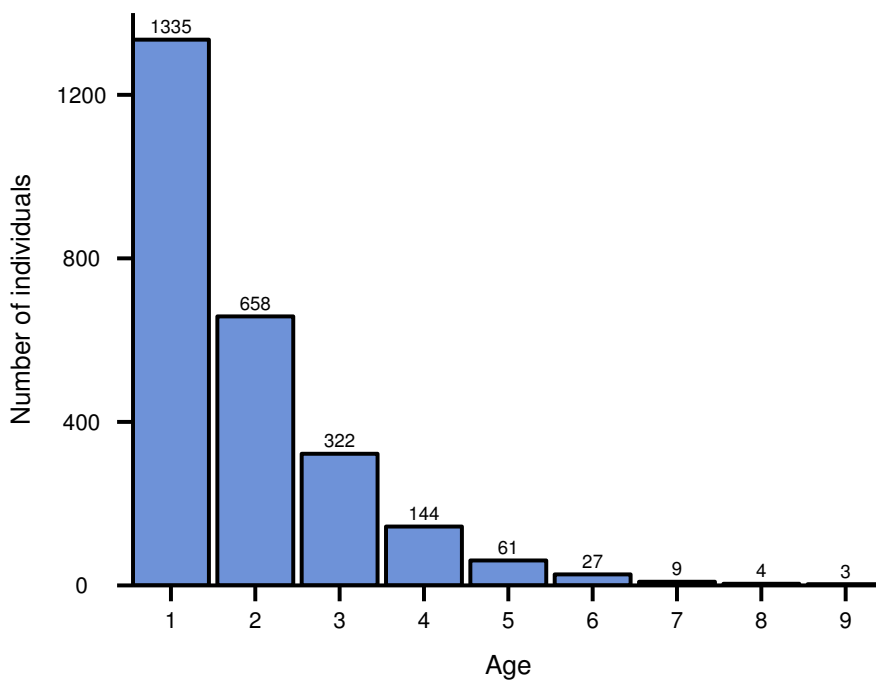
(a)
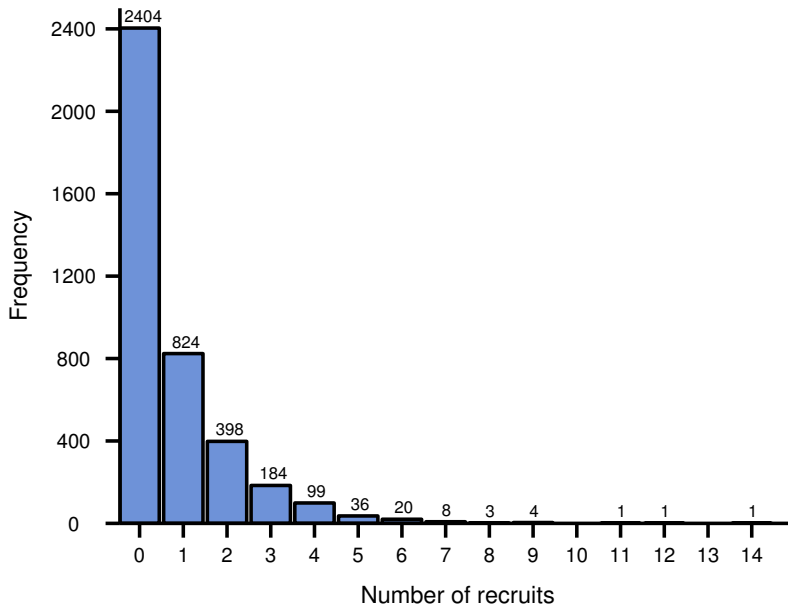
(b)
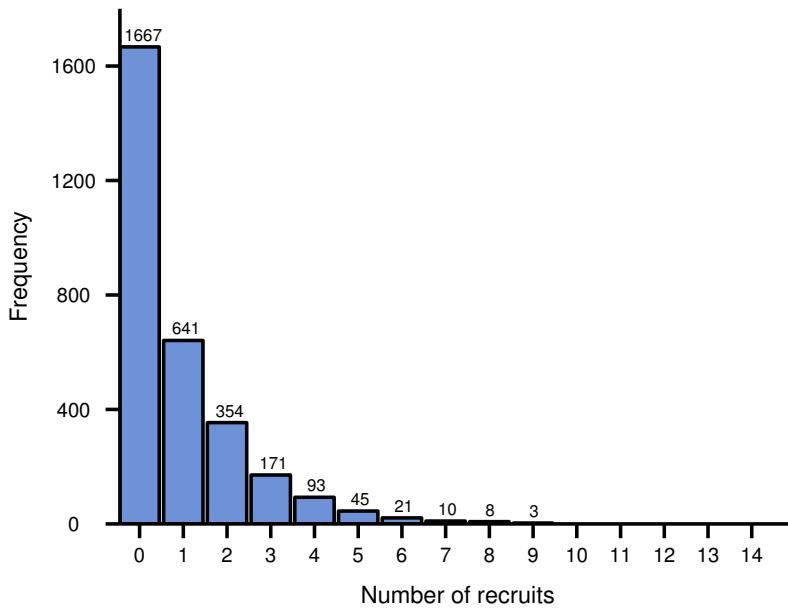
Figure A.2: Distributions of all recruits in dataset. Recruits in age class 1 and 2, in (a) and (b), respectively.

Figure A.3: Distribution of age of all individuals on Hestmannøy for 20 years

Appendix B   Parentage analysis

The pedigrees for the populations Handnesøy, Linesøya, Løkta, Rånes and Røvass had to be established. For all the other study islands, pedigrees were already available.

Materials and methods

To make a pedigree for a given population, I needed to determine the recruits from a given breeding season, and their potential candidate parents. The parent candidates in a given year were assumed to be all adult individuals caught or observed during, or right after, breeding season for the year in question. Also individuals that were ringed in a previous year, and then captured or observed in a later, were included as candidate parents. The recruits from a given year were all individuals caught, or observed, during February-March the following year, excluding any previously ringed and surviving adults. In addition to knowledge of recruits and candidate parents, it is also necessary to have information on the genotypes of all individuals. DNA from the blood samples was extracted and analysed, using 14 unlinked polymorphic microsatellite markers. Genotypes based on allelic variation at these microsatellites, were scored using the software GeneMapper 4.0 (Applied Biosystems) (Billing *et al.* 2012; Jensen *et al.* 2013). The work was done by the technicians, Margit Dagsdatter Haugsnes and Randi Røsbak. To get the number of candidate parents, since a capture rate at 90% is assumed, the observed number of candidates is multiplied by 1.10 to account for the non-captured individuals. The software CERVUS 3.0 (Kalinowski *et al.* 2007) was used to determine parentage based on candidates and their genotype data. The genotype frequencies used in the parentage analysis, were calculated from all years of data available for each population. The assignment of parent pairs to recruits was set to a confidence limit of 0.9, meaning that they on average will be correct in at least 90 % of the cases (see also Jensen *et al.* (2008, 2013); Billing *et al.* (2012); Hagen *et al.* (2013)). For recruits that did not get assigned a parent pair, possible mother and father candidates (with $> 90\%$ confidence) were compared, and the individual that was the most likely a parent, was assigned to the recruit. The missing parents are probably due to unknown candidate parents in the population, that the recruits immigrating from other populations, or error in the scoring of genotypes, which was estimated to be ≤ 2.5 %. Further, information on, or estimates of, how related candidate mothers are to other females, and how related candidate fathers are to other males is needed. A traditional way to calculate relatedness, is to look at the probability of alleles to be identical by descent from a common ancestor in a pedigree (Speed and Balding 2014). When there is little, or no information on pedigree and population structure, which is often the case for natural populations, relatedness estimates can be applied (Wang 2007). To estimate the proportion of relatives among candidate parents, and the average relatedness among relatives, the R-package *related* version 0.8 (Pew *et al.* 2014; Frasier *et al.* 2014), which is

based on the software package COANCESTRY (Wang 2011) was used. The pairwise relatedness, was calculated with the relatedness estimator *trioml*, a triadic likelihood estimator based on genotype frequencies, that have been shown to be precise and robust (Wang 2007), and account for both genotyping error and inbreeding, which increase the credibility of the relatedness estimates. The relatedness was determined using annual genotype frequencies for each population. All individuals with relatedness larger than zero were included in the estimate of the proportion of relatives among candidate parents.

Results

The number of recruits in the five populations was relatively stable across the study years (Table B.1) stay stable, even though the number of parent candidates decreased from one year to the next in Handnesøy, Røvass. Løkta is a special case, as it had a steep increase in both number of candidate parents and number of recruits in 2013 due to the inclusion of more farms on the island as part of the study population. The assignment rate of parent pairs tended to be lower for the first year, but increased for most populations in the second, except for Linesøya were there was a 5 % decrease. On average, parents tend to be approximately as related (0.14) as is expected of first cousins (0.125), except for on Løkta in 2012 where the relatedness was higher, but the proportion related was quite low compared to

Table B.1: Results from annual parentage analysis of the five populations that lacked pedigrees. Listed are the number of recruits and candidate parents (*n*), the percentage of recruits assigned (*Ass.*) a parent pair, the proportion (*Prop.*) related individuals within each sex, and the relatedness (*Rel.*) among these related individuals.

Population	Year	Recruits		Candidate mothers			Candidate fathers		
		n	Ass.	*n*	Prop.	Rel.	*n*	Prop.	Rel.
Handnesøy	2011	34	18 %	63	0.431	0.093	58	0.412	0.102
	2012	26	35 %	35	0.393	0.092	39	0.359	0.087
	2013	34	59 %	31	0.368	0.086	32	0.357	0.113
Linesøya	2012	51	45 %	45	0.417	0.106	45	0.399	0.102
	2013	30	40 %	44	0.367	0.136	44	0.402	0.105
Løkta	2011	8	38 %	12	0.273	0.085	14	0.244	0.162
	2012	5	60 %	9	0.071	0.595	11	0.111	0.296
	2013[a]	21	43 %	32	0.345	0.129	35	0.381	0.097
Røvass	2011	10	22 %	17	0.321	0.115	17	0.282	0.125
	2012	10	50 %	12	0.222	0.149	11	0.194	0.103
	2013	11	45 %	9	0.133	0.018	13	0.200	0.294
Rånes	2012	40	20 %	31	0.372	0.115	24	0.317	0.084
	2013	43	53 %	32	0.355	0.110	26	0.297	0.149

[a] More farms were included this year

previous and following year. On average, a third (0.31) of the parents were related, across populations and years.

Appendix C   Sensitivity analysis

There are two main types of sensitivity analysis, local and global, and choice of type depends on interest and assumptions of the model. Local analyses measure the effect a given input has on the output, and is often based on the partial derivatives of the model parameters. Traditionally, most sensitivity analyses are local, some inappropriately so, because they only explore one point of the parameter space. The parameters are changed one-at-the-time (OAT), while all other inputs are held at a nominal value (Saltelli *et al.* 2004). The computational cost for this method is low, but it cannot detect interactions between inputs, and tend to have a high bias for non-linear models (Yang 2011). Global analysis on the other hand, varies all inputs simultaneously, explores the entire parameter space, and accounts for interactions between input parameters (Sobol' 2001). An accurate method of sensitivity analysis should be model independent, be able to cope with differences in dimensions, and consider all interaction effects among input parameters. One type of global sensitivity analysis is variance-based, and has been found to be a method that fulfils these requirements (EPA Council for Regulatory Environmental Modeling 2009).

Global variance-based methods have a long history, starting with Cukier *et al.* (1973) and then formalised by Sobol' (1990, 1993). Later, there have been several improvements by Jansen *et al.* (1994), Jansen (1999), Saltelli (2002), Sobol' *et al.* (2007) and Saltelli *et al.* (2010), among others. Variance based methods are quantitative in principle, as long as the sample sizes are large enough to tell how much more important factor *A* is, relative to factor *B* (Saltelli *et al.* 2004). Some of the commonly used variance-based methods are the Sobol' method (Sobol' 1990, 1993), the Fourier Amplitude Sensitivity Testing (FAST) (Cukier *et al.* 1973; Saltelli *et al.* 1999), and several different regression and correlation methods. The Sobol' method has been found to be very robust when it comes to quantifying sensitivity, and ranking inputs by using sensitivity indices (Tang *et al.* 2007; Yang 2011; Lagerwall *et al.* 2014). For complex models the Sobol' method can be computational heavy, as it requires a high number of model runs to estimate the first and total order sensitivity indices (Saltelli 2002). The first order index is the main effect of a input on the output, while the total order index also includes all higher order indices, which are contributions to variance in the output through interactions among inputs (Sobol' 1990, 1993). The Sobol' method have been found to work well with biological data, and can handle both continuous and discrete inputs (Lagerwall *et al.* 2014). Ranking of inputs is most easily done by estimating the first order indices (Equation (12)), but these indices do not include possible interactions among inputs, and might lead to an erroneous ranking. Two, or more inputs are per definition interacting when their joint effect differs from their individual effects combined. Higher order indices include interactions among inputs, e.g. second order indices are interactions between two, third order are interactions among three, and so on. As the number of interactions among inputs increase geometrically (2^p) with the number of inputs, it is easier to compute the total index of a parameter (Saltelli *et al.* 2010), which includes the first and all higher order indices of an input (Sobol'

2001). To illustrate, if there is a model with three inputs, A, B and C, the total sensitivity index of parameter A is: $S_{TA} = S_A + S_{AB} + S_{AC} + S_{ABC}$. The total sensitivity index in this example includes the first, second and third order effect, or in other words: all possible ways parameter A can contribute to the output (Chan *et al.* 1997).

Saltelli *et al.* (2010) tested some of the estimators used to calculate sensitivity indices, and concluded that the Jansen estimator (Jansen 1999) was the best. In all the comparisons, it had the highest efficiency and lowest mean absolute error. The Jansen estimator equals the *soboljansen* estimator in the *sensitivity* package, which is the estimator used for the analyses in this study. The *soboljansen* estimator is based on the work of Sobol' (1990, 1993), improved upon by Jansen (1999), and later updated by Saltelli *et al.* (2010). This updated Jansen-Sobol' scheme uses a Sobol' quasi-random sequence for sampling of inputs from their distributions, which were found to outperform standard Monte Carlo sampling (Saltelli *et al.* 2010). The *soboljansen* estimator has a cost of $(p + 2)n$ model runs, where p is the number of input parameters, and n is the number of parameter samples. The *soboljansen* estimator requires a function that takes a data frame where each column is a parameter, and each row a new combination of all parameters (each cell is a random draw from the respective distribution). The output of the function must be a vector with the same length as the number of rows in the data frame (Pujol and Janon 2015).

The Sobol' method use a Monte Carlo estimation of the indices, or a so-called pick-freeze method. This method was adapted by Homma and Saltelli (1996) to calculate the total indices. This is a method where the Sobol' index is regarded as the regression coefficient between the output and a pick-freeze replication. A pick-freeze replication is when one, or several inputs are kept at a certain value (frozen), while the others are sampled from their respective distributions (picked) (Sobol' 1993, 2001). The decomposition of variance in the Sobol' method is done through evaluation of multidimensional integrals, estimated by Monte Carlo integrals (Sobol' 2001). To obtain these Monte Carlo estimates, two independent matrices, or data frames, with parameter values sampled from their respective probability distributions are needed. These matrices have dimensions (n, p) where n is the number of samples (rows) and p is the number of parameters (columns) (Chan *et al.* 1997). There are several sampling methods, e.g. random sampling, Monte Carlo sampling, Latin Hypercube Sampling and a whole array of possible sampling schemes or sequences. The data for the two random sampled matrices needed for the Sobol' method is usually generated by a Sobol' quasi-random sampling scheme. It is called quasi-random, even though it is not random at all, and in contrast to true random sampling, it remembers previously sampled data points, and fill in the gaps between them (Saltelli *et al.* 2010). Such sequences are characterized by having enhanced convergence (Sobol' 2001), which is preferable, as it reduces the total number of model runs. When using a Monte Carlo estimation, or pick-freeze method, to calculate sensitivity indices, one need to consider how many samples is in order to achieve convergence of parameter values (Nossent and Bauwens 2012).

The Sobol' method requires a large number of model runs to get convergence, typically in the order of thousands (Saltelli 2002). To monitor the convergence, and estimate confidence intervals of the indices, one can re-sample, e.g. by bootstrapping, as done in this thesis.

Appendix D Probability density functions (PDF)

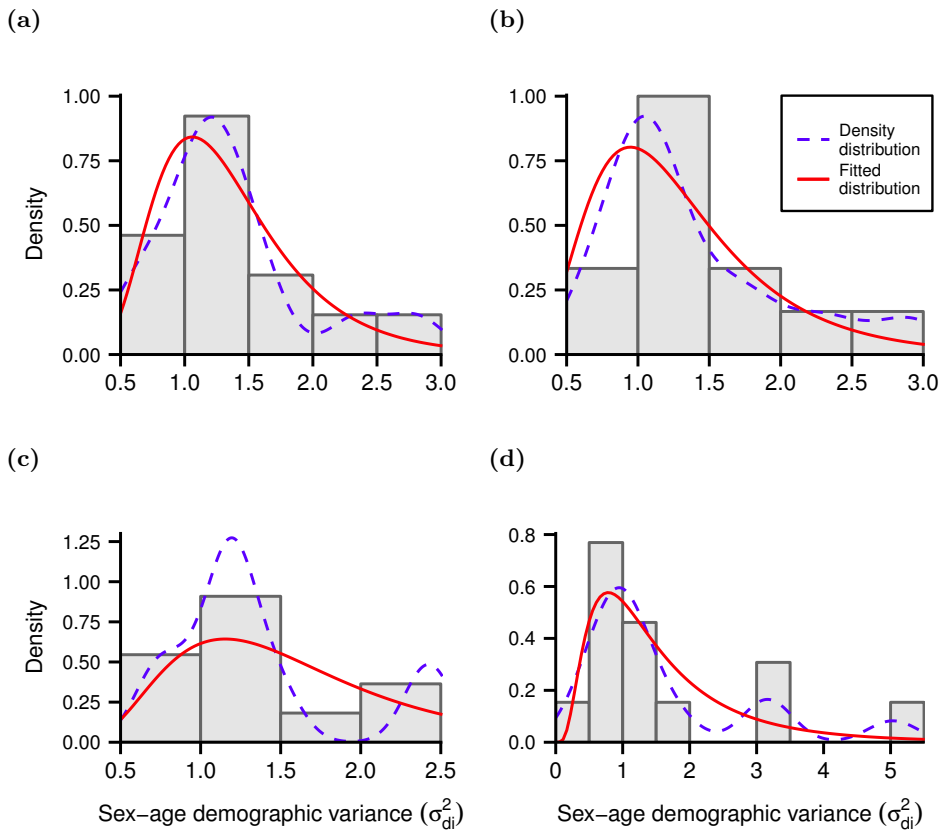All parameter PDF's follows, except for survival, J_i, which was binomially distributed.
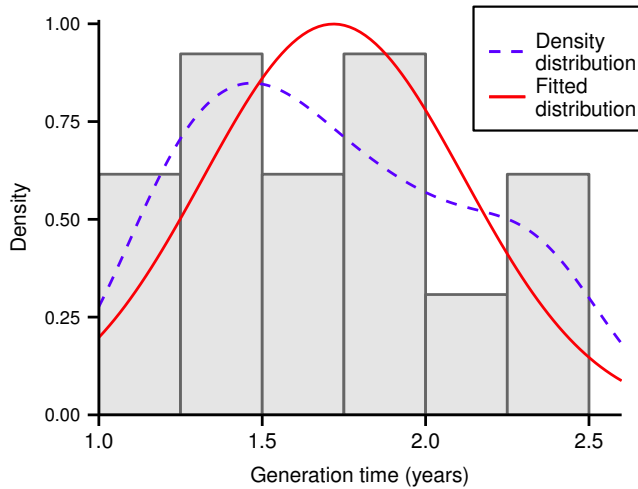
Figure D.1: Observed density distribution of generation time, T, based on the data from 13 populations, and the fitted distribution.
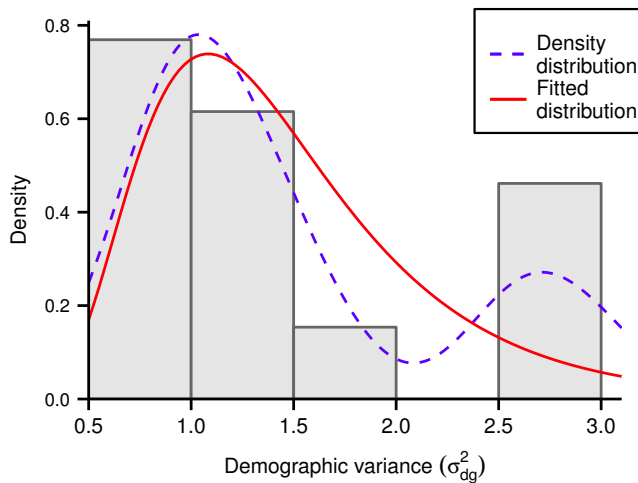
Figure D.2: Observed density of population specific demographic variance, σ_{dg}^2, based on data from 13 populations, and the fitted distribution.
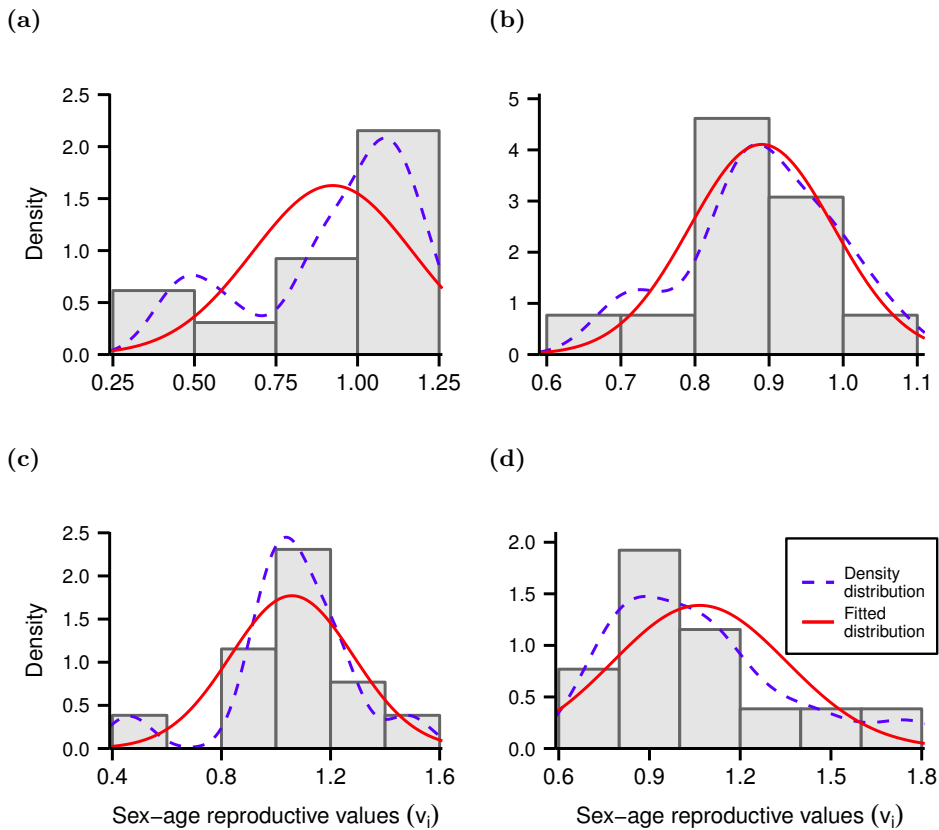
Figure D.3: Observed density of sex-age class demographic variance, σ^2_{dgi}, based on data from 13 populations, and their fitted distributions. Panels (a) and (b) are the distributions of females and males in age class 1, respectively, while panels (c) and (d) are the distributions of females and males in age class 2, respectively.

(a)

(b)

(c)

(d)
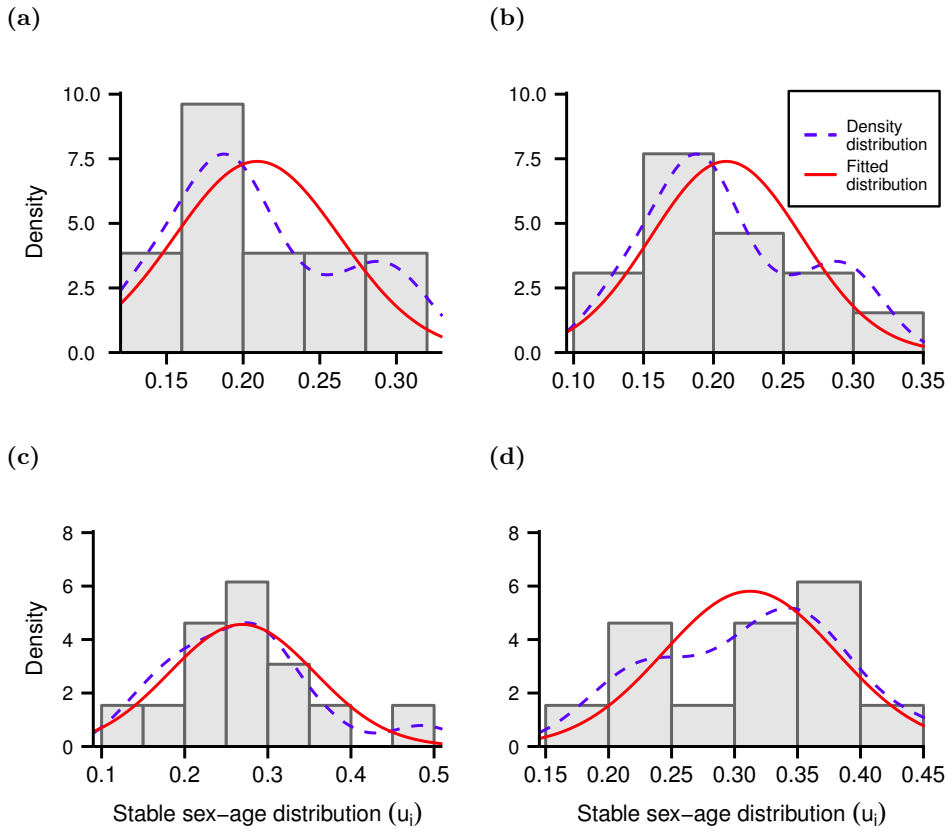
Figure D.4: Observed density of stable sex-age distribution, u_i, based on data from 13 populations, and their fitted distributions. Panels (a) and (b) are the distributions of females and males in age class 1, respectively, while panels (c) and (d) are the distributions of females and males in age class 2, respectively.

(a)

(b)

(c)

(d)

Figure D.5: Observed density of sex-age class specific reproductive value, v_i, based on data from 13 populations, and their fitted distributions. Panels (a) and (b) are the distributions of females and males in age class 1, respectively, while panels (c) and (d) are the distributions of females and males in age class 2, respectively.

(a)

(b)

(c)

(d)
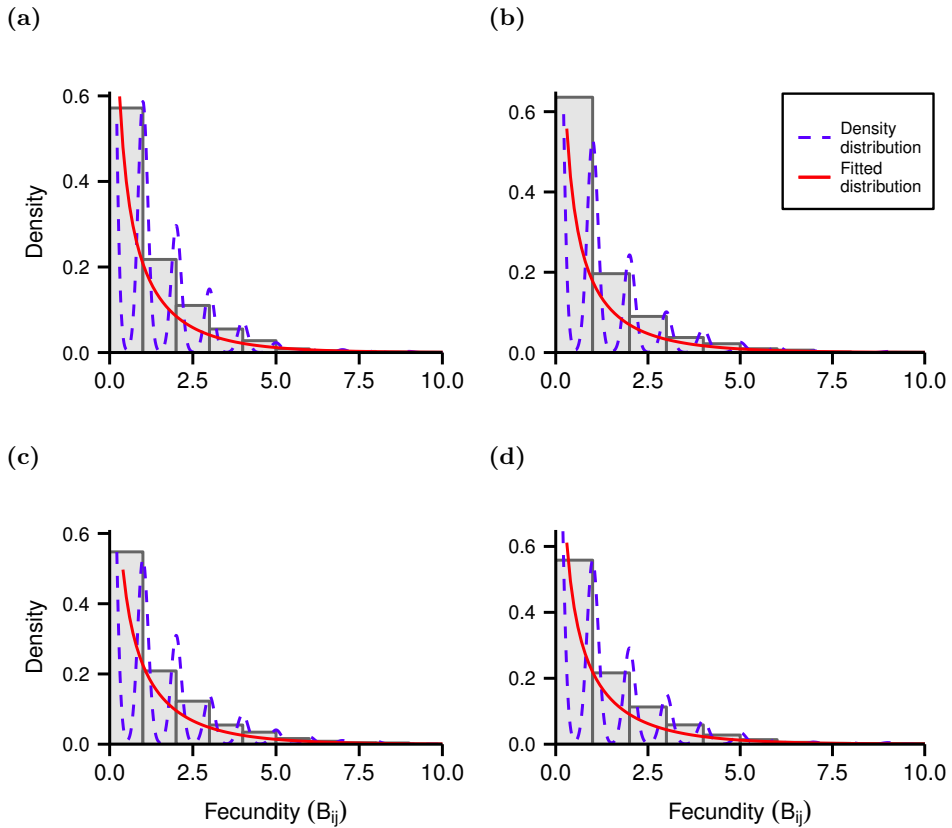
Figure D.6: Observed density of individual fecundity, B_{ij}, based on data from 13 populations, and their fitted distributions. Panels (a) and (b) are the distributions of females and males in age class 1, respectively, while panels (c) and (d) are the distributions of females and males in age class 2, respectively.

Appendix E Parameters

Table E.1: All sex-age class parameters for all 13 populations in the dataset; stable sex-age distribution, u_i, sex-age specific reproductive value, v_i, and sex-age class demographic variance, σ^2_{dgi}.

Population	i	Parameters		
		u_i	v_i	σ^2_{dgi}
Aldra	f_1	0.200	0.864	1.308
Aldra	f_2	0.254	0.954	1.243
Aldra	m_1	0.200	0.958	1.076
Aldra	m_2	0.345	1.137	1.768
Gjerøy	f_1	0.189	1.060	1.265
Gjerøy	f_2	0.307	1.010	1.507
Gjerøy	m_1	0.189	0.928	1.093
Gjerøy	m_2	0.315	0.998	1.216
Handnesøy	f_1	0.184	0.619	0.568
Handnesøy	f_2	0.277	1.049	1.176
Handnesøy	m_1	0.184	0.738	1.014
Handnesøy	m_2	0.355	1.295	0.825
Hestmannøy	f_1	0.197	0.922	0.992
Hestmannøy	f_2	0.289	0.974	1.326
Hestmannøy	m_1	0.197	0.986	1.065
Hestmannøy	m_2	0.316	1.081	1.348
Indre Kvarøy	f_1	0.165	1.097	1.221
Indre Kvarøy	f_2	0.316	1.257	1.178
Indre Kvarøy	m_1	0.165	0.845	1.089
Indre Kvarøy	m_2	0.353	0.797	0.934
Leka	f_1	0.279	0.899	2.339
Leka	f_2	0.203	1.217	3.160
Leka	m_1	0.279	0.837	1.808
Leka	m_2	0.238	1.125	3.180
Linesøya	f_1	0.208	0.479	0.728
Linesøya	f_2	0.142	0.462	0.793
Linesøya	m_1	0.208	0.890	1.215
Linesøya	m_2	0.442	1.469	0.942
Løkta	f_1	0.143	1.193	1.080
Løkta	f_2	0.486	1.116	0.690
Løkta	m_1	0.143	0.891	0.797
Løkta	m_2	0.228	0.699	0.383
Nesøy	f_1	0.128	1.093	1.004
Nesøy	f_2	0.365	1.178	1.150
Nesøy	m_1	0.128	0.854	0.715
Nesøy	m_2	0.379	0.846	0.844

Continued on next page

Table E.1: Continued from previous page

| Population | i | Parameters | | |
		u_i	v_i	σ^2_{dgi}
Rånes	f_1	0.302	0.453	1.305
Rånes	f_2	0.162	0.927	2.466
Rånes	m_1	0.302	0.996	2.315
Rånes	m_2	0.235	1.757	5.034
Røvass	f_1	0.246	1.049	1.538
Røvass	f_2	0.214	1.487	0.994
Røvass	m_1	0.246	0.696	0.465
Røvass	m_2	0.294	0.859	0.592
Vega	f_1	0.298	1.084	2.811
Vega	f_2	0.209	1.055	3.186
Vega	m_1	0.298	0.890	2.908
Vega	m_2	0.195	0.979	3.146
Ytre Kvarøy	f_1	0.180	1.198	1.602
Ytre Kvarøy	f_2	0.274	1.074	2.382
Ytre Kvarøy	m_1	0.180	1.061	1.603
Ytre Kvarøy	m_2	0.365	0.816	1.087