

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

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1 Title page:

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4 **in House Sparrow Populations**

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22 Running title: Sensitivity of effective population size

23 Abstract

24 The ratio between the effective and the census population size, N_e/N , is an important
25 measure of the long-term viability and sustainability of a population. Understanding
26 which demographic processes that affect N_e/N most will improve our understanding of
27 how genetic drift and the probability of fixation of alleles is affected by demography. This
28 knowledge may also be of vital importance in management of endangered populations
29 and species. Here, we use data from 13 natural populations of house sparrow (*Passer*
30 *domesticus*) in Norway to calculate the demographic parameters that determine N_e/N . By
31 using the global variance-based Sobol' method for the sensitivity analyses, we found that
32 N_e/N was most sensitive to demographic variance, especially among older individuals.
33 Furthermore, the individual reproductive values (that determine the demographic variance)
34 were most sensitive to variation in fecundity. Our results draw attention to the applicability
35 of sensitivity analyses in population management and conservation. For population
36 management aiming to reduce the loss of genetic variation, a sensitivity analysis may
37 indicate the demographic parameters towards which resources should be focused. The
38 result of such an analysis may depend on the life history and mating system of the
39 population or species under consideration, since the vital rates and sex-age classes that
40 N_e/N is most sensitive to may change accordingly.

41 Introduction

42 A growing number of natural populations face threats originating from human activities
43 (Primack 2010), many of which lead to increased fragmentation and decreased population
44 size (Frankham *et al.* 2010). Small populations are more vulnerable to extinction due
45 to increased inbreeding, more rapid loss of genetic variation due to genetic drift, and a
46 decreased resilience when faced with environmental change (Lande *et al.* 2003; Legendre
47 *et al.* 2008). Processes affecting population size (N) (e.g. survival, reproduction, and
48 migration, Tuljapurkar & Caswell 1997), depend on both genes and the environment
49 (Caswell 2001), and the effective population size (N_e) influence evolutionary processes in
50 the population through rate of loss of genetic variation. By maximising both N_e and N ,
51 the resilience to change is expected to be maintained in the population, and the risk of
52 extinction will then decrease (Frankham *et al.* 2010; Allendorf *et al.* 2012).

53 In population genetics, knowledge of N_e , which depends on both ecological and genetic
54 factors, is crucial to make both short- and long-term predictions regarding loss of genetic
55 variation due to drift as well as the probability of fixation of advantageous alleles due to
56 selection (Shaffer 1981; Nunney & Elam 1994; Palstra & Fraser 2012). As a consequence,
57 it is important to identify the parameters that influence N_e most, i.e. the parameters
58 to which N_e is most sensitive to (Caswell 2001; Saltelli *et al.* 2004). N_e is defined as
59 the size of a Wright-Fisher ideal population that experiences the same rate of genetic
60 drift and loss of heterozygosity as the observed population (Wright 1931). Such an
61 ideal population is a conceptual panmictic population with constant size, consisting of
62 monoecious diploid individuals that have discrete generations, Poisson distributed family
63 sizes, and no selection or mutations in autosomal loci (Nunney 1993; Caballero 1994;
64 Wang & Caballero 1999; Kalinowski & Waples 2002; Frankham *et al.* 2010). Natural
65 populations usually violate the ideal conditions in several ways (Harris & Allendorf 1989;
66 Wang & Caballero 1999; Frankham *et al.* 2010), and most populations therefore behave as
67 if they were a lot smaller than their census size (Halliburton 2003; Freeman & Herron 2007;

68 Frankham *et al.* 2010). Of all deviations from the ideal population, variation in N has been
69 shown to often reduce N_e most (Kalinowski & Waples 2002; Engen *et al.* 2005b; Frankham
70 *et al.* 2010), followed by variation in family size, and skewed sex ratios (Caballero 1994;
71 Frankham 1995; Frankham *et al.* 2010). Other factors that affect N_e include mating
72 system, overlapping generations, generation time (Nunney 1993; Engen *et al.* 2005b),
73 and population age-structure. Environmental stochasticity indirectly affect the effective
74 population size by amplifying fluctuations in population size (Lande *et al.* 2003). Random
75 variation in survival and reproduction within years, termed demographic stochasticity,
76 may also cause deviations from an ideal population and reduce N_e (Lebreton *et al.* 1992;
77 Ardren & Kapuscinski 2003; Frankham *et al.* 2010; Myhre *et al.* 2016). Demographic
78 stochasticity, measured by demographic variance (σ_d^2), increases the rate of genetic drift,
79 and is especially important for small populations (Lande *et al.* 2003; Engen *et al.* 2005b;
80 Shpak 2007).

81 Following the approach of Pollak (2000) considering the dynamics of a subgroup of
82 individuals bearing a rare neutral allele, Engen *et al.* (2005b) derived a formula for
83 the effective population size per generation based on the demographic variance, $N_e =$
84 $N/(\sigma_{dg}^2 T)$, where the subscript g indicates that the demographic variance also has a
85 genetic component due to Mendelian segregation, and T is the generation time. Based
86 on the realization that the dynamics of age-structured density-independent populations
87 could well be approximated by the dynamics of the total reproductive value (Engen *et al.*
88 2007a), Engen *et al.* (2010) derived formulas for the ratio of effective to actual size.
89 This provided an extension of previous models (Felsenstein 1971; Hill 1972, 1979) for
90 genetic drift in age-structured populations without assuming a stable age-distribution or
91 no environmental fluctuations.

92 In this study, data from a long-term study on Norwegian populations of house sparrow
93 (*Passer domesticus*) was used to estimate the variance N_e and the effective to census
94 population size ratio, N_e/N (Engen *et al.* 2010). The demographic parameters used to

95 estimate N_e include generation time and demographic variance, where the latter is given
96 by the sum of sex-age specific variances in individual reproductive values weighted by
97 the stable sex-age distribution. A sample-based Sobol' method was used for a global
98 variance-based sensitivity analysis, to determine the sensitivity of N_e/N to each of the
99 demographic parameters. The principle of global analyses is that all inputs are varied
100 simultaneously, the entire parameter space is explored, and any interactions between input
101 parameters are accounted for (Sobol' 2001). We believe management efforts to regulate
102 populations should be focused on the demographic parameters that N_e/N is most sensitive
103 to, and that this study will provide insight on identification of these parameters.

104 Materials and methods

105 Study system

106 The data in this study were collected from 13 populations of house sparrow located along
107 the Norwegian coast (Fig. 1). Six of the northernmost populations were located in a
108 long-term study system consisting of an insular metapopulation of house sparrows at the
109 Helgeland coast (66°N, 13°E). The remaining seven study populations were located on
110 the mainland, and on islands to the south of this insular metapopulation. See Ringsby
111 *et al.* (1999), Ringsby *et al.* (2002) and Pärn *et al.* (2012) for more details about the study
112 area.

113 The dataset included 4074 individuals, with an average of seven years of data per population
114 and with a range of two to twenty years. The data encompassed populations with highly
115 different histories. One of the populations, on the island Aldra (population 1 in Fig.), was
116 founded in 1998 by one female and three males, and suffers from substantial inbreeding
117 (Billing *et al.* 2012), while the population at Ytre Kvarøy (population 13 in Fig. 1) went
118 extinct in 2000 (Ringsby *et al.* 2006). Two other populations, Leka and Vega (population
119 6 and 12 in Fig. 1), were part of an experiment in 2002-2005 (Kvalnes *et al.* in review)
120 where approximately 60 % of the individuals in each population were removed each year
121 following artificial selection on tarsus length. Individuals with short or long tarsi were
122 removed on Leka and Vega, respectively (Kvalnes *et al.* in review). These four islands
123 were included to increase the range of variation, within natural limits, in the dataset.

124 Study species

125 The house sparrow is a socially monogamous species, with some extra-pair mating (Jensen
126 *et al.* 2008), where both parents contribute to brooding and feeding of nestlings (Ringsby
127 *et al.* 2009). In the study area, the breeding season is from May-August, and each pair

128 produce 1-3 clutches with an average of five eggs per clutch during this time (Ringsby *et al.*
129 2002; Husby *et al.* 2006). Only 15-20 % of fledglings survive their first winter (i.e. still
130 alive after 1 February) to become recruits in the next years' breeding population (Ringsby
131 *et al.* 2002). The average generation time is 1.97 years in this system (Jensen *et al.* 2008)
132 with an annual adult survival rate at approximately 50 % (Ringsby *et al.* 1999). After
133 the post-natal and post-breeding moult, adult and juvenile house sparrows are impossible
134 to discriminate (Anderson 2006). Hence, all full-grown individuals were assumed to be
135 hatched in the most recent completed breeding season upon first capture (see Table S1,
136 Supporting information). For islands with many years of data this assumption should
137 be of little concern, but it will affect the estimated generation time in populations with
138 few years of data (see *Results* and *Discussion*). The natal dispersal rates among islands
139 within the metapopulation system are low; only around 10 % of the juveniles disperse,
140 and adult dispersal is negligible (Altwegg *et al.* 2000; Pärn *et al.* 2009, 2012). Among the
141 dispersers, approximately 60 % of them travel distances shorter than 13 km (Tufto *et al.*
142 2005).

143 **Data collection and handling**

144 Most of the data was collected during the breeding season. Adults and fledged juveniles
145 were caught using mist nets, while nestlings were caught in the nests. All individuals were
146 marked with a numbered metal ring, and a unique combination of three coloured plastic
147 rings for later identification in the field (Ringsby *et al.* 2002; Jensen *et al.* 2004). A blood
148 sample of 25 µl was drawn from the brachial vein underneath the wing, and provided
149 the DNA necessary to genotype individuals on 14 unlinked polymorphic microsatellite
150 markers for genetic parentage analyses (Jensen *et al.* 2003). Genetic pedigrees for the
151 populations Handnesøy, Linesøya, Løkta, Rånes and Røvass, were established (see Table
152 S2 and *Parentage analyses* in Supporting information), while genetic pedigrees for the
153 remaining populations were already available, see Jensen *et al.* (2003), Billing *et al.* (2012),

154 Jensen *et al.* (2013) and Holand *et al.* (2015). The pedigrees in tandem with individual
155 capture and observation data, provided information on annual survival, fecundity and
156 census population size estimated as the number of adult individuals captured and/or
157 observed before or during breeding season in a given year. These estimates are assumed
158 to be accurate as the annual capture rates in the study system are above 70% and usually
159 close to 100% (Jensen *et al.* 2006, 2013).

160 The females and males in the dataset were split into two age classes each, (1) yearlings
161 of age one, and (2) all individuals of age two years or older. In total there were four
162 groups, hereafter addressed as sex-age classes, denoted by $i = (f_1, f_2, m_1, m_2)$ for females
163 and males in age class 1 and 2. The pooling of individuals into a terminal age class was
164 done to exclude the effect of small sample sizes of older individuals. This approach has
165 little effect on estimates of N_e , because the vital rates vary little with age (Engen *et al.*
166 2010). The sex-ratio at birth (q) given as the proportion of females, was assumed to be
167 0.5 (Husby *et al.* 2006), hence, the total number of recruits divided by two could be used
168 in the calculations (Engen *et al.* 2010). In accordance with Engen *et al.* (2007, 2009), we
169 assumed that the population dynamics were density-independent, and that there were no
170 temporal autocorrelations in vital rates. All data handling and statistical analyses were
171 done in the software R version 3.1.3 (R Core Team 2016).

172 Demographic parameters

173 For all populations, N_e/N was estimated following the method for age-structured populations
174 with two sexes in Engen *et al.* (2010):

$$175 \quad \frac{N_e}{N} = \frac{1}{\sigma_{dg}^2 T}, \quad (1)$$

176 where σ_{dg}^2 is the population specific demographic variance, and T is the generation time.
177 The subscript g in σ_{dg}^2 denotes that the demographic variance has a genetic component

178 due to Mendelian segregation in diploid species, as explained in Engen *et al.* (2005b). This
 179 definition of variance N_e has both theoretically and by simulations been shown to predict
 180 the correct amount of genetic drift (Engen *et al.* 2005b, see also Myhre *et al.* 2016). To
 181 calculate σ_{dg}^2 , we used data on individual survival and fecundity to build the expected
 182 population projection matrix, \mathbf{l} , for each population:

$$183 \quad \mathbf{l} = \begin{bmatrix} \frac{1}{2}q\bar{B}_{f_1} & \frac{1}{2}q\bar{B}_{f_2} & \frac{1}{2}q\bar{B}_{m_1} & \frac{1}{2}q\bar{B}_{m_2} \\ \bar{J}_{f_1} & \bar{J}_{f_2} & 0 & 0 \\ \frac{1}{2}(1-q)\bar{B}_{f_1} & \frac{1}{2}(1-q)\bar{B}_{f_2} & \frac{1}{2}(1-q)\bar{B}_{m_1} & \frac{1}{2}(1-q)\bar{B}_{m_2} \\ 0 & 0 & \bar{J}_{m_1} & \bar{J}_{m_2} \end{bmatrix} \quad (2)$$

184 The matrix included the mean number of total recruits produced by individuals in each of
 185 the sex-age classes (\bar{B}_i) and the mean specific survival probabilities of each sex-age class
 186 (\bar{J}_i), where i signifies the four different sex-age classes. The fecundities are multiplied by
 187 0.5 to account for the Mendelian segregation as offspring receive half its genes from each
 188 parent. As mentioned, q is the proportion of females, so $1-q$ is the proportion of males at
 189 birth, which in this study were assumed to be equal ($q = 0.5$). The asymptotic population
 190 growth rate (λ) was calculated as the real dominant eigenvalue of \mathbf{l} . The left and right
 191 eigenvectors of \mathbf{l} , \mathbf{u} and \mathbf{v} , are the stable sex-age distribution and reproductive values of
 192 each sex-age class i , provided that these are scaled so that $\sum u_i = 1$, and $\sum u_i v_i = 1$
 193 (Caswell 2001). Both \mathbf{u} and \mathbf{v} are conceptual values for a population at equilibrium,
 194 such that when the population has obtained its stable sex-age distribution, the census
 195 population size equals the total reproductive value of the population (Felsenstein 1971;
 196 Engen *et al.* 2010).

197 The number of offspring from males and females must necessary be exactly the same.

198 Hence, there are constraints on the vital rates in the matrix \mathbf{I} to ensure that the asymptotic
 199 growth rate of the male (λ_m) and female (λ_f) subpopulation are exactly the same (conditioned
 200 on the sex ratio at birth, q). When this is true we have that $\lambda = \lambda_f = \lambda_m$, and this was
 201 achieved by scaling the recruit production by males ($\bar{B}_{m_1}, \bar{B}_{m_2}$) by a constant, c . We
 202 introduced the constant c to the Euler-Lotka equation, $cq \sum \lambda^{-i} l_i m_i = 1$, and solved it
 203 using the Newtons method for the growth rate of the female subpopulation ($c = 1$). Then
 204 the male growth rate was set equal to λ_f and the equation solved for c with q replaced
 205 by $q - 1$. The R-package *lmf*, version 1.2 (Engen *et al.* 2012) was used to calculate λ , \mathbf{u}
 206 and \mathbf{v} .

207 To estimate σ_{dg}^2 , the individual contributions to the future population growth was needed.
 208 This can be calculated as the individual reproductive value (Engen *et al.* 2009) which for
 209 an individual j in sex-age class i , is defined as:

$$210 \quad W_{ij} = J_{ij}v_{i+1} + \frac{1}{2}B_{ij}v_1 + \frac{1}{2}B_{ij}v_3. \quad (3)$$

211 The individual reproductive value gives the annual individual contribution to the total
 212 reproductive value of the population the following year. Here, there are two age classes
 213 per sex, and $i = 1, 2$ represent females of age 1 and 2, respectively, while $i = 3, 4$ represent
 214 males of age 1 and 2, respectively. J is an individual's own survival (1 if it survives,
 215 otherwise 0), B is the number of recruits produced, and $v(i+1)$, v_1 and v_3 is the age-sex
 216 specific reproductive values, with recruiting females and males in sex-age class 1 and
 217 3. Since $q = 0.5$, half of the recruits were expected to be female and half to be male,
 218 which gave $B/2$. The value v_{i+1} , could due to the number of age classes in this case,
 219 maximally take the value v_2 for females, and v_4 for males. Since W_{ij} was calculated from
 220 observed data on viability and fecundity, the annual demographic variance for each sex-age
 221 class ($\sigma_{dgi}^2(t)$), will not only capture variance due to demographic stochasticity, but also
 222 sampling error and variance governing selection pressures. $\sigma_{dgi}^2(t)$ can be estimated as the

223 sum of squares (Engen *et al.* 2009):

$$224 \quad \sigma_{dgi}^2(t) = \frac{1}{m_{ti} - 1} \sum_{j=1}^{m_{ti}} (W_{ij} - \bar{W}_{ti})^2, \quad (4)$$

225 where m_{ti} is the total number of individuals in sex-age class i in year t , and \bar{W}_{ti} is the
 226 mean value of the W_{ij} in year t . The sex-age class specific demographic variance, σ_{dgi}^2 , is
 227 the weighted mean of $\sigma_{dgi}^2(t)$ over all years with $m_{ti} - 1$ as weights:

$$228 \quad \sigma_{dgi}^2 = \frac{\sum \sigma_{dgi}^2(t) m_{ti} - 1}{\sum m_{ti} - 1} \quad (5)$$

229 The total demographic variance of the population, σ_{dg}^2 , is the weighted mean of σ_{dgi}^2 with
 230 weights u_i ,

$$231 \quad \sigma_{dg}^2 = \sum \sigma_{dgi}^2 u_i. \quad (6)$$

232 The population specific generation time, T , was calculated as the mean age of all adults
 233 with recruits in each population (Lande *et al.* 2003). The N_e/N ratios of all populations
 234 were calculated by setting the values of σ_{dg}^2 into equation (1), with both the population
 235 specific T , and the average T across multiple populations and years in the study system
 236 ($T = 1.97$, Jensen *et al.* 2008).

237 Sensitivity analysis

238 A global variance-based method was used in the sensitivity analysis as it provides quantitative
 239 measures, is model independent, and there are no assumptions about linearity, monotonicity
 240 or independence of inputs (Saltelli & Annoni 2010). This approach with few assumptions
 241 suits biological data well, as biological parameters often are dependent on each other
 242 (Caswell 2001). The variance-based method can be illustrated with a general model:
 243 $Y = f(X)$, where Y is the output with an unconditional variance $\text{var}(Y)$, f is the
 244 function, and $X = (x_1, x_2, \dots, x_n)$ are the inputs. In general, global sensitivity analyses are

245 performed as follows: (i) the model is defined, (ii) the input parameters X are assigned
246 probability density functions, from which (iii) they are sampled randomly, and (iv) the
247 relative influence of the input parameters on the output is assessed by the preferred
248 method (Chan *et al.* 1997). In this study, we chose the Sobol' method as it has been
249 proven robust (Tang *et al.* 2007; Yang 2011).

250 Sobol's method

251 Sobol's method (Sobol' 1990, 1993) use Sobol' indices, or sensitivity indices, to quantitatively
252 measure the importance of inputs. It is based on variance decomposition of the total
253 variance, $\text{var}(Y) = V$, into partial, or conditional variances, $\text{var}(Y|x_p) = V_p$. The smaller
254 the conditional variance is, but the larger influence it has on the total variance, the more
255 important the input is. Ranking of inputs is most easily done by estimating the first order
256 indices (Sobol' 2001):

$$257 \quad S_p = \frac{V_p}{V}, \quad (7)$$

258 where the first order index S_p , is the main effect of input parameter p . However, these
259 indices do not include possible interactions among inputs, and might lead to erroneous
260 ranking. To account for the effect of possible interactions, it is preferable to use the
261 total-order index S_{Tp} , which is calculated as:

$$262 \quad S_{Tp} = 1 - \frac{V_{\sim p}}{V} = 1 - S_{\sim p}, \quad (8)$$

263 where $\sim p$ is all input parameters, except p (Homma & Saltelli 1996; Chan *et al.* 1997).
264 The interaction effect of a parameter, $\Delta S = S_{Tp} - S_p$ (Nossent & Bauwens 2012), was
265 considered significant if $\Delta S \geq 0.05$ (see Chu-Agor *et al.* 2011). The input parameters for
266 the analysis were sampled from their respective distributions with a Sobol' quasi-random
267 sampling scheme (Saltelli *et al.* 2010). Each parameter was sampled $n = 5000$ times, and
268 bootstrapped 10,000 times to ensure convergence of the indices (Saltelli 2002; Yang 2011).

269 Parameter distributions

270 The R-package *fitdistrplus* (Delignette-Muller & Dutang 2015) was used to evaluate each
271 parameters' density function which were used in the sensitivity analyses. Due to few
272 data points for most parameters (because we had data from 13 populations), the best
273 parameter distribution was not always clear. In tandem with considering the biological
274 process underlying the parameter, a suitable distribution was chosen (see Table S3,
275 Supporting information, for information on the distribution chosen for each parameter).
276 All parameters, except survival that is binomially distributed, were evaluated as continuous
277 due to the high number of individuals and the long timespan of the dataset.

278 Estimation of indices

279 To estimate the sensitivity indices, the *soboljansen* estimator in the R-package *sensitivity*
280 version 1.11 (Pujol & Janon 2015) was used. The *soboljansen* estimator has been shown
281 to be a computationally efficient estimator with low mean absolute error (Saltelli *et al.*
282 2010), and is suitable for large first-order indices, and large and small total indices (Pujol &
283 Janon 2015). All inputs for the estimation of the indices were sampled from the parameter
284 distributions (Table S3, Supporting information). We used a hierarchical approach in our
285 sensitivity analysis to better understand what parameters N_e/N was most sensitive to.
286 First we examined the sensitivity of N_e/N to T and σ_{dg}^2 (eqn 1). Then generation time
287 was fixed at the average generation time in the study system ($T = 1.97$), and we examined
288 the sensitivity of N_e/N to σ_{dg}^2 's components σ_{dgi}^2 and u_i (eqn 6). Since a stochastic annual
289 function was too complex for the chosen sensitivity estimator, the annual input parameter
290 $\sigma_{dgi}^2(t)$ (eqn 4) was not included in the sensitivity analysis. Instead, our sensitivity analysis
291 continued at the individual level (eqn 3), where the sensitivity of W_{ij} to J_{ij} and B_{ij} was
292 evaluated, with the v_i 's fixed at their average values.

293 Results

294 Demographic parameters

295 The demographic parameters used to estimate N_e/N , are summarised in Tables 1, 2 and
296 S4 (Supporting information). The mean population size over all years of data varied from
297 19 to 170 individuals (Table 3), and annual population sizes ranged between 4 and 336
298 (see Table S1, Supporting information).

299 The population specific generation time, T , ranged from 1.20 to 2.39 years, with a mean of
300 1.72 years (Table 1). T was highest (> 2.1 years) for Aldra, Gjerøy and Nesøy, and lowest
301 (< 1.5 years) for Handnesøy, Linesøya, Løkta, Rånes and Røvass. The relatively large
302 range in T among these populations, are probably partly due to the length of data series;
303 the four populations with low T all had $n < 4$ years of data (Table 3). The asymptotic
304 population growth rate was positive ($\lambda > 1$) in four populations (Aldra, Leka, Rånes and
305 Vega), while for all other populations the estimated growth rate was negative ($\lambda < 1$).

306 The demographic variance, σ_{dg}^2 , ranged from 0.62 to 2.98 in different populations, with a
307 mean of 1.45 (Table 1). Four populations had a higher σ_{dg}^2 than the overall mean, and
308 three of them were populations with special demographic histories: the inbred population
309 of Aldra, and the two artificially selected populations Leka and Vega. Rånes also had
310 a high σ_{dg}^2 ($\sigma_{dg}^2 = 2.64$), but this may be due to chance, as there were only 2 years of
311 data for this population (Table 3). For the sex-age class specific demographic variance,
312 σ_{dgi}^2 , both the mean and the variance were highest in the two oldest sex-age classes (Table
313 2). The highest value of σ_{dgi}^2 was found for older males on Rånes (Table S4, Supporting
314 information).

315 Both the stable sex-age distribution, u_i , and the sex-age class specific reproductive values,
316 v_i , had estimate means that were highest in age class 2 for both sexes (Table 2). Moreover,
317 the variance of the estimates were very low (< 0.1) for all classes. In general (12 out of 13
318 populations) one or both sexes in age class 2 had larger \mathbf{u} values than age class 1 (Tables

319 2 and S4, Supporting information). For \mathbf{v} , there was a tendency for age class 2 to have
320 higher values than age class 1 for one or both sexes (11 out of 13 populations; Tables 2
321 and S4, Supporting information).

322 For survival, J , the mean was approximately the same (≈ 0.50) for all sex-age classes, and
323 the difference between the highest and lowest mean value was small ($\Delta J = 0.03$, Table 2).
324 Furthermore, the variance was the same for all age classes (Table 2). For the fecundity,
325 B , the highest mean value was found in older females ($f_2 = 0.94$), while it was lowest for
326 young males ($m_1 = 0.69$). Age class 2 had the highest mean values for both sexes, but
327 the difference between age classes was smaller for females ($\Delta B = 0.11$), than for males
328 ($\Delta B = 0.19$). Finally, the highest variance in B was found in older females, whereas the
329 lowest was found in young males (Tables 2 and S4, Supporting information).

330 N_e/N

331 In general, N_e/N calculated with $T = 1.97$ tended to be lower than when calculated
332 with the population specific T (range of N_e/N ($T = 1.97$): 0.17-0.82, range of N_e/N
333 (population specific T): 0.22-1.35), but the opposite was true for three populations with
334 high population specific T . Hestmannøy and Indre Kvarøy had population specific T close
335 to $T = 1.97$, hence the ratio was approximately the same using either estimate (Table 1).

336 Sensitivity analysis

337 In the first sensitivity analysis of N_e/N , with input parameters being the population
338 specific estimates of σ_{dg}^2 and T , the demographic variance was found to be the most
339 important parameter (Fig. 2, Table S5, Supporting information). The total order indices
340 showed that N_e/N was significantly more sensitive to σ_{dg}^2 than to T (σ_{dg}^2 : 95% CI
341 [0.671, 0.795], T : 95% CI [0.259, 0.316]) (Fig. 2). Because $\Delta S < 0.05$, interactions
342 between the input parameters were not likely to be important (Table S5, Supporting

343 information).

344 In the second sensitivity analysis of N_e/N with input parameters σ_{dgi}^2 and u_i (eqn 6), the
345 demographic variance of age class 2 was most important (Fig. 3, Table S6, Supporting
346 information). In particular, N_e/N was most sensitive to the demographic variance of
347 males in age class 2, followed by females in the same age class. The total order indices
348 of these two input parameters, σ_{dgm2}^2 and σ_{dgf2}^2 , were significantly different (m_2 : 95% CI
349 [0.513, 0.576], f_2 : 95% CI [0.421, 0.477]; Fig. 3). The total order index for males in age
350 class 1 was not significantly different from females in the same age class (m_1 : 95% CI
351 [0.035, 0.044], f_1 : 95% CI [0.037, 0.046]; Fig. 3). Both σ_{dgf2}^2 and σ_{dgm2}^2 had significant
352 interaction effects ($\Delta S \geq 0.05$) between parameters (Table S6, Supporting information),
353 which might be related to the importance of having individuals of both sexes in age class
354 2, due to their higher reproductive success and the socially monogamous mating system
355 of the house sparrow.

356 In the third level of sensitivity analysis, the response variable was the individual reproductive
357 value W_{ij} for a given sex-age class, and J_{ij} and B_{ij} were input parameters. In all four
358 analyses, fecundity, B , was significantly more important than the other input parameters
359 as none of the 95% CI's overlapped (Fig. 4). Interactions between the input parameters
360 were only found to be significant ($\Delta S \geq 0.05$) for age class 1, which is possibly explained
361 by the importance of surviving to age class 2, which have higher reproductive success.

362 To investigate whether the highest sex-age specific demographic variance of older males
363 on Rånes (Table S4, Supporting information) affected the results, we re-analysed the
364 data when this population was removed. We also re-analysed the data with subsets that
365 excluded populations with less than 4 years of data, the population that went extinct,
366 and the two populations that had undergone selection. These analyses did not change
367 the conclusions from the main sensitivity analyses (results not shown). Nevertheless,
368 including as many populations as possible is important to make realistic assumptions
369 regarding the parameter distributions. We also believe the variation observed in the 13

370 populations reflects true variation as natural populations are founded, go extinct, and
371 undergo strong selection events.

For Review Only

372 Discussion

373 We found that N_e/N was most sensitive to the demographic variance, σ_{dg}^2 (Fig. 2),
374 indicating that variation in individual fitness within years is important for the process of
375 genetic drift in this system. More specifically, N_e/N was most sensitive to the demographic
376 variance of individuals in the terminal age class, especially the male's (Fig. 3). When we
377 decomposed σ_{dgi}^2 into survival and fecundity, it was found that the individual reproductive
378 values, W_{ij} , and implicitly N_e/N (Engen *et al.* 2010), was most sensitive to fecundity in
379 all four sex-age classes (Fig. 4). As the contribution to the total demographic variance
380 of the population show large age-specific variation (Sæther *et al.* 2013), this indicates
381 that age-dependence in demographic traits strongly affect the genetic drift in natural
382 populations.

383 N_e/N and sensitivity analysis

384 The mean values of N_e/N (Table 1) were similar to the mean values estimated in six
385 house sparrow populations in the same study system ($N_e/N = 0.37$, and $N_e/N = 0.50$
386 with $\lambda = 1$, Engen *et al.* 2007b). Furthermore, Engen *et al.* (2010) used the same approach
387 and estimated a $N_e/N = 0.69$ in a growing population of Finnish Siberian jays (*Perisoreus*
388 *infaustus*). N_e/N of different passerines has been found to range from 0.09-0.80, with an
389 average of 0.49 (see O'Connor *et al.* 2006, Table 2). In a review by Frankham (1995), it
390 was found that the average N_e/N in birds and mammals was 0.37 and 0.47, respectively.
391 Hence, our N_e/N ratios (calculated with $T = 1.97$) are well within the range of N_e/N
392 values found in mammals and other birds. There are many methods to estimate N_e/N ,
393 and as shown by Schmeller & Merilä (2007) the estimates can vary a lot between methods.
394 For example, in a previous study we used genetic data and methods to estimate N_e in a
395 set of insular house sparrow populations (some of which were also included in the present
396 study), and found that genetic estimates of N_e in general were similar to, or even larger

397 than N (Baalsrud *et al.* 2014). This pattern was likely due to the genetic consequences
398 that immigration had in the local populations (see also Gilbert & Whitlock 2015). Here
399 we used annual demographic estimates to ensure correct link between N_e and N (Waples
400 2005; Palstra & Fraser 2012), and used only the individuals assumed to be part of the
401 active breeding population, since these are the individuals that ultimately determine N_e
402 (Palstra & Fraser 2012). Importantly, the current study and other studies that use similar
403 demographic methods to estimate N_e/N show that N_e/N can vary between populations
404 of the same species in a restricted geographic area (Table 1; Kaeuffer *et al.* 2004; Cutrera
405 *et al.* 2006; Engen *et al.* 2007b; Schmeller & Merilä 2007). This is also true for studies that
406 have used genetic estimates of N_e and N_e/N (e.g. Palstra & Fraser 2012; Prado-Martinez
407 *et al.* 2013; Baalsrud *et al.* 2014).

408 We found that N_e/N was significantly more sensitive to σ_{dg}^2 than T (Fig. 2). This
409 strongly suggests that variation among individuals in their contribution to future breeding
410 populations, both directly through survival, and indirectly through production of recruits,
411 affects the effective size of populations. It is also caused by the large age-dependent
412 variation in the contribution to the demographic variance found in most populations
413 (Sæther *et al.* 2013). Our result is consistent with other studies, both theoretical (e.g.
414 Nomura 2002; Hedrick 2005) and empirical (e.g. Ardren & Kapuscinski 2003; Kaeuffer
415 *et al.* 2004; Araki *et al.* 2007), where demographic variance and variation in reproductive
416 success was found to influence N_e/N most. Lee *et al.* (2011) showed theoretically that for
417 populations with short generation time (i.e. $T < 3$, as studied here), changes in mating
418 system realized through changes in male reproductive success and hence demographic
419 variance, markedly changed the N_e/N ratio, irrespective of whether or not there were
420 persistent differences in male quality. When demographic variance increased, N_e/N
421 decreased, which is in accordance with our results (Table 1). We used a demographic
422 model to estimate N_e/N , but this ratio has also been estimated by genetic methods
423 in (partly) the same study system (Baalsrud *et al.* 2014). In that study, Baalsrud *et al.*
424 (2014) found that demographic characteristics of the house sparrow populations were able

425 to explain 31-71% of the observed variance in N_e/N based on different genetic estimators.
426 Importantly, sex ratio, which is closely linked to variation in reproductive success and
427 demographic variance, was found to affect N_e/N . Comparing our estimates of σ_{dg}^2 and
428 T with the harmonic mean of the preferred genetic estimator (the LDNE-estimator) by
429 Baalsrud *et al.* (2014) shows a high correlation for σ_{dg}^2 ($r = -0.846$), and a modest
430 correlation for T ($r = 0.185$). The mean value of σ_{dg}^2 found here (1.45, Table 1) is
431 similar to σ_{dg}^2 's found in other bird species with similar life history to the house sparrow,
432 e.g. blue tit (*Cyanistes caeruleus*) ($\sigma_{dg}^2 = 1.70$, Sæther *et al.* 2004) and great tit (*Parus*
433 *major*) ($\sigma_{dg}^2 = 1.14$, Engen *et al.* 2003). It is also worth noting that in the current
434 study, demographic variance was positively correlated with the mean contribution to the
435 next generation, i.e. the asymptotic population growth rate, λ (Table 1). Although the
436 sensitivity of N_e/N to λ could not be evaluated directly as it is not a parameter in the
437 equations used to calculate N_e/N here, the relationship with demographic variance may
438 suggest that the mean contribution of individuals to the next generation has an important
439 role on the effective size of a population.

440 The mean generation time found in our study (Table 1), was lower than the average
441 generation time ($T = 1.97$) found by Jensen *et al.* (2008) in the same study system.
442 Since the age of individual house sparrows can only be determined if they have been
443 marked as nestling or juvenile, and given the 50% annual adult mortality, the true age
444 of most ($\approx 94\%$) individuals is known after 4 years. For the 5 populations with less
445 than 4 years of data, the mean was 1.32 years, while for the 8 populations with more
446 than 4 years of data, the mean was 1.97 years, which equals the value found by Jensen
447 *et al.* (2008) in the same study system. Underestimating T may lead to an upward
448 bias in the estimate of N_e/N , which argues that using the average T of a species may
449 be more appropriate when few years of data is available. Although N_e/N was more
450 sensitive to the demographic variance than to generation time, we found that the latter
451 was far from unimportant. Indeed, generation time is considered one of the important
452 factors affecting the between-life-histories variation in effective population size (Nunney

453 1991, 1993; Caballero 1994). Theoretically, the contemporary ratio N_e/N decreases (or
454 sometimes increases) with increasing generation time, before it approaches a value of 0.5
455 (Nunney 1993; Caballero 1994; Lee *et al.* 2011, but see Waite & Parker 1996). This
456 relationship may be caused by the reduction in variance in reproductive success, and/or
457 change in other life history traits often accompanied by an increase in generation time
458 (Waples *et al.* 2013). Since most of these findings are based on different life histories
459 aligned along the fast-slow continuum, they encompass a much greater span of generation
460 time than experienced within most species. Actually, a change in T within the limits of
461 our values is not expected to create great changes (> 0.1) in N_e/N (Nunney 1993; Lee
462 *et al.* 2011), unless there are permanent differences in the mating success of individuals
463 (Lee *et al.* 2011). Taking this into consideration, N_e/N was almost surprisingly sensitive
464 to variation in generation time. This may be explained by the use of population specific
465 estimates of T to define the distribution of which samples were taken in the first sensitivity
466 analysis ($T \sim N(1.718, 0.399)$; Table S3, Supporting information). Due to the assumption
467 that all adults were 1 year old in their first year of capture, this distribution most likely
468 possessed a larger variance than the true variance in house sparrows, which could explain
469 the relatively high sensitivity of N_e/N to variation in T (Fig. 2).

470 In the second analysis of N_e/N , the demographic variances of the terminal age class were
471 found to be of higher importance for the ratio N_e/N than the demographic variances of
472 the first age classes and the stable sex-age distributions (Fig. 3). Particularly, N_e/N
473 was sensitive to the demographic variance of older males. The high estimated variance
474 of σ_{dgi}^2 in males (Table 2) was due to a few values, especially that of older males on
475 Rånes (Table S4, Supporting information). Removal of this value reduced the estimate
476 variance of older males (m_2 : 0.89), but it did not affect the outcome of the sensitivity
477 analysis. This shows that the analysis was not strictly dependent on the level of variance
478 in the data, and that N_e/N was significantly more sensitive to older males than females,
479 even when their estimated variances were almost equal. Older males was found to
480 be the age class that affects N_e/N most, and this is consistent with other studies on

481 species with similar life history and mating system (e.g. Green 2001; Geslin *et al.* 2004).
482 Given that mating system (Nunney 1993; Nomura 2002; Lee *et al.* 2011) and life history
483 parameters (Orive 1993; Waples *et al.* 2011, 2013) are important determinants of effective
484 population size, the sex-age class specific demographic parameters with largest effect,
485 should probably vary accordingly. For instance, in many species senescence negatively
486 affects reproductive output (e.g. the common lizard (*Lacerta vivipara*), Richard *et al.*
487 2005; and European badgers (*Meles meles*), Dugdale *et al.* 2011), suggesting that N_e/N
488 would be more sensitive to young or middle age-classes.

489 The age-class of highest importance for N_e/N will depend on the sampling scheme, that
490 is, whether a population is sampled just before or after reproduction. For instance, using
491 post-reproduction census in populations with high fecundity and type III survival curves
492 (high mortality in early life stages), we could expect N_e/N to be most sensitive to the
493 survival to adulthood by younger age classes (Gaggiotti & Vetter 1999). However, using
494 pre-reproduction census, such life histories often imply very large variance in reproductive
495 success among adults (in terms of production of recruits) which is one of the main causes of
496 low N_e/N ratios in such species (Hedgcock 1994; Hedgcock & Pudovkin 2011). Hence, if
497 sampling is performed right before reproduction (as in this study), survival to recruitment
498 will be included in the variance in reproductive success by the adult age-class(es), in which
499 case we could expect the result to be similar as in the current study.

500 In the sensitivity analyses of the individual reproductive values, all four sex-age classes
501 were most sensitive to fecundity, implying that fecundity was important for N_e . Accordingly,
502 fecundity has also earlier been found to be one of the main factors that affect N_e (Caballero
503 1994; Frankham *et al.* 2010), and variation in fecundity should generally decrease the
504 effective size of a population (Nunney 1996). Effects of fecundity and variance in reproductive
505 success on effective population size and genetic drift have been found in a diverse set of
506 species (e.g. many marine organisms, Hauser *et al.* 2002). Here, because we considered
507 production of recruits, the fecundity measures includes a survival component by offspring.

508 Although survival of adults were of less importance than adult fecundity, the survival rates
509 of juveniles to recruitment may be essential for this species' genetic diversity. Populations
510 at different points in the fast-slow continuum may exhibit different trade-offs between
511 survival and reproduction, in which current reproduction may come at the cost of either
512 future reproduction (slow species) or survival (fast species) (Ricklefs 2000; Bleu *et al.*
513 2016). This may suggest that the ratio N_e/N could be more sensitive to adult survival
514 relative to fecundity or variance in reproductive success in populations with slower life-histories.
515 Moreover, a negative effect on N_e by increased variance in reproductive success may be
516 compensated for by delayed maturity (Broquet *et al.* 2009), but this may again depend
517 on the juvenile survival rates (Lee *et al.* 2011).

518 **Demographic parameters affecting N_e/N**

519 Our dataset included both a recently founded population, a population that went extinct,
520 and two artificially selected populations (Table 3), thus the range for each of the parameters
521 was expected to be large, but biologically reasonable. By including these four populations,
522 our results may reflect the relative sensitivity of N_e/N to different demographic histories
523 which may occur both in isolated populations, and in dynamic metapopulations. The
524 habitat quality varied among the 13 populations, and they differed in quality of nesting
525 sites, food availability and shelter (Jensen *et al.* 2013). It is likely that this resulted in
526 differences among the populations in demography and life-history, e.g. population growth
527 rates, mean population sizes, and age structure (Table 3).

528 Our result shows that the reproductive success of breeders increase with age for both sexes,
529 and this is consistent with several other studies of mammals (e.g. European badgers,
530 Dugdale *et al.* 2011), several bird species (e.g. Rockwell *et al.* 1993; Forslund & Pärt
531 1995; McCleery *et al.* 2008), and fish species (e.g. Hixon *et al.* 2014; Waples 2016). Many
532 studies on life history parameters only consider female reproductive success, but there are
533 some exceptions. In birds, examples include the Australian brown thornbills (*Acanthiza*

534 *pusilla*), where only males improved their reproductive success with age (Green 2001),
535 in French bluethroats (*Luscinia svecica*) both sexes improved, but males improved most
536 (Geslin *et al.* 2004), and in North-American house sparrows, males and females improved
537 their reproductive success equally with age (Hatch & Westneat 2007).

538 Increased feeding of chicks by older males, especially in the first days after hatching, is
539 one of the reasons males have the highest increase in reproductive value with age in brown
540 thornbills and bluethroats (Green 2001; Geslin *et al.* 2004). In house sparrows there is
541 a positive relationship between feeding rates and visible badge size in males (Ringsby
542 *et al.* 2009), and both total and visible badge size has been shown to increase from age
543 class 1 to age class 2 (Jensen *et al.* 2006). Furthermore, there is a positive relationship
544 between badge size, mating success and recruit production (Jensen *et al.* 2004, 2008).
545 The relationship between age and reproductive success in males, probably explain why
546 the demographic variance in older males was the parameter N_e/N was most sensitive to
547 (Fig. 3, Table S6, Supporting information).

548 Survival was also identified as an important factor for W_{ij} , and thus N_e/N (Fig. 4). The
549 interaction effect of the two parameters was only significant ($\Delta S \geq 0.5$) in age class 1
550 (Table S7, Supporting information), and it might be related to the importance of surviving
551 to age class 2, where on average, individuals have higher reproductive success (Table 2).
552 Accordingly, we found that age class 2 of both sexes had the highest mean age-specific
553 reproductive values, v_i (Table 2), which reflect the expected future contribution from
554 an individual in a specific sex-age class to the long-term population growth (Keyfitz &
555 Caswell 2005). Three of the estimated parameters were from the population projection
556 matrix, \mathbf{I} (eqn 2): the asymptotic population growth rate, λ , the reproductive values
557 of the sex-age classes, v_i , and the stable sex-age distribution, u_i . The eigenvector v_i
558 was fixed at the average values for the dataset (Table 2) and thus not evaluated in the
559 sensitivity analysis. The other eigenvector u_i , is part of the definition of N_e/N (equations
560 1 and 6) and was included as a parameter in the sensitivity analysis, but was not found

561 to be of significant importance (Figs. 3 and Table S6, Supporting information). This
562 might be because it is truly non-important for variation in N_e/N , or simply because the
563 importance is not observable for a population at equilibrium. It would be possible to do
564 a perturbation analysis of the parameter to see if an increase in variance would affect the
565 outcome of the sensitivity analysis, but as we used the global variance-based method, an
566 increase in conditional parameter variance would most likely not change the result (see
567 section *Sensitivity analysis* in *Methods*).

568 The model used to estimate N_e/N in the house sparrow populations rest on a few
569 simplifying assumptions, particularly the assumptions of density independent vital rates
570 and isolated populations. We do not believe that the former should be of great concern
571 in the current study as there is little evidence for a relationship between ΔN and N in
572 any of the viable populations with more than 4 years of data (although at Gjerøy, there
573 was a slight relationship, (linear regression: $\beta = -0.731 \pm 0.309, p = 0.050$)). Also, in
574 the study system the environment fluctuates considerably between years, which seems
575 to be an important factor affecting population size, particularly through its effects on
576 juvenile survival probabilities (Ringsby *et al.* 1999). This effect is accounted for in the
577 demographic variance. The second assumption (no gene flow) is violated for most of the
578 populations and will affect the effective population size and rate of genetic drift if migrants
579 successfully produce recruits. Migration has previously been shown to affect genetic
580 estimators in the same study system, causing them to give higher N_e estimates than
581 the demographic estimator (Baalsrud *et al.* 2014). This may be attributed to the effect
582 successful migrants can have on the genetic stochasticity compared to the demographic
583 stochasticity. The demographic effects of an immigrant will be captured by our method
584 through the fecundity and survival measures, probably causing a reduction in the estimate
585 of demographic N_e since immigrant males seems to have lower fitness in the study system
586 (Pärn *et al.* 2009). However, it will not capture the direct (positive) effect a reproducing
587 immigrant may have in slowing the rate of genetic drift. On the other hand, the genetic
588 estimators will most probably be biased upwards by immigration in this study system

589 (see Baalsrud *et al.* 2014 for further discussion), which makes it likely that our estimates
590 of N_e/N in the different populations are somewhat conservative, but not considerably
591 biased due to this assumption.

592 Management

593 In population management, it is of great importance to determine factors that affect
594 N_e . The demographic model we used to estimate N_e/N is based on annual demographic
595 data, which is mainly affected by demographic stochasticity, but also by selection, causing
596 variation in survival and reproductive success between individuals within a year. Nevertheless,
597 it is important to acknowledge that N_e/N will be affected by environmental stochasticity
598 in the long-run (Engen *et al.* 2010). As a consequence, it is important to keep in mind that
599 N_e/N is affected not only by the species specific life history (Lee *et al.* 2011) and mating
600 system (Nunney 1991, 1993; Nomura 2002; Engen *et al.* 2003; Kaeuffer *et al.* 2004), but
601 also external factors such as human activities (Therkildsen *et al.* 2010).

602 Depending on the management goals for the species or population in question, a manager
603 might want to improve N_e or N_e/N . Given a specific population size, N_e should be
604 maximised to be as close to N as possible to minimise the genetic stochasticity in the
605 population. There are many ways to achieve this, e.g. manipulation of the sex ratio
606 (Caballero 1994; Frankham *et al.* 2010), limit fluctuations in N (Kalinowski & Waples
607 2002; Engen *et al.* 2005b), and reduce variance in the mean family size (Manning *et al.*
608 2000; Gayet *et al.* 2016), as little to no variance will give a N_e that is larger than N
609 (Wright 1984; Frankham *et al.* 2010). Under random mating, the number of inbreeding
610 events is independent of N , and the increase in N_e due to inbreeding avoidance diminishes
611 as N increases (Caballero & Hill 1992). In other words, for managers of small populations,
612 inbreeding avoidance is important to increase N_e , but for larger populations, the efforts
613 to maximise N_e should be focused elsewhere. However, in most management situations
614 it is N that is observed and manipulated. Due to problems related to small population

615 sizes, such as high influence of demographic stochasticity and drift that increase the
616 probability of extinction (Engen *et al.* 2005a; Legendre *et al.* 2008), it is therefore desirable
617 to maximise N as well as N_e . The relative value of N_e/N can be used to assess population
618 persistence based on influence of demographic, genetic and ecological factors (Kalinowski
619 & Waples 2002; Palstra & Fraser 2012). Of course, N_e/N can be numerically increased by
620 reducing N (Kuparinen *et al.* 2016), but as the two are strongly correlated, a reduction in
621 N will also reduce N_e , leading an unchanged, or even reduced ratio. As small populations
622 can have a high ratio, and enormous populations can have tiny ratios (see Hauser *et al.*
623 2002), its value is only informative in combination with information on N . However,
624 the ratio is expected to be more predictable in species with low variance in reproductive
625 success (Frankham 1995; Frankham *et al.* 2014), but the relationship between N_e and N
626 is still not well enough known to make inferences based on N_e or N alone (Luikart *et al.*
627 2010). For managers to extrapolate from an estimated N_e to N , they have to consider
628 the life history of the species in question. For instance, Waples *et al.* (2013) found that
629 up to half the variation in N_e/N can be explained by age at maturity and adult lifespan.
630 Combined with data on cross-generational fluctuations in N , it can provide more precise
631 extrapolations and informative N_e/N estimates (Frankham *et al.* 2014).

632 Our sensitivity analysis suggest that for species with life histories resembling the house
633 sparrow, management and conservation actions should focus on the demographic stochasticity
634 of older individuals, especially males. It is important to keep in mind that different
635 parameters can be important for a population depending on the time-scale (e.g. age
636 structure is most important in the short-term, Waples 2010). To increase N_e , σ_{dgm2}^2 must
637 be reduced through manipulation of fecundity, but also survival (Fig. 4d, Table S7,
638 Supporting information). Specific management actions in this study system would be to
639 maintain suitable habitat, which often are dairy farms. It could also be possible to decrease
640 variance in reproductive success by increasing chick survival to recruits, e.g. by increasing
641 the number of nest boxes and subject them to flea removal, have supplemental feeding
642 stations and remove predators such as feral cats. This study shows, as others before (e.g.

643 Taylor *et al.* 2012), that sensitivity analysis provides a useful, and perhaps vital tool to
644 assure the desired outcome in management and conservation. Implementing management
645 action without such information could result in ineffective (Carter *et al.* 2007; Cook *et al.*
646 2010; Walsh *et al.* 2012), or even devastating effects (e.g. supplementary feeding of female
647 kakapos (*Strigops habroptilus*), Robertson *et al.* 2006) of management actions.

648 We believe incorporation of empirical data that reflects the expected rate of loss of
649 genetic variation through genetic drift, such as N_e and N_e/N , together with traditional
650 knowledge-based management (Cook *et al.* 2010), will be important for conservation
651 and management in the future. This provides an area where sensitivity analyses can
652 be especially useful. For a manager, sensitivity analyses indicates the critical parameters
653 in a model (Tuljapurkar & Caswell 1997), and this insight can contribute to more effective
654 and better decisions (Cook *et al.* 2010). In absence of data, or lack of resources to collect
655 annual and individual data, it is possible to use samples to estimate the demographic
656 parameters (Engen *et al.* 2010). The importance of number of generations and years of
657 data was not evaluated in this study, but to be able to maximize the output of management
658 efforts, it should be further studied.

659 Conclusion

660 A population's resilience and vulnerability to extinction is determined by N and N_e , and
661 our results provide knowledge on which demographic parameters that are important for
662 the rate of genetic drift in natural populations. Our study also shows the value of applying
663 sensitivity analyses in population management, as they might identify where efforts
664 and resources should be focused. Due to the relatively extensive range of demographic
665 characteristics of the populations in this study, the results may be relevant to other
666 isolated, fragmented, and perhaps threatened populations and species with similar life
667 histories and demography.

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993 **Data accessibility**

994 Data will be submitted to dryad when this manuscript is accepted for publication.

For Review Only

995 **Author contributions**

996 M.W.S. wrote analysis scripts, performed parentage and sensitivity analyses, and wrote
997 the paper with A.M.M. and H.J. Both H.H. and T.K. contributed with advice and inputs
998 to the statistical analyses and the parentage analysis. B.E.S., H.J. and T.H.R conceived
999 the research question and acquired funding. All authors contributed to the fieldwork and
1000 comments on the manuscript.

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1001 Tables

Table 1: Population level parameters for each of the populations.

Population	N_e/N (fix. T) ^a	N_e/N (pop. T) ^b	T	σ_{dg}^2	λ
Aldra	0.36	0.30	2.35	1.42	1.05
Gjerøy	0.40	0.36	2.19	1.28	0.91
Handnesøy	0.56	0.74	1.49	0.90	0.79
Hestmannøy	0.42	0.42	1.95	1.22	0.79
Indre Kvarøy	0.47	0.48	1.94	1.09	0.79
Leka	0.20	0.22	1.75	2.55	1.07
Linesøya	0.82	1.35	1.20	0.62	0.74
Løkta	0.69	1.11	1.23	0.74	0.60
Nesøy	0.54	0.44	2.39	0.95	0.88
Rånes	0.19	0.30	1.25	2.64	1.03
Røvass	0.60	0.83	1.44	0.85	0.77
Vega	0.17	0.22	1.55	2.98	1.17
Ytre Kvarøy	0.31	0.38	1.63	1.62	0.72
Mean values	0.44	0.55	1.72	1.45	0.87

T and σ_{dg}^2 , population specific generation time and demographic variance, respectively
 λ , asymptotic population growth rate from the projection matrix l (eqn 2)

^a N_e/N calculated with $T = 1.97$ (Jensen *et al.* 2008)

^b N_e/N calculated with the population specific T

Table 2: Sex-age class specific parameters averaged across all populations.

Parameter	i^a	Values			
		Min	Mean	Max	Var
σ_{dgi}^2	f_1	0.62	1.35	2.73	0.38
	f_2	0.70	1.67	3.19	0.87
	m_1	0.52	1.27	3.00	0.42
	m_2	0.45	1.54	3.75	1.26
u_i	f_1	0.05	0.20	0.31	4.62×10^{-3}
	f_2	0.05	0.26	0.46	9.25×10^{-3}
	m_1	0.05	0.20	0.31	4.62×10^{-3}
	m_2	0.18	0.34	0.85	2.66×10^{-2}
v_i	f_1	0.59	0.90	1.13	2.46×10^{-2}
	f_2	0.58	1.06	1.44	3.97×10^{-2}
	m_1	0.60	0.90	1.13	2.44×10^{-2}
	m_2	0.85	1.04	1.19	1.20×10^{-2}
J_{ij}	f_1	0.00	0.47	1.00	0.25
	f_2	0.00	0.49	1.00	0.25
	m_1	0.00	0.49	1.00	0.25
	m_2	0.00	0.50	1.00	0.25
B_{ij}	f_1	0.00	0.83	14.00	1.74
	f_2	0.00	0.94	8.00	1.99
	m_1	0.00	0.69	11.00	1.44
	m_2	0.00	0.88	9.00	1.81

Mean, variance, minimum and maximum values are given

σ_{dgi}^2 , sex-age specific demographic variance

u_i and v_i , stable sex-age distribution and reproductive values, respectively

J_{ij} and B_{ij} , individual survival and fecundity, respectively

^a sex-age classes

Table 3: Overview of study populations and their mean population sizes, N .

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 Fig. 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 review)

^e Went extinct in 2000 (Ringsby *et al.* 2006)

1002 Figures

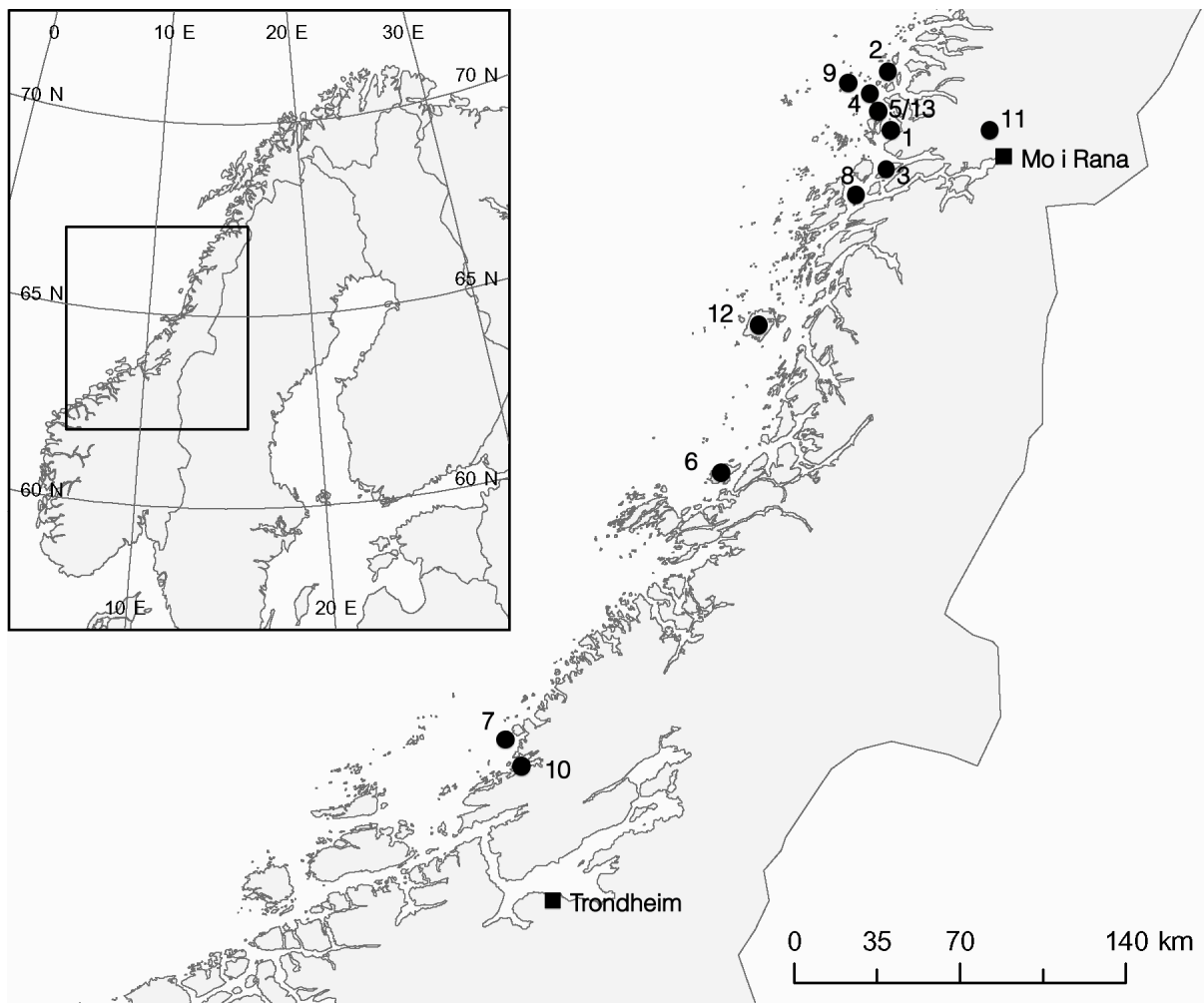


Figure 1: The 13 populations in the dataset are spread out along the Norwegian coast, from Trondheim (63°N, 10°E) in the south, to near Mo i Rana (66°N, 13°E) in the north (also see Table 3).

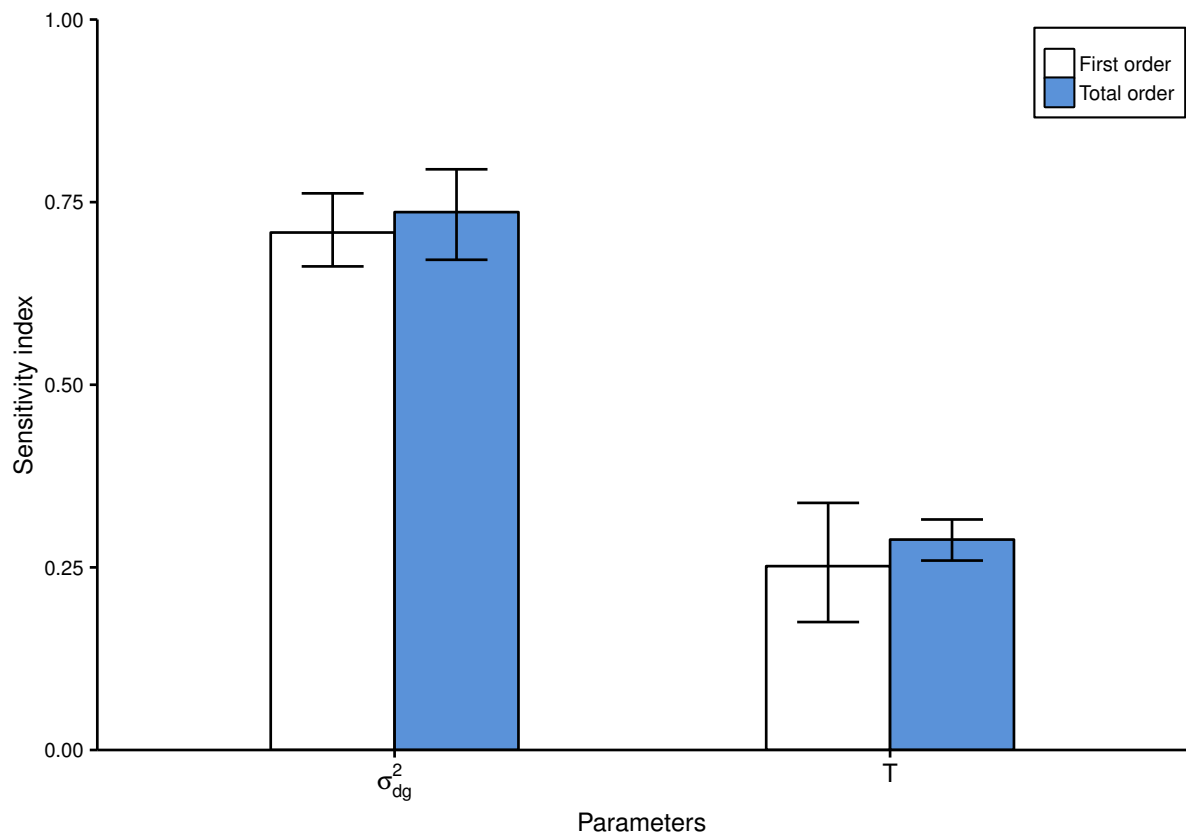


Figure 2: Results from the variance-based sensitivity analysis of N_e/N , with demographic variance, σ_{dg}^2 , and generation time, T , as input parameters, shown by first, S_p , and total order, S_{Tp} , sensitivity indices. The error bars show the 95% confidence intervals of the indices.

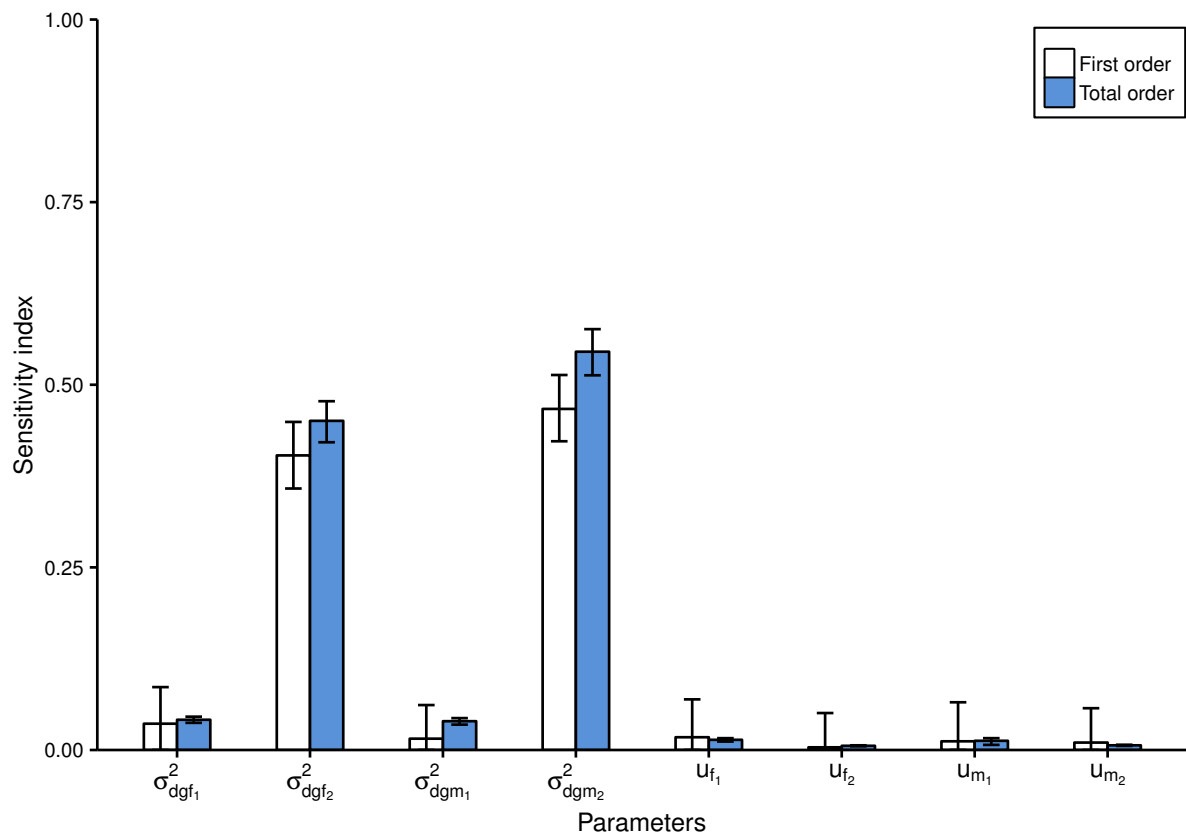


Figure 3: Results from the variance-based sensitivity analysis of N_e/N , where $T = 1.97$ and with sex-age class specific demographic variance, σ_{dgi}^2 , and stable sex-age distribution, u_i , as input parameters, shown by first, S_p , and total order, S_{Tp} , sensitivity indices. The error bars show the 95% confidence intervals of the indices

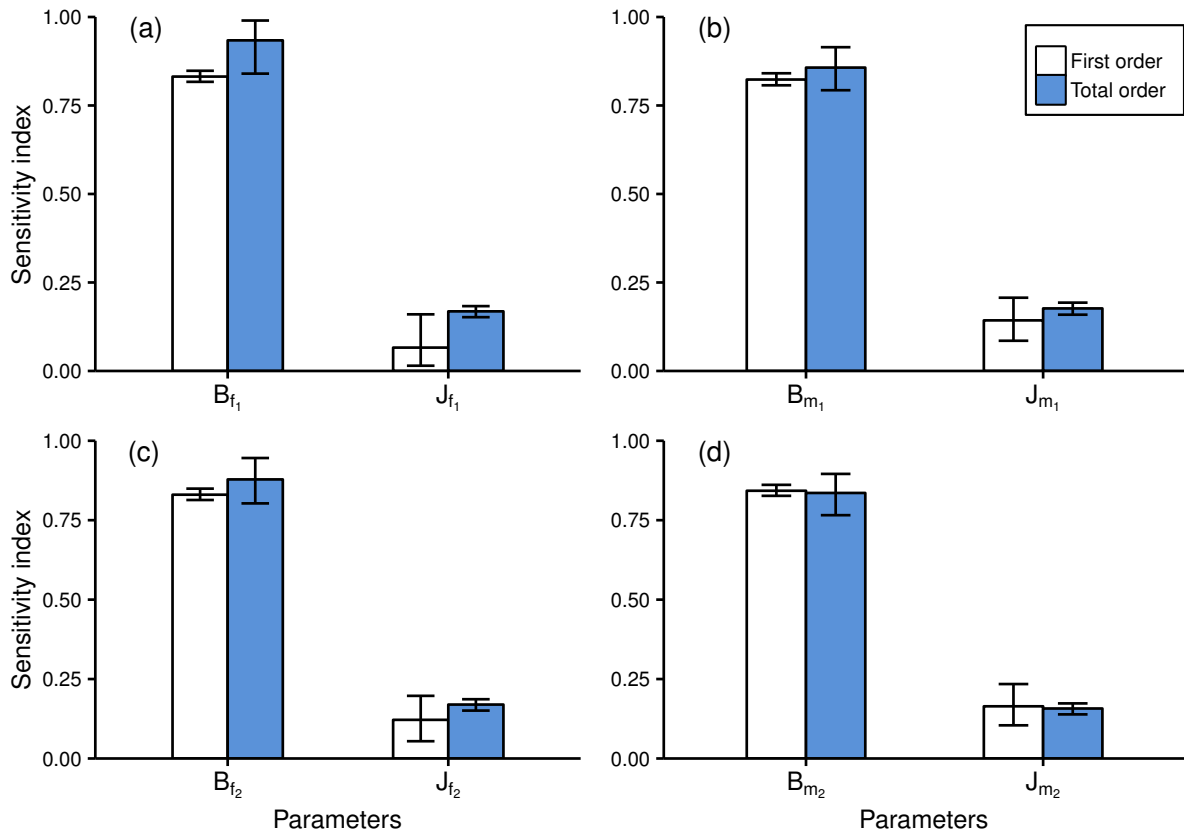


Figure 4: Results four variance-based sensitivity analyses of individual reproductive value, W_{ij} , with fecundity, B , and survival, J , as input parameters. The panels (a) and (b) show the results from females and males in age class 1, respectively, while panels (c) and (d) show the results from 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.