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Population characteristics and estimates of effective population size in a house sparrow metapopulation

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ABSTRACT

Effective population size (N_e) is a fundamental concept for understanding evolutionary dynamics and can be defined as the size of an ideal Wright-Fisher population in which the rate of genetic drift is the same as in the observed population. Natural populations are not ideal so that N_e is often < N_c. A low N_e can lead to inbreeding depression and reduced potential for adaptive evolutionary change in a population, thus it is essential to know N_e for threatened populations as N_e influences their probability of long-term survival. N_e can be estimated using genetic or demographic data. In this study I compared four different genetic estimators (LDNE, ONeSAMP, MLNE and CoNe) and a demographic estimator based on Engen et al. (2005) using data from a natural house sparrow metapopulation. These estimators all estimate N_e reflecting the current rate of genetic drift. How N_e related to N_c was also examined. All four genetic estimators seemed to be upwardly biased. However, LDNE often produced estimates in the expected range (N_e < N) and thus appeared to be less biased. Genetic N_e was much higher than demographic N_e, probably due to the greater effect of immigration on genetic than demographic processes. To understand how characteristics of natural populations may affect the rate of genetic drift it is important to examine what influence the N_e/N_c-ratio. Thus, I investigated whether population characteristics such as population size, sex ratio, immigration rate, variance in population size and population growth rate explained variation in the N_e/N ratio for the different genetic estimators. A general result was that the immigration rate had a positive effect on the N_e/N_c-ratio. The apparent upward bias of genetic N_e estimates and the positive effect of immigration rate on N_e/N_c-ratio suggest that gene flow between subpopulations within the study metapopulation was of significant importance for the local rate of genetic drift. Genetic estimators of N_e seem like promising tools. However, if no knowledge of the ecology of the population in question exists, N_e should be interpreted cautiously. When assumptions underlying estimators are violated this can lead to erroneous conclusions about genetic processes in the population.

SAMMENDRAG

Et fundamentalt begrep innenfor biologi er effektiv bestandsstørrelse (N_e), definert som den bestandsstørrelsen der genetisk drift skjer like raskt som i en tilsvarende ideell Wright-Fisher bestand. Potensielle konsekvenser av en lav N_e er innavlsdepresjon, samt en redusert evne til evolusjonære tilpasninger og dermed redusert overlevelse av bestanden i fremtiden. Man kan bruke enten demografiske eller genetiske data for å estimere N_e. Her ble data fra en naturlig oppsplittet gråspurvbestand, fordelt på 15 ulike øyer, brukt til å sammenlikne fire genetiske N_e-estimatorer (LDNE, ONeSAMP, MLNE, CoNe) og en demografisk estimator basert på fremgangsmåten i Engen et al. (2005). I tillegg ble forholdet mellom N_e og observert bestandsstørrelse (N_c) undersøkt. Alle de genetiske estimatorene ga generelt verdier høyere enn det som var forventet ut ifra teorien ($N_e<N_c$), med unntak av LDNE som ofte ga estimater lavere enn N_c. Genetisk N_e var mye høyere enn demografisk N_e, antakeligvis fordi immigranter har større effekt på genetiske enn demografiske prosesser. For å forstå om demografiske parametere for en bestand påvirker genetisk drift er det viktig å undersøke hva som kan påvirke N_e/N_c-forholdet. Derfor undersøkte jeg om deler av variasjonen i N_e/N_c for hver enkelt estimator kunne forklares ut ifra demografiske parametere slik som bestandsstørrelse, kjønnsforhold, immigrasjonsrate, varians i bestandsstørrelse og bestandsvekst. Et generelt resultat var at immigrasjonsrate hadde en positiv innvirkning på N_e/N_c. Dette antyder at genflyt mellom lokale bestander i dette øy-systemet har en viktig betydning for hvor raskt genetisk drift skjer. Genetiske estimatorer av N_e er nyttige verktøy, men fordi de ofte overestimerer bør man være forsiktig med å bruke estimatene som beslutningsgrunnlag i forbindelse med forvaltning.

INTRODUCTION

Effective population size (N_e) is a fundamental concept in evolutionary biology. N_e determines the expected rate of random genetic drift in a population, the increase through time in the degree of inbreeding and the loss of selectively neutral heterozygosity. It also affects the evolutionary effects of selection through influencing the fixation probabilities of advantageous, as well as deleterious mutations (Wright 1931; Crow and Kimura 1970; Lande 1976; Ewens 1982). N_e is defined as the size of an ideal Wright-Fisher population in which the rate of change in heterozygosity or allele frequencies is the same as in the observed population (Wright 1931). Thus, it is the size of an idealized population experiencing the same amount of inbreeding or genetic drift as the population in question (Kimura and Crow 1963). An ideal Wright-Fisher population is a population with discrete generations, diploid individuals, sexual reproduction, and where the population size is constant across generations, there is no migration, mating is random, there are no mutations, the sex ratio is 1:1, there is no selection and the average number of recruits produced by each individual is Poisson distributed with a mean and variance of 2 (Fisher 1930; Wright 1931). Usually in natural populations a number of these assumptions are violated, resulting in $N_e << N$ (Wright 1931; Wright 1938; Frankham 1995; Nunney 1995; Vucetich et al. 1997).

In an infinite population not exposed to selection and with no mutations or migration, the allele and genotype frequencies will not change from one generation to another, resulting in a constant level of genetic variation over time. Natural populations are on the other hand finite in size, and thus allele and genotype frequencies will change even in the absence of selection through random sampling errors known as random genetic drift (Crow and Kimura 1970; Wang 2005). Over time genetic variation will decrease unless introduced by mutation or immigration, mutations being the ultimate source of genetic variation (Nei 1987). A general result from theoretical population genetic models is that genetic variation is lost at the rate of $1/(2N_e)$ per generation. Consequently, over time neutral genetic variation is lost in a population of finite size at an exponential rate roughly described by the following equation:

$$\frac{H_t}{H_0} = \left[1 - \frac{1}{2N_e}\right]^t \sim e^{-t/2N_e} \qquad (1)$$

where H_t is the heterozygosity at generation t and H_0 is the original heterozygosity (Crow and Kimura 1970). This equation has also been shown to apply to additive genetic variation (Frankham 1996). In addition, N_e determines the relative influence of natural selection compared to genetic drift; if N_e is sufficiently small then advantageous mutations may be lost and deleterious mutations may become fixed in the population, due to chance effects (Kimura 1983; Otto and Whitlock 1997; Small et al. 2007; Ellegren 2009).

N_e is thus a key parameter to understand the viability of endangered populations and evolution in small populations (Frankham 1996; Frankham 2010). One advantage of using N_e instead of the census size (N_c) is that N_e allows for the measuring of the strength of genetic drift across all real populations with different life histories using a common reference (Hare et al. 2011). More importantly, population genetic theory relating to population size is dependent on N_e and not N_c (Charlesworth 2009). Given that the rate of genetic drift is inversely proportional to effective population size (eqn. 1), populations with small N_e risk losing genetic variation at a greater rate than new variation is introduced to the population. This has the short term effect of reducing the average fitness in the population due to inbreeding (mating between biological relatives) and the long term effect of reducing the population's evolutionary potential (Franklin and Frankham 1998; Willi et al. 2006). Inbreeding depression is a reduction in fitness accompanying inbreeding, and can significantly increase the extinction probability of small populations (Charlesworth and Charlesworth 1999; Willi et al. 2006; Evans and Sheldon 2008). The reason for this is believed to be that inbreeding leads to increased homozygosity, increasing the probability of expressing recessive deleterious alleles (Charlesworth and Charlesworth 1987; Charlesworth and Charlesworth 1999). Empirical studies do indeed show that endangered populations have lower genetic variation on average than non-endangered populations, and this is related to small population size (Frankham 1996). Thus, it is essential to know the effective population size of endangered populations or species, so that the importance of negative genetic effects mentioned above can be evaluated and minimized if necessary and possible. For instance, the effective population size can be maximized by artificially increasing gene-flow or carrying out strict breeding regimes (Templeton and Read 1984; Schwartz et al. 2007; Palstra and Ruzzante 2008; Hedrick and Fredrickson 2010).

Depending on which aspect of genetic drift is considered, there are different ways of defining N_e (Crow 1954; Crow and Denniston 1988), the two most commonly used being the inbreeding N_e (N_{el}) and the variance N_e (N_{eV}). The various definitions of N_e have different properties and implications for further interpretation. N_{el} is used to predict the rate at which heterozygosity is lost, whereas N_{eV} reflects the variance of change in allele frequency from one generation to the next. N_{el} depends more on the number of individuals in the parent generation, whereas N_{eV} depends more on the number of offspring (Kimura and Crow 1963). Furthermore, N_{eV} is more sensitive to reductions in population size, and thus more relevant for monitoring endangered species (Schwartz et al. 2007). However, N_{el} and N_{eV} should be equal in a single isolated population of constant size (Kimura and Crow 1963).

In addition to the conceptual varieties of N_e, there are many different methods of estimating N_e, which can be roughly divided into two categories; those using demographic ecological data and those using genetic markers (Anderson and Garza 2009). The demographic approach gives an estimate reflecting the current rate of genetic drift, but most methods (e.g. Felsenstein 1969; Hill 1972; Engen et al. 2005) require extensive data on ecological parameters such as population size, variance in reproductive success, sex ratio etc. Such data

are rarely obtainable for most natural populations (Nunney and Elam 1994). This is why considerable effort has been put into developing estimators based on genetic data to estimate N_e in recent years. This development has been fueled by a revolution in the advancement of techniques to efficiently genotype individuals in a population on polymorphic molecular markers (Anderson and Garza 2009).

Estimators based on genetic data can be based on a single sample (in time), which gives a N_{el} estimate, or multiple samples spaced by one or more generations (temporal method), which gives a N_{eV} estimate (Waples and Yokota 2007). The temporal method is generally considered to be superior to single sample methods (Waples 2010). However, the disadvantage of the temporal method is that it requires samples separated by several generations, which for some populations (e.g. mammals, birds and perennial plants) can be many years or even decades (Waples 2010). The disadvantage with most of the genetic methods is that they assume closed populations with random mating and discrete generations. For more extensive reviews on genetic N_e estimators, see Nunney and Elam (1994); Wang (2005); Anderson and Garza (2009); Charlesworth (2009); and Luikart et al. (2010).

Because of the fundamental importance of N_e in conservation, population genetics and evolutionary biology knowledge of its size, and in particular how large N_e in general is relative to N_c is needed. Hence, the ratio of effective population size to census size (N_e/N_c) is interesting to biologists. If N_e/N_c is known this has several practical applications. Firstly, N_e or N_c can be inferred by knowing the other if the N_e/N_c-ratio is known. This is however only appropriate if the N_e/N_c-ratio is relatively constant over time and across populations, which may not be valid for some species (Engen et al. 2007; Luikart et al. 2010). Secondly, one can use the N_e/N_c-ratio to determine how different population characteristics influence the rate of genetic drift and in this way increase our understanding of this important process (Kalinowski and Waples 2002). Third, it can be used to develop management strategies to reduce the rate of genetic drift and retain genetic variation (Araki et al. 2007; Tanaka et al. 2009). It is also imperative to compare genetic estimators of N_e, because there are many of them in the scientific literature, and they all aim at measuring the same quantity, N_e. However, they differ in what they actually measure and in how well they measure it (Anderson and Garza 2009). Erroneous estimates may lead to wrong conclusions regarding evolutionary processes (Leberg 2005). Having quantitative knowledge of the correspondence between various genetic estimators is therefore important. Such knowledge will for instance enable assessing the reliability of using non-invasive sampling methods (DNA samples from hair, feces, feathers etc.) to estimate N_e for endangered populations or species, where extensive ecological studies are unfeasible (Pauli et al. 2010). If N_e is overestimated and the resulting genetic effects of a lower N_e are ignored the risk of extinction could be underestimated and inappropriate management strategies implemented (Frankham 2005).

In this study data from a long-term house sparrow metapopulation study at Helgeland, Norway, was used to estimate N_e with four different genetic estimators. This dataset is exceptional because of its metapopulation structure (the main study system consist of 18 different island populations) and timespan (data has been collected from 1993 to 2011 in the main study system). Because a large proportion of all birds on the study islands are individually marked and followed from hatching to death, and individual genotypes exist at 15 presumably neutral molecular markers, individual information on key parameters such as sex, survival, reproductive success and dispersal is available in this study system. This provides population level information such as census population size (N_c), sex-ratio, migration rates, and inter- and intra-individual genetic variation (Jensen et al. 2003; Jensen et al. 2004; Husby et al. 2006; Engen et al. 2007; Jensen et al. 2007; Jensen et al. 2008; Pärn et al. 2009), which can be used to estimate the current rate of genetic drift in a population. The study system thus presents a unique opportunity to not only compare different genetic estimators of N_e, but also examine which population characteristics that are most important in explaining any deviation between N_e and N_c (i.e. N_e/N_c). Furthermore, it allows comparing of genetic estimates strongly affected by the history of the population with the current N_e based on demographic data. I used two single sample estimators; the linkage disequilibrium method LDNE (Waples and Do 2008; Waples and Do 2010) and an approximate Bayesian computation (ABC) approach ONeSAMP (Tallmon et al. 2008). Two temporal estimators were also used; a pseudo-maximum-likelihood method MLNE (Wang 2001; Wang and Whitlock 2003) and a coalescent based approach CoNe (Berthier et al. 2002; Anderson 2005). These methods all give estimates of N_e on a contemporary time scale.

My objectives are to examine the congruence of different genetic estimators of N_e by comparing estimates from different methods based on the same data set. I will then relate the different estimates of N_e to the actual population size (N_c), and examine whether different population characteristics can explain the difference between genetic estimates of N_e and N_c in subpopulations within this metapopulation. Finally, I will examine if N_e based on analyses of genetic data agrees with demographic estimates of N_e (Engen et al. 2007). In this way, I can explore whether differences in genetic estimates of N_e strongly affected by processes affecting genetic variation over long periods of time can be explained by short-term variation in population dynamics known to affect demographic estimates of N_e.

MATERIALS AND METHODS

Study system

The main study area consisted of eighteen islands along the coast of Northern Norway. The northernmost island was Myken (66°46´N, 12°29´E) and the southernmost island was Sleneset (66°22´N, 12°36´E), and the whole archipelago covered approximately 1600 km^2. These eighteen islands were populated continuously or periodically by house sparrows during the study period (1993-2009; Table A3). Out of these eighteen islands, three were excluded due to insufficient sampling, leaving fifteen islands included in this study (Fig. 1). The house sparrow populations on ten of the islands (Gjerøy, Hestmannøy, Indre Kvarøy, Lovund, Lurøy, Myken, Nesøy, Onøy, Sleneset and Træna) persisted throughout the study period. Aldra was colonized in 1998 and was populated continuously thereafter (Billing et al. In press). Populations on two islands, Sundøy and Ytre Kvarøy, went extinct in 2000 (Ringsby et al. 2006), and the Selvær population went effectively extinct in 2000 as there were only four males present on the island. However, the Selvær population was swiftly restored by immigration from other islands in later years. Selsøyvik has experienced several bottleneck events, with population sizes ranging from 2 to 15 over the study period (Ringsby et al. unpublished results).

In this study system the house sparrow is easily studied due to its close association to human settlements, in small villages or farms (mainly dairy farms). This way individual-based information on a large proportion of individuals present in the populations can be collected with relatively little effort. In this study area the breeding season usually starts in May and ends in August, with 1-3 clutches per breeding pair (Husby et al. 2006). House sparrows are socially monogamous and both females and males contribute in raising the young (Ringsby et al. 2009). There is however variation among males in mating success (Jensen et al. 2008) due to extra-pair copulations (Larsen et al. manuscript). Accordingly, although variation in lifetime reproductive success seems similar for males and females, a higher proportion of variation in lifetime reproductive success seems explained by variation in annual reproductive success in males than in females in this meta-population system (Jensen et al. 2004). The sex ratio in complete broods deviates slightly, but not significantly, from 1:1, with on average 54.9% males (Husby et al. 2006). After one year the house sparrows become reproductively active, and the recruitment rate is 15-20% (Ringsby et al. 2002). The dispersal rate is relatively low (approx. 10%) and seems similar for males and females (Pärn et al. 2009). Dispersal outside of the study system is very rare (Tufto et al. 2005; Jensen et al. unpublished results). Immigrant males have significantly lower reproductive success than resident males, whereas female immigrants do not differ from resident females in reproductive success (Pärn et al. 2009). For more extensive information regarding this study

system, see Sæther et al. (1999); Ringsby et al. (2002); Jensen et al. (2004); Jensen et al. (2007); Pärn et al.(2009) ; Pärn et al. (2012).

Data collection and sampling scheme

Adult and fledged juvenile individuals have been captured using mist nets, whereas nestlings were sampled directly from the nest. From each individual a blood sample was drawn (approximately 25 µL) from the underside of the wing. These blood samples were stored in a standard buffer (used 1993-1999; Jensen et al. 2003) or 96% ethanol (used 2000 and onwards). A metal ring with a unique number was put on each bird's left or right tarsus and used to identify each individual. In addition, 3 colored plastic rings were combined with the metal ring on the two tarsi and used for subsequent unique identification of free ranging individuals by observation. This allowed for estimation of demographic parameters such as survival, dispersal and population size from recapture and observation data.

The data used in this study span from 1993 to 2009. As the average generation time for the house sparrow is approximately 2 years (Jensen et al. 2008) I assumed that samples spaced by 3 years were from separate generations. Accordingly, this minimized the possibility that the same individuals were represented in subsequent samples. The following six years were selected to represent six generations: 1994, 1997, 2000, 2003, 2006 and 2009. For the single sample estimators of N_e, one point estimate was obtained for each island population in each of those years. For the temporal estimators of N_e, two samples were included for each island population, with either 1, 4 or 7 generations between samples (for the different combinations of years and islands see Table A3 and Table A4). Thus, spatio-temporal trends in N_e could be plotted and compared with spatio-temporal trends in N_c, and the correspondence between different N_e estimators could be examined at different time spans between sampling events.

Population characteristics

Population size

The population size in this study was defined as the number of adults in a population; juveniles were excluded because they do not contribute genetically to the population, unless they become recruits the following breeding season (Luikart et al. 2010). Census population size (N_c) was estimated in two ways depending on the sampling effort on a given island. On the islands where the sparrows mostly live on farms (Aldra, Gjerøy, Hestmannøy, Indre Kvarøy, Nesøy, Sundøy and Ytre Kvarøy), the percentage of marked individuals is high enough (>70%, and often close to 100%) that N_c could simply be estimated as the number of marked individuals present in each population. Individuals not observed or captured in a given year on an island would still be regarded as present if they were observed or captured in later years (Jensen et al. 2006). For the islands where the sparrows are found mainly in villages (Lovund, Lurøy, Myken, Onøy, Selsøyvik, Selvær, Sleneset and Træna) N_c was estimated by counting adult birds each spring before the breeding season begins. This

census population size estimate was compared with $\widehat{N}_e$ for the single sample estimator. For temporal estimators, $\widehat{N}_e$ was compared with the harmonic mean population size (N_H) across the years since the previous sampling event (both years of sampling included). This is because the single sample $\widehat{N}_e$ represents N_e at the time of sampling, whereas the temporal $\widehat{N}_e$ represents the harmonic mean N_e in the time interval considered (Waples 2010). Also, N_e/N_H relates to the N_e/N_c-ratio per generation, and thus corresponds to the N_e/N_c-ratio for single sample estimators (Kalinowski and Waples 2002).

The variance in population size ($\sigma^2_{N_c}$) was calculated as:

$$\sigma^2_{N_c} = \sum_{i=1}^{t} \frac{(N_i - \overline{N})^2}{t-1} \quad (2)$$

where t is the number of years and $\overline{N}$ is the arithmetic mean from N_1 to N_t. For single sample $\widehat{N}_e$, N_1 was the population size in the year representing the previous generation before sampling and N_t the population size in the year of sampling. For temporal $\widehat{N}_e$, N_1 was the population size in the year of the first sample and N_t was the population size in the year of the last sample. Population growth rate (dN/dt) was calculated as:

$$\frac{dN}{dt} = \frac{N_2 - N_1}{N_1} \quad (3)$$

For single sample $\widehat{N}_e$, N_1 was the population size in the year representing the previous generation before sampling and N_2 the population size in the year of sampling. For temporal $\widehat{N}_e$, N_1 was the population size in the year of the first sample and N_2 was the population size in the year of the last sample (Table 1).

Sex ratio

The sex ratio (*SR*) was defined as the proportion of males in the population. For single sample $\widehat{N}_e$, *SR* was simply the *SR* in the year of sampling. For temporal $\widehat{N}_e$ I used the average *SR* for the two years at the start and at the end, respectively, in the relevant time interval (e.g. for the interval 1997-2000 *SR* would be the average *SR* for the years 1997 and 2000).

Immigration

A disperser was defined as any nestling or juvenile marked on an island one year, and captured or observed on a different island in the subsequent calendar year. Consequently, any breeding dispersal (adult dispersers) was excluded. Because breeding dispersal is rare in the study system (Pärn et al. 2009) this was not likely to introduce any bias. The immigration rate (m) was estimated differently according to whether it would be compared with single sample estimates of N_e or temporal estimates of N_e. In the first case, m was estimated as the number of new immigrants to the island population in the three years prior to the year of sampling (e.g. immigrants arriving in 1998, 1999 and 2000 for N_e estimate of 2000) divided by N_c in the year of sampling. In the latter case, m was estimated as the sum of the annual

immigration rate (number of new immigrants to an island population in one year divided by N_c in the same year) over the same time interval as N_e was estimated for, and dividing that sum by the number of years in that time interval.

Molecular analyses

DNA was extracted from proteinase K digested blood samples using a Silica-gel based procedure carried out in 96-well plates, as described in Elphinstone et al. (2003). The DNA was then available for PCR-amplification. Intra-individual genetic variation was determined by genotyping 15 microsatellite loci; Ase18 (Griffith et al. 2007), Pdoμ1, Pdoμ3 (Neumann and Wetton 1996), Pdoμ5 (Griffith et al. 1999), Pdo10 (Griffith et al. 2007), Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo33, Pdo40, Pdo44, Pdo47 (Dawson et al. In press). The PCR amplification was executed on Applied Biosystems GeneAmp PCR system 9700 PCR machines (Applied Biosystems, USA). Ase18, Pdoμ1, Pdoμ3, Pdoμ5, Pdo10, Pdo33, and Pdo40 were multiplexed with the avian sex-determination primers P2 and P8 (Griffiths et al. 1998) in multiplex Panel 1, whereas Pdo16, Pdo17, Pdo19, Pdo22, Pdo27, Pdo32, Pdo44 and Pdu47 were multiplexed in multiplex Panel 2. Included in each reaction mixture (10μL) were 5μL 2x QIAGEN Multiplex PCR Master Mix (QIAGEN Inc, USA), 5μL MilliQ H_2O, 0.125μM of each primer, and approximately 20ng of genomic DNA. For both multiplex panels PCR was carried out using a touchdown profile: a denaturing step at 94^{o}C for 15 minutes followed by 12 cycles at 94^{o}C for 30 seconds; an annealing step initially at 62^{o}C for 30 seconds (successively reduced by 1^{o}C each cycle); and an elongation step at 72^{o}C for 60 seconds. Following this were 19 cycles with 94^{o}C for 30 seconds, 50^{o}C for 30 seconds and 72^{o}C for 60 seconds. Finally, the PCR machine ran for 5 minutes at 60^{o}C, and the PCR-product was thereafter kept at 4^{o}C. For each sample, 1μL of the PCR products in a multiplex panel was mixed with 0.5μL of a size ladder (GeneScan LIZ 600, Applied Biosystems, USA), and 10μL Hi-Di Formamide solution (Applied Biosystems, USA). The separation of PCR products was by electrophoresis in an automated 16 capillary electrophoretic analysis system: ABI Prism 3130xl Genetic Analyzer (Applied Biosystems, USA). Alleles were visualized by fluorescently labeling the forward primer, with either FAM (Pdoμ1, Pdoμ5, Pdo19, Pdo22, Pdo44), NED (P2P8, Pdoμ3, Pdo16, Pdo27, and Pdo33), VIC (Ase18, Pdo10, Pdo32, Pdo40 and Pdo47) or PET (Pdo17). Genotypes of all individuals on each of the microsatellite loci were determined using the software package GENEMAPPER 4.0 (Applied Biosystems, USA). Pdo32 and Pdo33 were excluded from further analyses because of scoring difficulties. Allele frequencies of the remaining 13 microsatellite loci did not deviate significantly from Hardy Weinberg equilibrium expectations across years within the largest population Hestmannøy (n = 560). The only exception was Pdo17 which had a slight deficiency of heterozygotes (H_e = 0.89, H_o = 0.87). Furthermore, these 13 loci are likely to either be located on different chromosomes or far apart on the same chromosome and hence not physically linked (Dawson et al. In press). These loci are therefore likely to be suitable for estimating genetic effective population size (see also Jensen et al. (2003); Jensen et al. (2007); Hermansen et al. (2011); Kekkonen et al.

(2011); and Schrey et al. (2011) for use of these loci in molecular ecological and population genetic studies).

Estimation of genetic N_e

Estimates of effective population size ($\widehat{N}_e$) based on a single sample were obtained for each population and year of sampling (Table A3) using the linkage disequilibrium method implemented in the program LDNE (Waples and Do 2010) and the ABC method implemented in the ONeSAMP program (Tallmon et al. 2008). Temporal estimates were obtained for each population for the different combinations of sampling years using the pseudo-likelihood method implemented in the MLNE program (Wang 2001; Wang and Whitlock 2003) and the coalescent based method implemented in the program CoNe (Berthier et al. 2002; Anderson 2005).

Single sample estimators

The LDNE program implements a method for estimating N_e based on random linkage disequilibrium (*LD*) that arises due to random genetic drift in a finite population (Waples and Do 2008; Waples and Do 2010). *LD* can be defined as the non-random association of alleles at different loci (Lewontin and Kojima 1960). *LD* is often approximated by *r*, which is the correlation coefficient for alleles at different gene loci, and often r^2 is used when interested in the magnitude of *LD* rather than the direction (Waples and Do 2008; Waples and Do 2010). For this method N_e is estimated as a function of the expected value of $\hat{r}^2$, based on the theoretical relationship between $\hat{r}^2$ and N_e:

$$E(\hat{r}^2) \approx \frac{1}{3N_e} + \frac{1}{S} \qquad (4)$$

where *S* is the sample size (Hill 1981). Thus N_e is inversely proportional to *LD*. The performance of the estimator depends on estimating $\hat{r}^2$ accurately, with rare alleles being the worst source of bias (see below). The key assumption of this method is that *LD* only arises from genetic drift. However, *LD* can also arise as a result of migration, selection, overlapping generations and population admixture (Service et al. 2006). In the estimation procedure, random mating or monogamy was assumed. In the random mating model each progeny is the result of a mating between a randomly, independently selected male and a randomly, independently selected female, chosen without replacement from the population. In the monogamy model each progeny is the result of a randomly selected, with replacement, permanently bonded male-female pair (Waples 2006). Here I assumed random mating, as the house sparrows in this study system do not establish life-long pair-bonds, and are not necessarily sexually monogamous (Jensen et al. 2008), although they do form socially monogamous pairs each season (Husby et al. 2006). Another setting is the P_{crit} value, which is a criterion for excluding rare alleles; alleles with a frequency lower than P_{crit} were excluded from the analysis. To include rare alleles may increase precision, but could result in estimates that are biased slightly upwards. There is an interaction between bias, P_{crit} and sample size, *S* (Waples 2006; Waples and Do 2010). Following recommendations by Waples

and Do (2010) P_{crit} was chosen to be 0.02 for $S > 25$, and for $S \leq 25$ P_{crit} was chosen so that $1/(2S) \leq P_{crit}$, rounded to the nearest two decimal places.

The ONeSAMP program implements approximate Bayesian computation to estimate N_e by comparing eight summary statistics obtained for the population in question with the same statistics calculated for 50 000 simulated populations (Tallmon et al. 2008). Population genetics theory and simulations were used by Tallmon et al. (2008) to select eight summary statistics which relate to N_e: the number of alleles divided by allele length range, the difference of the natural logarithms of variance in heterozygosity and allele length, expected heterozygosity (H_e), number of alleles per locus, Wright's inbreeding coefficient (F_{IS}), the mean and variance of multilocus homozygosity, and $\hat{r}^2$ (a measure of *LD*, see above). The program requires a lower and an upper prior to be specified (even numbers). Because N_e theoretically can be at most twice as high as N_c[1], $2N_c$ was chosen as the upper limit. 2 was chosen as the lower limit. The repeat motif was specified for each locus (for repeat motif for the different loci, see Neumann and Wetton (1996); Griffith et al. 2007; Dawson et al. (In press)). Monomorphic loci or individuals with missing data at more than one locus needed to be excluded from the ONeSAMP input (Table A1).

Multiple samples estimators/temporal methods

For both temporal methods, an upper limit was needed. For each sample the upper limit was chosen to be $2N_c$ for the sampling year with the highest N_c, so that it would be comparable with the priors set for the ONeSAMP method.

The MLNE software obtains $\widehat{N}_e$ using a pseudo-likelihood method, which assumes that temporal changes in allele frequencies are caused by genetic drift alone (Wang 2001; Wang and Whitlock 2003). The full maximum likelihood of N_e calculated from temporal samples was developed by Williamson and Slatkin (1999). Their method is based on the Wright-Fisher model, assuming discrete generations, no immigration and constant population size. The drawback of the full maximum likelihood method is that it is computationally demanding, and only applicable to biallelic markers. Wang (2001) extended this model to include multiallelic loci and simplified the computation by using a pseudo-likelihood approach: a locus with k number of alleles was transformed into k biallelic loci. Pseudo-likelihood refers to the approximation of the joint probability of all the data by the product of marginal probabilities. Extensive simulations have shown that this represents a good approximation to the full likelihood (Wang 2001). I also assumed non-equilibrium between drift and migration equilibrium, because the populations are relatively small and the effects of migration and drift are not expected to cancel each other out, but rather to vary in relative strength in shaping the genetic variation of each population across time and space.

[1] In an ideal population the family size is Poisson distributed with a mean (k) and variance (V_k) of 2, and N_e is given by: $N_e = (4N_c - 2)/(V_k + 2)$. However, from this equation it can be seen that if $V_k < 2$ then $N_e > N_c$, and the highest potential N_e is $2N_c$ (Wright 1938).

The program CoNe gives the likelihood of N_e given genetic data sampled from the same population at different points in time (Anderson 2005). This method is based on coalescent theory; going backwards in time from the time the last sample was taken to the first sample was taken, some of the gene lineages may have coalesced, due to genetic drift. The probability of two lineages coalescing is $1/2N_e$ (Kingman 1982). Berthier et al. (2002) introduced a maximum likelihood method of estimating N_e based on the coalescent instead of the Wright-Fisher population approach used by Williamson and Slatkin (1999), see above. Berthier et al. (2002)s´ model was further extended by Beaumont (2003), however both approaches are extremely computationally demanding. The CoNe implements a more efficient Monte Carlo approximation to the likelihood than of that described in Berthier et al. (2002). This method assumes that coalescent events are only caused by genetic drift. CoNe calculates a Monte Carlo estimate of the likelihood curve, obtaining a maximum-likelihood estimate of N_e (Anderson 2005).

Estimation of demographic N_e

Early methods for estimating N_e based on demographic data (Felsenstein 1969; Hill 1972; Emigh and Pollak 1979; Hill 1979; Nunney 1991; Nunney 1993) were based on rather restrictive assumptions (e.g. constant population and stable age-structure). The applicability of the demographic approach was greatly improved when Engen et al. (2005) developed a method for deriving formulas for N_e from the infinitesimal variance of a diffusion approximation. However, these formulas still involve a large number of parameters. Here I base my estimates on the approach by Engen et al. (2007), which assumes constant adult survival rates and constant mean vital rates independent of age. This simplifies the estimation procedures considerably. N_e was calculated for each sex separately, due to the recognition that even monogamous species can have differences in reproductive success due to extra-pair copulations and sex-specific survival (Promislow et al. 1992). Sexual selection may thus contribute significantly to N_e. N_e for females (N_{ef}) was based on a simplification of Engen et al. (2005) and is given by:

$$N_{ef} = \frac{N_f}{\sigma^2_{dgf} T_f} = \frac{N_f}{\left[b_f/4 + \sigma^2_f/4 + s_f(1 - s_f) + c_f\right] T_f} \quad (5)$$

where N_f is the number of females, σ^2_{dgf} is the demographic variance of a hypothetical female subpopulation of heterozygotes carrying a rare allele, b_f is the mean number of female offspring born to each female, σ^2_f is the variance in number of female offspring per female, s_f is the probability of survival for females, c_f is the covariance between an individual's number of offspring and the indicator variable (0 or 1) for its survival, and T_f is the generation time for the female population given by $T_f = \lambda/(\lambda - s_f)$ where λ is the deterministic growth rate. N_e for males (N_{em}) was calculated in the same way. Second, the N_e of the total population was then calculated by using a formula, based on Wright's formula for uneven sex ratios, but modified to allow for non-overlapping generations:

$$N_e = \frac{4\lambda^2 b N_{ef} N_{em}}{b_f N_{ef} + b_m N_{em}} \quad (6)$$

This approach avoids the increased complexity introduced by age structure in a population with overlapping generations (Engen et al. 2005). Estimates from this method, $\widehat{N}_{e(demographic)}$, represent N_{eV} and are thus comparable with the temporal genetic $\widehat{N}_e$. Therefore $\widehat{N}_{e(demographic)}$ was obtained from the same sampling intervals as temporal genetic $\widehat{N}_e$, by multiplying the mean population size for each sampling interval with the N_e/N_c ratios given for each island in Engen et al. (2007). These ratios were only available for 6 of the islands, namely Aldra, Gjerøy, Hestmannøy, Indre Kvarøy, Nesøy and Ytre Kvarøy. Note that this approach assumes a constant N_e/N_c-ratio across years.

Statistical analyses

Pearson's correlation coefficient (r) was used to investigate the relationship between estimates from the two single sample estimators ($\widehat{N}_{e(LDNE)}$ and $\widehat{N}_{e(ONeSAMP)}$), and between estimates from the two temporal estimators ($\widehat{N}_{e(MLNE)}$ and $\widehat{N}_{e(CoNe)}$). Spearman's rank correlation coefficients (ρ) were also estimated, but as this gave similar results only Pearson's correlation coefficients are presented. Similarly, Pearson's correlation coefficient was used to explore the relationship between single sample $\widehat{N}_e$ and N_c, as well as between temporal $\widehat{N}_e$ and N_H. The temporal $\widehat{N}_e$ were also compared with $\widehat{N}_{e(demographic)}$ using Pearson's correlation coefficient.

The precision of each estimator was represented by the coefficient of variation (*CV*), defined as the range of the 95% confidence limits (given in the estimators' output) divided by $\widehat{N}_e$ and expressed as a percentage. The *CV* values were plotted against population size to examine how the variance in the estimates of each estimator related to population size. In order to determine the importance of population characteristics for the relative magnitude of $\widehat{N}_e$ to N (i.e. N_c or N_H), $\widehat{N}_e/N_c$ and $\widehat{N}_e/N_H$ was modeled as a function of the following predictor variables: sex ratio (*SR*), immigration rate (m), population size (single sample = N_c, temporal = N_H), population growth rate (dN/dt), temporal variance in population size ($\sigma^2_{N_c}$) and the number of generations between samples (T, only for temporal estimates). Additionally, two interactions were included in the *a priori* global models: $N_c \times SR$ and $N_c \times m$ (for single sample estimators) or $N_H \times SR$ and $N_H \times m$ (for temporal estimators). These interaction terms were included in the model because I suspected that effect of sex ratio and immigration rate on $\widehat{N}_e/N$ could vary with population size. Both generalized linear models (GLM) with a Gaussian error structure (using the lm function in R; R Development Core Team 2011) and generalized linear mixed models (GLMM, with a Gaussian error structure, using the nlme package (Pinheiro et al. 2011)) with population as a random factor, i.e. accounting for any inter-dependency between estimates from the same island population), were used. As GLMs and GLMMs gave similar results only the results from the GLMs are presented.

Model selection was done by Akaike's Information Criterion with a correction for smaller sample sizes (AIC_C), which is defined as:

$$AIC_C = -2L + 2K + \frac{2K(K+1)}{n-K-1} \quad (7)$$

where K is the number of parameters in the model, n is the sample size and L is the maximum log-likelihood of the model (Burnham and Anderson 2002). L is a measure of the fit of the model to the data. Every candidate model nested under the global model was ranked by the relative deviance in AIC_C from the best model (Δ_i). The candidate models for which $\Delta_i < 2$ were examined more closely to determine which model was the best model (given the set of candidate models), as all models $\Delta_i < 2$ are considered to have considerable evidence in the data (Burnham and Anderson 2002). Another measurement of the strength of evidence for each model is provided by Akaike's weights (w_i), which was also calculated:

$$w_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{r=i}^{R} e^{-\frac{1}{2}\Delta_r}} \quad (8)$$

where Δ_r is the sum of Δ_i over all j to R models (R being the number of tested models). From this the evidence ratio (ER) for the "best" model relative to model i was calculated as w_i for the best model divided by w_i for the model i. The evidence ratio can be interpreted as how much "better" the "best" model is relative to model i.

65 point estimates were obtained for the LDNE method, and 70 point estimates were obtained for the ONeSAMP method (out of 70 possible). The LDNE method gave 5 estimates with negative values indicating infinity for either the point estimate or the confidence limits (Table A1). Infinite estimates is a result of too little information in the sample so that the genetic signal found in the data is due to sampling error rather than genetic drift (Waples and Do 2010). 86 point estimates were obtained for the MLNE method and 33 point estimates were obtained for the CoNe method, out of 89 possible estimates (Table A1).

All statistical analyses were carried out using R (R Development Core Team 2011). Several outliers were removed from the dataset. Analyses were carried out with and without outliers, but results were similar and only the results without outliers are shown here. For an overview of removed data, including justification for removing outliers, see Table A1.

RESULTS

Single sample estimates of N_e

Estimates of effective population size from a single sample ($\widehat{N}_{e(LDNE)}$ and $\widehat{N}_{e(ONeSAMP)}$) along with 95% confidence limits are presented in Table A2.

There was a significant, positive correlation between $\widehat{N}_{e(LDNE)}$ and $\widehat{N}_{e(ONeSAMP)}$ (r = 0.62, p<<0.001; Fig. 2). $\widehat{N}_{e(ONeSAMP)}$ were generally higher than $\widehat{N}_{e(LDNE)}$. There was however a great deal of variation, and approximately 23% of $\widehat{N}_{e(LDNE)}$ were higher than $\widehat{N}_{e(ONeSAMP)}$.

$\widehat{N}_{e(LDNE)}$ and $\widehat{N}_{e(ONeSAMP)}$ were both significantly positively correlated with N_c (r = 0.63, p<<0.001 and r = 0.93, p<<0.001, respectively; Fig. 3). $\widehat{N}_{e(LDNE)}$ were generally lower than N_c (Fig. 3a) whereas $\widehat{N}_{e(ONeSAMP)}$ were mostly higher than N_c (Fig. 3b). $\widehat{N}_{e(LDNE)}/N_c$-values ranged from 0.21 to 3.14 with a mean and median of 0.90 and 0.69, respectively. $\widehat{N}_{e(ONeSAMP)}/N_c$-values were in the range 0.55-2.78 with a mean and median of 1.22 and 1.19, respectively. The two estimators showed opposite patterns; $\widehat{N}_{e(ONeSAMP)}$ were typically higher than N_c in large populations in contrast to $\widehat{N}_{e(LDNE)}$ which were mostly lower than N_c in large populations (Fig. 3). At some threshold value of N_c ($N_c \approx 25$) the relative magnitude of $\widehat{N}_e$ and N_c changed for both estimators; $\widehat{N}_{e(ONeSAMP)}$ became lower and $\widehat{N}_{e(LDNE)}$ became higher than N_c below this threshold, respectively (Fig. 3).

CV for the two estimators plotted against N_c showed opposite relationships (Fig. 4). CV_{LDNE} decreased with increasing N_c (r = -0.34, p = 0.005; Fig. 4a), suggesting that precision increased as N_c increased. However, the relationship between CV_{LDNE} and N_c was not linear; at small values of N_c (below approx. 25) the CV_{LDNE} -values varied enormously. In contrast, there was a strong positive relationship between $CV_{ONeSAMP}$ and N_c (r = 0.96, p<<0.001; Fig. 4b), indicating that precision actually decreased as N_c increased. Furthermore, there was in general higher uncertainty in $\widehat{N}_{e(LDNE)}$ than in $\widehat{N}_{e(ONeSAMP)}$ as indicated by the larger magnitude and range of CV_{LDNE}-values compared to $CV_{ONeSAMP}$-values (Table A3). Mean and median *CV* for $\widehat{N}_{e(LDNE)}$ were 99.80 and 52.55, respectively. The divergence between these two values indicates a positively skewed distribution. Mean and median *CV* for $\widehat{N}_{e(ONeSAMP)}$ were 58.25 and 55.70, respectively. The similar values indicate a symmetric distribution of $CV_{ONeSAMP}$-values (Table A3).

Temporal estimates of N_e

Estimates from the temporal methods ($\widehat{N}_{e(MLNE)}$ and $\widehat{N}_{e(CoNe)}$) along with 95% confidence limits are shown in Table A4.

There was a significant, positive relationship between $\widehat{N}_{e(MLNE)}$ and $\widehat{N}_{e(CoNe)}$ (r = 0.79, p<<0.001; Fig. 5). There was considerable variation between the two estimators; for some populations the CoNe method gave estimates twice as high as MLNE, but the MLNE method also frequently estimated N_e much higher than the CoNe method.

$\widehat{N}_{e(MLNE)}$ and $\widehat{N}_{e(CoNe)}$ were both significantly positively correlated with N_H (r = 0.83, p<<0.001 and r = 0.43, p = 0.015, respectively; Fig. 6). Both estimators gave $\widehat{N}_e$ higher than N_H; for $\widehat{N}_{e(MLNE)}$ this relationship seemed fairly constant with population size (Fig. 6a) whereas for $\widehat{N}_{e(CoNe)}$ the estimates were higher than N_H, especially at lower N_H-values (Fig. 6b). $\widehat{N}_{e(MLNE)}/N_H$-values spanned from 0.65-5.72, however only one value was lower than 1. Mean and median $\widehat{N}_{e(MLNE)}/N_H$ were 2.43 and 2.33, respectively. $\widehat{N}_{e(CoNe)}/N_H$-values covered the largest range of $\widehat{N}_e/N_H$-values of all four estimators, from 0.50-8.53, with mean and median values of 2.88 and 2.10. Overall the MLNE and CoNe method thus seemed to produce quite similar estimates.

For the two temporal methods the uncertainty (*CV*) in the estimates were differently related to N_H (Fig. 7). CV_{MLNE} was positively correlated with N_H (r = 0.57, p<<0.001; Fig. 7a). In other words precision decreased with increasing population size. On the other hand, due to extreme variation in the CV_{CoNe}-values (many >200) across the range of N_H there was no significant relationship between CV_{CoNe} and N_H (r = -0.27, p = 0.15; Fig. 7b), indicating that the precision of $\widehat{N}_{e(CoNe)}$ did not change with population size. Mean and median CV_{MLNE} were 39.55 and 34.80, respectively, indicating an almost symmetric distribution of CV_{MLNE}-values. For the CoNe method, mean and median *CV*-values were 182.90 and 109.24, respectively. The large difference between these values indicates that extreme values resulted in a positively skewed distribution.

Population characteristics and variation in N_e/N_c

The most parsimonious model explaining variation in $\widehat{N}_{e(LDNE)}/N_c$ included two parameters in addition to the intercept: sex ratio (*SR*) and immigration rate (*m*) (model 1, Table 2a). The other candidate models were all more parameterized than model 1. There were 4 models with AIC_C-values within 2 units higher than model 1, (models 2-5, Table 2a). Thus, one cannot exclude the possibility that they were equally "good" models, although model 1 was 1.36, 1.61, 1.74, and 2.01 times more likely to be the "best" model than model 2, 3, 4 or 5, respectively. These 5 models all included the parameters *SR* and *m*. Given that the fit was not really improved by adding more parameters, as indicated by the similar *L*-values, Ockham's razor dictates that the less complicated model should be chosen as the "best" model (Burnham and Anderson 2002). Additionally, when looking at the parameter estimates of each model it was apparent that the added parameters (parameters not included in model 1) had slopes not significantly different from zero (p>0.09). Thus it seems that the most important population characteristics explaining variation in $\widehat{N}_{e(LDNE)}/N_c$ are *SR* and *m* (model 1, Table 2a). The parameter estimates for each variable in model 1, which explained 35% of the variance in $\widehat{N}_{e(LDNE)}/N_c$ (model r^2 = 0.35), are given in Table 3a. There

was a positive effect of *SR* (β_1 = 2.083) and m (β_2 = 6.563) on $\widehat{N}_{e(LDNE)}/N_c$, meaning that $\widehat{N}_{e(LDNE)}$ was relatively higher compared to N_c when the population was more male biased and there were more immigrants.

The only parameter included in the most parsimonious model explaining variation in $\widehat{N}_{e(ONeSAMP)}/N_c$ was N_c (model 1, Table 2b). Model 2 included N_c and $\sigma^2_{N_c}$, and had an AIC_C-value less than 2 units higher than the most parsimonious model. However, model 2 had considerably lower w_i and the evidence ratio in favor of model 1 showed that this model was 1.97 more likely to be the "best". Furthermore, the fit (*L*) of model 2 was not improved by adding the parameter $\sigma^2_{N_c}$. Finally, the parameter estimate for $\sigma^2_{N_c}$ was not significantly different from zero (p = 0.36). These points considered, model 1 was chosen as the "best model", with associated parameter estimates shown in Table 3b. This model explained 31% of the variance in $\widehat{N}_{e(ONeSAMP)}/N_c$ (model r^2 = 0.31) and showed that N_c had a positive effect on $\widehat{N}_{e(ONeSAMP)}/N_c$ (β_1 = 0.007). This means that $\widehat{N}_{e(ONeSAMP)}$ was relatively higher compared to N_c at higher values of N_c.

Model 1 had the lowest AIC_C among the models tested and suggested that variation in $\widehat{N}_{e(MLNE)}/N_H$ was explained by population size (N_H), sex ratio (*SR*), immigration rate (*m*) and population growth rate (*dN/dt*; Table 4a). Models 2-11 had AIC_C-values less than 2 units higher than model 1, which also was the most parsimonious model among them (with the exception of model 7 which had 5 parameters just like model 1). Thus, all 11 models can be said to be relevant for explaining variation in $\widehat{N}_{e(MLNE)}/N_H$. As judged by w_i model 1 was 1.04, 1.09, 1.47, 1.47, 1.50, 1.67, 2.06, 2.12, 2.40, and 2.57 more likely in a Kullback-Leibler sense to be the "best" compared to models 2-11, respectively. When inspecting the models more closely it was evident that all 11 had the following parameters in common: N_H, *SR* and *m*. Furthermore, only model 1 include exclusively parameters with parameter estimates that differed significantly from zero (all other models included explanatory variables for which parameter estimates had p>0.09). Also the fit (*L*) of the more parameterized models were not better than model 1. Thus, model 1 was chosen as the "best" model, with parameter estimates shown in Table 5a. In model 1, which explained 0.35% of the variance in $\widehat{N}_{e(MLNE)}/N_H$ (model r^2 = 0.35), $\widehat{N}_{e(MLNE)}/N_H$ was negatively related to N_H and *SR* (β_1 = -0.017 and β_2 = -2.992, respectively), and positively related to *m* and *dN/dt* (β_3 = 7.004 and β_4 = 0.260, respectively). This implied that $\widehat{N}_{e(MLNE)}$ was relatively lower compared to N_H at higher population sizes and at higher proportions of males, and relatively higher than N_H when the population was growing and when there were many immigrants.

The most parsimonious model explaining variation in $\widehat{N}_{e(CoNe)}/N_H$ included population size (N_H), immigration rate (*m*), population growth rate (*dN/dt*) and the interaction term $N_H \times m$ (model 1, Table 3b). Model 2 differed from model 1 by adding $\sigma^2_{N_c}$, i.e. it had more parameters. Model 2 had AIC_C-values less than 2 units higher than model 1, and both models are thus likely to be "best" at explaining variation in $\widehat{N}_{e(CoNe)}/N_H$ among the candidates. Model 1 was however 1.49 times more likely than model 2 to be the "best" according to the

evidence ratio. The parameters that were shared by both models (N_H, *m, dN/dt,* and $N_H \times m$) were all significantly different from zero, but the main effect of N_H was not. The $\sigma^2_{N_c}$ parameter included in model 2 was not significantly different from zero (p = 0.19), nor did including it improve the fit to the data as the *L*-value was slightly lower for this model. Given this, model 1 was selected as the "best" model explaining $\widehat{N}_{e(CoNe)}/N_H$. 71% of the variance in $\widehat{N}_{e(CoNe)}/N_H$ was explained by this model (model r^2 = 0.71). Parameter estimates for model 1 (Table 5b) showed that *m* and *dN/dt* had a positive effect on $\widehat{N}_{e(CoNe)}/N_H$ (β_2 = 52.220 , β_3 = 0.938, respectively), whereas N_H and the interaction term $N_H \times m$ had negative parameter estimates (β_1 = -0.015 and β_4 = -0.549, respectively). However, the main effect of N_H was not significant (*p* = 0.20). In other words, $\widehat{N}_{e(CoNe)}$ was relatively higher compared to N_H when number of immigrants increased and with higher population growth rate. Furthermore, the magnitude of the positive effect of *m* on $\widehat{N}_{e(CoNe)}/N_H$ was reduced when population size increased.

The relationship between genetic and demographic N_e

The estimates of N_e from the demographic method was significantly positively correlated with estimates from the MLNE method (*r* = 0.83, *p*<<0.001), and estimates from the CoNe method (*r* = 0.63, *p* = 0.002). Thus, this suggests that these methods reflect the current rate of drift in these populations. However, there was absolutely no overlap between the $\widehat{N}_e$ obtained from the two genetic temporal methods and $\widehat{N}_{e(demographic)}$; both the MLNE method and the CoNe method gave estimates that were much higher than the $\widehat{N}_{e(demographic)}$ (Fig. 8).

DISCUSSION

All four genetic estimators of effective population size included in this study were positively correlated with population size, and N_e estimates were in general higher than census population size (Fig. 3, Fig. 6). Only the single sample estimator LDNE gave N_e estimates below N_c over most of its range (Fig. 3a). There was a positive relationship between the estimates given by the two single sample estimators (Fig. 2) and between the two temporal estimators (Fig. 5). Temporal genetic N_e was always higher than demographic N_e (Fig. 8). Furthermore, precision was positively correlated with N_c for the LDNE method (Fig. 4a), unrelated to N_c for the CoNe method (Fig. 7b) and negatively correlated with N_c for the ONeSAMP and MLNE methods (Fig. 4b and Fig. 7a, respectively). The population characteristics explaining the variation in $\widehat{N}_e/N_c$ differed between estimators (Table 3, Table 5). Sex ratio, population size, immigration rate and population growth rate were included among the explanatory variables. Population growth rate had a positive effect on $\widehat{N}_e/N_c$ for the two temporal N_e estimators (Table 2). The effect of sex ratio on $\widehat{N}_e/N_c$ was opposite for the two estimators for which it was important (Table 3, Table 5). A general result seemed, however, to be that immigration had a positive effect on the magnitude of N_e relative to N_c, as this was true for three of the four genetic estimators (Table 3, Table 5).

Bias and precision of the estimators

A good estimator should be unbiased as well as precise. Estimation bias (also called systematic error) refers to when the estimated value deviates from the true value (West 1999; Walther and Moore 2005). In this study, a genetic estimator of N_e that gives estimates unequal to the true value of N_e is biased. Estimation bias should decrease with increasing sampling effort (Walther and Moore 2005). Precision is on the other hand independent of the true value and describes a measure of the statistical variation (variance, standard error, coefficient of variation etc.) of an estimation procedure (West 1999). Here the precision of the N_e estimates was measured by the coefficient of variation, *CV* (derived from the 95% confidence limits); a low *CV* indicates high precision. In general, the precision of an estimator should increase with sampling effort (Walther and Moore 2005). Specifically, as the signal from genetic drift is inversely proportional to N_e, precision is expected to be negatively correlated with N_e and thus also with N_c (Waples 1989; Waples 2002). Sample size is often close to N_c in this study system (see Table A3), so imprecision due to sampling should be minimal and rather caused by a relatively weaker signal from genetic drift as N_c increases. Precision was indeed negatively correlated with N (N_c or N_H) for the ONeSAMP method (Fig. 4b) and the MLNE method (Fig. 7a) and this is concordant with results obtained by others (Waples and Do 2010; Barker 2011). However the opposite relationship was shown for the LDNE method (Fig. 4a). It is important to note that if an estimator is biased, then the confidence limits may not include the true value of N_e and the estimator thus contains little

information even if it is very precise. Also, there could be a relationship between precision and bias, further complicating interpretation.

To evaluate the bias of the estimators is difficult as the true value of N_e is unknown. Previous studies have carried out simulations to test for bias in the estimates from the estimators I have used here (Williamson and Slatkin 1999; Turner et al. 2001; Waples and England In press). These simulation studies generally found that bias decreases with increased sample size (with respect to number of individuals genotyped, number of loci and number of alleles per loci). Another general result is that maximum likelihood and Bayesian methods are less biased than moment-based methods. For an empirical study such as this, potential bias can be assessed by comparing estimates to population size or estimators known to be unbiased. Theory states that N_e should usually be less than N_c unless family size is equalized in the population (Wright 1931; Templeton and Read 1984; Kalinowski and Waples 2002). As N_e estimates in this study were generally higher than N_c (Fig. 3, Fig. 5) and temporal estimates were always higher than $\widehat{N}_{e(demographic)}$ (Fig. 8), all four estimators seem to suffer from an upward bias. The bias was more severe for the temporal methods, and LDNE was the least biased estimator as 69% of its estimates were < N_c. The upward bias found here was most likely caused by violating one or more of the different assumptions underlying the different estimators, e.g. no immigration, no subdivision of the population, no mutations, no selection, constant population size, unlinked and statistically independent markers, loci sampled at random, the population sampled at random and discrete generations. All four genetic estimators included in this study make these assumptions, the exception being that CoNe may be more appropriate for organisms with overlapping generations (Anderson 2005). However the consequence of violating these assumptions may vary, some estimators may be more robust when it comes to ignoring certain assumptions than others (Fraser et al. 2007). I will discuss which assumptions that are possibly violated in this study, and the effect this may have had on the estimates given by the different estimators.

If loci are physically linked, *LD* could be overestimated, causing a downward bias of N_e (Waples 2005). However, in this study loci are probably not linked so this assumption should not be violated (Dawson et al. In press). The effect of selection on loci (or genes linked to the loci) included in estimation of N_e is complex. Directional selection will result in a higher loss of genetic variation than expected under drift only, and thus an underestimation of N_e. Balancing selection, on the other hand, would maintain genetic variation and counteract genetic drift, thus leading to an overestimation of N_e. Either way, the potential bias introduced by selection should be minimal unless the selection is very strong (Waples 1989). I cannot exclude the possibility that markers used for estimating genetic N_e in this study were affected by selection, as selection has been found to operate on for instance morphological traits in this population (Jensen et al. 2008). However, the likelihood that any markers I used are tightly linked to genes affecting traits under strong selection seems low. In support of this, 12 out of 13 markers used in this study did not significantly deviate from Hardy-Weinberg equilibrium expectations in the largest population (see Material and

Methods). Selection did therefore probably not introduce much bias to the N_e estimates. The assumption of no mutations is also probably not violated, as the mutation rate would need to be extremely high and even higher than documented for microsatellites (Ellegren 2004; Chistiakov et al. 2006), to introduce much bias in such a short timeframe (Waples 1989; Waples 2002). Furthermore, as a very high proportion of individuals present in the population (often nearly 100%) were sampled in this study (Table A3) I conclude that the samples represented a random and highly representative sample of the populations' genetic composition. In contrast, loci are often not chosen at random as highly polymorphic loci are often selected due to their suitability for genetic analyses (Griffith et al. 2007). However this is not likely to introduce much bias (Luikart et al. 2010). Population subdivision can increase inbreeding because locally breeding individuals are more likely to be related (Ovaskainen and Hanski 2004). This would result in a downward bias of N_e. Most of the island populations in this study were probably not subdivided, with Gjerøy and Hestmannøy being possible exceptions. The bias introduced by population subdivision is more serious if some subpopulations are overrepresented in the samples (Nei and Tajima 1981; Luikart et al. 2010). This problem was probably avoided in this study as most individuals present were sampled both within and across populations (Table A3).

Following the discussion above there are three potential sources of bias left in this study, namely violating the assumptions of overlapping generations, immigration, and fluctuations in population size. The house sparrow has overlapping generations; the assumption of discrete generations is thus violated. The bias that may result from overlapping generations is very complex. In this study I aimed at sampling individuals representing different generations as samples were spaced by three years, which is more than one generation ($T \approx 2$; Jensen et al. 2008). This means that any bias will depend on the co-variation of genetic relationships between cohorts and the number of generations between samples (Jorde and Ryman 1995; Jorde and Ryman 1996). Waples and Yakota (2007) showed that bias due to overlapping generations for the temporal estimators will be minimized if samples are spaced by at least three to five generations. However, too many generations between samples could result in an upward bias (Antao et al. 2011). The survivorship pattern of the population also influences this bias; given a type II survivorship (roughly age-independent survival rate) which is common for birds, N_e could suffer from a downward bias (Waples and Yokota 2007). Concerning the LDNE method, Waples and Do (2010) argue that if the number of cohorts represented in a sample is roughly equal to generation time, then $\widehat{N}_e$ should conform to N_e for one generation. In this study system the maximum recorded age is 9 years (Jensen et al. 2004). Furthermore, the recruitment rate is 0.15-0.20 (Sæther et al. 1999; Ringsby et al. 2002) and adult survival rate is on average approximately 0.6 (Sæther et al. 1999). The number of cohorts represented in a sample will therefore generally exceed the generation time (2 years). However, most individuals sampled (approx. >70%) will be from the two cohorts produced since the previous year of sampling (Jensen et al. unpublished results), so the bias introduced by this may be minimal. Overall, violating the assumption of overlapping generations in this study could have introduced a negative bias, not a positive bias. This

means that violating the assumption of overlapping generations did probably not cause the upward bias found for all four estimators (see above). This leaves immigration and fluctuations in population size as potential explanations for the upward bias.

The influence of immigration on estimates of N_e is not clear cut. For the MLNE and CoNe methods, if the immigrants come from a genetically distinct population, then immigration will mimic drift and a downward bias will be the result. However, in the long run immigration tend to offset genetic drift by (re-)introducing genetic variation and hence result in an overestimation of N_e for a subpopulation (Wang and Whitlock 2003). Similarly, gene flow can influence *LD* in two opposing ways. Single sample estimators estimate the effective number of parents which produced the cohort from which the sample was drawn (Waples 2005). If the sample contains immigrants, then this sample is drawn from a larger pool of parents than just the local breeders. This will lead to an overestimation of N_e. On the other hand, genetically different immigrants can increase *LD* due to population admixture, which will lead to an underestimation of N_e. The latter effect is operating when migration is rare, whereas the first effect is more prominent if migration is common. I expect that an overestimation would be the result in this study system as migration is relatively common, with an average ecological immigration rate of approximately 0.1 across years and populations (Pärn et al. 2009; Pärn et al. 2012). Simulations have shown that if the immigration rate is less than 0.05-0.1 then the estimates from the LDNE method will not be affected (Waples and England In press). As ONeSAMP is also based largely on *LD* this might apply to this method as well. Similar conclusions were reached by Wang and Whitlock (2003) for the MLNE method. Overestimation is especially serious if migrants are not a part of the breeding population.

Fluctuations in population size are expected to influence N_{el} (single sample) and N_{eV} (temporal) differently, as variance in allele frequencies and inbreeding relates differently to population dynamics (Crow and Denniston 1988). Changes in N_{eV} are expected to follow changes in N_c because variance in allele frequency is directly dependent on N_c, whereas N_{el} will lag by at least one generation, as it relates to the number of parents that produced the sample. Assuming stable population size is inappropriate for most natural populations, including the island populations in this study (e.g. Pärn et al. 2012). Nevertheless, the potential bias arising from this is poorly understood. Luikart et al. (2010) recommends comparing N_{el} and N_{eV} to detect if this assumption is robust, given no prior knowledge of variation in population size is known. In general, if there has been a recent bottleneck N_{el} will tend to overestimate N_e. On the other hand, if the population has recently recovered from a period of low population size, then N_{eV} may overestimate N_e if none of the samples were taken during the bottleneck (Templeton and Read 1984).

An upward bias has been established for all four estimators, but the extent of this bias is hard to quantify. However, considerable research has gone into estimating how N_e relates to N_c in natural populations. Nunney (1993) derived an N_e/N_c ratio of 0.5 when accounting for

mating system and overlapping generations. An empirical review by Frankham (1995) found an average N_e/N_c of 0.10-0.11, for birds it was a little higher (0.21). Engen et al. (2007) showed that when accounting for overlapping generations, unequal sex ratio and variation in reproductive success N_e/N_c was in the range 0.20-0.48 for a selection of the island populations considered here. Assuming that N_e estimated by the genetic estimators in this study was for the local population (see discussion on immigration above) I found that only LDNE produced a considerable proportion of its estimates (69%) within this range. ONeSAMP also gave estimates within this range when N_c was small, but generally gave N_e much higher than N_c (71% of $\widehat{N}_{e(ONeSAMP)} \geq N_c$). MLNE and CoNe always overestimated N_e compared to the expectations from previous studies. This is especially clear when looking at Fig. 8; all the temporal genetic estimates were much higher than the demographic estimates. LDNE thus seems to perform better than the other estimators when it comes to bias. This is unexpected as one would expect the three maximum likelihood methods (ONeSAMP, MLNE, and CoNe) to be less biased, because they use more of the information in the data than the moment estimator LDNE. This result is however concordant with the results in Antao et al. (2011), who also concluded that LDNE was a better estimator than the temporal methods. When rare alleles are included, although increasing precision, a bias may result, both for methods based on *LD* (England et al. 2006) and the temporal methods (Turner et al. 2001). LDNE excludes rare alleles to avoid this problem (Waples 2006), but the other three methods considered here do not implement such a bias correction. This might explain why the LDNE method was less biased.

To sum up the discussion with respect to bias, immigration seems to be the main cause of the overestimation of genetic N_e. When looking at the relationship between the temporal genetic estimates and the demographic estimates of N_e (Fig. 8) it is apparent that the demographic estimates do not seem to be affected by immigration in the same way, as the values of N_e fall within what is expected with respect to N_H ($N_e < N_H$). The demographic method is sensitive to demographic parameters such as mean and variance in vital rates and deviation from a 1:1 sex ratio, so that if these parameters are affected by immigrants, for instance because immigrants have a different demography than residents, then immigration will indirectly affect the estimate of demographic N_e (Engen et al. 2005; Engen et al. 2007). However, even if demographic parameters were different for immigrants and residents, the effect on estimates of N_e was not likely to be as substantial. On the other hand, genetic N_e will be directly affected by immigration. Immigrants may introduce new genetic variation to the population, and thus counteract the effect of genetic drift. This could explain why genetic estimates of N_e are higher than expected in this metapopulation. As stated earlier, there was an upward bias in the temporal genetic estimates. However, the true N_e may lie somewhere between N_e estimated using the demographic approach, which accounts for demographic processes in the population, and N_e estimated using genetic methods, which are directly affected by the genetic consequences of immigration.

The apparent upward bias detected here in the genetic N_e estimators can have serious implications. Overestimation is more severe than underestimation of N_e if the purpose of estimating N_e is to determine where conservation efforts should be directed, because it may lead to a failure in detecting populations most likely to experience reduced viability due to loss of genetic variation. Caution should thus be exercised when interpreting genetic estimates of N_e for management purposes (Frankham 2005; Leberg 2005).

Population characteristics and variation in N_e/N_c

Even if the genetic estimators overestimate N_e to a certain degree, there was still considerable variation in N_e/N_c across years and populations (Fig. 3, Fig. 5). Although this relationship seemed to be shifted upwards it may still be possible to identify population characteristics that influence the magnitude of N_e relative to N_c. Accordingly, the results showed that population characteristics explained between 31 and 71 % of the observed variance in N_e/N_c for the different genetic estimators. This pattern is however complicated, as the population characteristics affecting the N_e/N_c-ratio differed between estimators.

Population size and population growth rate

According to theory there should be no relationship between N_e/N_c and N_c (Kalinowski and Waples 2002). However, N_c positively affected N_e/N_c for the ONeSAMP method (Table 3b) and negatively affected N_e/N_c for the MLNE and CoNe method (Table 5). Because the effect of an explanatory variable is estimated accounting for the effect of any other explanatory variables included in the model, this may explain why the MLNE and CoNe methods showed the opposite relationship between N_c and N_e/N_c compared to ONeSAMP. However, Palstra and Ruzzante (2008) reviewed temporal genetic methods and found a negative relationship between N_e/N_c and N_c similar to what was found here. Accordingly, Beebee (2009) found a negative relationship for N_e/N_c and N_c. Similar findings have been reported elsewhere (Pray et al. 1996; Ficetola et al. 2010). Palstra and Ruzzante (2008) attributed this negative relationship between N_e/N_c and N_c to genetic compensation, which is a higher than expected N_e at low values of N_c because reproductive variance may be lower in small populations. Ardren and Kapuscinski (2003) reached the same conclusion in their study. However, reproductive variance may not decrease in smaller populations, as suggested by Lande et al. (2003) reproductive variance is actually expected to increase in smaller populations. Furthermore, as pointed out by Palstra and Ruzzante (2008), the negative relationship between N_c and N_e/N_c might be a mathematical artifact of plotting a fraction against its denominator. The positive relationship between N_e/N_c and N_c obtained for ONeSAMP thus seems inconsistent with previous studies. The explanation could of course be that the upward bias in the ONeSAMP method previously mentioned is increasing with N_c (see Fig. 3b), and this explains the relatively higher N_e values at higher values of N_c. This is consistent with results obtained by Phillipsen et al. (2011) and Haag et al. (2010), which found a positive relationship between sample size and N_e/N_c for this estimator.

For the two temporal methods my analyses also showed a positive effect of population growth rate on N_e/N_c. Because the temporal methods estimate N_{eV}, which is predicted to closely follow changes in N_c (see above; Crow and Denniston 1988), the positive effect of population growth rate is as expected from theory.

Sex ratio

A prediction from Wright's theory is that a skewed sex ratio will decrease N_e toward the effective size for the rarest sex (Wright 1931; Wright 1938). Individuals of the rare sex have relatively higher reproductive success than individuals of the common sex, leading to an overall increase in variance in reproductive success, causing a reduction in N_e (Wright 1938). Empirical studies have reported that unequal sex ratio had a negative effect on N_e/N_c (Frankham 1995). However, the effect of sex ratio on N_e/N_c needs to be viewed in light of variance in reproductive success and mating system (Nunney 1993). The house sparrow mating system is likely some sort of dominance polygyny, resulting in higher variance in reproductive success for males than females (Anderson 2006). Accordingly, in this study system a clutch often has more than one genetic father (Larsen et al. manuscript) causing considerable variation in mating success among males (Jensen et al. 2008). As a consequence, a higher proportion of variation in lifetime reproductive success seems to be explained by variation in annual reproductive success for males than for females in this metapopulation system (Jensen et al. 2004). For species with dominance polygyny it is expected that the maximum value of N_e/N_c is obtained in a male biased population (Nunney 1993). This is concordant with the results for the LDNE method, where sex ratio (i.e. proportion of males) affected N_e/N_c positively (Table 3a). However, for MLNE the opposite result was found (Table 5a). This could be due to confounding effects of the other parameters included in the model (population size, immigration and population growth rate), as other factors could influence the relationship between sex ratio and N_e/N_c.

Immigration

Immigration rate had a positive effect on N_e/N_c for three of the estimators: LDNE, MLNE and CoNe (Table3a, Table 5). This should be seen in the context of violating the assumption of a closed population mentioned above and thus be interpreted as a confirmation of positive bias of N_e estimates due to immigration. In any case, this positive relationship between immigration rate and N_e/N_c could be a direct consequence of the increased genetic variation introduced by immigrants. The effect of immigration depends on the genetic differentiation between the source population and recipient population. An average F_{ST} value of 0.02 have been reported for this metapopulation, indicating little or moderate genetic differentiation (Kristiansen et al. manuscript). Immigration rates thus seems low enough to uphold genetic differentiation across populations in this metapopulation system, but high enough that immigration is an important factor reducing the effect of genetic drift in each island population. Given the consistent effect of immigration on N_e/N_c across estimators it would be interesting to know the metapopulation N_e. However, this may be very difficult to estimate as the metapopulation N_e is not equal to the sum of all the subpopulation N_e-values

(Hedrick and Gilpin 1997). Under Wright's island model, N_e for a metapopulation is actually higher than the equivalent panmictic population. However, if extinction-recolonization dynamics are accounted for, metapopulation N_e will be smaller than its panmictic counterpart (Hedrick and Gilpin 1997; Whitlock and Barton 1997; Ovaskainen and Hanski 2004). Trying to estimate metapopulation N_e would nevertheless be an important extension of the present study, because my results strongly indicates the importance of identifying the proper spatial scale for estimating N_e; if unaware of metapopulation dynamics one might risk either overestimating local N_e or underestimating metapopulation N_e (see also Fraser et al. 2007; Palstra and Ruzzante 2011).

Conclusions and implications

The four genetic estimators used in this study all seemed to suffer from a considerable upward bias, but LDNE less so. Given that LDNE is also a simpler estimator to use than the other methods because it requires only one sample in time and the estimation procedure is user friendly, LDNE may be a better choice than the other estimators. If genetic N_e is estimated with proper caution shown with respect to potential biases or imprecisions, then information on N_e can be used to guide management decisions (Leberg 2005). Identifying N_e is vital for conservation biologists, but not sufficient. The factors causing low values of N_e also need to be identified (Wang 2009), as well as knowledge of how N_e can be maximized by management. From my analyses it is clear that population size itself is an important factor, as N_e increased with N_c for all estimators. Frankham (1995) and Vucetich et al. (1997) conclude that fluctuations in population size is the most important factor responsible for depressing the N_e/N_c ratio. Immigration had a positive effect on N_e/N_c, thus facilitating gene flow in fragmented habitats may be an important conservation measure to reduce loss of genetic variation. I suggest that more effort should be put into estimating N_e for metapopulations, both with respect to N_e for the local populations and for the total metapopulation. Because more populations will become fragmented in the future and metapopulation structure will be more common, increasing our understanding of how different factors affect the rate of genetic drift in such populations will be essential (Hedrick and Gilpin 1997).

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TABLES

Table 1: Notation used.

H_e	Expected heterozygosity
LD	Linkage disequilibrium
ML	Maximum likelihood
ABC	Approximate Bayesian computation
CV	Coefficient of variation
N_e	Effective population size
N_c	Census population size
N_{eI}	Inbreeding effective population size
N_{eV}	Variance effective population size
N_H	Harmonic mean population size
$\widehat{N}_e$	Estimate of effective population size
$\widehat{N}_{e(LDNE)}$	Estimate of effective population size from the linkage disequilibrium method
$\widehat{N}_{e(ONeSAMP)}$	Estimate of effective population size from the ABC method
$\widehat{N}_{e(MLNE)}$	Estimate of effective population size from the pseudo-maximum-likelihood method
$\widehat{N}_{e(CoNe)}$	Estimate of effective population size from the coalescent based method
$\widehat{N}_{e(demographic)}$	Estimate of effective population size from the demographic method
SR	Sex ratio (the proportion of males in the population)
$\frac{dN}{dt}$	Population growth rate
$\sigma^2_{N_C}$	Temporal variance in population size
m	Immigration rate
T	Number of generations

Table 2: Modeling variation in $\widehat{N}_{e(LDNE)}/N_c$ and $\widehat{N}_{e(ONeSAMP)}/N_c$ as a function of population size (N_c), sex ratio (SR), variance in population size ($\sigma^2_{N_c}$), immigration rate (m), population growth rate (dN/dt), the interaction between N_c and SR, the interaction between N_c and m, and intercept (β_0). The global models are model 6 and 3, respectively. Models nested within the global models were tested (52 for $\widehat{N}_{e(LDNE)}/N_c$ and 52 for $\widehat{N}_{e(ONeSAMP)}/N_c$), however only a subset containing the "best" models along with the null model (including only intercept) and the global model are shown. K denotes the number of parameters, L is the log Likelihood of the model, AIC_C is Aikaike's information criterion for small sample sizes, Δ_i is the difference in AIC_C between the best model and model i, w_i is the Aikake weight of model i, and the evidence ratio is the evidence that the "best" model is better than model i.

Dependent variable	Mdl	Predictor variables: β_0	N_c	SR	$\sigma^2_{N_c}$	m	$\frac{dN}{dt}$	$N_c \times SR$	$N_c \times m$	K	L	AIC_C	Δ_i	w_i	ER
a) $\frac{\widehat{N}_{e(LDNE)}}{N_c}$	**1**	**X**		**X**		**X**				**3**	**-43.96**	**96.61**	**0.00**	**0.155**	**1.00**
	2	X	X	X		X		X		5	-41.87	97.24	0.63	0.114	1.36
	3	X		X		X	X			4	-43.26	97.57	0.96	0.096	1.61
	4	X	X	X		X				4	-43.34	97.72	1.11	0.089	1.74
	5	X	X	X		X	X	X		6	-40.99	98.02	1.41	0.077	2.01
	6	X	X	X	X	X	X	X	X	8	-40.70	102.79	6.18	0.007	22.14
	7	X								1	-57.53	119.06	22.44	0.000	∞
b) $\frac{\widehat{N}_{e(ONeSAMP)}}{N_c}$	**1**	**X**	**X**							**2**	**-20.41**	**47.19**	**0.00**	**0.227**	**1.00**
	2	X	X		X					3	-19.96	48.55	1.36	0.115	1.97
	3	X	X	X	X	X	X	X	X	8	-19.13	59.37	12.18	0.001	227.00
	4	X								1	-33.14	70.28	23.09	$2.2\text{x}10^{-6}$	103181

Table 3: Parameter estimates (coefficient) for explanatory variables for the "best" generalized linear models (GLMs) explaining variance in the relationship between population characteristics and a) $\widehat{N}_{e(LDNE)}/N_c$ and b) $\widehat{N}_{e(ONeSAMP)}/N_c$, respectively. Explanatory variables included in the "best" models were sex ratio (*SR*) and immigration rate (*m*) for $\widehat{N}_{e(LDNE)}/N_c$, and census population size (N_c) for $\widehat{N}_{e(ONeSAMP)}/N_c$ (see Table 2). *SE* is the standard error of the parameter estimates. All the explanatory variables are continuous so that the associated coefficient values indicates whether $\widehat{N}_e/N_c$ increases ($\beta>0$) or decreases ($\beta<0$) with increased values of the explanatory variables.

Model	Variable	Coefficient	*SE*	*p*-value
a) $\frac{\widehat{N}_{e(LDNE)}}{N_c} = \beta_0 + \beta_1 SR + \beta_2 m + e$	**Intercept**	$\beta_0 = -0.502$	0.368	0.178
	SR	$\beta_1 = 2.083$	0.674	0.003
	m	$\beta_2 = 6.563$	1.489	<0.001
b) $\frac{\widehat{N}_{e(ONeSAMP)}}{N_c} = \beta_0 + \beta_1 N_c + e$	**Intercept**	$\beta_0 = 0.934$	0.066	<<0.001
	$\boldsymbol{N_c}$	$\beta_1 = 0.007$	0.001	<0.001

Table 4: Modeling variation in $\widehat{N}_{e(MLNE)}/N_H$ and $\widehat{N}_{e(CoNe)}/N_H$ as a function of population size (N_H), sex ratio (SR), variance in population size ($\sigma^2_{N_c}$), immigration rate (m), number of generations (T), population growth rate (dN/dt), interaction between N_H and SR, interaction between N_H and m, and intercept (β_0). Models (Mdl) number 12 and 3, respectively, are the initial, global models. Models nested within the global models were tested (104 for $\widehat{N}_{e(MLNE)}/N_H$ and 104 for $\widehat{N}_{e(CoNe)}/N_H$), however only a subset containing the "best" models along with the null model (including only intercept) and the global model are shown. K denotes the number of parameters, L is the log likelihood of the model, AIC_C is Aikaike's information criterion for small sample sizes, Δ_i is the difference in AIC_C between the best model and model i, w_i is the Aikake weight of model i, and the evidence ratio (ER) is the evidence that the "best" model is better than model i.

Dependent variable	Mdl	Predictor variables									K	L	AIC_C	Δ_i	w_i	ER
		β_0	N_H	SR	$\sigma^2_{N_C}$	m	T	$\frac{dN}{dt}$	$N_H \times SR$	$N_H \times m$						
a) $\frac{\widehat{N}_{e(MLNE)}}{N_H}$	**1**	**X**	**X**	**X**		**X**		**X**			**5**	**-93.70**	**200.47**	**0.00**	**0.072**	**1.00**
	2	X	X	X	X	X		X		X	7	-91.35	200.56	0.09	0.069	1.04
	3	X	X	X	X	X		X			6	-92.61	200.65	0.18	0.066	1.09
	4	X	X	X	X	X		X	X	X	8	-90.44	201.25	0.78	0.049	1.47
	5	X	X	X		X		X		X	6	-92.91	201.25	0.78	0.049	1.47
	6	X	X	X	X	X				X	6	-92.93	201.30	0.83	0.048	1.50
	7	X	X	X	X	X					5	-94.22	201.50	1.03	0.043	1.67
	8	X	X	X		X		X	X		6	-93.23	201.89	1.42	0.035	2.06
	9	X	X	X		X		X	X	X	7	-92.10	201.97	1.50	0.034	2.12
	10	X	X	X	X	X		X	X		7	-92.17	202.21	1.74	0.030	2.40
	11	X	X	X	X	X			X	X	7	-92.26	202.38	1.91	0.028	2.57
	12	X	X	X	X	X	X	X	X	X	9	-90.44	203.82	3.35	0.014	5.14
	13	X									1	-112.50	229.01	28.53	$4.6\text{x}10^{-8}$	1.6×10^{6}
b) $\frac{\widehat{N}_{e(CoNe)}}{N_H}$	**1**	**X**	**X**			**X**		**X**		**X**	**5**	**-70.64**	**155.44**	**0.00**	**0.232**	**1.00**
	2	X	X		X	X		X		X	5	-69.64	156.23	0.79	0.156	1.49
	3	X	X	X	X	X	X	X	X	X	9	-67.42	161.13	5.69	0.013	17.85
	4	X									1	-98.78	201.56	46.12	0.000	∞

Table 5: Parameter estimates (coefficient) for explanatory variables included in the "best" generalized linear models (GLMs) explaining variance in the relationship between population characteristics and a) $\widehat{N}_{e(MLNE)}/N_H$ and c) $\widehat{N}_{e(CoNe)}/N_H$, respectively. Explanatory variables included in the "best" models were population size (N_H), sex ratio (SR), immigration rate (m) and population growth rate (dN/dt) for $\widehat{N}_{e(MLNE)}/N_H$, and population size ($N_H$),variance in population size ($\sigma^2_{N_c}$), immigration rate (m) and $N_H \times m$ for $\widehat{N}_{e(CoNe)}/N_H$ (see Table 4). *SE* is the standard error of the parameter estimates. All the explanatory variables are continuous so that the associated coefficient values indicates whether $\widehat{N}_e/N_H$ increases ($\beta>0$) or decreases ($\beta<0$) with increased values of the explanatory variables.

Model	Variable	Coefficient	*SE*	*p*-value
a) $\frac{\widehat{N}_{e(MLNE)}}{N_H} = \beta_0 + \beta_1 N_H + \beta_2 SR + \beta_3 m + \beta_4 \frac{dN}{dt} + e$	**Intercept**	$\beta_0 = 4.352$	0.787	<0.001
	$\boldsymbol{N_H}$	$\beta_1 = -0.017$	0.003	<0.001
	SR	$\beta_2 = -2.992$	1.369	0.032
	m	$\beta_3 = 7.004$	2.646	0.010
	$\boldsymbol{\frac{dN}{dt}}$	$\beta_4 = 0.260$	0.120	0.033
b) $\frac{\widehat{N}_{e(CoNe)}}{N_H} = \beta_0 + \beta_1 N_H + \beta_2 m + \beta_3 \frac{dN}{dt} + \beta_4 N_H \times m + e$	**Intercept**	$\beta_0 = 2.574$	0.600	<0.001
	$\boldsymbol{N_H}$	$\beta_1 = -0.015$	0.011	0.197
	m	$\beta_2 = 52.220$	10.268	<<0.001
	$\boldsymbol{\frac{dN}{dt}}$	$\beta_3 = 0.938$	0.310	0.004
	$\boldsymbol{N_H \times m}$	$\beta_4 = -0.549$	0.248	0.032

FIGURES

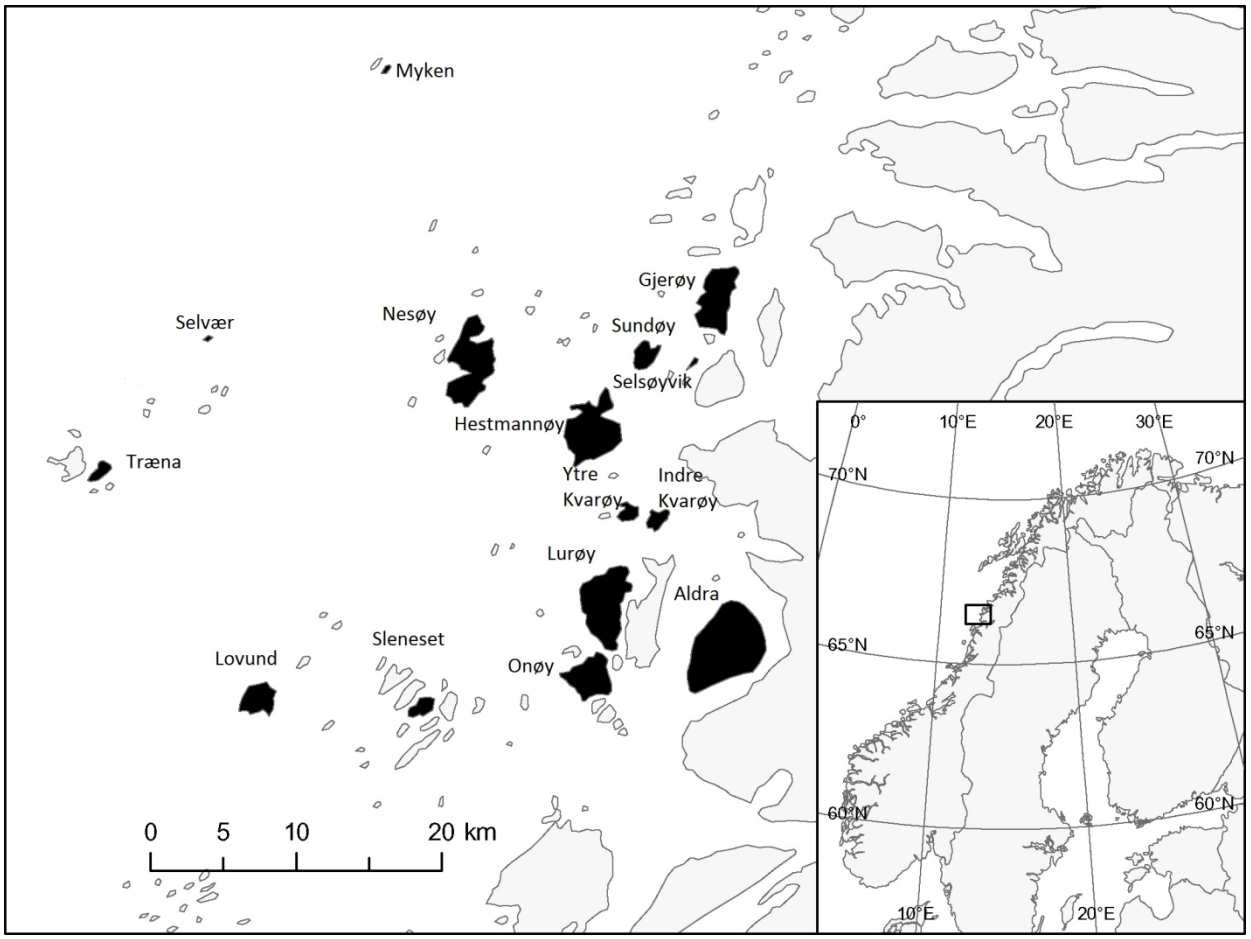

Figure 1: The study system off the coast of Northern Norway. The 15 islands included in this study are named and shown in black.

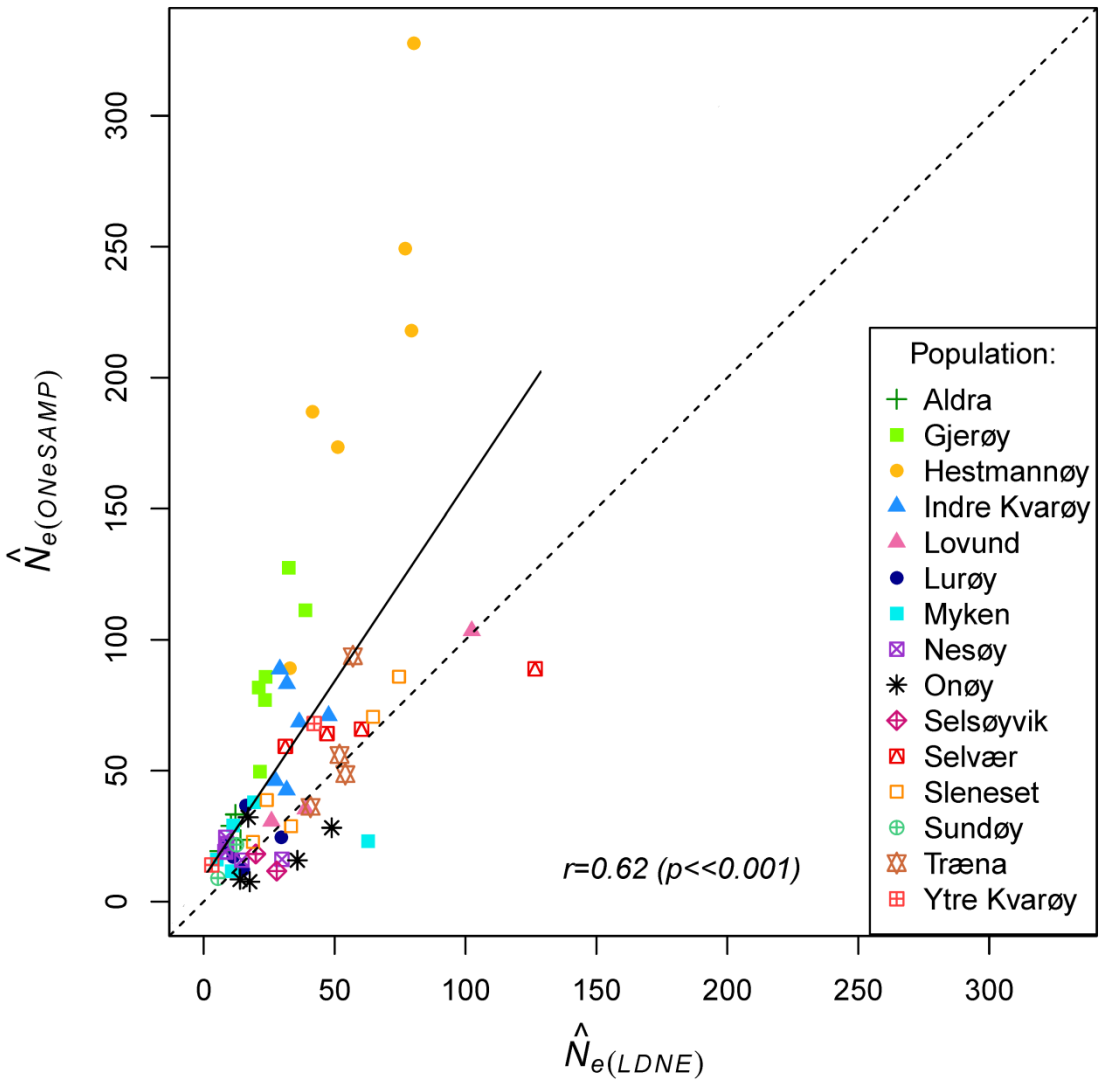

Figure 2: The relationship between $\hat{N}_{e(ONeSAMP)}$ and $\hat{N}_{e(LDNE)}$. Pearson's correlation coefficient *r* is shown along with its associated *p*-value. The solid line represents the correlation, whereas the dotted line represents a perfect 1:1 relationship. Each population is represented by a unique symbol; for each island there are multiple estimates spaced by three years.

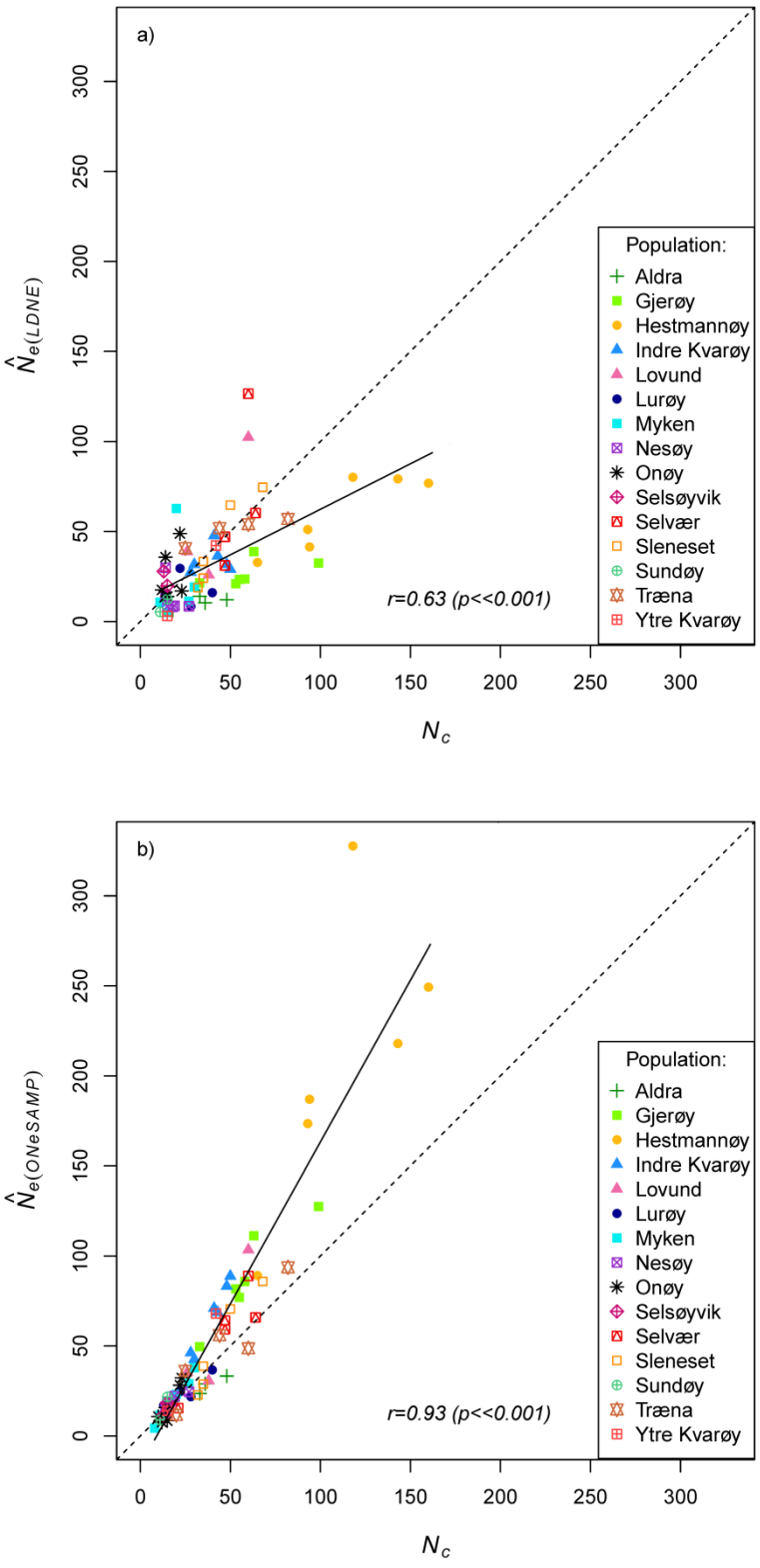

Figure 3: The relationship between a) $\hat{N}_{e(LDNE)}$ and N_c and b) $\hat{N}_{e(ONeSAMP)}$ and N_c. Pearson's correlation coefficient *r* is shown along with its associated p-value in each figure. The solid line represents the correlation, whereas the dotted line represents a perfect 1:1 relationship. Each population is represented by a unique symbol; for each island there are multiple estimates spaces by three years.

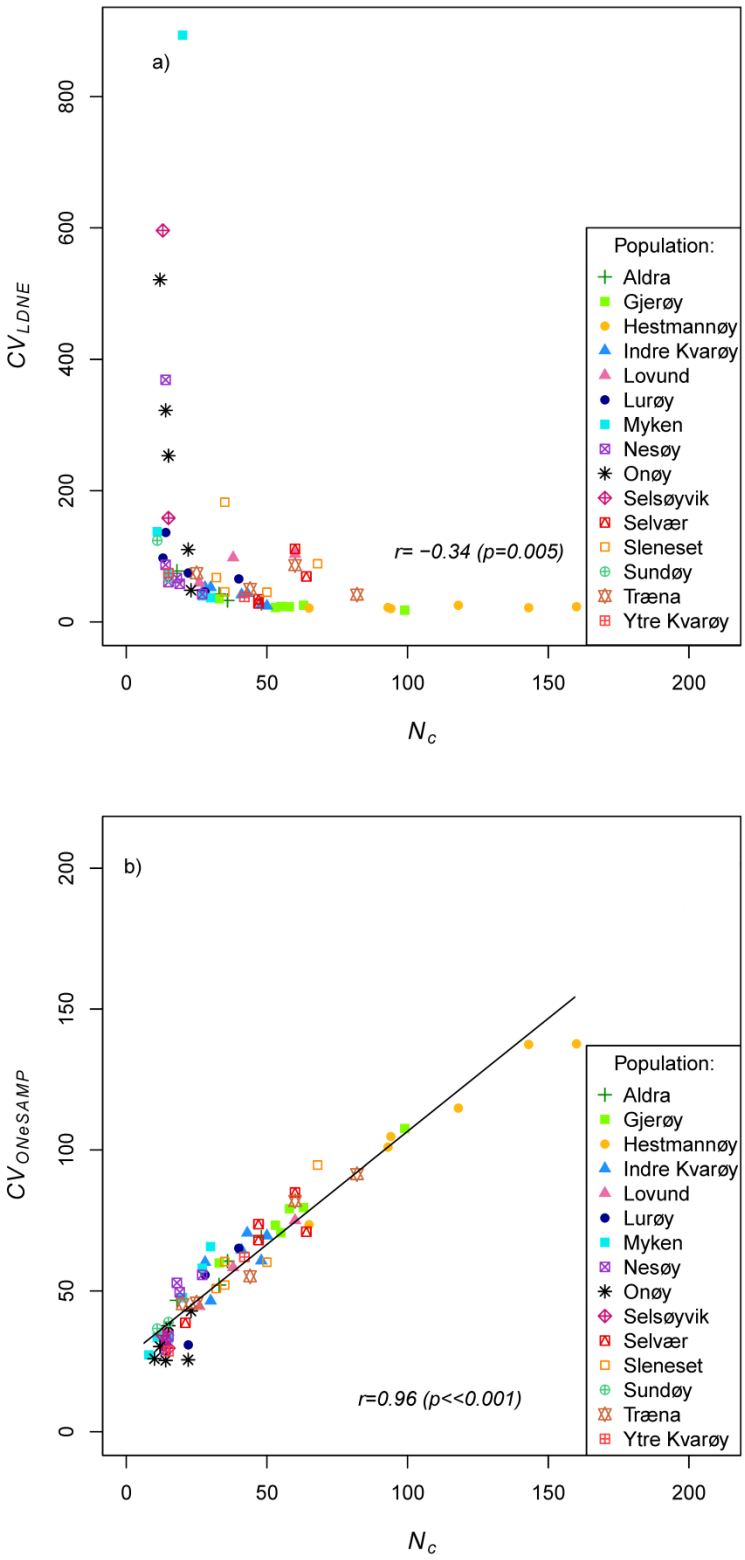

Figure 4: The precision (*CV*) in the single sample $\widehat{N}_e$ plotted against N_c with the correlation between the two variables represented by the solid line. Pearson's correlation coefficient (*r*) is shown along with the associated *p*-value. Each population is represented by a unique symbol; for confidence limits for the different estimates, see Table A3. Notice different scales on the y-axis for a) and b).

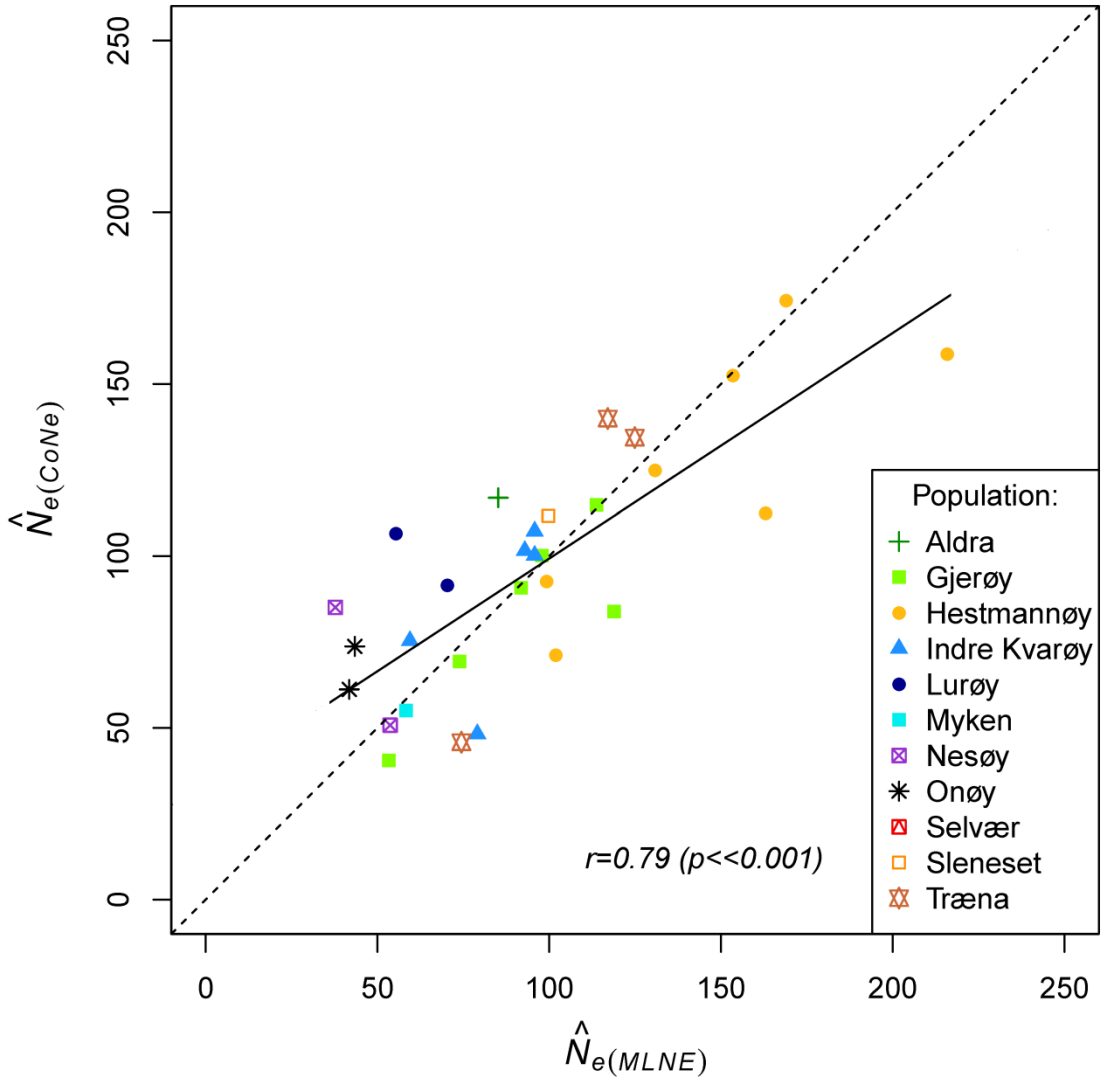

Figure 5: The relationship between $\hat{N}_{e(CoNe)}$ and $\hat{N}_{e(MLNE)}$. Pearson's correlation coefficient *r* is shown along with its associated *p*-value. The solid line represents the correlation, whereas the dotted line represents a perfect 1:1 relationship. Each population is represented by a unique symbol; there are several estimates for each population for different combinations of years, see table A4. Notice that there are only 11 populations.

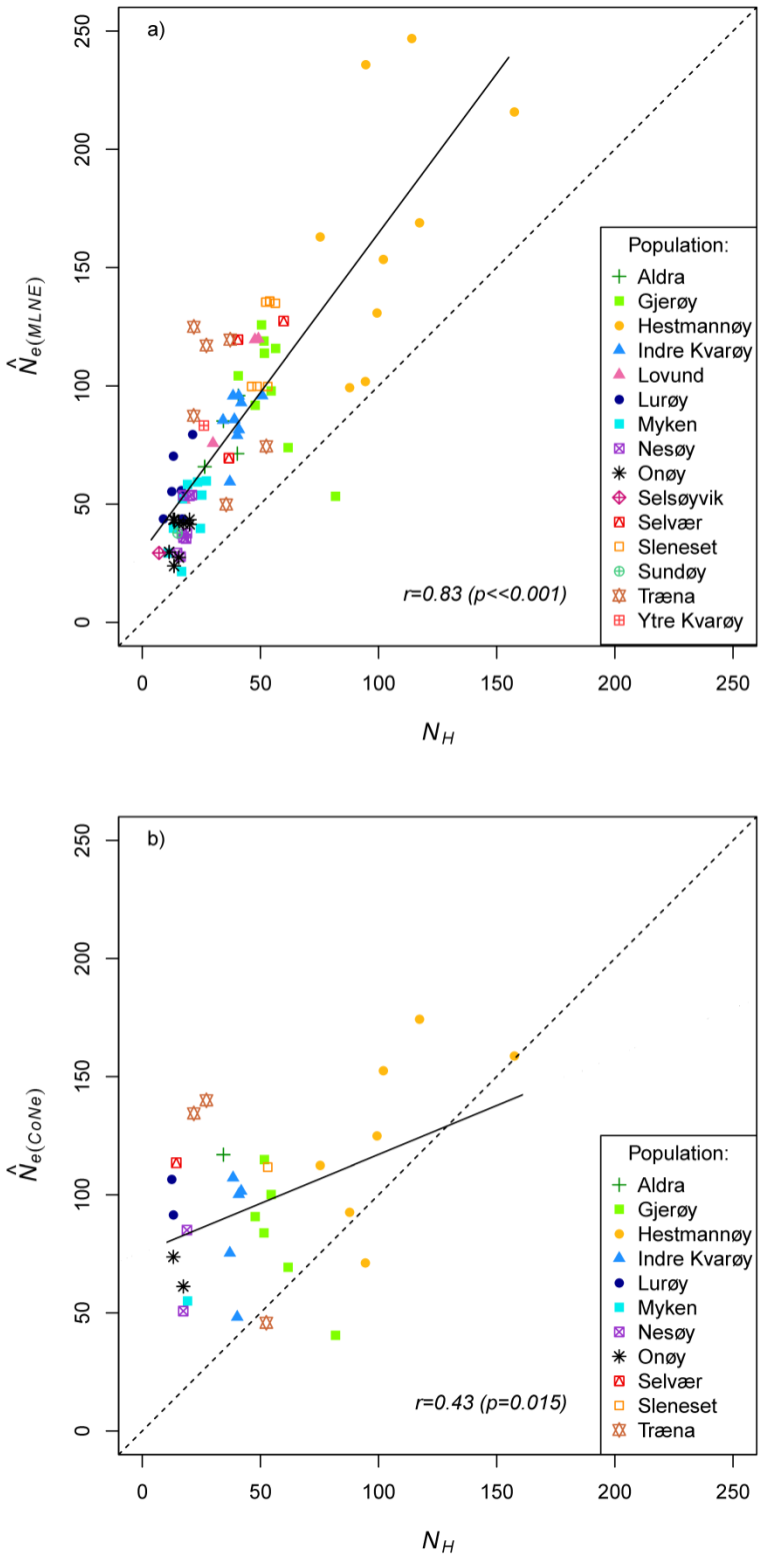

Figure 6: The relationship between a) $\widehat{N}_{e(MLNE)}$ and N_H and b) $\widehat{N}_{e(CoNe)}$ and N_H. Pearson's correlation coefficient *r* is shown along with its associated p-value in each figure. The solid line represents the correlation, whereas the dotted line represents a perfect 1:1 relationship. Each population is represented by a unique symbol; there are several estimates for each population for different combinations of years, see table A4. Notice that in b) there are only 11 populations.

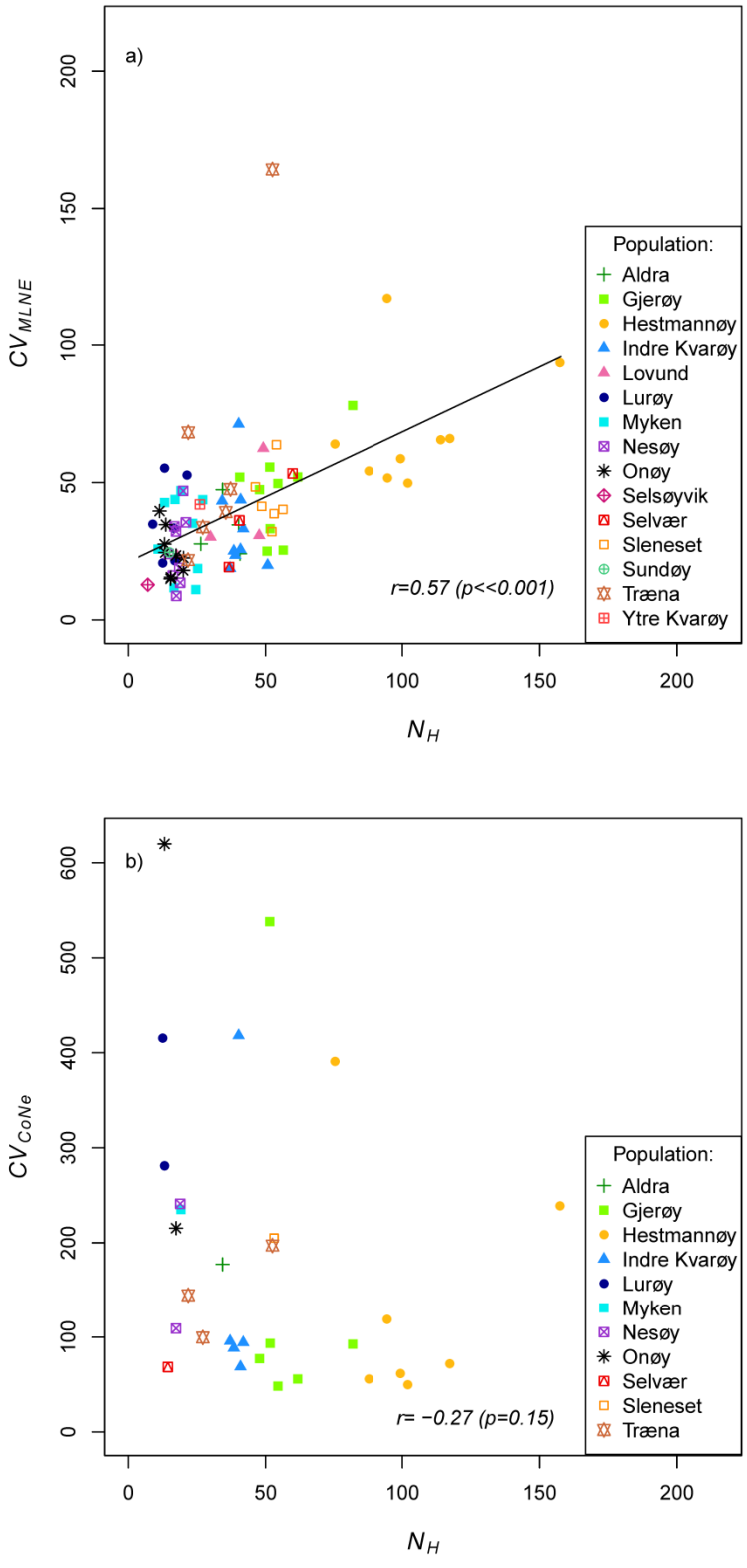

Figure 7: The precision (*CV*) in the temporal $\widehat{N}_e$ plotted against N_H with the correlation between the two variables represented by the solid line. Pearson's correlation coefficient (*r*) is shown along with the associated *p*-value. Each population is represented by a unique symbol; for confidence limits for the different estimates, see table A4. Notice different scales on the y-axis for a) and b).

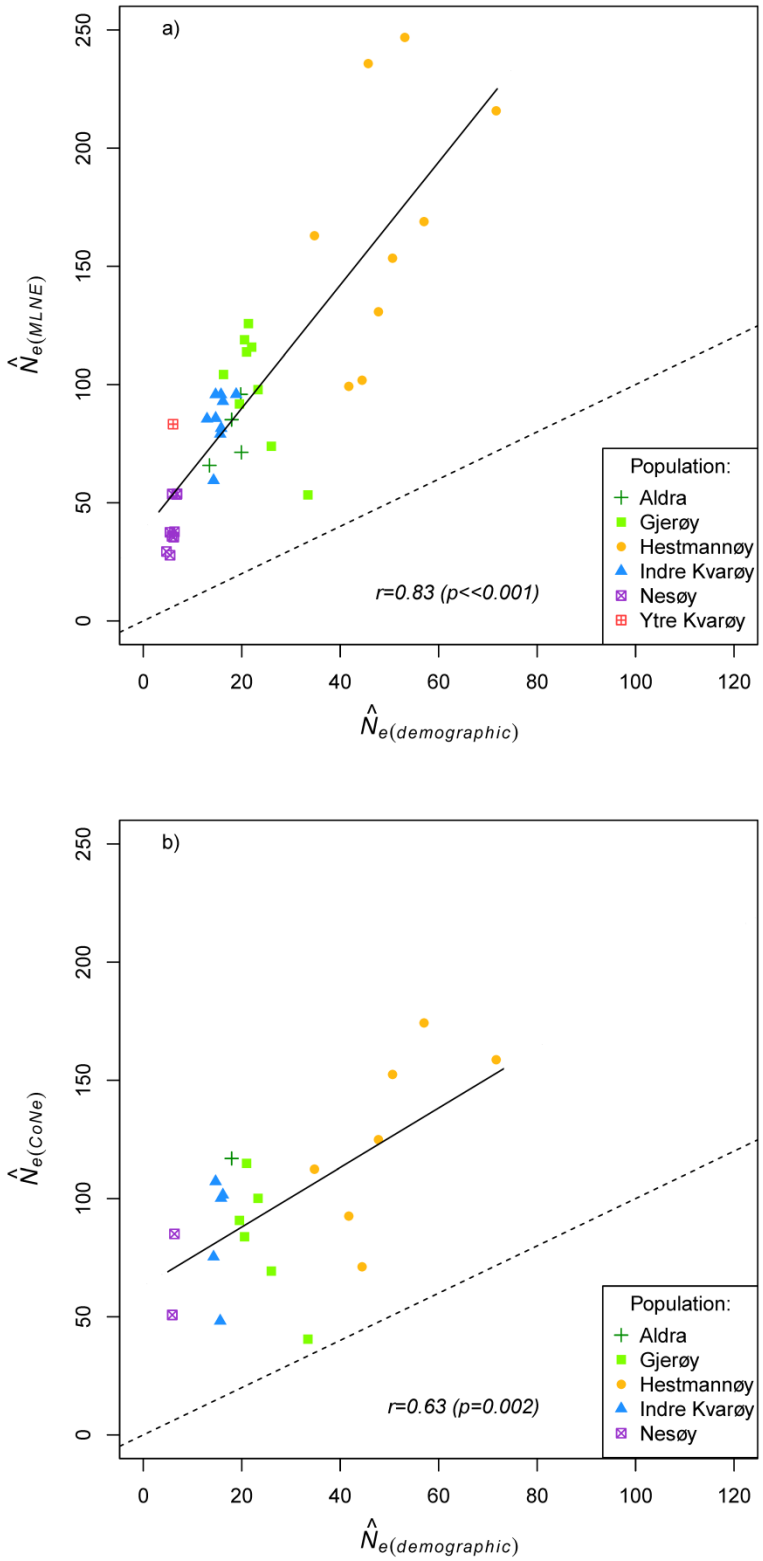

Figure 8: The relationship between a) $\hat{N}_{e(MLNE)}$ and $\hat{N}_{e(demographic)}$ and b) $\hat{N}_{e(CoNe)}$ and $\hat{N}_{e(demographic)}$. Pearson's correlation coefficient *r* is shown along with its associated *p*-value in each figure. The solid line represents the correlation, whereas the dotted line represents a perfect 1:1 relationship. Each population is represented by a unique symbol; there are several estimates for each population for different combinations of years, see table A4. Notice that in a) there are 6 populations, whereas in b) there are only 5 populations.

APPENDIX 1: MISSING/EXCLUDED DATA

Table A1: Data excluded from the ONeSAMP analyses due to individuals with too few genotypes and/or loci with too little information. Population and year is given where the sample size is reduced, with ring number of the excluded individual and/or the excluded loci.

Population	Year	Excluded individual	Excluded locus
Aldra	2000	-	Pdo19
Gjerøy	2000	8681361	-
Gjerøy	2009	8L89161	Ase18
Hestmannøy	2000	8732651	-
Hestmannøy	2009	-	Ase18
Lovund	2009	-	Ase18
Onøy	2009	-	Ase18
Selsøyvik	2009	-	Ase18
Selvær	2009	-	Ase18
Sleneset	2009	-	Ase18
Sundøy	1994	-	Pdo20
Sundøy	1997	-	Pdo21
Træna	2006	8L30301	-
Træna	2009	8981657	-
Træna	2009	-	Ase18

The ONeSAMP method requires that monomorphic loci or individuals with missing data at two or more loci are excluded from the data set. Table A1 shows which individuals and/or loci that were removed.

For the single sample estimators (LDNE and ONeSAMP), 5 and 2 data points were removed, respectively, due to missing data on one or more of the predictor variables (Table A2). These data points were excluded from the dataset used in analyses of population characteristics and N_e/N_c, but included in the correlation between estimators and N_c, and variance in estimators and N_c.

For the CoNe method 37 estimates had infinite upper confidence limits (Table A2). These estimates were excluded from the correlations between $\widehat{N}_{e(CoNe)}$ and $\widehat{N}_{e(MLNE)}$, N_H, $\widehat{N}_{e(demographic)}$, respectively. However, these estimates were included in the GLM explaining variance in $\widehat{N}_{e(CoNe)}/N_H$. This was a result of a trade-off between precision and sample size; excluding 37 estimates would have given the GLM little power in explaining $\widehat{N}_{e(CoNe)}/N_H$, but it is important to note that many of these estimates are extremely uncertain.

For the temporal estimators MLNE and CoNe, 3 and 5 outliers were removed, respectively, because the residuals were more than 2 standard deviations from the mean (Table A2). For both methods 3 of the removed estimates were for the Selvær population. Selvær

experienced a severe bottleneck event in year 2000, effectively going extinct with only 4 males present on the island. However, the population quickly recovered by receiving immigrants from nearby islands. So the estimates that span this bottleneck event but do not include samples from the years when the bottleneck took place may overestimate N_e for this interval. N_H on the other hand will be depressed by this bottleneck. The result is N_e/N_H values that are beyond what is reasonable, as high as 20 (for the CoNe method). Additionally, for the CoNe method one estimate each was excluded from the Myken and Sleneset population, respectively. Although these estimates were excluded from the analyses as they were examples of extreme estimates, it does highlight a general concern with N_e estimators; without any knowledge of the history of a population, $\widehat{N}_e$ can be biased without the researcher ever detecting it. Thus, $\widehat{N}_e$ should be interpreted even more cautiously if no other information exists.

Table A2: An overview of number of possible estimates and the actual number used for the GLMs. Also given is the amount of data not included in the analyses due to infinite estimates or confidence limits, no estimates, missing data on predictor variable(s) or being defined as an outlier.

			Number of excluded data points			
Estimator	Potential number of estimates	Number of estimates in GLMs	Infinite estimate/no estimate	Infinite confidence limits	Missing data on predictor variable(s)	Outliers
LDNE	70	60	3	2	5	0
ONeSAMP	70	68	0	0	2	0
MLNE	89	86	0	0	0	3
CONE	89	46	38	19	0	5

APPENDIX 2: ESTIMATES OF EFFECTIVE POPULATION SIZE

Table A3: Estimates of effective population size (N_e) using single samples from the LDNE method and the ONeSAMP method, for 15 populations from 1994-2009, 95% confidence limits are given in brackets. Population size (N_c) and sample size for each population each year is also given. For the ONeSAMP estimator the upper prior was the census size multiplied by two.

Population	Year	N_c	Sample size	$\widehat{N}_{e(LDNE)}$	$\widehat{N}_{e(ONeSAMP)}$
Aldra	2000	18	18	6 (4-9)	19 (16-25)
Aldra	2003	33	33	14 (12-18)	24 (19-31)
Aldra	2006	36	36	10 (9-12)	29 (24-41)
Aldra	2009	48	47	12 (11-14)	33 (26-49)
Gjerøy	1994	53	52	21 (19-24)	82 (63-123)
Gjerøy	1997	33	32	22 (18-26)	50 (39-69)
Gjerøy	2000	63	61	39 (34-44)	111 (84-173)
Gjerøy	2003	55	46	23 (21-26)	77 (62-116)
Gjerøy	2006	58	55	24 (21-27)	86 (68-135)
Gjerøy	2009	99	94	33 (30-36)	128 (97-234)
Hestmannøy	1994	93	87	51 (46-57)	174 (122-298)
Hestmannøy	1997	65	65	33 (30-37)	89 (71-136)
Hestmannøy	2000	118	111	80 (71-91)	328 (238-615)
Hestmannøy	2003	94	86	42 (38-46)	187 (137-334)
Hestmannøy	2006	143	138	79 (71-89)	218 (148-448)
Hestmannøy	2009	160	129	77 (69-87)	249 (173-516)
Indre Kvarøy	1994	50	50	29 (26-33)	89 (69-131)
Indre Kvarøy	1997	48	48	32 (28-36)	83 (67-117)
Indre Kvarøy	2000	28	27	27 (22-36)	46 (36-64)
Indre Kvarøy	2003	43	35	37 (30-46)	69 (54-103)
Indre Kvarøy	2006	41	39	48 (39-59)	71 (57-103)
Indre Kvarøy	2009	30	30	32 (25-42)	43 (35-55)
Lovund	2000	15	8	-	11 (10-14)
Lovund	2003	26	24	39 (30-53)	35 (31-47)
Lovund	2006	60	35	102 (71-176)	103 (78-156)
Lovund	2009	38	18	26 (18-43)	31 (25-43)
Lurøy	1994	28	22	9 (7-11)	22 (18-30)
Lurøy	1997	13	13	11 (7-18)	17 (15-20)
Lurøy	2000	22	21	30 (22-44)	25 (22-29)
Lurøy	2003	14	11	15 (9-30)	12 (11-15)
Lurøy	2006	40	18	16 (12-23)	37 (29-53)
Myken	1994	8	5	16 (3-∞)	4 (4-5)
Myken	1997	15	15	5 (3-7)	16 (14-19)

Population	Year	N_c	Sample size	$\widehat{N}_{e(LDNE)}$	$\widehat{N}_{e(ONeSAMP)}$
Myken	2000	30	30	19 (16-23)	38 (31-55)
Myken	2003	27	26	11 (9-14)	29 (24-41)
Myken	2006	20	17	63 (31-592)	23 (20-31)
Myken	2009	11	10	11 (6-21)	12 (10-14)
Nesøy	1994	18	15	8 (6-11)	19 (16-26)
Nesøy	1997	19	17	9 (7-12)	22 (18-29)
Nesøy	2000	27	23	9 (7-11)	25 (20-33)
Nesøy	2003	14	12	30 (15-126)	16 (14-19)
Nesøy	2006	14	14	15 (10-23)	16 (14-19)
Nesøy	2009	15	15	8 (6-11)	19 (16-23)
Onøy	1994	23	23	17 (14-22)	32 (27-41)
Onøy	1997	14	13	36 (19-135)	16 (14-18)
Onøy	2000	22	21	49 (33-87)	28 (25-32)
Onøy	2003	10	9	64 (20-∞)	11 (10-13)
Onøy	2006	12	7	18 (8-100)	8 (7-9)
Onøy	2009	15	8	14 (7-42)	9 (7-11)
Selsøyvik	2000	13	9	28 (14-180)	12 (10-14)
Selsøyvik	2009	15	13	20 (12-43)	18 (16-21)
Selvær	1994	47	47	31 (27-36)	59 (46-89)
Selvær	1997	47	47	47 (40-56)	64 (52-96)
Selvær	2003	21	11	-	16 (13-19)
Selvær	2006	60	40	127 (85-226)	89 (69-145)
Selvær	2009	64	34	60 (45-87)	66 (53-100)
Sleneset	1997	35	16	33 (20-81)	29 (24-41)
Sleneset	2000	50	48	65 (53-82)	71 (58-100)
Sleneset	2003	35	27	24 (20-31)	39 (31-52)
Sleneset	2006	68	32	75 (53-119)	86 (63-144)
Sleneset	2009	32	19	19 (14-27)	23 (19-31)
Sundøy	1994	11	11	5 (3-10)	9 (8-11)
Sundøy	1997	15	15	13 (9-18)	22 (19-27)
Træna	1994	60	24	54 (39-85)	49 (38-78)
Træna	1997	25	24	41 (30-60)	36 (31-47)
Træna	2000	20	8	-	12 (10-15)
Træna	2006	82	48	57 (47-71)	94 (66-152)
Træna	2009	44	38	52 (41-68)	56 (46-77)
Ytre Kvarøy	1994	42	40	42 (35-51)	68 (53-96)
Ytre Kvarøy	1997	15	15	3 (3-5)	14 (12-16)

Table A4: Estimates of effective population size (N_e) using two samples from the MLNE method and the CoNe method, for 15 populations from 1994-2009, 95% confidence limits are given in brackets. The number of generations between samples, the harmonic mean population size (N_H) and upper limit are also given. The upper limit is the maximum N_e allowed in the estimation procedure and was set as the highest census population size in each time interval multiplied by two. Sample sizes for the different populations in different years are given in Table A3.

Population	Years	Generations between samples	N_H	Upper limit	$\widehat{N}_{e(MLNE)}$	$\widehat{N}_{e(CoNe)}$
Aldra	2000-2003	1	26	66	66 (48-66)	-
Aldra	2000-2009	4	34	96	85 (56-96)	117 (68-276)
Aldra	2003-2006	1	40	72	71 (47-72)	115 (33-∞)
Aldra	2006-2009	1	41	96	96 (73-96)	-
Gjerøy	1994-1997	1	41	106	104 (52-106)	116 (40-∞)
Gjerøy	1994-2003	4	48	110	92 (66-110)	91 (64-134)
Gjerøy	1994-2009	7	54	198	98 (77-126)	100 (79-127)
Gjerøy	1997-2000	1	51	126	126 (95-126)	-
Gjerøy	1997-2006	4	52	116	114 (78-116)	115 (79-186)
Gjerøy	2000-2003	1	51	126	119 (60-126)	84 (41-492)
Gjerøy	2000-2009	4	62	198	74 (58-96)	69 (54-92)
Gjerøy	2003-2006	1	56	116	116 (87-116)	-
Gjerøy	2006-2009	1	82	198	53 (39-80)	40 (27-64)
Hestmannøy	1994-1997	1	75	186	163 (82-186)	112 (57-497)
Hestmannøy	1994-2003	4	88	188	99 (77-131)	93 (72-123)
Hestmannøy	1994-2009	7	102	320	154 (121-197)	152 (119-195)
Hestmannøy	1997-2000	1	95	236	236 (114-236)	157 (80-∞)
Hestmannøy	1997-2006	4	99	286	131 (100-177)	125 (95-172)
Hestmannøy	2000-2003	1	94	236	102 (67-186)	71 (45-130)
Hestmannøy	2000-2009	4	117	320	169 (125-237)	174 (125-251)
Hestmannøy	2003-2006	1	114	286	247 (124-286)	212 (102-∞)
Hestmannøy	2006-2009	1	157	320	216 (118-320)	159 (87-466)
Indre Kvarøy	1994-1997	1	51	96	96 (77-96)	-
Indre Kvarøy	1994-2003	4	42	96	93 (65-96)	102 (69-164)
Indre Kvarøy	1994-2009	7	41	96	96 (72-96)	100 (74-143)
Indre Kvarøy	1997-2000	1	40	96	79 (40-96)	48 (24-226)
Indre Kvarøy	1997-2006	4	38	96	96 (72-96)	107 (73-168)
Indre Kvarøy	2000-2003	1	34	86	86 (49-86)	139 (45-∞)
Indre Kvarøy	2000-2009	4	37	60	60 (49-60)	75 (51-124)
Indre Kvarøy	2003-2006	1	39	86	86 (66-86)	-
Indre Kvarøy	2006-2009	1	41	82	82 (46-82)	117 (38-∞)
Lovund	2000-2003	1	18	52	52 (40-52)	-
Lovund	2000-2009	4	30	76	76 (53-76)	-
Lovund	2003-2006	1	48	120	120 (83-120)	-
Lovund	2006-2009	1	49	120	120 (45-120)	85 (27-∞)
Lurøy	1994-1997	1	17	56	56 (37-56)	-

Population	Years	Generations between samples	N_H	Upper limit	$\widehat{N}_{e(MLNE)}$	$\widehat{N}_{e(CoNe)}$
Lurøy	1994-2003	4	12	56	55 (45-56)	107 (54-497)
Lurøy	1997-2000	1	17	44	44 (35-44)	-
Lurøy	1997-2006	4	13	80	70 (41-80)	92 (49-307)
Lurøy	2000-2003	1	9	44	44 (29-44)	71 (20-∞)
Lurøy	2003-2006	1	21	80	80 (38-80)	-
Myken	1994-1997	1	11	30	29 (22-30)	-
Myken	1994-2003	4	17	54	52 (31-54)	190 (62-∞)
Myken	1994-2009	7	17	22	22 (20-22)	-
Myken	1997-2000	1	23	60	59 (39-60)	-
Myken	1997-2006	4	25	40	40 (36-40)	1322 (123-∞)
Myken	2000-2003	1	27	60	60 (34-60)	106 (28-∞)
Myken	2000-2009	4	19	60	58 (33-60)	55 (30-159)
Myken	2003-2006	1	25	54	54 (44-54)	-
Myken	2006-2009	1	13	40	40 (23-40)	79 (15-∞)
Nesøy	1994-1997	1	17	38	38 (25-38)	239 (26-∞)
Nesøy	1994-2003	4	19	36	35 (29-36)	-
Nesøy	1994-2009	7	17	36	36 (33-36)	-
Nesøy	1997-2000	1	21	54	54 (35-54)	-
Nesøy	1997-2006	4	19	38	38 (33-38)	85 (47-252)
Nesøy	2000-2003	1	20	54	54 (29-54)	32 (14-∞)
Nesøy	2000-2009	4	17	54	54 (37-54)	51 (33-88)
Nesøy	2003-2006	1	16	28	28 (24-28)	-
Nesøy	2006-2009	1	15	30	29 (23-30)	-
Onøy	1994-1997	1	20	42	42 (33-42)	-
Onøy	1994-2003	4	17	42	42 (32-42)	61 (34-166)
Onøy	1994-2009	7	15	42	42 (36-42)	-
Onøy	1997-2000	1	20	44	43 (36-44)	-
Onøy	1997-2006	4	15	28	28 (24-28)	-
Onøy	2000-2003	1	14	44	43 (29-44)	-
Onøy	2000-2009	4	13	44	43 (32-44)	74 (35-492)
Onøy	2003-2006	1	13	24	24 (18-24)	-
Onøy	2006-2009	1	11	30	30 (18-30)	-
Selsøyvik	2000-2009	4	7	30	29 (26-30)	-
Selvær	1994-1997	1	37	70	70 (57-70)	160 (58-∞)
Selvær	1994-2003	4	10	64	64 (50-64)	107 (53-477)
Selvær	1994-2009	7	14	128	109 (80-128)	114 (83-161)
Selvær	1997-2006	4	10	120	119 (98-120)	206 (121-459)
Selvær	2003-2006	1	40	120	120 (77-120)	-
Selvær	2006-2009	1	60	128	127 (60-128)	369 (56-∞)
Sleneset	1997-2000	1	49	100	100 (59-100)	-
Sleneset	1997-2006	4	52	136	135 (93-136)	581 (151-∞)
Sleneset	2000-2003	1	46	100	100 (52-100)	156 (42-∞)
Sleneset	2000-2009	4	53	100	100 (61-100)	112 (62-290)

Population	Years	Generations between samples	N_H	Upper limit	$\widehat{N}_{e(MLNE)}$	$\widehat{N}_{e(CoNe)}$
Sleneset	2003-2006	1	56	136	135 (82-136)	-
Sleneset	2006-2009	1	54	136	136 (49-136)	-
Sundøy	1994-1997	1	15	38	38 (29-38)	-
Træna	1994-1997	1	37	120	120 (63-120)	-
Træna	1994-2009	7	27	120	117 (81-120)	140 (94-234)
Træna	1997-2000	1	36	50	50 (30-50)	158 (20-∞)
Træna	1997-2006	4	22	164	125 (79-164)	134 (83-277)
Træna	2000-2009	4	22	88	87 (69-88)	-
Træna	2006-2009	1	52	164	74 (42-164)	46 (26-116)
Ytre Kvarøy	1994-1997	1	26	84	83 (49-84)	-