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Effective/census population size ratio estimation: a compendium and appraisal

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Abstract

With an ecological-evolutionary perspective increasingly applied toward the conservation and management of endangered or exploited species, the genetic estimation of effective population size (N_e) has proliferated. Based on a comprehensive analysis of empirical literature from the past two decades, we asked: (i) how often do studies link N_e to the adult census population size (N)? (ii) To what extent is N_e correctly linked to N? (iii) How readily is uncertainty accounted for in both N_e and N when quantifying N_e/N ratios? and (iv) how frequently and to what degree might errors in the estimation of N_e or N affect inferences of N_e/N ratios? We found that only 20% of available N_e estimates (508 of 2617; 233 studies) explicitly attempted to link N_e and N; of these, only 31% (160 of 508) correctly linked N_e and N. Moreover, only 7% (41 of 508) of N_e/N ratios (correctly linked or not) reported confidence intervals for both N_e and N; for those cases where confidence intervals were reported for N_e only, 31% of N_e/N ratios overlapped with 1, of which more than half also reached below $N_e/N = 0.01$. Uncertainty in N_e/N ratios thus sometimes spanned at least two orders of magnitude. We conclude that the estimation of N_e/N ratios in natural populations could be significantly improved, discuss several options for doing so, and briefly outline some future research directions.

Background: why are effective and census population sizes important?

In many research instances in ecology and evolution, two important variables to be estimated in natural populations are the effective population size (N_e) and the adult census size (N). As species ranges and abundances are continuously fragmented and/or reduced by human-induced environmental change, N_e and N will play key roles in determining the degree to which populations can avoid extinction from demographically, environmentally, or genetically stochastic events, such as temporary recruitment failures, environmental catastrophes, inbreeding depression, or a loss of genetic diversity at low population size (Soulé 1987; Boyce 1992; Frankham et al. 2003). Effective population size may also dictate whether populations can maintain adequate genetic variance for adaptive evolution in quantitative traits, and hence will affect responses to environmental change (Franklin 1980; Lynch and Lande 1997; Newman and Pilson 1997).

Knowledge of the relative magnitudes of these two parameters, as expressed by the ratio N_e/N, is important for disentangling the relative risks that demographic, environmental, and genetic factors might pose for population persistence, particularly because N_e is generally much lower than N in natural populations (Frankham 1995; Palstra and Ruzzante 2008). Understanding N_e/N ratios may also reveal what ecological factors drive N_e below N, insights which might facilitate more effective conservation and management decision-making (Kalinowski and Waples 2002). If simple conversions exist between N_e and N among taxonomic groups or intraspecific populations, much time and money could also be saved on the estimation of one variable to infer both (Luikart et al. 2010). Yet, several recent studies have suggested that no simple relationship between N_e and N may exist, either because

of habitat factors or because of population expansion and contraction (Ardren and Kapuscinski 2003; Watts et al. 2007; Fraser et al. 2007b; Belmar-Lucero et al. 2012).

The precision and accuracy of various N estimators have seen extensive evaluation over the past century (Ricker 1975; Seber 1982; Pollack et al. 1990); so too has the estimation of N_e from genetic data in recent years, based on theoretical considerations (England et al. 2006; Waples and Do 2008), simulations (Jorde and Ryman 2007; Waples and Yokota 2007), and empirical data (Fraser et al. 2007a; Palstra and Ruzzante 2008). Now is the time to assess (i) the extent to which studies have linked N_e to the adult census population size (N); (ii) the extent to which N_e has been correctly linked to N; (iii) the degree to which uncertainty is accounted for in both N_e and N when quantifying N_e/N ratios; and (iv) the frequency with which errors in the estimation of N_e or N affect inferences of N_e/N ratios. These objectives form the present quantitative review, which considers the state of the field of empirical N_e/N estimation and its future. Indeed, Frankham (2010) recently highlighted the updating of meta-analyses of N_e/N ratios in the wild as a top priority scientific need in conservation genetics.

Trends in published empirical estimates

Trends in N_e estimation

We extended a previously compiled database of empirical estimates on contemporary N_e within natural populations based on genetic data (Palstra and Ruzzante 2008). New estimates were added through literature searches performed in ISI Web of Science (up to April 30th 2012), using the search terms "effective population size" and "microsatellites" or "allozymes", and by performing queries on citations of key articles, usually on the methodology of estimating contemporary N_e. We also browsed the Online Early sections of many relevant journals.

Our search located 2617 contemporary N_e estimates (1837 new estimates since 2008) published in 233 studies (151 new publications since 2008). A steady increase in publications reporting N_e estimates has occurred over the past 20 years (Fig. 1a), since empirical methods for estimating contemporary N_e started being applied using genetic data. Recent years have seen the development (Tallmon et al. 2008; Wang 2009) or refinement (Waples and Do 2008) of these methods using single samples, which affords the practical estimation of N_e based on a random sample of genotyped individuals (Hill 1981). This is reflected in the growing use of single sample approaches relative to temporal methods that require at least two samples separated usually by multiple generations (Fig. 1b). An important distinction is whether estimates generated from these approaches reflect N_e or the effective number of breeders (N_b), two properties that are not equal but frequently confused (Table 1). We treat and discuss N_e and N_b separately whenever appropriate.

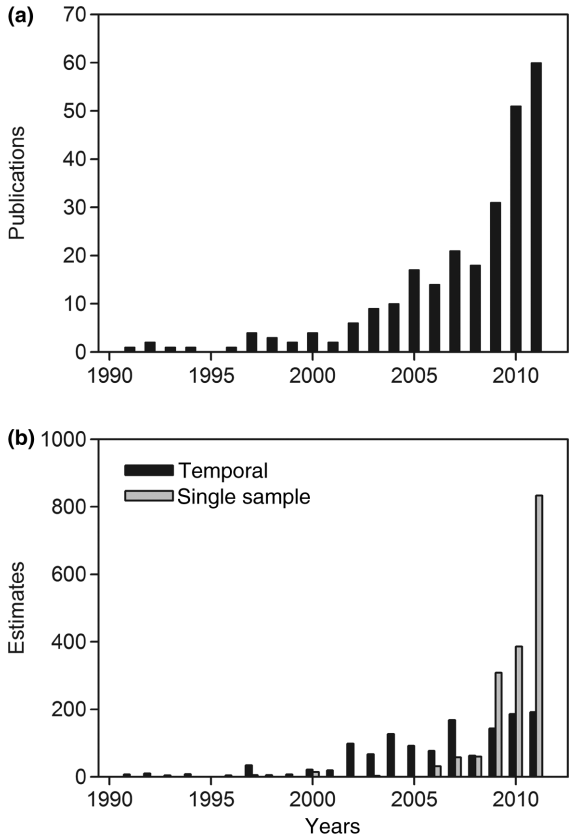

Figure 1. Annual trends of empirical studies on contemporary N_e based on genetic data. Given are (a) the number of N_e studies from 1990 to 2011 and (b) the number of published N_e estimates based on temporal methods and on single samples during the same time period. Data for 2012 are not shown as this year is still ongoing and therefore the summary of estimates is likely incomplete.

Trends in N_e/N estimates

Only 28% of published studies with N_e estimates (66 of 233 publications) have explicitly attempted to link N_e to N. The 508 N_e/N estimates reported in these 66 studies (240, or 47% of 508, new estimates since 2008, Table S1) comprise about 20% of all published N_e estimates using genetic data and these are analyzed in detail below.

Correctly linked N_e/N ratios

A considerable number of N_e/N ratios reported to date have improperly linked N_e to N, despite the existence of

Table 1. Overview of relevant population parameters and their definitions (and the abbreviation symbols used to refer to them in this manuscript). References provided whenever possible and relevant.

Parameter	Symbol	Definition	References
Annual census population size	N_a	The number of reproductively mature individuals in a population that may reproduce and hence contribute to the cohort of individuals born in that year. Not to be confused with (i) total annual census population size (adults and juveniles) and (ii) annual census population size based on breeders, nonbreeders, and senescents	Frankham (1995)
Arithmetic mean		$\bar{X} = \frac{1}{n}\sum_{i=1}^{n} x_i$	
Cohort		A group of individuals born in a given year, thus having the same age	Caswell (2001)
Effective population size	N_e	The size of an ideal population experiencing the same rate of random genetic change over time as the real population under consideration. For the purpose of this review, we limit ourselves to contemporary effective population size	Wright (1931), Wright (1938)
Effective number of breeders	N_b	The effective number of breeders contributing to a sample of offspring. When this offspring sample constitutes one single cohort, then N_b represents the effective number of breeders in a given year	Waples & Teel (1990)
Generation length		The average age of parents in the population, i.e., the reproductive output weighted by the age distribution of the parents.	Felsenstein (1971)
Harmonic mean		$\tilde{X} = \frac{n}{\sum_{i=1}^{n} \frac{1}{x_i}}$	

guiding literature (Waples 2005). The relationship between N_e and N depends on both the nature of samples analyzed and the age structure of the population studied. Single sample methods based on linkage disequilibrium (Hill 1981; Waples and Do 2008) and relatedness (Wang 2009) estimate the number of adults that produced the sample, so when a population has discrete generations, this estimate applies to N in the previous generation. Temporal methods (e.g., Waples 1989; Wang and Whitlock 2003) generally apply to the harmonic mean generational N during the period delimited between the two samples (Kalinowski and Waples 2002). The important detail here is that the most recent generational N is *not* included in this calculation, for it has not yet been introduced to genetic drift. This situation becomes more complex in species with overlapping generations, a point we will return to later. For now, one important conclusion is that, regardless of the approach chosen to estimate N_e, genetic and demographic data collected from exactly the same time period are not directly related (see also Nunney 1995). Hence, they are generally not compatible for the calculation of N_e/N, unless one can explicitly assume that population size has been constant. Such an assumption is unlikely to be commonly justified in empirical studies of contemporary N_e, as these are typically motivated by drastic declines in abundances of the study species (e.g., Ardren and Kapuscinski 2003; Johnson et al. 2004; Alo and Turner 2005; Fraser et al. 2007b; Henry et al. 2009; Riccioni et al. 2010; Zschokke et al. 2011). Under such circumstances, the untenable assumption of constant population size is most likely to yield upwardly biased N_e/N ratios.

Using the recommendations of Waples (2005), we found that 31% of reported N_e/N ratios (160 of 508 estimates) can be presumed free of bias caused by improper linking between N_e and N. These 160 estimates are roughly equally divided into estimates of N_b/N_a and N_e/N, where N_a is the adult census population size in a given year (Table 1). After further accounting for age structure in N_e estimation using temporal methods, only slightly over half of these N_e/N ratio estimates remain, which is less than 4% of all published N_e estimates (93 of 2617).

Degree of uncertainty in N_e/N ratios and implications for inferring N_e/N ratios

Even if N_e and N are correctly linked, both parameters need to be estimated with accuracy and precision. However, our survey suggests that uncertainty in N_e or N estimates (e.g., 95% confidence intervals [CI] or credible regions) has been insufficiently translated explicitly into uncertainty in N_e/N ratios. For example, after accounting for uncertainty in N_e, plots of 95% CI for N_e versus N show that these often range anywhere from nearly zero to 1 (Fig. 2a). In fact, 31% of estimated N_e/N ratios overlap with 1, of which more than

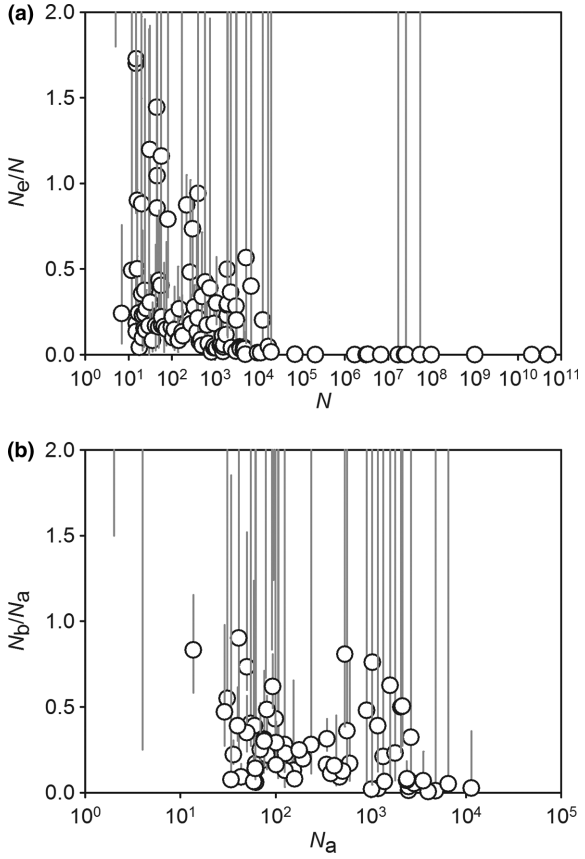

Figure 2. Uncertainty in estimates of the ratio of (a) N_e to adult census population size (N) and (b) N_b to annual census population size (N_a), quantified by including the 95% confidence intervals surrounding N_e or N_b estimates, respectively. Note that some point estimates of these ratios where much larger than 2.0, but the *y*-axis scales were not extended to avoid blurring any trends at lower values.

half also reach below $N_e/N = 0.01$. A similar result is obtained when considering the ratio between N_b estimates and annual census population size (N_a) (Fig. 2b; see also Table 1), with 45% of N_b/N_a ratios overlapping with 1 (11% of which also reach below $N_b/N_a = 0.01$). The uncertainty in N_e/N ratios thus frequently spans a minimum of two orders of magnitude.

A similar trend is observed when accounting for uncertainty in N estimates, even when N_e estimates are precise and accurate. We could only locate six empirical studies that reported CI for N (Jehle et al. 2001, 2005; Miller and Waits 2003; Charlier et al. 2011; Belmar-Lucero et al. 2012, Moyer et al. 2012). Of the 41 N_e/N or N_b/N_a ratios reported in these studies, 67% of comparisons contained an N_e estimate significantly smaller than the estimate of N (i.e., the 95% CI for the two parameters did not overlap), but this is just 5.5% (28 of 508) of all N_e/N estimates and only 1.1% of all published N_e estimates.

Unfortunately, the challenge of incorporating a known (and the likely large) variance in N into the variance of N_e/N has so far received scant attention in the literature. Possibly this situation could be improved in the future with the application of the Delta method (Oehlert 1992).

So what are 'typical', correctly linked N_e/N ratios?

In light of the inherent imprecision often surrounding N_e and/or N estimates, given that previous assessments of N_e/N ratios (Palstra and Ruzzante 2008) did not account for improper linking of N_e to N, and given the large amount of new estimates published, we think it is justified to revisit this question with the present data. Available data on correctly linked N_e/N ratios include 31 N_e/N estimates and 62 N_b/N_a estimates, where median values for N_e/N and N_b/N_a ratios were found to be 0.231 and 0.225, respectively. These median values are higher than previously reported values of 0.14 for genetic (Palstra and Ruzzante 2008) and 0.11 for mainly demographic N_e estimates (Frankham 1995). Hence, correctly linking the two parameters might increase the general magnitude of the N_e/N ratio by a factor two (see also Nunney 1995) and bring them closer to theoretically expected values (Nunney 1993, 1996). We also observe that these values differ substantially from the medians based on all available estimates ($N_e/N = 0.123$ and $N_b/N_a = 0.163$) and analyses of variance indicate that the former are also more precise (despite being based on far fewer data points). Overall, although tempting as it may be to make a statement about the general magnitude of N_e/N for natural populations, we necessarily reiterate, as have others in the past (Frankham 1995; Palstra and Ruzzante 2008), that our estimated N_e/N medians should be interpreted with extreme caution: their taxonomic coverage is limited (based on fishes, amphibians, and insects only) and their range is considerable (0.01–0.95). Furthermore, our data plots combine all taxa and there are good reasons to suspect that N_e/N ratios will differ among populations within species, among related species, and among different taxonomic groups, especially those characterized by different life history survival curves (cf. Palstra and Ruzzante (2008)).

Is there a relationship between N_e and N?

This is certainly a relevant question to explore because if simple conversions exist between N_e and N, limited conservation resources could be saved on the estimation of one variable to infer both, as pointed out in a recent review (Luikart et al. 2010). We therefore regressed the two parameters using only those data points that were

correctly linked and unbiased due to age structure. Figure 3a,c shows that no simple linear relationship exists between estimates of N_e and N or N_b and N_a (simple linear regression, $r^2 = 0.11$, $P = 0.556$, $r^2 = 0.05$, $P = 0.739$, respectively). Interestingly, log-linear relationships are a better fit for both data sets (N_e vs. N, $r^2 = 0.43$, $P = 0.019$; N_b vs. N_a, $r^2 = 0.21$, $P = 0.063$), suggesting that a positive, albeit variable, relationship between N_e and N may only exist at (very) low abundances (Fig. 3b, d). Moreover, correlation coefficients were always lower for regression analyses based on all data points (results not shown), which encouragingly suggests that additional correctly linked N_e/N (and N_b/N_a) ratios in future studies could enhance our understanding of these ratios for natural populations. Naturally, these analyses ignore the large variation in life history that is contained in the database, which may have weakened any real biological relationships present in species with similar life histories. Nevertheless, our quantitative survey underscores that until similar surveys are conducted in the future with the addition of substantially more N_e/N data, researchers should be extremely cautious when making inferences about N_e based on N, and vice versa.

Recommendations and considerations

Our compendium and appraisal contains two salient conclusions. First, there is a need to better report uncertainty in both N_e and N, but particularly the latter, in studies linking N_e to N. Second, more attention needs to be paid to correctly linking N_e and N. How to do this was not well understood before Waples's (2005) criteria and since then, correctly linked N_e/N ratios have encouragingly increased from 14.8% (26 of 179 estimates) to 38.4% (126 of 328 estimates). Yet, this final value suggests that researchers should continue to pay meticulous attention to the issue.

The overall lower scrutiny applied to N estimation in the same studies that estimate N_e is probably due to a number of common factors relating to the difficulty in estimating N in organisms: (i) characterized by secretive or obscure behaviors; (ii) inhabiting environments that make conducting population censuses challenging; and/or importantly (iii) having overlapping generations or repeat breeding (iteroparity). The ratio N_e/N obviously depends on which definition of N is used (Nunney and Elam

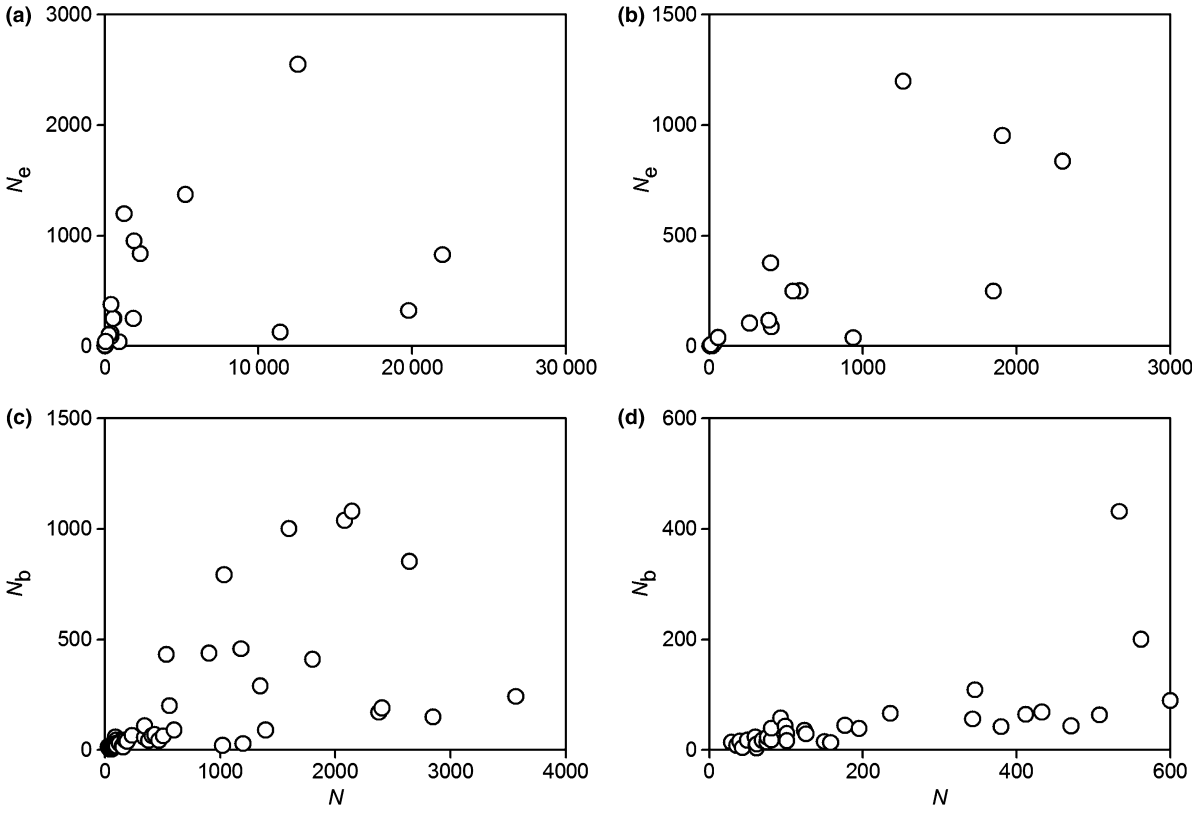

Figure 3. Relationships between (a) effective population size (N_e) and generational census size and (c) effective number of breeders (N_b) and annual census size based on the subset of empirical estimates that were correctly linked and free of bias due to age structure. For clarification, the same data are also displayed at smaller scales (b,d).

1994). Here, we propose that, where feasible, N should reflect the number of reproductively mature adults in a population, as it is their ecology and reproductive biology that principally shape N_e (Frankham 1995). For semelparous species, these calculations are relatively straightforward and have, for example, helped elucidating the effects of variance in recruitment and population growth rate on the N_e/N ratio (Waples 2002; Waples et al. 2010).

For iteroparous species with overlapping generations, some of the challenges related to calculating N_e/N may be overcome through careful a priori consideration of the sampling design. It is often much easier to census adults breeding in a given season, and a single cohort sample applies to just such a property. A drawback is that these estimates will reflect the annual effective breeder size (N_b) and much still remains to be understood on how this parameter relates to N_e (see Waples 1990, Waples et al. 2011). Hence, more empirical genetic studies that explicitly compare N_b and N_e will be needed. For example, genetic monitoring should facilitate sampling designs of several consecutive cohorts to estimate N_b using single sample approaches, with consecutive cohorts being analyzed jointly to estimate N_e using a temporal cohort model (Jorde and Ryman 1995; Jorde 2012). Alternately, researchers could analyze samples that aim to characterize the genetic make-up of an entire generation length, by pooling several annual samples of mixed cohorts (e.g., Palstra et al. 2009).

Finally, life table analyses (reviewed in Caswell 2001) continue to be an exception rather than the rule in empirical genetic studies of N_e. This is unfortunate, as they can be used to directly estimate both N and N_e (Age N_e, Waples et al. 2011) as well as provide demographic parameters to genetically estimate N_e using the cohort model. They will facilitate the interpretation of empirical N_e estimates in the context of population dynamics and species biology and, importantly, aid in the formulation of management recommendations.

Where the challenges highlighted above in estimating N_e for semelparous and iteroparous species can be practically overcome (reviewed or detailed in Jorde and Ryman 1995; Waples 2005; Palstra et al. 2009; Wang 2009; Waples et al. 2010, 2011), we note that there is an extensive, century-old literature on estimation of N, predominantly through the use of various mark-and-recapture methods (Ricker 1975; Seber 1982; Pollack et al. 1990). We do not review this rich literature here, but as in the estimation of N_e, we strongly urge authors to carefully consider the sampling assumptions underlying the estimation of N more explicitly in the future when linking N_e and N. Researchers should also (i) provide more details on the methods used to calculate N, (ii) report the measure of uncertainty surrounding N estimates, and (iii) distinguish whether N is based on only adult breeders or breeders and senescent individuals (see Table 1). An excellent review (Luikart et al. 2010) also exists on how molecular genetic data may be utilized to noninvasively estimate N for species where it is impossible or harmful to handle the number of individuals required for traditional estimation.

The reality though is that some of the issues highlighted above (i.e., the difficulties in estimating N or N_e due to overlapping generations), and others, such as linking N_e to N in iteroparous species, may not be easily overcome without the use of considerable resources (multiyear field work and genotyping, parentage analysis, etc.). Whether this is deemed a major concern in a given situation may depend on the research question, the study system, or how large N_e and N are likely to be. For instance, if the goal of the research is to compare populations over several orders of magnitude of size (N_e, N), it may not be that problematic if N_e/N ratios are off by an order of magnitude due to incorrect linking or estimation of either N_e or N, provided that the assumptions are acknowledged and the errors are proportional across all populations sampled (e.g., Belmar-Lucero et al. 2012). Conversely, if the conservation fate of a species or population is being interpreted through N_e and/or N data, great caution relating to uncertainty is warranted. For example, in salmonid fishes, a group of related, socioeconomically important species for which the most N_e/N estimates were available ($n = 98$, of which 65 were independent, whether free of bias or not), the range of N_e/N estimates across populations within five species had a fourfold to 100-fold difference (Table S2). Clearly, such variation could translate into vastly different conservation implications when using one variable to infer the magnitude of the other (N_e from N, and vice versa). Overall, our hope in raising these issues here is to stimulate further discussion on such important topics in the future of conservation genetics in general, and of N_e/N estimation in particular.

Conclusion

There is now an extensive set of genetic tools available for estimating N_e (Waples 1989; Beaumont 2003; Wang and Whitlock 2003; Leberg 2005; Wang 2005, 2009; Jorde and Ryman 2007; Tallmon et al. 2008; Waples and Do 2008, 2010; Luikart et al. 2010). Encouragingly, the 2617 N_e estimates from the 233 studies we could locate suggest that empirical researchers are taking full advantage of these approaches. However, our quantitative survey suggests that research into N_e estimation could place a stronger focus on simultaneously estimating and correctly linking N_e and N as an additional step. This will stimulate considerations of N_e and N in the broader conservation

context and will facilitate a better understanding of the relative importance of the various stochastic and deterministic forces that shape population persistence (see below). Apart from the need for meticulous calculation of both N_e and N, we also suggest that several important research areas will be enriched from doing so, both for new and expert researchers alike.

Some of these research topics have been reviewed or discussed in other, recent papers, such as understanding (i) the range and conditions over which N_e/N can be assumed to be constant within populations (Vucetich et al. 1997; Waples 2005); (ii) the biological plausibility of genetic compensation or other factors that might lead to shifting N_e/N ratios within populations (Ardren and Kapuscinski 2003; Fraser et al. 2007b; Watts et al. 2007); (iii) the variation in N_e/N ratios across populations within species (Wright 1938; Frankham 1995; Shrimpton and Heath 2003; Palstra and Ruzzante 2008; Luikart et al. 2010; Belmar-Lucero et al. 2012); (iv) the role that life history plays in affecting the N_e/N ratio in species (Lee et al. 2011), particularly for species with extremely low N_e/N ratios such as marine fishes (e.g., Hauser et al. 2002; Turner et al. 2002); and (v) the likely possibility that N_e/N is reduced by multiple factors which can act in tandem, whether due to interactions between population size and/or variance in reproductive success, reproductive biology, or anthropogenic pressures such as fisheries-induced size-selective mortality (Therkildsen et al. 2010; Lee et al. 2011; Belmar-Lucero et al. 2012).

Finally, some research topics are just emerging and therefore demand further investigation. For example, we still know little about how demographic (N) and evolutionary potential (N_e) can feedback on one another within populations. Factors facilitating positive population growth at low N, and hence long-term viability, can result in a few individuals contributing disproportionately to the next generation in genetic terms, reducing N_e (Lee et al. 2011). In another case, reduced N_e/N associated with a more complex age structure was found to actually confer greater resilience to environmental stochasticity (Gaggiotti and Vetter 1999). Whether such trade-offs are sufficiently strong to affect evolutionary potential awaits further empirical investigation but their recognition may help to guide the balancing of demographic and genetic goals in conservation.

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Overview of publications with empirical Ne/N ratio estimates on wild populations.
Table S2. Variability of empirical Ne/N ratio estimates within wild populations of salmonid fish species.

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