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# Effective population size/adult population size ratios in wildlife: a review

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## Summary

The effective population size is required to predict the rate of inbreeding and loss of genetic variation in wildlife. Since only census population size is normally available, it is critical to know the ratio of effective to actual population size ($N_e/N$). Published estimates of $N_e/N$ (192 from 102 species) were analysed to identify major variables affecting the ratio, and to obtain a comprehensive estimate of the ratio with all relevant variables included. The five most important variables explaining variation among estimates, in order of importance, were fluctuation in population size, variance in family size, form of $N$ used (adults *v.* breeders *v.* total size), taxonomic group and unequal sex-ratio. There were no significant effects on the ratio of high *v.* low fecundity, demographic *v.* genetic methods of estimation, or of overlapping *v.* non-overlapping generations when the same variables were included in estimates. Comprehensive estimates of $N_e/N$ (that included the effects of fluctuation in population size, variance in family size and unequal sex-ratio) averaged only 0·10–0·11. Wildlife populations have much smaller effective population sizes than previously recognized.

## 1. Introduction

Finite population size results in inbreeding and loss of genetic variation. Its genetic effects are predicted to depend on the effective population size ($N_e$) rather than the actual size ($N$). The predicted relationships of genetic variation and inbreeding with effective population size are given by equation (1) (Falconer, 1989)

$$H_t/H_0 = [1-1/2N_e)]^t = 1-F, \quad (1)$$

where $H_t$ is heterozygosity after $t$ generations, $H_0$ is initial heterozygosity, and $F$ is the inbreeding coefficient.

Since census sizes are the only demographic data available for most populations, the ratio of $N_e/N$ is a critical parameter for evolutionary genetics and wildlife management. For example, a minimum ratio of 0·2 is assumed in the Mace–Lande criteria for endangerment (Mace & Lande, 1991), and assumptions for $N_e/N$ are inherent in estimates of minimum viable population size (Nunney & Campbell, 1993). Unequal sex-ratios, variance in family sizes, and fluctuations in population size over generations are all predicted to affect $N_e/N$ (Wright, 1969; Falconer, 1989). Experimental tests have validated these predictions (Borlase *et al.* 1993; Briton *et al.* 1994; Woodworth *et al.* 1994).

Widely divergent views have been expressed about the magnitude of $N_e/N$. Empirical estimates were reported to be 0·5–0·8 (Falconer, 1989; Spiess 1989), 0·2–0·4 (Denniston, 1978; Mace, 1986), 0·2–0·5 (Mace & Lande, 1991), 0·25–1·0 (Nunney & Campbell, 1993), or 0·56–1·27 (Nunney & Elam, 1994), while values as low as $10^{-6}$ have been reported (Hedgecock, Chow & Waples, 1992). Nunney (1993) predicted that special circumstances would be required for the ratio to be much less than 0·5, Nunney & Campbell (1993) suggested that it would usually be greater than 0·25, while Nei & Tajima (1981) suggested that it would be less than 0·1 in small organisms. In spite of the critical importance of $N_e/N$ ratios in conservation and evolutionary biology, there has been no recent comprehensive review of estimates.

To predict the effects of finite population size on inbreeding and loss of genetic variation, estimates must encompass the effects of unequal sex-ratio, variance in family size and fluctuation in population size (comprehensive estimates). A range of genetic and demographic methods have been used to estimate $N_e$ (see below). Typically genetic estimates have included all three relevant variables, while most demographic estimates have not included the effects of fluctuations in population size. Consequently, many available estimates of $N_e/N$, particularly demographic ones, may be overestimates.

Wildlife species differ in life history characteristics, so they may differ in $N_e/N$ ratios. High fecundity species might be expected to have lower ratios due to high variance in family sizes, and perhaps greater fluctuations in population size over generations. Species exhibiting polygamy would be expected to have lower ratios than monogamous species due to unequal sex-ratio and high variance of male gametic contributions.

The objectives of this contribution were to review estimates of $N_e/N$ in order to identify the major variables affecting the ratio, and to obtain a reliable comprehensive estimate of the ratio. In particular, they were to test the hypotheses that (i) sex-ratio, variance in family size, and fluctuating population size affect the ratio; (ii) taxonomic groups differ in ratio; (iii) life history characteristics affect the ratio and (iv) different methods yield different estimates. Estimates were compared with the 0·5 and 0·25 values predicted above. Means for comprehensive estimates were computed by two methods. $N_e/N$ averaged only 0·10–0·11, much smaller than previously recognized.

## 2. Methods of estimating $N_e$

The concept of effective population size was introduced by Wright (1931, 1938, 1939) and has been refined by others, especially Crow and co-workers (see Crow & Kimura, 1970; Caballero, 1994). $N_e$ is defined as the size of an idealized population that would give rise to the same variance of gene frequency, or rate of inbreeding as in the actual population under consideration (see Falconer, 1989; Caballero, 1994). Three effective sizes have been defined: inbreeding, variance and eigenvalue. Estimates from the former two are the same under random mating and constant size over generations, but can differ when population sizes are changing, and also differ from the eigenvalue estimate (see Caballero, 1994; Templeton & Read, 1994).

Unequal sex-ratio (SR), variance in family size (VFS), and fluctuations in population size (FPS) are the major variables predicted to affect $N_e$ (Wright, 1969; Lande & Barrowclough, 1987; Falconer, 1989). Their effects are given by equations 2–4 below.

$$N_e = 4N_f N_m/[N_f + N_m], \tag{2}$$

where $N_f$ and $N_m$ are the number of female and male parents of the next generation.

$$N_e = N/[1 + (V_k - m_k)/m_k^2], \tag{3}$$

where $N$ is the number of sexually mature, non-senescent adults, $m_k$ is the mean number of gametes per individual contributing to production of mature individuals in the next generation, and $V_k$ is the variance in gametic contributions (Gowe, Robertson & Latter, 1959).

$$1/N_e = [1/N_{e1} + 1/N_{e2} + 1/N_{e3} + \ldots 1/N_{ei} \ldots 1/N_{et}]/t, \tag{4}$$

where $N_{ei}$ is the effective population size in the $i$th generation.

Equations to accommodate overlapping generations have been developed by Hill and others (see Caballero 1994; Nunney & Elam, 1994), and one to include the effects of selfing by Heywood (1986).

Demographic estimates of $N_e$ have relied on one or more of equations 2–4. Very few such estimates have included all these variables. Genetic estimates have been made from changes in allozyme heterozygosity (or quantitative genetic variation) over time using equation 1 (Briscoe *et al.* 1992), from drift variances among populations for allozymes (Easteal & Floyd, 1986), from linkage disequilibrium (Hill, 1981; Bartley *et al.* 1992), lethal allelism (Malpica & Briscoe, 1981), and from changes in pedigree inbreeding over time (Tomlinson *et al.* 1991). Typically genetic estimates were comprehensive estimates.

The time frame of interest in conservation biology is several generations to a few hundred generations. The genetic estimates reviewed here reflect this time frame. Long-term species estimates of $N_e$, based on either a neutral interpretation of allozyme variation (Nei & Graur, 1984; Schoen & Brown, 1991), a drift-heterokaryotype disadvantage model of karyotype evolution (Lande, 1979; Barrowclough & Shields, 1984), or DNA sequence divergence (Avise, Ball & Arnold, 1988) operate over hundreds of thousands to millions of generations, and require additional assumptions, so they have not been included in the survey in the Appendix. However, the mean of the Nei & Graur (1984) estimates has been computed to compare with estimates from the data in the Appendix.

## 3. Data

There are 192 published estimates of the $N_e/N$ ratio from 102 species of insects, molluscs, amphibians, reptiles, birds, mammals and plants listed in the Appendix along with estimation methods, the variables they include, and the $N$ value used. The values reported for the Japanese human population (Imaizumi, Nei & Furusho, 1970) were restricted to mothers' birth dates prior to 1910 as birth control affected values after that. Estimates based on the use of segregating mutations (Nozawa, 1963, 1970; Wright, 1977, 1978; Wade, 1980; Pray *et al.* 1995) are given for comparative purposes, but were not included in statistical analyses as they may have been influenced by natural selection, and such estimates were not available outside insects. $N_e/N$ estimates for white spruce and black spruce that included only the effects of maternal-to-seed sampling, rather than seedling establishment, were not included (Cheliak, Pitel & Murray, 1985; Barrett, Knowles & Cheliak, 1987).

Values for domestic animal populations and mutant stocks were excluded. The estimate for *Rana pipiens* from Merrell (1968) was not used in the statistical analyses as it was only an estimate of the ratio of breeding adults to all adults.

Estimates varied widely in methods used, variables included, precision, and in the value of $N$ used. Few demographic estimates were based on paternities that had been verified with genetic markers. Many early estimates were based on limited data, and are little better than guesses. Details of what had been done, or what $N$ was used for the divisor were sometimes unclear (and the authors could not always clarify such matters!). The information in the Appendix represents my best attempt to glean the details for the published estimates. Apart from one case, the values of $N_e$ and $N$ given by the authors have been accepted.

Three different values of $N$ have been used in $N_e/N$ estimates, total census size ($N_T$ = adults+juveniles), number of adults ($N_A$ = breeding+senescent adults), and number of breeding adults ($N_B$ = sexually mature adults, including sterile individuals and non-breeding helpers). No one measure of $N$ fits all needs, and there is a clear need to specify carefully which $N$ is used. For comparative purposes, a single type of $N$ must be used. $N_A$ is probably the most appropriate value for this purpose (Nunney & Elam, 1994). Conversely, for conservation purposes, the census size ($N_c$) is the most appropriate divisor, as the ratio of $N_e/N_C$ is required to translate census size into $N_e$. The census population size may be $N_A$, $N_B$ or $N_T$, depending on the organisms being considered. Wherever possible $N_A$ or $N_B$ has been reported herein, with 60 estimates using $N_A$, 90 $N_B$ and 24 $N_T$. The effects of using different $N$ values were tested in the analyses described below.

The specification of $N$ when population size fluctuates is also a difficult issue. Since we wish to extrapolate from observed population sizes to $N_e$, the mean population size seems the appropriate value to insert; this is what I have used. The issue is more vexed where there have been large increases or decreases in population size. In the northern hairy-nosed wombat (Taylor, Sherwin & Wayne, 1994), the population dropped from several thousands to 20–30 adults by 1981 and has subsequently increased to 53 adults (A. Taylor *pers. comm.*). To be conservative, I have used the mean of 25 and 53 = 39 as the divisor for the $N_e/N$ ratios for this species in the Appendix.

Data were inappropriate to test directly for the effects of polygamy on an individual species basis, as breeding systems were often not specified, or not known. A weak test of the effects of polygamy *v.* monogamy was provided by comparing mammals with birds, as the former group is commonly polygamous, while the latter is reputed to be largely monogamous (see Briton *et al.* 1994).

In some cases repeat estimates were available on the same populations (Malpica & Briscoe, 1981 and Briscoe *et al.* 1992; Tomlinson *et al.* 1991; Reed *et al.* 1993 and Blackwell *et al.* 1995; Crow & Morton, 1955 and Nei & Murata, 1966; Imaizumi *et al.* 1970; MacCluer & Shull, 1970 and Nei, 1970; Felsenstein, 1971, Emigh & Pollak, 1979 and Charlesworth, 1980; Taylor *et al.* 1994 and Taylor *pers. comm.*; Husband & Barrett, 1992). Analyses were generally done on both the full data set and on the data set where repeat estimates on the same population were pooled.

## 4. Statistical analyses

All statistical analyses were done using the MINITAB statistical package (release 7). Where a range was given for an estimate, statistical analyses were based on means of the individual estimates, or the mid-point of this range where no further information was available. The main analyses were done on four data sets; the full data set that included 165 estimates with complete information, including repeat estimates on the same populations, but excluding one outlier (see below). The pooled data set had 135 estimates; repeat estimates on the same population were pooled and the mean on the transformed scale (see below) used. The full comprehensive data set consists of the 56 estimates that had the effects of all relevant variables included (FPS, VFS and SR). The pooled comprehensive data set had 36 entries with repeat estimates pooled as above. The estimates for the plant *Eichhornia paniculata* (Husband & Barrett, 1992) had all relevant variables included and so were included in comprehensive estimates, but they were monoecious so they were not considered to include the effects of unequal sex-ratio.

### (i) *Normality and outliers*

As the data were not normally distributed (sigmoid normal probability plot between NSCOR and data), they were arcsine square root transformed (radians) prior to analyses. Data were normally distributed on this scale (linear relationship between NSCOR and transformed data, correlation = 0·997). One clear outlier was identified (see Fig. 1), the estimate of 0·9

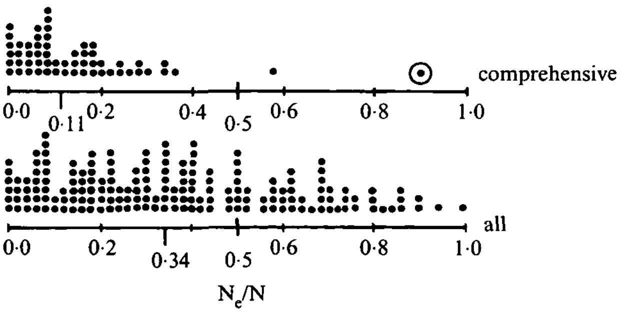

Fig. 1. Distributions of estimates of effective/actual population size ($N_e/N$) ratios. Comprehensive estimates (that include the effects of fluctuation in population size, variance in family size and unequal sex-ratio) are above and all estimates below. The circled outlier is for a pair mated rainbow trout (*Oncorhynchus mykiss*) population. Means of estimates are indicated below vertical lines.

for pair mated rainbow trout (Bartley *et al.* 1992). As this was a managed population, while all the others were relatively unmanaged, it was omitted prior to statistical analyses, except for overall mean and the *t*-test of all data versus 0·5. Otherwise the number of potential outliers identified by regressions or analyses of variance were within the numbers expected. The two remaining estimates with the highest standardized residuals were 0·78–0·93 for the plant *Chaemacrista fasciculata* and 0·09 for the bird *Melanerpes formicivorous*. There were no clear biological reasons to omit these values. The minimum estimate ($10^{-6}$ for the Pacific oyster *Crassostrea gigas*) was not identified as an outlier.

### (ii) *Identifying major variables affecting* $N_e/N$

Stepwise multiple regressions were performed to identify the most important variables explaining differences in $N_e/N$. Independent variables were inclusion *v.* exclusion of the effects of fluctuation in population size, variance in family size, unequal sex-ratio and overlapping generations, plus method of estimation, high *v.* low fecundity, taxonomic group, and $N_B$ *v.* $N_A$ *v.* $N_T$. Where more than one degree of freedom was associated with an effect, single degree of freedom indicator variables were generated and used in the analyses. The effect of different methods of estimation (genetic *v.* demographic) was tested in the full data set by one way analysis of variance, and after the effects of FPS, VFS, *N*, taxonomic group and SR had been removed in a general linear model (GLM) analysis of variance. Comprehensive estimates were tested for the full range of effects of method, for demographic *v.* genetic and among genetic estimation methods using GLM analyses of variance with form of *N* and method as the variables. The effect of plants *v.* animals in the comprehensive data set was also tested using a one-way analysis of variance.

### (iii) *Computation and testing of means*

Means were computed on the transformed scale and de-transformed means reported. Comprehensive estimates were computed in two ways. Means for those estimates containing the effects of all relevant variables (FPS, VFS and SR) were computed for both the full data set and the pooled data set. Multiple regressions were done on the full and pooled data sets with FPS, VFS and SR effects entered in this order, and estimates of the comprehensive $N_e/N$ derived from the multiple regression equations. Means were also computed for those estimates that included only the effects of VFS, only SR, and only VFS and SR.

Tests of means against predictions were done using *t*-tests (all estimates *v.* 0·5, estimates that included VFS and SR, but not FPS *v.* 0·5, comprehensive estimates *v.* 0·25). Comprehensive estimates were compared with estimates that did not include all variables using a two sample *t*-test.

The mean of the estimates made by Nei & Graur (1984) was obtained by subjecting them to arcsine square root transformation (excluding 13 estimates of 0 and setting two estimates of greater than unity to 1·0), computing means, and de-transforming them. Confidence intervals were computed on the transformed scale, and de-transformed.

## 5. Results

### (i) *Factors accounting for variation in* $N_e/N$

Estimates of $N_e/N$ ranged from $10^{-6}$ in Pacific oysters (*Crassostrea gigas*) to 0·994 in humans and averaged 0·34 (Table 1). A major reason for the large variation among estimates was that they were estimating different things (Appendix). They included or excluded SR, VFS, and FPS, and different values of *N* ($N_B$, $N_A$ or $N_T$) were used as divisors. Less than one third were comprehensive estimates that included the effects of all relevant variables. Comprehensive estimates showed a much lower variance than all estimates (Fig. 1).

The most important variables explaining differences in $N_e/N$ in the pooled data set, in order of importance, were fluctuation in population size, variance in family sizes, $N_B$ *v.* $N_A$ and $N_T$, plants *v.* animals, unequal sex ratio, and birds *v.* other animals as revealed by

Table 1. *Mean estimates of* $N_e/N$ *for the effects of fluctuations in population size (FPS), variance in family size (VFS), unequal sex-ratios (SR), and their combinations, plus form of* N, *plants v. animals, and birds v. other animals*

| Estimates | Mean | | |
|---|---|---|---|
| SR + VFS + FPS | | | |
| – Comprehensive estimates | 0·11* † | | |
| – Multiple regression | 0·10* † | | |
| SR + VFS only | 0·35 | | |
| VFS only | 0·46 | | |
| SR only | 0·64 | | |
| All data | 0·34 | | |
| GLM estimates‡ | Inclusion | Exclusion | |
| FPS | 0·14 | 0·40 | |
| VFS | 0·14 | 0·40 | |
| SR | 0·20 | 0·33 | |
| $N_B$ *v.* $N_A$ *v.* $N_T$ | 0·39 | 0·25 | 0·16 |
| Plants *v.* animals | 0·16 | 0·39 | |
| Birds *v.* other animals | 0·21 | 0·32 | |

* Mean for the pooled data set.

† Mean for the full data sets.

‡ Means below all generated following GLM analysis of variance with FPS, VFS, *N*, plants *v.* animals, SR and birds *v.* other animals.

Table 2. *Stepwise multiple regression analyses to identify the variables explaining variation in effective/actual population size* ($N_e/N$) *ratios. The variables entered were fluctuation in population size* (*FPS*), *variance in family size* (*VFS*), *unequal sex-ratio* (*SR*), *taxonomic group, value of* N *used, overlapping v. non-overlapping generations and high v. low fecundity groups. The data set with pooling of repeat estimates on the same population was used. Values given are the regression coefficients, their corresponding t-test values* (*all $P < 0·05$*), *the standard deviation about the regression line* (*S*) *and the proportion of variation accounted for* ($r^2$)

| Step | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Constant | 0·739 | 0·987 | 0·961 | 0·945 | 1·071 | 1·052 |
| FPS | −0·364 | −0·366 | −0·332 | −0·327 | −0·287 | −0·302 |
| *t* | −8·6 | −9·2 | −8·1 | −8·3 | −6·9 | −7·2 |
| VFS | — | −0·274 | −0·317 | −0·291 | −0·326 | −0·303 |
| *t* | — | −4·4 | −5·1 | −4·8 | −5·4 | −5·0 |
| $N_B$ *v.* $N_A$ and $N_T$ | — | — | 0·103 | 0·197 | 0·147 | 0·188 |
| *t* | — | — | 2·7 | 4·2 | 3·1 | 3·6 |
| Plants *v.* animals | — | — | — | −0·162 | −0·215 | −0·253 |
| *t* | — | — | — | −3·6 | −4·4 | −4·9 |
| SR | — | — | — | — | −0·142 | −0·123 |
| *t* | — | — | — | — | −2·6 | −2·2 |
| Birds *v.* other animals | — | — | — | — | — | −0·131 |
| *t* | — | — | — | — | — | −2·0 |
| *S* | 0·226 | 0·211 | 0·206 | 0·198 | 0·194 | 0·191 |
| $r^2$ | 0·36 | 0·44 | 0·47 | 0·42 | 0·54 | 0·55 |

Table 3. *General linear model analysis of variance for the effective/actual population size* ($N_eN$) *ratios* (*full data set*) *to determine the effects of fluctuation in population size* (*FPS*), *variance in family size* (*VFS*), *unequal sex-ratio* (*SR*), *taxonomic group, value of* N *used, method of estimation* (*demographic v. genetic*) *and overlapping v. non-overlapping generations. F tests and probabilities* (*P*) *are shown*

| Source | D.F. | Sequential sum of squares | Adjusted mean square | F | P |
|---|---|---|---|---|---|
| FPS | 1 | 6·006 | 0·983 | 26·5 | < 0·001 |
| VFS | 1 | 0·804 | 0·545 | 14·7 | < 0·001 |
| $N_B$ *v.* $N_A$ *v.* $N_T$ | 2 | 0·489 | 0·406 | 11·0 | < 0·001 |
| Taxonomic group | 7 | 1·324 | 0·230 | 6·2 | < 0·001 |
| SR | 1 | 0·263 | 0·236 | 6·4 | 0·013 |
| Overlapping *v.* non- | 1 | 0·079 | 0·031 | 0·8 | 0·362 |
| Method | 1 | 0·010 | 0·010 | 0·3 | 0·603 |
| Error | 150 | 5.560 | 0·037 | — | — |
| Total | 164 | 14·535 | — | — | — |

stepwise multiple regression (Table 2). These variables accounted for 55% of the variation in $N_e/N$. Overlapping *v.* non-overlapping generations, and high *v.* low fecundity did not significantly improve this prediction. Analyses of both the pooled and the full data sets yielded similar conclusions (Tables 2, 3).

### (ii) *Effects of method of estimation*

Demographic estimates were significantly higher than genetic ones ($F_{1,169} = 77·4$, $P < 0·001$) in the one way analysis of variance for the full data set. However, when allowance was made for differences in variables included in estimates, the effect of method of estimation was non-significant (Table 3). For comprehensive estimates, there was a significant effect of method of estimation ($F_{5,48} = 3·3$, $P = 0·012$), and for differences among genetic methods ($F_{4,33} = 3·4$, $P = 0·021$), but not for genetic *v.* demographic estimates ($F_{1,52} = 2·4$, $P = 0·13$). Estimates from linkage disequilibrium and lethal allelism were higher than other genetic estimates (Table 4).

Table 4. *Effects of different methods of estimation on* $N_e/N$ *ratio, determined from analyses of comprehensive estimates using GLM analysis of variance with adjustment for form of* N. *De-transformed means and sample sizes* (*n*) *are shown*

| Method | *n* | Means (de-transformed) |
|---|---|---|
| Genetic | | |
| Temporal loss of heterozygosity | 20 | 0·052 |
| Variance in gene frequency | 2 | 0·015 |
| Lethal allelism | 12 | 0·144 |
| Linkage disequilibrium | 5 | 0·228 |
| Pedigree inbreeding | 1 | 0·073 |
| Demographic | 16 | 0·122 |

### (iii) *Effects of life history variables and taxonomic groups*

After correcting for FPS, VFS, and SR, and $N$ there was no significant effect of high *v.* low fecundity, or of overlapping *v.* non-overlapping generations. There were two significant taxonomic effects; plants were less than animals, and birds were less than other animals. Both these effects are equivocal. The birds *v.* other animals effect had a probability of 0·05 in the GLM analysis of variance with FPS, VFS, $N$, and plants *v.* animals included. Plants and animals did not differ in the pooled comprehensive data set ($F_{1,34} = 0·13$, $P = 0·72$). The difference between birds and mammals was in the opposite direction from that expected from the effects of polygamy *v.* monogamy (0·32 *v.* 0·47; these come from a different GLM analysis to those in Table 1).

### (iv) *Comprehensive estimates of* $N_e/N$

The mean of $N_e/N$ estimates that included all relevant variables was 0·11 in both the full- and pooled comprehensive data sets (Table 1). The estimate of $N_e/N$ from the multiple regression equation utilizing fluctuation in population size, variance in family size and unequal sex-ratios was 0·10 for both the full data set and the pooled data set. Explicitly correcting the above estimates so that they had $N_A$ as a divisor resulted in essentially no change. The mean of the estimates given by Nei & Graur (1984) was 0·06, not significantly different from the means above (95% confidence interval of 0·02–0·11).

### (vi) *Testing estimates against predicted values*

All estimates (mean 0·34) were significantly less than 0·5 ($t = -7·1$, D.F. = 171, $P < 0·0001$), as were estimates including VFS and SR, but not FPS (0·35, $t = -4·3$, D.F. = 18, $P = 0·004$). Comprehensive estimates were significantly less than 0·25 ($t = -6·4$, D.F. = 34, $P < 0·0001$), and significantly lower than non-comprehensive estimates (0·11 *v.* 0·45, $t = -10·8$, D.F. = 76, $P < 0·0001$).

## 6. Discussion

There were two major findings of this study. First, the most important variable reducing $N_e/N$ was fluctuation in population size, followed by variance in family size, form of $N$ used, taxonomic group and unequal sex-ratio. Secondly, comprehensive estimates of $N_e/N$ were much less than previously recognized (means 0·10–0·11).

Are low values of $N_e/N$ realistic? They have been criticized by Nunney (1993) and Nunney & Campbell (1994). However, the number of low estimates continues to rise (56 comprehensive estimates, and 36 pooled comprehensive ones; both means 0·11). Very similar estimates were obtained from the multiple regression equation for the full and pooled data sets (165 and 135 estimates). Further, the mean of 64 long-term species estimates made by Nei & Graur (1984) was 0·06. The low values were not due to method of estimation as demographic and genetic methods yielded similar estimates when similar variables were included. It is hard to escape the conclusion that comprehensive $N_e/N$ is of the order of 0·1.

While it has been suggested that natural selection on genetic marker loci may be responsible for low genetic estimates of $N_e/N$ (Nunney, 1993), this can be refuted for short to medium term estimates herein. Explicit tests of predicted changes of allozyme heterozygosity in finite populations over periods of 8–10 generations and over 50 generations have been in accord with theoretical predictions of equation 1 (Borlase *et al.* 1993; Briton *et al.* 1994; Woodworth *et al.* 1994; Montgomery *et al.* in preparation). In the limited number of cases where selection on allozyme polymorphisms have been identified, it has generally been weak and in favour of heterozygotes (Brookfield & Sharp, 1994). The net effect of such selection on estimates of $N_e$ in finite populations depends on the equilibrium frequency. It will slow fixation for alleles with equilibrium frequencies in the 0·2–0·8 range, but will accelerate fixation for alleles with equilibrium frequencies outside this range (Robertson, 1962).

Why are comprehensive estimates of $N_e/N$ so low? The overall reduction was due to the cumulative effects of fluctuation in population size, variance in family size, and to a lesser degree unequal sex-ratio. Wright (1969) predicted that 'If $N$ varies widely, as in the annual cycle in many insects, effective $N$ may be very much smaller than apparent $N$.' He cited a theoretical example where $N_e/N$ was 0·0003. Extreme fluctuations in population size are also well known for small mammals. However, they also occur in large mammals and plants due to climatic extremes such as droughts, extreme winters, floods, hurricanes, parasites and disease (Young, 1994). While there is higher variance in population size per year in smaller than larger mammals, different sized animals have similar variance in population size when measured on a per generation basis (Sinclair, 1995). Fluctuation in population size was identified as the most important variable affecting the ratio by my analyses. Wright (1978) recognized that variance in family size may also reduce $N_e/N$ substantially; he attributed empirical estimates of $N_e/N$ for the moth *Panaxia dominula* of 0·26 and 0·08 to this factor. This was identified as the second most important factor reducing the ratio.

The published estimates do not support Nunney's (1993) suggestion that estimates should only be less than 0·5 in exceptional circumstances, as they were significantly less than this value. Comprehensive estimates were significantly less than Nunney & Campbell's (1993) prediction of a minimum of 0·25. These authors suggested that values could be less than this if population sizes fluctuated significantly. This seems to be the case. This study identified fluctuation in population size as the most important variable affecting the ratio.

Surprisingly, life history characteristics showed little evidence of effects of $N_e/N$. The effects of high *v.* low fecundity, overlapping *v.* non-overlapping generations, and polygamy *v.* monogamy (from mammals *v.* birds) showed no clear effects. The only significant taxonomic effects were those of plants *v.* animals and birds *v.* other animals, and there is some doubt about the reality of both those effects. The effects of life history characteristics and taxonomic group should be reevaluated when more estimates (especially comprehensive ones) accumulate.

Estimates of $N_e/N$ from demographic and genetic methods did not differ when the same variables were included, in agreement with Husband & Barrett's (1992) findings. There were significant differences among genetic methods in analyses of comprehensive estimates; estimates from lethal allelism and linkage disequilibrium were higher than other genetic estimates. Falconer (1989) obtained similar estimates of $N_e$ from temporal changes in heterozygosity, drift in gene frequencies and pedigree inbreeding in pedigreed mouse population. In *Drosophila*, similar estimates from temporal changes in heterozygosity and pedigree inbreeding (Borlase *et al.* 1992; Woodworth *et al.* 1994), and among temporal changes in heterozygosity, quantitative genetic variation, and from lethal allelism have been found (Briscoe *et al.* 1992). Conversely, Begon, Krimbas & Loukas (1980) concluded that estimates from lethal allelism and an ecological method were concordant, while a lower estimate from temporal genetic change was attributed to directional selection on two allozyme loci. In birds, Blackwell *et al.* (1995) found lower $N_e/N$ estimates from pedigree inbreeding than from demographic estimates, possibly as a consequence of the population structure. While there may be real differences among methods, they do not alter the conclusion that comprehensive estimates of $N_e/N$ are low.

Estimates of $N_e$ are expected to depend on the environmental conditions experienced by populations. Climatic conditions are likely to affect birth and death rates, variance in family sizes, and perhaps mating patterns in different years and habitats. Further, crowding is likely to affect demographic variables. Lower $N_e/N$ ratios at higher densities have been reported in *Drosophila* (Nozawa, 1963, 1970), *Tribolium* (Wade, 1980; Pray *et al.* 1995), the moth *Panaxia dominula* (Wright, 1978) and the plant *Eichhornia paniculata* (Husband & Barrett, 1992). Bird populations in different habitats had different ratios (Reed *et al.* 1993). Such factors deserve more attention than they have hitherto received.

These observations have important conservation implications. First, $N_e/N$ ratios are even lower than previously suspected. Most current estimates of the ratio ignore the effects of fluctuation in population size, and are thus serious overestimates. Consequently, wildlife populations are in a worse state genetically than is currently recognized. Secondly, criteria such as the Mace–Lande criteria for endangerment and minimum viable population size estimates need to be revised to take account of the lower than assumed $N_e/N$ values. Typical values of $N_e$ are about one order of magnitude less than adult population sizes. The form of census sizes differs among taxonomic groups, typically being $N_A$ in insects and plants, $N_A$ or $N_B$ in birds and $N_T$ in mammals. Consequently, the required adjustment will be even greater in mammals as most census size estimates include both adults and juveniles. For humans, the required further downward adjustment is approximately 1/3, based on 1/3 of the census size being sexually mature adults, 1/3 juveniles, and 1/3 beyond reproductive age (Jorde, 1980). For birds, either adults or breeding pairs are recorded. An upwards adjustment is required if $N$ is breeding pairs. It is of critical importance that the form of $N$ be specified when reporting estimates of $N_e/N$, and that the proportion of adults be specified if census size estimates contain other than adults, so that the adjustment factor can be calculated to estimate $N_e$ from census numbers.

In conclusion, comprehensive values of $N_e/N$ are much smaller than has previously been recognized.

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## Appendix

*Estimates of effective/actual population size* ($N_e/N$) *ratios in different species, along with method of estimation, variables included in the estimate, the form of population size* ($N$) *used as divisor, and the reference. Common names are given in brackets*

| Species | $N_e/N$ ratio | Method* | Variables† | $N$‡ | Reference |
|---|---|---|---|---|---|
| **Insects High fecundity** | | | | | |
| *Ceratitis capitata* (Mediterranean fruit fly) | 0·41 | D | VFS, n | A | Debouzie (1980) |
| *Coelopa frigida* (Seaweed fly) | 0·0047, 0·0009 | GT | SR, VFS, FPS, o | T | Butlin & Day (1989) |
| *Dacus oleae* (Olive fruit fly) | 0·18 | GT | SR, VFS, FPS, o | A | Nei & Tajima (1981) |
| *Drosophila melanogaster* (Fruit fly) | 0.256, ∞§ | GL | SR, VFS, FPS, o | A | Prout (1954) |
| *D. melanogaster* | 0·48, 0·71, 0·72, 0·74, 0·85, 0·85, 0·90 | D | VFS, n | B | Crow & Morton (1955) |
| *D. melanogaster* | 0·38, 0·23 | GM | SR, VFS, n | B | Nozawa (1963) |
| *D. melanogaster* | 1·07, 0·98, 0·80, 0·32, 0·14, 0·73, 0·72, 0·72, 0·35, 0·16 | GM | VFS, n | B | Nozawa (1970) |
| *D. melanogaster* | 0·138 | GL | SR, VFS, FPS, o | A | Murata (1970) |
| *D. melanogaster* | 0·83, 0·72, 0·67, 0·75, 0·69, 0·46 | GM | VFS, n | B | Wright (1977) |
| *D. melanogaster* | 0·36 | GD | SR, VFS, FPS, o | A | Hill (1981) |
| *D. melanogaster* | 0·038, 0·077, 0·079, 0·085 0·225, 0·250 | GL | SR, VFS, FPS, o | A | Malpica & Briscoe (1981) |
| *D. melanogaster* | 0·078, 0·122, 0·151, 0·285, ∞§ | GL | SR, VFS, FPS, o | A | López-Fanjul & Torroja (1982) |
| *D. melanogaster* | 0·037, 0·051, 0·004, 0·016 | GT | SR, VFS, FPS, o | A | Briscoe *et al.* (1992) |
| *D. pseudoobscura* | 0·012, 0·036 | GT | SR, VFS, FPS, o | A | Briscoe *et al.* (1992) |
| *D. subobscura* | 0·083–0·097‖ | D | SR, VFS, FPS, n | B | Begon (1977) |
| *Panaxia dominula* (Moth) | 0·077, 0·256 | GM | SR, VFS, n | A | Wright (1978) |
| *Tribolium castaneum* (Red flour beetle) | 0·76–0·95 | GM | VFS, n | B | Wade (1980) |
| *Tribolium castaneum* | 1·04, 0·98, 0·96, 0·95, 0·91, 0·78, 0·75 | GM | VFS, n | B | Pray *et al.* (1955) |
| **Molluscs High fecundity** | | | | | |
| *Cepaea nemoralis* (Snail) | 0·5 | D | VFS, n | A | Greenwood (1974) |
| *Crassostrea gigas* (Pacific oyster) | $< 10^{-6}$ | GV | SR, VFS, FPS, o | A | Hedgecock, Chow & Waples (1992) |
| *Lymnea columella* (Snail) | 0·75 | D | VFS, n | B | Crow & Morton (1955) |
| **Fish High fecundity** | | | | | |
| *Atractoscion nobilis* (Sea bass) | 0·27–0·40 | GD | SR, VFS, FPS, o | A | Bartley *et al.* (1992) |
| *Oncorhynchus kisutch* (Coho salmon) | 0·24 | D | SR, VFS, n | A | Simon, McIntyre & Hemmingsen (1986) |
| *Oncorhynchus mykiss* (Rainbow trout) | 0·90 | GD | SR, VFS, FPS, o | A | Bartley *et al.* (1992) |
| *Oncorhynchus tshawytscha* (Chinook salmon) | 0·013, 0·043 | GD | SR, VFS, FPS, o | A | Bartley *et al.* (1992) |
| **Amphibians High fecundity** | | | | | |
| *Bufo marinus* (Great toad) | 0·016–0·088 | GV | SR, VFS, FPS, o | A | Easteal & Floyd (1986) |
| *Notophthalmus viridescens* (Red-spotted newt) | 0·073 | D | SR, VFS§, FPS, n | A | Gill (1978) |
| *Rana pipiens* (Leopard frog) | 0·01–0·67 | D | n | A | Merrell (1968) |
| *Rana sylvatica* (Wood frog) | 0·44 | D | SR, FPS, n | B | Berven & Grudzien (1990) |
| **Reptiles High fecundity** | | | | | |
| *Sceloporus olivaceus* (Rusty lizard) | 0·22 | D | VFS, o | A | Kerster (1964) |
| *Uta stansburiana stejnegera* (Lizard) | 0·61–0·74 | D | VFS, n | B | Tinkle (1965) |
| **Birds Low fecundity** | | | | | |
| *Accipiter gentilis* (Northern goshawks) | 0·41 | D | ?, o | B | Reed, Doerr & Walters (1986) |
| *Aphelocoma coerulescens* (Florida scrub jay) | 0·48 | D | VFS, o | B | Koenig (1988) |
| *Cairina scutulata* (White-winged wood duck) | 0·052 | GP | SR, VFS, FPS, o | T | Tomlinson *et al.* (1991) |
| *Cairina scutulata* | 0·094 | D | SR, VFS, FPS, o | T | Tomlinson *et al.* (1991) |

| Species | $N_e/N$ ratio | Method* | Variables† | $N$‡ | Reference |
|---|---|---|---|---|---|
| *Geospiza conirostris* (Darwin's large cactus finch) | 0·28 | D | VFS, n | B | Grant & Grant (1989) |
| *Geospiza fortis* (Darwin's medium ground finch) | 0·31 | D | SR, VFS, n | B | Grant & Grant (1992) |
| *Geospiza scandens* (Darwin's cactus finch | 0·40 | D | SR, VFS, n | B | Grant & Grant (1992) |
| *Grus japonensis* (Red-crowned crane) | 0·45 | D | SR, VFS, n | A | Mace (1986) |
| *Gymnorhinus cyanocephalus* (Pinyon jay) | 0·74 | D | VFS, n | B | Marzluff & Balda (1989) |
| *Malurus splendens* (Splendid fairy-wren) | 0·30 | D | SR, VFS, o | A | Rowley, Russell & Brooker (1993) |
| *Melanerpes formicivorous* (Acorn woodpecker) | 0·09 | D | VFS, o | B | Koenig (1988) |
| *Parus major* (Great tit) | 0·67 | D | ?, o | A | Nunney & Elam (1994) |
| *Passer domesticus* (House sparrow) | 0·74 | D | VFS, n | B | Fleischer (1983) |
| *Picoides borealis* (Red-cockaded woodpecker) | 0·63, 0·80 | D | SR, VFS, o | B | Reed *et al.* (1993) |
| *Piciodes borealis* | 0·32–0·46 | GP | SR, VFS, o | B | Blackwell *et al.* (1995) |
| *Puffinus puffinus* (Manx shearwater) | 0·70 | D | ?, o | A | Nunney & Elam (1994) |
| *Strix occidentalis* (Spotted owl) | 0·39 | D | VFS, o | B | Koenig (1988) |
| *Zonotrichia leucophrys* (White-crowned sparrow) | 0·324 | D | SR, VFS, o | B | Baker (1981) |
| **Mammals Low fecundity** | | | | | |
| *Alces alces* (Moose) | 0·27–0·55 | D | SR, VFS, o | A | Ryman *et al.* (1981) |
| *Bison bison* (Bison) | 0·084–0·296 | D | SR, VFS, o | T | Shull & Tipton (1987) |
| *Bison bison* | 0·069 | D | SR, VFS, FPS, n | A | Berger & Cunningham (1995) |
| *Cercocebus galeritus* (Tana River crested mangabey) | 0·19–0·29 | D | SR, VFS, FPS, n | A | Kinnaird & O'Brien (1991) |
| *Cervus elaphus* (Elk) | 0·23 | D | SR, o | A | Reed *et al.* (1986) |
| *Cervus elaphus* | 0·41 | D | SR, VFS, o | A | Glenn (1990) |
| *Connochaetes taurinus* (Wildebeest) | 0·5 | D | SR, n | T | Ralls & Ballou (1983) |
| *Cynomys ludocicianus* (Prairie dog) | 0·83 | D | SR, n | A | Chepko-Sade *et al.* (1987) |
| *Dipodyms spectabilis* (Banner-tailed kangaroo rat) | 0·56 | D | ?, o | A | Nunney & Elam (1994) |
| *Enhydra lutris* (California sea otters) | 0·36–0·75 | D | SR, n | A | Ralls, Ballou & Brownell (1983) |
| *Equus caballus* (Horse) | 0·8 | D | SR, n | B | Berg (1987) |
| *Equus caballus* | 0·82 | D | SR, o | A | Nunney & Elam (1994) |
| *Equus grevyi* (Grevy's zebra) | 0·28 | D | SR, VFS, n | A | Mace (1986) |
| *Helogale parvula* (Mongoose) | 0·16** | D | SR, VFS, n | A | Chepko-Sade *et al.* (1987) |
| *Homo sapiens* (Human) | 0·69, 0·76, 0·79, 0·95 | D | VFS, n | B | Crow & Morton (1955) |
| *Homo sapiens* | 0·65 | D | o | T | Nei & Imaizumi (1966) |
| *Homo sapiens* | 0·52 | D | VFS, n | B | Nei & Murata (1966) |
| *Homo sapiens* | 0·69–0·76, 0·90–1·18 | D | VFS, n | B | Imaizumi *et al.* (1970) |
| *Homo sapiens* | 0·2–0·5 | D | VFS, o | T | MacCluer & Shull (1970) |
| *Homo sapiens* | 0·44 | D | VFS, o | T | Nei (1970) |
| *Homo sapiens* | 0·34 | D | VFS, o | T | Felsenstein (1971) |
| *Homo sapiens* | 0·21–0·46 | D | VFS, n | T | Salzano (1971) |
| *Homo sapiens* | 0·33, 0·34, 0·37 | D | VFS, n | T | Salzano (1971) |
| *Homo sapiens* | 0·123 | ? | ? | T | Morton & Lalouel (1973) |
| *Homo sapiens* | 0·41 | D | VFS, o | T | Emigh & Pollak (1979) |
| *Homo sapiens* | 0·60 | D | VFS, o | B | Charlesworth (1980) |
| *Homo sapiens* | 0·49 | D | SR, VFS, o | T | Wood (1987) |
| *Lasiorhinus krefftii* (N. hairy-nosed wombat) | 0·18 | GT | SR, VFS, FPS, o | A | Taylor *et al.* (1994) |
| *Lasiorhinus krefftii* | 0·59 | GD | SR, VFS, FPS, o | A | Taylor *pers. comm.* (1995) |
| *Macaca fuscata and M. mulatta* (Japanese and rhesus monkeys) | 0·65 | D | SR, VFS, n | A | Nozawa (1972) |
| *Macaca mulatta* | 0·45–0·53 | G? | ?, o | T | Harpending & Cowan (1986) |
| *Mirounga augustirostrus* (N. elephant seal) | 0·22 | D | SR, VFS, o | A | Nunney (1993) |
| *Odocoileus virginianus* (White-tailed deer) | 0·52–0·65 | D | SR, VFS, o | A | Ryman *et al.* (1981) |
| *Oryctolagus cuniculus* (Rabbit) | 0·42, 0·55–0·65 | D | SR, FPS, o | A | Daly (1981) |
| *Oryx dammah* (Scimitar-horned oryx) | 0·20 | D | SR, VFS, n | A | Mace (1986) |
| *Ovis canadiensis* (Bighorn sheep) | 0·44 | D | SR, FPS, n | A | FitzSimmons, Buskirk & Smith (1995) |
| *Panthera tigris* (Tiger) | 0·41 | D | SR, VFS, n | B | Smith & McDougal (1991) |

| Species | $N_e/N$ ratio | Method* | Variables† | $N$‡ | Reference |
|---|---|---|---|---|---|
| *Perameles gunnii* (E. barred bandicoot) | 0·135 | D | SR, VFS. o | A | Sherwin & Brown (1990) |
| *Pteropus rodricensis* (Rodrigues fruit bat) | 0·18–0·43 | D | SR, VFS, FPS, o | T | Carroll & Mace (1988) |
| *Rhinoceros unicornis* (Greater one-horned rhinoceros) | 0·61 | D | SR, n | A | Dinerstein & McCracken (1990) |
| *Sciurus caroliniensis* (Gray squirrel) | 0·59 | D | VFS, o | B | Charlesworth (1980) |
| *Urocyon littoralis* (Island fox) | 0·50 | D | ?, o | ? | Wayne *et al.* (1991) |
| *Ursus americanus* (Black bear) | 0·69 | D | SR, n | A | Chepko-Sade *et al.* (1987) |
| *Ursus arctos* (Grizzly bear) | 0·28 | D | SR, VFS, o | T | Allendorf, Harris & Metzgar (1991) |
| **Plants†† High fecundity** | | | | | |
| *Agrostemma githargo* | 0·676, 0·510‡‡ | D | VFS, n | B | Heywood (1986) |
| *Anagallis minima* | 0·413, 0·260‡‡ | D | VFS, n | B | Heywood (1986) |
| *Astrocaryum mexicanum* (Tropical palm) | 0·18–0·43 | D | VFS, o | A | Eguiarte *et al.* (1993) |
| *Avena fatua* (Wild oats) | 0·51 | D | VFS, n | B | Jain & Rai (1974) |
| *Bidens cernua* | 0·511, 0·343‡‡ | D | VFS, n | B | Heywood (1986) |
| *Bidens tripartata* | 0·517, 0·349‡‡ | D | VFS, n | B | Heywood (1986) |
| *Blackstonia perfoliata* | 0·212, 0·119‡‡ | D | VFS, n | B | Heywood (1986) |
| *Cardamine hirsuta* | 0·585, 0.376, 0·414‡‡, 0·232‡‡ | D | VFS, n | B | Heywood (1986) |
| *Centaurium erythraea* | 0·379, 0·234‡‡ | D | VFS, n | B | Heywood (1986) |
| *Chaenorhinum minus* | 0·188, 0·104‡‡ | D | VFS, n | B | Heywood (1986) |
| *Chamaecrista fasciculata* | 0·78–0·93 | D | VFS, n | A | Fenster (1991) |
| *Cicendia filiformis* | 0·676, 0·511‡‡ | D | VFS, n | B | Heywood (1986) |
| *Crassula tilaea* | 0·605, 0·433‡‡ | D | VFS, n | B | Heywood (1986) |
| *Damasonium alisma* | 0·485, 0·321‡‡ | D | VFS, n | B | Heywood (1986) |
| *Diamophora smallii* | 0·431, 0·275‡‡ | D | VFS, n | B | Heywood (1986) |
| *Eichhornia paniculata* | 0·054, 0·015, 0·093, 0·002, 0·146, 0·164, 0·174, 0·086, 0·160, 0·168 | GT | VFS, FPS, o | B | Husband & Barrett (1992) |
| *Eichhornia paniculata* | 0·114, 0·080, 0·290, 0·008, 0·191, 0·066, 0·341, 0·139, 0·191, 0·184 | D | VFS, FPS, n | B | Husband & Barrett (1992) |
| *Gaillardia pulchella* | 0·386, 0·239‡‡ | D | VFS, n | B | Heywood (1986) |
| *Impatiens pallida* | 0·344, 0·208‡‡ | D | VFS, n | B | Heywood (1986) |
| *Kickxia elatine* | 0·265, 0·152‡‡ | D | VFS, n | B | Heywood (1986) |
| *Kickxia spuria* | 0·140, 0·075‡‡ | D | VFS, n | B | Heywood (1986) |
| *Lapsana communis* | 0·379, 0·234‡‡ | D | VFS, n | B | Heywood (1986) |
| *Legousia hybrida* | 0·194, 0·108‡‡ | D | VFS, n | B | Heywood (1986) |
| *Linum catharticum* | 0·146, 0·079‡‡ | D | VFS, n | B | Heywood (1986) |
| *Linanthes androsaceus* | 0·306, 0·181‡‡ | D | VFS, n | B | Heywood (1986) |
| *Ludwigia leptocarpa* | 0·227, 0·128‡‡ | D | VFS, n | B | Heywood (1986) |
| *Matricaria matricarioides* | 0·31, 0·19‡‡ | D | VFS, n | B | Heywood (1986) |
| *Moenchia erecta* | 0·62, 0·45‡‡ | D | VFS, n | B | Heywood (1986) |
| *Myosurus minimus* | 0·63, 0·46‡‡ | D | VFS, n | B | Heywood (1986) |
| *Papaver dubium* (Poppy) | 0·07 | D | VFS, n | A | Crawford (1984) |
| *Papaver dubium* | 0·251, 0·144‡‡ | D | VFS, n | B | Heywood (1986) |
| *Papaver rhoeas* | 0·317, 0·188‡‡ | D | VFS, n | B | Heywood (1986) |
| *Phlox drummondii* | 0·355, 0·216‡‡ | D | VFS, n | B | Heywood (1986) |
| *Picea glauca* (White spruce) | 0·19 | D | VFS, n | B | Brown & Schoen (1992) |
| *Radiola linoides* | 0·391, 0·243‡‡ | D | VFS, n | B | Heywood (1986) |
| *Saxifraga tridactylites* | 0·502, 0·335‡‡ | D | VFS, n | B | Heywood (1986) |
| *Senecio sylvaticuls* | 0·619, 0·448‡‡ | D | VFS, n | B | Heywood (1986) |
| *Solanum nigrum* | 0·216, 0·121‡‡ | D | VFS, n | B | Heywood (1986) |
| *Stephanomeria exiuga* | 0·299, 0·210‡‡ | D | VFS, n | B | Heywood (1986) |
| *Veronicá hederaefolia* | 0·660, 0·493‡‡ | D | VFS, n | B | Heywood (1986) |

* Methods used to estimate $N_e$ were D = demographic, GD = linkage disequilibrium, GL = lethal allelism, GM = analyses of populations segregating for mutations, GP = pedigree, GT = changes in genetic variation over time, and GV = variance in gene frequencies.

† Variables included are SR = sex-ratio variation, VFS = variation in family sizes, FPS = fluctuations in population size over generations, n = non-overlapping generations, o = overlapping generations, and ? = unclear what was included.

‡ $N$ = population size used; A = adults, B = breeding adults, T = total adults + juveniles).

§ Estimates of ∞ are presumed to reflect contamination of populations, and were omitted from analyses.

‖ Where ranges are given, analyses were based on means if available, otherwise the mid-point of the range.

¶ Variance in family size was from variance among demes.

** Recalculated using equation 3 to determine the effect of VFS.

†† All plants were annuals, apart from *Astrocaryum mexicanum* and *Picea glauca*

‡‡ The two estimates for each species made by Heywood (1986) represented one assuming an inbreeding coefficient of 0, and the second a value of 1·0. Analyses were based on the former.

## References

Allendorf, F. W., Harris, R. B. & Metzgar, L. H. (1991). Estimation of effective population size of grizzly bears by computer simulation. *Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology* pp. 650–654.

Avise, J. C., Ball, R. M. & Arnold, J. (1988). Current versus historical population sizes in vertebrate species with high gene flow: a comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. *Molecular Biology and Evolution* **5**, 331–344.

Baker, M. C. (1981). Effective population size in a songbird: some possible implications. *Heredity* **46**, 209–218.

Barrett, J. W., Knowles, P. & Cheliak, W. M. (1987). The mating system in a black spruce clonal seed orchard. *Canadian Journal of Forest Research* **17**, 379–382.

Barrowclough, G. F. & Shields, G. F. (1984). Karyotypic evolution and long-term effective population sizes of birds. *Auk* **101**, 99–102.

Bartley, D., Bagley, M., Gall, G. & Bentley, B. (1992). Use of linkage disequilibrium data to estimate effective size of hatchery and natural fish populations. *Conservation Biology* **6**, 365–375.

Begon, M. (1977). The effective size of a natural *Drosophila subobscura* population. *Heredity* **38**, 13–18.

Begon, M., Krimbas, C. B. & Loukas, M. (1980). The genetics of *Drosophila subobscura* populations. XV. Effective size of a natural population estimated by three independent methods. *Heredity* **45**, 335–350.

Berg, W. J. (1987). Effective population size estimates and inbreeding in feral horses: a preliminary assessment. *Equine Veterinary Science* **6**, 240–245.

Berger, J. & Cunningham, C. (1995). Multiple bottlenecks, allopatric lineages and badlands bison *Bos bison*: consequences of lineage mixing. *Biological Conservation* **71**, 12–23.

Berven, K. A. & Grudzien, T. A. (1990). Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* **44**, 2047–2056.

Blackwell, B. F., Reed, J. M., Walters, J. R. & Doerr, P. D. (1995). Inbreeding rate and effective population size: a comparison of estimates from pedigree analysis and a demographic model. *Biological Conservation* **71**, 299–304.

Borlase, S. C., Loebel, D. A., Frankham, R., Nurthen, R. K., Briscoe, D. A. & Daggard, G. E. (1993). Modeling problems in conservation genetics using captive *Drosophila* populations: consequences of equalization of family sizes. *Conservation Biology* **7**, 122–131.

Briscoe, D. A., Malpica, J. M., Robertson, A., Smith, G. J., Frankham, R., Banks, R. G. & Barker, J. S. F. (1992). Rapid loss of genetic variation in large captive populations of *Drosophila* flies: Implications for genetic management of captive populations. *Conservation Biology* **6**, 416–425.

Briton, J., Nurthen, R. K., Briscoe, D. A. & Frankham, R. (1994). Modelling problems in conservation genetics using captive *Drosophila* populations: Consequences of harems. *Biological Conservation* **69**, 267–275.

Brookfield, J. F. Y. & Sharp, P. M. (1994). Neutralism and selectionism face up to DNA data. *Trends in Genetics* **10**, 109–111.

Brown, A. H. D. & Schoen, D. J. (1992). Plant population genetic structure and biological conservation. In *Conservation of Biodiversity for Sustainable Development* (ed. O. T. Sandlund, K. Hindar and A. H. D. Brown), pp. 88–104. Oslo: Scandinavian University Press.

Butlin, R. K. & Day, T. H. (1989). Environment correlates of inversion frequencies in natural populations of seaweed flies (*Coelopa frigida*). *Heredity* **62**, 223–232.

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

Carroll, J. B. & Mace, G. M. (1988). Population management of the Rodrigues fruit bat *Pteropus rodricensis* in captivity. *International Zoo Yearbook* **27**, 70–78.

Charlesworth, B. (1980). *Evolution in Age-Structured Populations.* Cambridge: Cambridge University Press.

Cheliak, W. M., Pitel, J. A. & Murray, G. (1985). Population structure and the mating system of white spruce. *Canadian Journal of Forest Research* **15**, 301–308.

Chepko-Sade, B. D., Shields, W. M., Berger, J., Halpin, Z. T., Jones, W. T., Rogers, L. L., Rood, J. P. & Smith, A. T. (1987). The effects of dispersal and social structure on effective population size. In *Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics* (ed. B. D. Chepko-Sade and Z. T. Halpin), pp. 287–321. Chicago, IL: University of Chicago Press.

Crawford, T. J. (1984). What is a population? In *Evolutionary Ecology* (ed. B. Shorrocks), pp. 135–173. Oxford: British Ecological Society Symposium No. 23, Blackwell.

Crow, J. F. & Kimura, M. (1970). *An Introduction to Population Genetics Theory.* New York: Harper & Row.

Crow, J. F. & Morton, N. E. (1955). Measurement of gene frequency drift in small populations. *Evolution* **9**, 202–214.

Daly, J. C. (1981). Effects of social organization and environmental diversity on determining the genetic structure of a population of wild rabbits, *Oryctolagus cuniculus. Evolution* **35**, 689–706.

Debouzie, D. (1980). Estimate of variance effective population size in a laboratory *Ceratitis* population. *Heredity* **45**, 297–299.

Denniston, C. (1978). Small population size and genetic diversity. Implications for endangered species. In *Endangered Birds: Management Techniques for Preserving Endangered Species* (ed. S. A. Temple), pp. 281–290. Madison, WI: University of Wisconsin Press.

Dinerstein, E. & McCracken, G. F. (1990). Endangered greater one-horned rhinoceros carry high levels of genetic variation. *Conservation Biology* **4**, 417–422.

Easteal, S. & Floyd, R. B. (1986). The ecological genetics of introduced populations of the giant toad, *Bufo marinus* (Amphibia: Anura): dispersal and neighbourhood size. *Biological Journal of the Linnean Society* **27**, 17–45.

Eguiarte, L. E., Burquez, A., Rodriguez, J., Martinez-Ramos, M., Sarukhan, J. & Pinero, D. (1993). Direct and indirect estimates of neighborhood and effective population size in a tropical palm *Astrocaryum mexicanum. Evolution* **47**, 75–87.

Emigh, T. H. & Pollak, E. (1979). Fixation probabilities and effective population numbers in diploid populations with overlapping generations. *Theoretical Population Biology* **15**, 86–107.

Falconer, D. S. (1989). *Introduction to Quantitative Genetics* (3rd ed.). Harlow: Longman.

Felsenstein, J. (1971). Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics* **68**, 581–597.

Fenster, C. B. (1991). Gene flow in *Chamaecrista fasciculata* (Leguminosae) II. Gene establishment. *Evolution* **45**, 410–422.

Fleischer, R. C. (1983). A comparison of theoretical and electrophoretic assessments of genetic structure in populations of the house sparrow (*Passer domesticus*). *Evolution* **37**, 1001–1009.

FitzSimmons, N. N., Buskirk, S. W., Smith, M. H. (1995). Population history, genetic variability, and horn growth in bighorn sheep. *Conservation Biology* **9**, 314–323.

Gill, D. E. (1978). Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Evolution* **32**, 839 849.

Glenn, T. C. (1990). *Genetic Variation in the Michigan Elk* (Cervus elaphus). M.Sc. thesis, University of Michigan.

Gowe, R. S., Robertson, A. & Latter, B. D. H. (1959). Environment and poultry breeding problems. 5. The design of poultry control strains. *Poultry Science* **38**, 462–471.

Grant, B. R. & Grant, P. R. (1989). *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galapagos*. Chicago, IL: University of Chicago Press.

Grant, P. R. & Grant, B. R. (1992). Demography and the genetically effective size of two populations of Darwin's finches. *Ecology* **73**, 766–784.

Greenwood, J. J. D. (1974). Effective population size in the snail *Cepaea nemoralis*. *Evolution* **28**, 513–526.

Harpending, H. & Cowan, S. (1986). Primate population structure: evaluation of models. *American Journal of Physical Anthropology* **70**, 63–68.

Hedgecock, D., Chow, V. & Waples, R. S. (1992). Effective population numbers of shellfish broodstocks estimated from temporal variance in allelic frequencies. *Aquaculture* **108**, 215–232.

Heywood, J. S. (1986). The effect of plant size variation on genetic drift in populations of annuals. *American Naturalist* **127**, 851–861.

Hill, W. G. (1981). Estimation of effective population size from data on linkage disequilibrium. *Genetical Research* **38**, 209–216.

Husband, B. C. & Barrett, S. C. H. (1992). Effective population size and genetic drift in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution* **46**, 1875–1890.

Imaizumi, Y., Nei, M. & Furusho, T. (1970). Variability and heritability of human fertility. *Annals of Human Genetics* **33**, 251–259.

Jain, S. K. & Rai, K. N. (1974). Population biology of *Avena*. IV. Polymorphism of small populations of *Avena fatua*. *Theoretical and Applied Genetics* **44**, 7–11.

Jorde, L. B. (1980). The genetic structure of subdivided human populations: A review. *Current Developments in Anthropological Genetics* **1**, 135–208.

Kerster, H. W. (1964). Neighborhood size in the rusty lizard, *Sceloporus olivaceus*. *Evolution* **18**, 445–457.

Kinnaird, M. F. & O'Brien, T. G. (1991). Viable populations for an endangered forest primate, the Tana River crested mangabey (*Cercocebus galeritus galeritus*). *Conservation Biology* **5**, 203–213.

Koenig, W. D. (1988). On determination of viable population size in birds and mammals. *Wildlife Society Bulletin* **16**, 230–234.

Lande, R. (1979). Effective deme size during long-term evolution estimated from rates of chromosomal rearrangement. *Evolution* **33**, 234–251.

Lande, R. & Barrowclough, G. F. (1987). Effective population size, genetic variation, and their use in population management. In *Viable Populations for Conservation* (ed. M. E. Soulé), pp. 87–123. Cambridge: Cambridge University Press.

López-Fanjul, C. & Torroja, E. (1982). Presion ambiental y reaccion genetica en caracteres cuantitativos. *Actas V Congr. Latinoam. Genetica* pp. 272–279.

MacCluer, J. W. & Shull, W. J. (1970). Estimating the effective size of human populations. *American Journal of Human Genetics* **22**, 176–183.

Mace, G. M. (1986). Genetic management of small populations. *International Zoo Yearbook* **24/25**, 167–174.

Mace, G. M. & Lande, R. (1991). Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. *Conservation Biology* **5**, 148–157.

Malpica, J. M. & Briscoe, D. A. (1981). Effective population number estimates of laboratory populations of *Drosophila melanogaster*. *Experientia* **37**, 947–948.

Marzluff, J. M. & Balda, R. P. (1989). Causes and consequences of female-biased dispersal in a flock-living bird, the Pinyon jay. *Ecology* **70**, 316–328.

Merrell, D. J. (1968). A comparison of the estimated and the 'effective size' of breeding populations of the leopard frog *Rana pipiens*. *Evolution* **22**, 274–283.

Morton, N. E. & Lalouel, J. M. (1973). Bioassay of kinship in Micronesia. *American Journal of Physical Anthropology* **38**, 709–720.

Murata, M. (1970). Frequency distribution of lethal chromosomes in small populations. *Genetics* **64**, 559–571.

Nei, M. (1970). Effective size of human populations. *American Journal of Human Genetics* **22**, 694–696.

Nei, M. & Graur, D. (1984). Extent of protein polymorphism and the neutral mutation theory. *Evolutionary Biology* **17**, 73–118.

Nei, M. & Imaizumi, Y. (1966). Genetic structure of human populations. II. Differentiation of blood group gene frequencies among isolated populations. *Heredity* **21**, 183–190.

Nei, M. & Murata, M. (1966). Effective population size when fertility is inherited. *Genetical Research* **8**, 257–260.

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

Nozawa, K. (1963). Competition between brown gene and its wild-type allele in *Drosophila melanogaster*. II. Estimation of relative viability of brown homozygotes and an analysis of change in gene-frequency. *Japanese Journal of Genetics* **38**, 6–20.

Nozawa, K. (1970). Estimation of the effective size in *Drosophila* experimental populations. *Drosophila Information Service* **45**, 117–118.

Nozawa, K. (1972). Population genetics of Japanese monkeys. I. Estimation of the effective troop size. *Primates* **13**, 381–393.

Nunney, L. (1993). The influence of mating system and overlapping generations on effective population size. *Evolution* **47**, 1329–1341.

Nunney, L. & Campbell, K. A. (1993). Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* **8**, 234–239.

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

Pray, L. A., Goodnight, C. J., Stevens, L., Schwartz, J. M. & Yan, G. (1995). The effect of population size on effective population size: an empirical study in the red flour beetle *Tribolium castaneum*. *Conservation Biology* (submitted).

Prout, T. (1954). Genetic drift in irradiated experimental populations of *Drosophila melanogaster*. *Genetics* **39**, 529–546.

Ralls, K. & Ballou, J, (1983). Extinction: lessons from zoos. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations* (ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde & L. Thomas), pp. 164–184. Menlo Park, CA: Benjamin/Cummings.

Ralls, K., Ballou, J. & Brownell, R. L. Jr. (1983). Genetic diversity in California sea otters: theoretical considerations and management implications. *Biological Conservation* **25**, 209–232.

Reed, J. M., Doerr, P. D. & Walters, J. R. (1986). Determining minimum population size for birds and mammals. *Wildlife Society Journal* **14**, 244–261.

Reed, J. M., Walters, J. R., Emigh, T. E. & Seaman, D. E. (1993). The effective population size in red-cockaded woodpeckers: Population and model differences. *Conservation Biology* **7**, 302–308.

Robertson, A. (1962). Selection for heterozygotes in small populations. *Genetics* **47**, 1291–1300.

Rowley, I., Russell, E. & Brooker, M. (1993). Inbreeding in birds. In *The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives* (ed. N. W. Thornhill), pp. 304–328. Chicago, IL: University of Chicago Press.

Ryman, N., Baccus, R., Reuterwall, C. & Smith, M. H. (1981). Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. *Oikos* **36**, 257–266.

Salzano, F. M. (1971). Demographic and genetic interrelationships among the Cayapo Indians of Brazil. *Social Biology* **18**, 148–157.

Schoen, D. J. & Brown, A. H. D. (1991). Intraspecific variation in population gene diversity and effective size correlates with the mating system in plants. *Proceedings of the National Academy of Sciences, USA* **88**, 4494–4497.

Sherwin, W. S. & Brown, P. R. (1990). Problems in the estimation of the effective size of a population of the Eastern Barred bandicoot (*Perameles gunnii*) at Hamilton, Victoria. In *Bandicoots and Bilbies* (ed. J. H. Seebeck, P. R. Brown, R. L. Wallis and C. M. Kemper), pp. 367–373. Chipping Norton, NSW: Surrey Beatty & Sons.

Shull, A. M. & Tipton, A. R. (1987). Effective population size of bison on the Whichita Mountains Wildlife Refuge. *Conservation Biology* **1**, 35–41.

Simon, R. C., McIntyre, J. D. & Hemmingsen, A. R. (1986). Family size and effective population size in a hatchery stock of Coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Science* **43**, 2434–2442.

Sinclair, A. R. E. (1995). Mammal populations: fluctuation, regulation and conservation. In *Frontiers of Population Ecology* (ed. R. Floyd, A. Shepherd and L. Lawrence). (in press) Canberra, ACT: CSIRO Publications.

Smith, J. L. D. & McDougal, C. (1991). The contribution of variance in lifetime reproduction to effective population size in tigers. *Conservation Biology* **5**, 484–490.

Spiess, E. B. (1989). *Genes in Populations* (2nd ed.). New York, Wiley.

Taylor, A. C., Sherwin, W. B. & Wayne, R. K. (1994). Genetic variation of microsatellite loci in a bottlenecked species: the northern hairy-nosed wombat *Lasiorhinus krefftii*. *Molecular Ecology* **3**, 277–290.

Templeton, A. R. & Read, B. (1994). Inbreeding: One word, several meanings, much confusion. In *Conservation Genetics* (ed. V. Loeschcke, J. Tomiuk and S. K. Jain), pp. 91–105. Basel: Birkhauser.

Tinkle, D. W. (1965). Population structure and effective size of a lizard population. *Evolution* **18**, 569–573.

Tomlinson, C., Mace, G. M., Black, J. M. & Hewston, N. (1991). Improving the management of a highly inbred species: the case of the white-winged wood duck *Cairina scutulata* in captivity. *Wildfowl* **42**, 123–133.

Wade, M. J. (1980). Effective population size: the effects of sex, genotype, and density on the mean and variance of offspring numbers in the flour beetle, *Tribolium castaneum*. *Genetical Research* **36**, 1–10.

Wayne, R. K., George, S. B., Gilbert, D., Collins, P. W., Kovach, S. D., Girman, D. & Lehman, N. (1991). A morphologic and genetic study of the Island fox, *Urocyon littoralis*. *Evolution* **45**, 1849–1868.

Wood, J. W. (1987). The genetic demography of the Gainj of Papua New Guinea. 2. Determinants of effective population size. *American Naturalist* **129**, 165–187.

Woodworth, L. M., Montgomery, M. E., Nurthen, R. K., Briscoe, D. A. & Frankham, R. (1994). Modelling problems in conservation genetics using *Drosophila*: consequences of fluctuating population sizes. *Molecular Ecology* **3**, 393–400.

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

Wright, S. (1938). Size of population and breeding structure in relation to evolution. *Science* **87**, 430–431.

Wright, S. (1939). Statistical genetics in relation to evolution. In *Exposés de Biométrie et de la Statistique Biologique XIII*, pp. 5–64. Paris: Hermann et Cie.

Wright, S. (1969). *Evolution and the genetics of populations*. Vol. 2. *The theory of gene frequencies*. Chicago, IL: University of Chicago Press.

Wright, S. (1977). *Evolution and the genetics of populations*. Vol. 3. *Experimental Results and Evolutionary Deductions*. Chicago, IL: University of Chicago Press.

Wright, S. (1978). *Evolution and the genetics of populations*, Vol. 4. *Variability within and among Natural Population*. Chicago, IL: University of Chicago Press.

Young, T. P. (1994). Natural die-offs of large mammals: Implications for conservation. *Conservation Biology* **8**, 410–418.