Wild populations are smaller than we think: a commentary on 'Effective population size/adult population size ratios in wildlife: a review' by Richard Frankham

TRUDY F. C. MACKAY*

Department of Genetics, North Carolina State University, Campus Box 7614, Raleigh, NC 27695, USA

Population genetics theory predicts the heterozygosity (H) of a finite population maintained for t generations at a constant size of $2N$ each generation, with a random distribution of family size, as:

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

where H_0 is the heterozygosity of the population before the bottleneck, H_t is the heterozygosity after t generations of maintenance with $2N$ individuals and F is the inbreeding coefficient (Falconer & Mackay, 1996). Clearly heterozygosity decreases, and inbreeding increases, as N decreases; and these effects accumulate over time. However, no real population fits the ideal model on which this theory is based, which includes self-fertilization in random amounts. The concept of effective population size enables us to utilize this expression by replacing the N in the equation with N_e, where N_e, the effective population size, is the number of individuals that would give rise to the same variance in gene frequency or rate of inbreeding as an ideal population of that size (Falconer & Mackay, 1996). Major departures from the ideal population model that affect N_e are unequal numbers of males and females, unequal numbers of individuals in different generations, non-random distribution of family size, and overlapping generations. Analytical expressions relating the census size of the population (N) to the effective population size have been derived for each of these cases (Frankham, 1995; Falconer & Mackay, 1996); under most scenarios $N_e < N$. Knowledge of the ratio of N_e to N is critical in wildlife populations and particularly endangered species, if we are to predict the rate of inbreeding and loss of heterozygosity. In this meta-analysis, Frankham (1995) synthesizes data from 192 estimates of N_e/N from 102 species.

The estimates of N_e/N from insects, molluscs, amphibians, reptiles, birds, mammals and plants ranged from 10^{-6} in Pacific oysters to 0·99 in humans, and averaged 0·34 overall. However, these studies differed in whether they included fluctuating population size, variable family size and/or different numbers of males and females – less than one-third of the studies included all three of these factors. In addition, different measures of census size were used as the denominator. Some studies utilized the total census size (N_T, the total number of adults and juveniles), some the number of adults (N_A, the number of breeding plus senescent adults), while others counted only the number of breeding individuals (N_B). Finally, both genetic and demographic methods were used. Frankham (1995) capitalized on this variability to perform stepwise regression analyses in order to determine the major variables affecting N_e/N. The significant variables, in decreasing order of importance, were fluctuating population size, variable family size, method of determining census number, taxonomic group, and the sex ratio. The most striking conclusion was that the comprehensive estimates of N_e/N in wild species, including all variables, were of the order of 10%. This is much smaller than had been thought previously and a cause for concern in terms of long-term population viability. This influential review stimulated many studies estimating N_e/N in a wide variety of wild species.

References

Falconer, D. S. & Mackay, T. F. C. (1996). *Introduction to Quantitative Genetics*, 4th edn. Harlow, Essex: Longman.
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* e-mail: trudy_mackay@ncsu.edu