

Third, heritabilities are often less than 0.5. Of traits in *Drosophila* and other non-domestic animals classified as life history, behaviour, physiology and morphology, only morphological traits in animals excluding *Drosophila* average about 0.5; all other categories are less (Roff, 1997). This is particularly important for traits closely related to reproductive fitness where heritabilities are typically 10–20% (Roff, 1997). Using Lande's (1995) discount factor of 90%, so that  $V_m = 10^{-4}V_E$ , then if we assume  $h^2 = 0.1$ ,  $N_e = 556$ , while for  $h^2 = 0.2$ ,  $N_e = 1250$ .

Wild populations need to be about an order of magnitude higher than these  $N_e$  values (i.e. about 5000–12 500) to maintain their evolutionary potential, as  $N_e/N$  ratios that contain all relevant variables average 0.10–0.11 (Frankham, 1995). This range sets a lower limit for the minimum size that populations should be maintained at for long-term viability (Soulé, 1987), and is within the range of values reached from consideration of environmental stochasticity and catastrophes (Nunney & Campbell, 1993) and from empirical observation (Thomas, 1990).

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## The critical effective size for a genetically secure population

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For practical reasons, managers and policy-makers have to make rapid decisions with limited information on the status of endangered species. Because of its relative ease of acquisition, the most common surrogate used to derive inferences about the risk of extinction is population size. This is not to say that population size is the best indicator of risk; other considerations, such as the recent rate of population decline, are of clear importance (Mace & Lande, 1991). A popular rule of thumb for the critical population

size necessary for the maintenance of adequate genetic variance for adaptive evolution in quantitative traits, originally espoused by Franklin (1980) and Soulé (1980), has been an effective population size ( $N_e$ ) of 500 individuals. More recent assessments, based on both empirical and theoretical developments, suggest that this number should be revised upwards to  $N_e \approx 1000$ –5000 (Lande, 1995a; Lynch, 1995; National Research Council, 1995; Bürger & Lynch, 1997). Here we address the arguments of Franklin & Frankham

(1998) that a critical  $N_e \simeq 500$ –1000 is adequate for conservation purposes.

In deriving a critical effective size of 500 individuals, Franklin & Frankham (1998) persist in the use of a model for the amount of quantitative genetic variance expected for a character under a balance between the forces of mutation and random genetic drift. The problem with this approach is that it fails to consider the significant role that selection plays in defining both the quantity and quality of genetic variation in natural populations. Consider, for example, the authors' first formula:

$$N_e = \frac{V_A}{2V_m}, \quad (1)$$

which defines the effective population size that yields an equilibrium additive genetic variance of  $V_A$  when the per-generation rate of input of new variation by mutations is  $V_m$ . A recent survey suggests that the ratio  $V_A/V_m$  for a variety of traits in a diversity of species is typically in the range of 30–300 (Houle, Morikawa & Lynch, 1996), which according to Eqn (1) would imply an  $N_e$  of 15–150 individuals. Even for bristle numbers in *Drosophila melanogaster*, the authors' example of choice,  $V_A/V_m$  is of the order of 500. It seems rather unlikely that the effective population size of this cosmopolitan species is anywhere near as small as 250, so something is clearly wrong with this approach.

For an equilibrium population (with a balance between the input of new variation by mutation and the loss by selection and random genetic drift), the ratio  $V_A/V_m$  is equivalent to the mean persistence time of a new mutation. In small populations, where drift is the primary mechanism influencing the fate of new mutations, the mean persistence time is simply  $2N_e$  generations, as shown in Eqn (1). In large populations, where the forces of selection prevail over drift, the mean persistence time is closely approximated by the reciprocal of the average selection coefficient against a new mutation (Crow, 1993). Thus, the results cited above imply that the average mutation entering a population is selected against with an intensity of 0.3–3.0%. Since these indirect estimates are consistent with direct observations from laboratory mutation-accumulation experiments (summarized by Lynch & Walsh, 1998), a logical conclusion is that a considerable fraction of the standing variation for quantitative traits simply reflects the recurrent introduction of mildly deleterious mutations prior to their removal by selection.

Technical limitations make it very difficult to experimentally measure the distribution of selection coefficients of newly arising mutations, but the existing data are consistent with the idea that a large fraction of new mutations falls in the class with mildly deleterious effects less than 1% (Keightley, 1994; Lande, 1994; Lynch & Walsh, 1998). If a large fraction of mutations have deleterious effects of the order of 0.1% or less, then it is clear that a target  $N_e$  of 500 would impede the efficiency of purifying selection, particularly if a large fraction of deleterious mutations are unconditionally so

(i.e. disadvantageous in all ecological settings). This is because such alleles are effectively neutral (Wright, 1969) and confer a high genetic load (Kimura, Maruyama & Crow, 1963).

An alternative approach to approximating the effective population size necessary for maintaining a genetically secure population is to simply ask the question, 'How large must a population be before it begins to behave genetically as though it were effectively infinite in size?' This is a potentially useful approach because it simultaneously deals with the issue of the maintenance of genetic variance that is available for adaptive evolution in a changing environment as well as with the issue of extinction risk due to deleterious-mutation accumulation. The technical issues have been evaluated in a number of recent publications (Lande, 1994, 1995a, b; Lynch, 1995; Lynch, Conery & Bürger, 1995a, b; National Research Council, 1995; Schultz & Lynch, 1997) and need only be summarized here, again noting that there are limitations to the conclusions that can be drawn in the absence of detailed empirical data on the distribution of allelic effects at loci underlying quantitative traits.

In terms of the *expected* level of genetic variance for quantitative traits, it appears that an effective population size of approximately 1000 individuals is nearly equivalent to a population of infinite size. Moreover, populations with effective sizes greater than this are highly unlikely to succumb to the accumulation of unconditionally deleterious alleles except on extremely long time scales. Nevertheless, a critical effective population size of 1000 individuals is likely to be too low for three reasons. First, unlike the situation in infinite populations, even in populations with constant sizes as large as  $N_e = 1000$ , the genetic variance can be subject to substantial random genetic drift, wandering around its expected value and sometimes remaining at low levels for prolonged periods of time (Bürger & Lande, 1994). Such transient periods of low genetic variability can be a very significant risk of extinction for populations that are adaptively challenged by changing environments (Bürger & Lynch, 1994). Second, the overall mutation rates for single-locus traits, such as disease resistance loci, are approximately three orders of magnitude lower than those for polygenic characters, so much larger populations may be required to maintain an adequate pool of utilizable alleles at such loci. Third, strong synergistic effects between demographic, environmental, and genetic sources of stochasticity in small populations can yield much higher risks of extinction than would be apparent on genetic grounds alone (Lynch, Conery & Bürger, 1995b; Schultz & Lynch, 1997).

Most genetic problems accumulate over tens or hundreds of generations, so the maintenance of populations below the critical effective size for a few generations will not necessarily lead to irreversible genetic problems. However, for populations maintained largely or entirely in captivity, additional problems can arise. First, since there is an economic premium on maintaining individuals in a viable and reproductive

state, managers of captive populations often provide their dependents with an array of services (including dieticians, veterinarians, dating-services, etc.). Such practices may often result in the relaxation of selection against new deleterious mutations, the cumulative effects of which might not be expressed until the population is released back into the wild. Since the recurrent mutational damage experienced by individuals appears to be of the order of 1% per generation (Lynch & Walsh, 1998), this is not a trivial problem on time scales of a dozen or more generations. Second, both during establishment and propagation, captive populations may experience direct selection for phenotypes that are conducive for life in captivity but liabilities with respect to survival and/or reproduction in nature (Arnold, 1995). Neither type of problem is likely to be mitigated by an increase in population size, and the second type of problem may even be exacerbated in larger populations since there will often be more opportunity for evolutionary change.

Given the limitations of our existing knowledge on both deleterious and beneficial mutations and given the still uncertain connection between  $N_e$  and the risk of extinction, we believe that the cautionary principle to err on the side of species should be applied. If the goal of a conservation program is to maintain the long-term genetic security of a species, a target effective size in the range of 1000–5000 appears to be justified, keeping in mind that the reliance on benign captive environments should be avoided. Since the effective size of a population is often of the order of one-third to one-tenth of the actual population size (Frankham, 1995), actual population sizes necessary for the maintenance of genetic integrity must be in excess of a few thousand. In particular cases, ecological and/or demographic considerations will warrant still higher numbers.

Because of resource limitations for the management of endangered species, there may be political and/or economic reasons to keep the critical effective population sizes for protected species below the numbers that we advocate. However, relying on a critical effective size of 500 individuals obviously only makes sense if it is justified on biological grounds. While critical numbers as large as a few thousand may be distressing for those needing to make decisions regarding endangered species, there seems to be little reason for understating things. One could argue, just as reasonably, that an awareness of a need for larger population sizes will in the long run yield more public awareness of the problem and more resources, provided that the convoluted logic that 'species below the critical effective size are doomed and should be ignored' is not applied.

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