Relationship of Genetic Variation to Population Size in Wildlife

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Abstract: *Genetic diversity is one of three levels of biological diversity requiring conservation. Genetic theory predicts that levels of genetic variation should increase with effective population size. Soulé (1976) compiled the first convincing evidence that levels of genetic variation in wildlife were related to population size, but this issue remains controversial. The hypothesis that genetic variation is related to population size leads to the following predictions: (1) genetic variation within species should be related to population size; (2) genetic variation within species should be related to island size; (3) genetic variation should be related to population size within taxonomic groups; (4) widespread species should have more genetic variation than restricted species; (5) genetic variation in animals should be negatively correlated with body size; (6) genetic variation should be negatively correlated with rate of chromosome evolution; (7) genetic variation across species should be related to population size; (8) vertebrates should have less genetic variation than invertebrates or plants; (9) island populations should have less genetic variation than mainland populations; and (10) endangered species should have less genetic variation than nonendangered species. Empirical observations support all these hypotheses. There can be no doubt that genetic variation is related to population size, as Soulé proposed. Small population size reduces the evolutionary potential of wildlife species.*

La Relación Entre la Variacion Genética y el Tamaño Poblacional en Vida Silvestre

Resumen: *La diversidad genética es uno de los tres niveles de diversidad biológica que requieren ser conservados. La teoría genética predice que los niveles de variación genética se incrementan con el tamaño de la población efectiva. Soulé (1976) reunió la primera evidencia convincente de que los niveles de variación genética en la fauna silvestre se relacionaban con el tamaño de sus poblaciones. Sin embargo, este tema sigue siendo controversial. La hipótesis de que la variación genética se relaciona con el tamaño poblacional conduce a las siguientes predicciones (1) la variación genética intraespecífica debe relacionarse con el tamaño de la población, (2) la variación genética intraespecífica debe relacionarse con el tamaño de la isle, (3) la variación genética debe relacionarse con el tamaño poblacional dentro de grupos taxonómicos, (4) especies ampliamente distribuidas deben tener mayor variación genética que especies de distribución restringida, (5) la variación genética en animales debe tener una correlación negative con el tamaño del cuerpo, (6) la variación genética debe correlacionarse negativamente con la tasa de evolución cromosómica, (7) la variación genética intraespecífica debe relacionarse con el tamaño de la población, (8) los vertebrados deben tener menos variación genética que los invertebrados o plantas, (9) poblaciones insulares deben tener menos variación genética que poblaciones continentales, (10) especies amenazadas deben tener menos variación genética que especies no amenazadas. Todas estas hipótesis están sustentadas por observaciones empíricas. Como propuso Soulé, no hay duda de que la variación genética se relaciona con el tamaño de la población. El tamaño pequeño de una población reduce el potencial evolutivo de las especies de fauna silvestre.*

1500

Introduction

Conservation of genetic diversity is a fundamental concern in conservation biology. Genetic variation is the raw material for evolutionary change within wildlife populations. It allows populations to evolve in response to environmental change, whether that be new or changed diseases, pests, parasites, competitors or predators or greenhouse warming, ozone layer depletion, or pollution. Consequently, the World Conservation Union has recognized genetic diversity as one of three levels of biological diversity requiring conservation (McNeely et al. 1990).

The level of genetic variation within a species represents a balance between mutation, drift, and natural selection. Genetic variation is generated by mutation and is lost from populations by genetic drift due to finite population size. Natural selection may either erode genetic variation by leading to fixation of alleles or promote its retention as a result of balancing or diversifying selection. Loss of neutral genetic variation due to finite population size in the short to medium term approximates an exponential decay process, described as follows:

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

where H_t is the heterozygosity at time t, H_0 the original heterozygosity, N_e the effective population size, and t the number of generations (Crow & Kimura 1970). Because the variance of heterozygosity is expected to increase in small populations, this relationship can be obscured unless there are numerous genetic markers and many replicates. Allozyme variation declined according to Eq. 1 in replicated pedigreed populations of *Drosophila melanogaster*, with effective sizes between 25 and 500 maintained for 50 generations (Montgomery et al., in preparation).

Additive genetic variation for quantitative characters should also decline according to Eq. 1 because it is directly proportional to heterozygosity (Falconer & Mackay 1996). Quantitative genetic variation for bristle characters in *D. melanogaster* behaved as predicted by Eq. 1, declining with generations (Briscoe et al. 1992) and declining more rapidly in populations with lower effective population sizes (Frankham 1996a).

The predicted equilibrium heterozygosity (H) between neutral mutation and genetic drift in the long term is given by Eq. 2, and the effective number of alleles at equilibrium (n_e) by Eq. 3:

$$H = 4N_e\mu/[4N_e\mu + 1] \qquad (2)$$

$$n_e = 4N_e\mu + 1, \qquad (3)$$

where μ is the mutation rate for neutral alleles (Crow & Kimura 1970). Equation 2 yields the sigmoid relationship between H and log N_e shown in Fig. 1. Because mutation rates are similar across diploid eukaryotic species (Weaver & Hedrick 1992), Eq. 2 predicts that heterozygosity will be related to the effective population size both across populations within species and across spe-

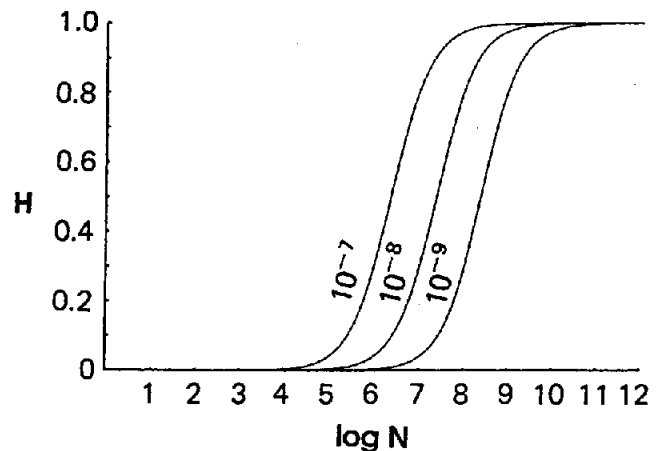*Figure 1. Predicted relationship between heterozygosity (H) and logarithm of effective population size (log N) for three different neutral mutation rates according to Eq. 2 (after Soulé 1976).*

cies. Provided that population size (*N*) is correlated with N_e, and that current *N* reflects past *N*, then a relationship between *H* and *N* similar to Fig. 1 is expected.

Surprisingly, empirical evidence on the relationship between population size and genetic variation in wildlife is equivocal. Soulé (1976) observed a strong positive correlation of 0.7 between heterozygosity and log *N* in animals, explaining approximately one-half of the variation in heterozygosity (Fig. 2). This is an example of Soulé's forte for mining the literature to great effect. Recognition of this important contribution has been sidetracked, largely because of the neutralist-selection controversy (see Kimura 1983; Gillespie 1991). Interestingly, Soulé transcended this controversy, accepting that at least some allozyme loci were subject to balancing natural selection (Soulé 1980), while recognizing that small population size reduced genetic variation.
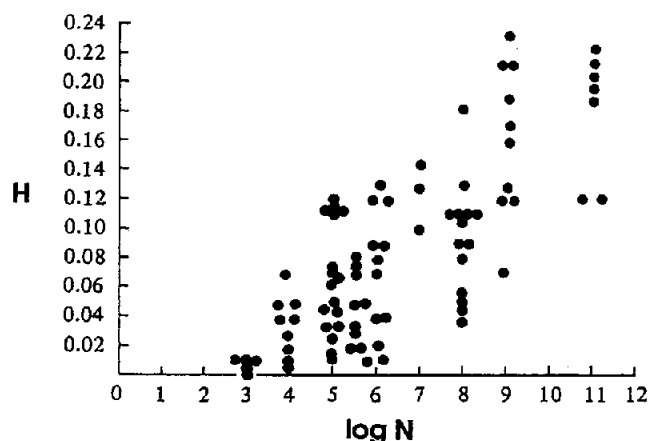

Figure 2. Correlation between heterozygosity (H) and logarithm of populations size (log N) for animal species, as given by Soulé (1976).

The reality of this relationship has been questioned. For example, Gillespie (1991) queried a similar relationship in data collected by Nei and Graur (1984). He noted that the lowest values of H were mainly from carnivores and the highest values from *Drosophila* species, so that the observed difference might reflect different ecologies and different selective forces. Several studies of the relationship between heterozygosity and log N in plants have yielded nonsignificant relationships (Ellstrand & Elam 1993). This could be due either to a lack of relationship or to a reflection of the noisy nature of the relationship due to large drift variance in small populations. This issue can be resolved only by analysis of data from many studies.

The strength of the relationship between genetic variation and population size is likely to vary for different categories of loci because they are subject to different intensities of selection. Selective forces on allozyme loci are weak (Kimura 1983; Gillespie 1991; Ohta 1992), with perhaps 50% of loci subject to weak selection favoring heterozygotes (Brookfield & Sharp 1994). Non-coding DNA regions and synonymous mutations appear to be subject to little selection. Mitochondrial DNA is expected to be subject to selective sweeps because it codes for essential functions and shows little or no recombination. Direct evidence of selective differences among mtDNA haplotypes has been found in *Drosophila* (Mac-Rae & Anderson 1988; Fos et al. 1990; Hutter & Rand 1995). Natural selection on quantitative genetic variation is weak for characters peripheral to reproductive fitness and strong for reproductive fitness itself (Falconer & Mackay 1996), although the intensify of the effect on individual loci is unclear because the number of loci over which selection is spread is unknown.

A correlation between heterozygosity and effective population size is expected for loci under heterozygote advantage selection in finite populations. The effect of heterozygote advantage on fixation probability depends on the equilibrium frequency of the alleles (Robertson 1962). Selection retards fixation for alleles with equilibrium frequencies in the 0.2–0.8 range. Conversely, selection accelerates fixation for alleles with equilibrium frequencies outside this range. Hence, heterozygote advantage in finite populations will slow fixation for some alleles and accelerate it for others. Alleles subject to natural selection approach effective neutrality as the effective population size drops—when the selection coefficient drops below $1/2N_e$ (Wright 1931; Kimura 1983). The effect of selection on individual alleles detected by electrophoresis or DNA sequence is generally weak, so they are likely subject to genetic drift unless population sizes are very large (Robertson 1962; Kimura 1983; Ohta 1992; Satta et al. 1994). The relationship between genetic variation and population size should be strongest for neutral genetic markers and poorest for the most strongly selected markers; non-coding nuclear DNA should show the best relationship, followed by allo-zymes, quantitative

genetic variation for peripheral characters, and mitochondrial DNA, with quantitative genetic variation for reproductive fitness characters showing the weakest relationship.

I tested predictions arising from the hypothesis that genetic variation is related to population size. In most cases population size data were not available, so correlates of population size such as island size, distribution (widespread versus restricted), body size, rate of chromosomal evolution (Lande 1979), and endangered versus nonendangered were used to extend the range of data that could be used. The following predictions were evaluated: (1) genetic variation within species will be related to population size; (2) genetic variation within species will be related to island size; (3) genetic variation among species will be related to population size within taxonomic groups; (4) widespread species will have more genetic variation than restricted species; (5) genetic variation in animals will be negatively correlated with body size; (6) genetic variation will be negatively related to rate of chromosome evolution; (7) genetic variation across species will be related to population size; (8) vertebrates will have less genetic variation than invertebrates or plants; (9) island populations should have less genetic variation than mainland populations; and (10) endangered species will have less genetic variation than nonendangered species.

Data Analyses

It has been traditional to correlate measures of genetic variation with log N, following Soulé (1976). The justification for using this rather than alternative relationships is not clear. From Eq. 2, $H/(1 - H)$ should be linearly related to N_e. Effective number of alleles per locus should be linearly related to N_e according to Eq. 3. To determine the most appropriate scales for presenting relationships between genetic variation and population size, I compared correlations of genetic variation measures with N_e, log N_e, and $(\log N_e)^2$ using our *Drosophila melanogaster* data. For gene diversity (expected heterozygosity), alleles per locus, and percent polymorphism, the highest correlation was with log N_e. All three correlations involving observed heterozygosity were essentially identical (all 0.46). A similar comparison of the relationships between H and log N and between $H/(1 - H)$ and N using the data of Nei and Graur (1984) also revealed a higher correlation for the former than the latter (0.73 versus 0.55). Consequently, I present correlations of genetic variation with log N or log island area, as have most authors.

I used all published data that could be located in testing the predictions. Where correlations between genetic variation and log N were not reported, they were computed from the data given. Correlations were computed between measures of genetic variation (gene diversity, observed heterozygosity, number of alleles per locus, and percent polymorphism) and the logarithm of popu-

lation size (N). The significance of each correlation was determined from the significance of the corresponding regression, with one-tailed tests because the predictions were directional. The data of Saura et al. (1973) was reanalyzed so that measures of genetic variation for the same 14 loci were used for all populations. Analyses of the data of Shapcott (1994) were restricted to Tasmanian mainland populations because there were significant island-mainland differences for some measures of genetic variation. Similar correlations were computed between genetic variation and logarithm of island size.

Over all data sets correlations are equally likely to be positive or negative under the null hypothesis that there is no correlation between genetic variation and population size (island area). Conversely, the alternative hypothesis of an association between genetic variation and population size predicts that correlations will be predominantly positive. I tested the number of positive and negative correlations for deviations from equality using a one-tailed chi-square test. This represents a simple version of meta-analysis of the form already used in conservation biology by Ralls and Ballou (1983). Although more powerful statistical methods are now available for meta-anal-

yses (Arnquist & Wooster 1995), it is inconceivable that they would alter the overall conclusions of these analyses.

Results

Prediction 1. Genetic variation within species will be positively correlated with population size

The correlation between allozyme genetic variation (H_e or H_o) and logarithm of population size was positive in 22 of 23 studies within species of plants and animals (Table 1). This represents a highly significant excess of positive correlations ($\chi^2 = 19.17$, 1 df, $p < 0.000025$). All measures of allozyme genetic variation showed significant associations with log N, as tested using sign tests. The average magnitude of the correlations between genetic variation and log N overall were not markedly lower than those found between genetic variation and log N_e in *Drosophila melanogaster*. The DNA fingerprint variation was significantly correlated with log N in red squirrels ($r = 0.75$, $p = 0.027$; Wauters et al. 1994) and nonsignificantly so in California Channel Island fox ($r = 0.71$, $p = 0.057$; Gilbert et al. 1990).

Table 1.   Correlations between genetic variation and logarithm of population size.[a]

Species location	H_e[b]	H_o[c]	A	P	Range of N	n	Reference
Mammals							
Ovis canadensis	0.89**	0.72*	0.89**	0.93**	100–1146	8	FitzSimmons et al. 1995
Peromyscus maniculatus	—	0.02	0.88**	0.74*	b	8	Gill 1980
Thomomys botae	—	0.69**	—	—	c	23	Patton & Yang 1977
Bird							
Piciodes borelais	0.48**	—	0.83**	0.51**	4–1122	26	Stangel et al. 1992
Insect							
Philaenus spumaris	—	0.34	0.34	0.27	90–30,000	7	Saura et al. 1973
Plants							
Acacia anomala	0.71	0.64	0.85*	0.74*	3–50	6	Coates 1988
Aconitum noveboracense	—	0.13	0.24	0.32	15–10,000	38	Dixon & May 1990
Atherosperma moschatum	0.13	0.13	0.08	0.06	c	16	Shapcott 1994
Eichhornia paniculata							
Brazil	—	0.20	0.15	0.17	8–5,000	49	Husband & Barrett unpublished data
Jamaica	—	0.41	0.45*	0.40	5–2,000	17	
Eucalyptus albens	0.70**	0.77**	0.69**	0.54**	14–6,000	22	Prober & Brown 1994
Eucalyptus caesia	0.22	—	0.58*	0.48*	7–550	13	Moran & Hopper 1983
Eucalyptus crucis	0.62*	0.61*	0.71*	0.80*	4–300	10	Sampson et al. 1988
Eucalyptus parvifolia	0.59	0.44	0.48	−0.07	12–427	8	Prober et al. 1990
Eucalyptus pendens	−0.35	−0.38	−0.32	0.06	27–3,000	7	Moran & Hopper 1987
Eucalyptus pulverulenta	0.75	0.66	0.91*	0.98*	15->500	4	Peters et al. 1980
Gentiana pneumonanthe	0.21	0.21	0.21	0.44**	1–20,000	25	Raijmann et al. 1994
Halocarpus bidwilli	0.94**	—	0.89**	0.89**	20–400,000	17	Billington 1991
Salvia pratensis	0.31	—	0.54*	0.62**	5–1,500	14	Bijlsma et al. 1994
Scabiosa columbaria	0.49	—	0.82**	0.71**	14–100,000	12	Bijlsma et al. 1994
Silene regia							Dolan 1994
east	0.71*	—	—	0.51	45–895	9	
west	0.14	—	—	0.21	41–1,302	9	
Washingtonia filifera	0.23	0.12	—	0.72*	1–82	16	McClenaghan & Beauchamp 1986
Means	0.46	0.36	0.54	0.50			
Drosophila melanogaster	0.56**	0.46*	0.86**	0.78**	25–500	23	Montgomery et al. in preparation

[a] *Genetic variation for allozymes was characterized as gene diversity (H_e), observed heterozygosity (H_o), allelic diversity (A), percentage of loci polymorphic (P). N is population size and n is number of populations.* *p < 0.05; **p < 0.01. Dash indicates correlation not available.*
[b] *Relative population sizes were estimated from the product of island area and trapping success.*
[c] *Correlation was with four categories of population size.*

Quantitative genetic variation was related to population size, although there were far fewer data than for allozyme variation. Responses to artificial selection were greater in larger populations of *Drosophila melanogaster* (Frankham et al. 1968; Jones et al. 1968; Hammond 1973; Franklin 1980; Weber 1990; Weber & Diggins 1990), mice (Eisen 1975), and maize (Silvela et al. 1989). Phenotypic variation will reflect quantitative genetic variation if environmental variation is similar across populations. Bijlsma et al. (1994) reported positive correlations between phenotypic variation (averaged over a number of morphological, growth, and reproductive characteristics) and population size in two plant species (0.92, $p = 0.0075$, in *Salvia pratensis*; 0.53, $p = 0.070$, in *Scabiosa columbaria*).

Prediction 2. Genetic variation will be positively correlated with island area

Significant positive correlations between genetic variation and logarithm of island area (or habitat island size) were reported in 16 of 19 studies involving mammals, birds, reptiles, and an insect (Table 2). This is a significant excess of positive correlations ($x^2 = 8.89$, $df = 1$, $p = 0.0014$). Eight studies reported significant correlations. The bird studies with negative correlations were based on very small sample sizes, 2–7 for *Camarhynchus parvulus* and 1–7 for *Geospiza magnirostris*.

Morphological variation showed a highly significant correlation of 0.81 with logarithm of island area in the

lizard *Uta stansburiana* (Soulé 1972), a highly significant correlation of 0.95 with log island area in the roof rat (*Rattus rattus*; Patton et al. 1975) and a nonsignificant correlation of 0.71 with log island area in the deer mouse (*Peromyscus maniculatus*; Aquadro & Kilpatrick 1981).

Prediction 3. Genetic variation will be related to population size within taxonomic groups

Soulé (1976) reported positive relationships between heterozygosity and population size in lizards, fish, mammals, marine invertebrates, and *Drosophila*. Nevo et al. (1984) found a significant relationship between heterozygosity and population size categories for vertebrates and plants but not for invertebrates. Within vertebrates there was a significant relationship for mammals and fish, but not for birds, reptiles, and amphibians. Cases with nonsignificant relationships were generally represented by few species. For vertebrates the population size category showed the highest correlation of 15 ecological, demographic, and life-history variables with both heterozygosity and percent polymorphism.

Prediction 4. Genetic variation will be greater in species with wider ranges

Populations within plant species with wider geographic ranges have higher allozyme variation (Table 3), and the widely distributed species have more overall allozyme variation (Hamrick & Godt 1989). Further, allozyme vari-

Table 2. Correlations between genetic variation and logarithm of island size.[a]

Species	H_e	H_o	A	P	n	Reference
Mammals						
Cynopterus brachyotis	0.03	0.01	0.25	0.25	6	Peterson & Heaney 1993
Haplonycteris fisheri	0.15	0.42	0.09	0.15	6	Peterson & Heaney 1993
Macaca fascicularis	0.86*	—	—	0.85*	7	Kawamoto et al. 1988
Microtus pennsylvanicus	—	−0.40	—	−0.60	7	Kilpatrick 1981
Mus musculus	—	0.55**	—	0.77**	19	Kilpatrick 1981
Peromycus maniculatus	—	0.40	—	0.35	7	Kilpatrick 1981
Rattus rattus	—	0.73*	—	—	8	Patton 1984
Birds						
Atalapetes brunneinuncha[b,c]	—	0.20	—	—	4	Peterson et al. 1992
Camarhynchus parvulus	—	−0.42	—	—	4	Yang & Patton 1981
Certhidea olivacea	—	0.996*	—	—	4	Patton 1984
Chlorospingus ophthalmicus[b,c]	—	0.60	—	—	4	Peterson et al. 1992
Geospiza fortis	—	0.16	—	—	8	Patton 1984
Geospiza fuliginosa	—	0.24	—	—	10	Patton 1984
Geospiza magnirostris	—	−0.62	—	—	4	Yang & Patton 1981
Reptiles						
Anolis cristatellus	—	0.60*	—	—	9	Soulé 1980
Lacerta melisellensis	—	0.76**	—	0.70**	12	Gorman et al. 1975
Trachydosaurus rugosus	0.55	0.04	0.45	0.35	5	Sarre et al. 1990
Uta stansburiana	—	0.647*	—	0.63**	14	Soulé & Yang 1973
Insect						
Parnassius mnemosyne[b]	0.83**	—	0.83**	0.52**	24	Descimon & Napolitano 1993

[a] *Genetic variation for allozymes was characterized as gene diversity (H_e), observed heterozygosity (H_o), allelic diversity (A) and percentage of loci polymorphic (P). Number of islands is n. *p < 0.05; **p < 0.01.*
[b] *Habitat islands on the mainland.*
[c] *Rank correlation.*

ation was significantly lower in restricted versus widespread plant congeners (Karron 1987).

For all species and for vertebrates, Nevo et al. (1984) reported lower levels of genetic variation in endemics than narrow, regional, and widespread species, the latter three not differing significantly.

Prediction 5. Genetic variation in animals will be negatively correlated with body size

Large animals typically have smaller populations than small animals. Consequently, a negative correlation between body size and heterozygosity is predicted. Wooten and Smith (1985) reported a significant negative correlation between body size and allozyme heterozygosity in mammals.

Prediction 6. Genetic variation will be negatively correlated with rate of chromosome evolution

Lande (1979) predicted that rate of chromosome evolution would be negatively related to effective population size. Chromosomal heterozygotes typically show heterozygote disadvantage and unstable equilibria, such that low population sizes are required to fix new chromosomal mutations. Lande (1979) and Barrowclough and Shields (1984) have used rates of chromosome evolution to estimate species effective population sizes. Consequently, heterozygosity is predicted to be negatively correlated with rate of chromosome evolution. Coyne (1984) found a significant negative correlation between heterozygosity and rate of chromosome evolution in animals.

Prediction 7. Genetic variation will be positively correlated with population size across species

Soulé (1976) reported a correlation of 0.7 between heterozygosity and estimates of log N in animals (Fig. 2). This conclusion is supported by analyses of data presented by Nei and Graur (1984) on gene diversity (minimum 20 loci) and population sizes for 77 animal, plant,
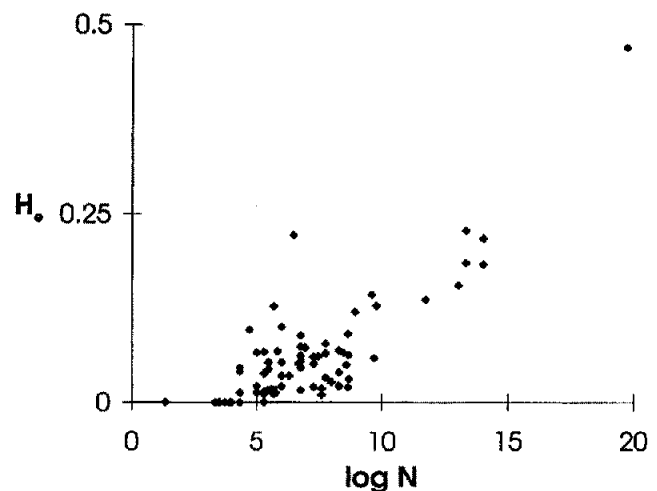
Table 3. Geographic range and genetic variation within plant populations.*

Geographic range	H_e	A	P	n
Endemic	0.063	1.39	26.3	100
	(0.006)	(0.03)	(2.1)	
Narrow	0.105	1.45	30.6	115
	(0.009)	(0.05)	(2.2)	
Regional	0.118	1.55	36.4	180
	(0.007)	(0.04)	(2.0)	
Widespread	0.159	1.72	43.0	85
	(0.013)	(0.07)	(3.3)	

Genetic variation for allozymes was characterized as gene diversity (H_e), allelic diversity (A), and percentage of loci polymorphic (P). Standard errors are given in parentheses and n is the number of species. (From Hamrick and Godt [1989]).

Figure 3. Relationship between gene diversity (expected diploid heterozygosity) (H_e) and logarithm of populations size (log N) across species for the data of Nei and Graur (1984). The point for Eschericia coli to the extreme right is plotted against half its population size because it is haploid.

and bacterial species (Fig. 3). The correlation between gene diversity and log N was 0.81 for the full data set and 0.73 with *Escherichia coli* omitted, very similar to the value reported by Soulé (1976). Both correlations were highly significant. Nevo et al. (1984) reported higher allozyme variation in larger populations for all species, vertebrates and plants, but a nonsignificant relationship in invertebrates. Mitochondrial DNA nucleotide diversity showed a significant correlation of 0.45 with log N (females) ($p = 0.032$) for data on 18 populations of 12 species of vertebrates (Avise 1992).

Prediction 8. Genetic variation will be lower in vertebrates than in invertebrates or plants

For species in which allozyme genetic variation has been measured, vertebrates generally have lower population sizes than invertebrates or plants and so should have lower genetic variation. Nevo et al. (1984) showed that vertebrates had significantly lower levels of allozyme variation than invertebrates (heterozygosities of 0.054 ± 0.0025 versus 0.100 ± 0.0048, respectively). The heterozygosity for vertebrates was significantly lower than the mean heterozygosity of 0.113 ± 0.005 for plant populations, reported by Hamrick and Godt (1989).

Prediction 9. Genetic variation should be less in island populations than mainland populations

Because island populations are typically smaller than mainland populations, they are predicted to have less genetic variation. A large and highly significant majority of island populations have less allozyme genetic variation than their mainland counterparts (165 of 203 com-

parisons; Frankham 1996*b*). Similar differences exist for other measures of genetic variation. Island endemic species showed lower allozyme variation than related mainland species in 34 of 38 cases.

Prediction 10. Genetic variation will be lower in endangered species than nonendangered species

By definition, endangered species typically have smaller populations than related nonendangered species and should have lower levels of genetic variation. Genetic variation was significantly reduced in endangered species compared with nonendangered species (Frankham 1995*a*), 32/38 endangered species being lower than their controls ($\chi^2 = 17.8$, 1 *df*, *p* < 0.0001).

Discussion

Nine of the 10 predictions of the hypothesis that genetic variation is related to population size were verified. The only prediction in which the evidence was equivocal was the taxonomic group; even here most comparisons were in the predicted direction. Consequently, there can be no doubt that genetic variation is related to population size; Soulé's (1976) conclusions have been amply vindicated. Data were most extensive for allozymes, but similar relationships were evident for mtDNA and for quantitative genetic variation.

It is implausible that reporting bias could explain all these positive associations because data were collected mostly for unrelated purposes. The Soulé (1976) and Nei and Graur (1984) analyses involved data collected in this way, as were the analyses for predictions relating to body size, rates of chromosome evolution, geographic range, endangered species, and the comparison of vertebrates versus invertebrates and plants. Only for predictions 1, 2, and 9 is reporting bias a potential problem. Even in these cases there seems to have been no impediment to reporting nonsignificant or negative correlations, or differences in the opposite direction to those predicted.

The positive correlations between genetic variation and population size variables probably represent causal relationships. Such a consistent relationship is predicted by population genetics theory. The only competing theory that predicts a similar relationship is diversifying selection favoring different genotypes in different habitats, and evidence for this is weak and inconsistent (Hedrick 1986). Widespread species would be expected to have greater niche diversity than more restricted species. Although this hypothesis is compatible with correlations between genetic variation and population size or island size within species, it stretches credibility to attribute all the correlations to this cause, especially those with body size and rates of chromosomal evolution and with the difference in genetic variation between vertebrates and invertebrates and plants. Alternative hypotheses for the

relationship can be rejected for our controlled experiment in *D. melanogaster*. Mean correlations between genetic variation and log *N* within wildlife species, and that for all species, were not markedly lower than those observed in our controlled *Drosophila* experiment. Positive correlations were found within species, among species within taxonomic groups, and across all species.

Population size is arguably the most important variable explaining differences in allozyme variation. Logarithm of population size explained 49% or more of the variation in heterozygosity in the data sets of Soulé (1976) and Neve and Graur (1984), whereas Nevo et al. (1984) accounted for only 20% of the variation in heterozygosity with a suite of 15 ecological, demographic, and life-history variables, several themselves related to population size. Further, geographic range, a close correlate of *N*, was the most important variable explaining differences in heterozygosity among plant species and was equally important as breeding system in explaining differences in heterozygosity among plant populations (Hamrick & Godt 1989). Conversely, in the analyses of Nevo et al. (1984), population size category was not one of the four significant explanatory variables for heterozygosity across all species. It was the most important explanatory variable for mammals and fish.

Soulé (1976) pointed out that the relationship between heterozygosity and log *N* was not sigmoid as predicted by Eq. 2. Analyses of the Nei and Graur (1984) data support this: there was a higher correlation between *H* and log *N* than between *H*/(1 − *H*) and *N* (0.73 versus 0.55), whereas the latter would give a higher correlation if the relationship was sigmoid. The predicted relationship is affected by natural selection, nonlinear relationships between N_e and *N*, N_e having narrower range than *N*, and populations not having sufficient time to reach equilibrium. Models with mildly deleterious and neutral mutations (the near neutral model) in finite populations give a near-linear relationship between heterozygosity and log N_e, at least up to an N_e of 10^6 (Kimura 1983: 244). The overall relationship between heterozygosity and log *N* would not be possible if N_e/N ratios varied widely among different species and taxa. Analyses of published estimates of N_e/N ratios failed to detect significant differences among animal taxa (Frankham 1995*b*). Plants differed from animals, but there was a question about the reality of this difference. A negative relationship between N_e/N and log *N* has been found in *Drosophila, Tribolium*, and the plant *Eichhornia paniculata* (Nozawa 1963, 1970; Husband & Barrett 1992; Pray et al. in preparation). The range of N_e is less than that for *N*; N_e/N estimates that include all relevant variables average 0.11 (Frankham 1995*b*). A model of mildly deleterious and neutral alleles and the negative relationship of N_e/N and log *N* seem to provide the most plausible reasons for the nonsigmoid relationship between heterozygosity and log *N*. In conclusion, genetic varia-

tion within species and among species is positively correlated with population size, confirming and amplifying the analysis of Soulé (1976).

This work provides compelling empirical support for conservation concerns about the genetic consequences of small population size. Theoretical prediction that reductions in population size reduce genetic variation have been amply verified. Consequently, reduction in population size will compromise the ability of populations to adapt genetically to changing environments.

Acknowledgments

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