# Do island populations have less genetic variation than mainland populations?

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Island populations are much more prone to extinction than mainland populations. The reasons for this remain controversial. If inbreeding and loss of genetic variation are involved, then genetic variation must be lower on average in island than mainland populations. Published data on levels of genetic variation for allozymes, nuclear DNA markers, mitochondrial DNA, inversions and quantitative characters in island and mainland populations were analysed. A large and highly significant majority of island populations have less allozyme genetic variation than their mainland counterparts (165 of 202 comparisons), the average reduction being 29 per cent. The magnitude of differences was related to dispersal ability. There were related differences for all the other measures. Island endemic species showed lower genetic variation than related mainland species in 34 of 38 cases. The proportionate reduction in genetic variation was significantly greater in island endemic than in nonendemic island populations in mammals and birds, but not in insects. Genetic factors cannot be discounted as a cause of higher extinction rates of island than mainland populations.

**Keywords:** allozymes, conservation, endemic species, extinction, genetic variation, islands.

## Introduction

Island populations have a much higher risk of extinction than mainland populations (Diamond, 1984; Vitousek, 1988; Flesness, 1989; Case *et al.*, 1992; World Conservation Monitoring Centre, 1992; Smith *et al.*, 1993). Recorded extinctions since 1600 show that a majority of extinctions of mammals, birds and reptiles were of insular forms, and substantial proportions of extinctions in invertebrates and vascular plants were of island forms (Table 1), even though island species represent a minority of total species in all groups. For example, only 20 per cent of all bird species are on islands, but 90 per cent of bird species driven to extinction in historic times have been island dwellers (Myers, 1979). Further, substantial proportions of endangered and vulnerable species are of insular species (Table 2). Endemic species are particularly prone to extinction or endangerment. Davis *et al.* (1986) reported 55–97 per cent of endemic plant taxa on 13 islands were extinct, endangered, rare or threatened, and Reid & Miller (1989) described 6–94 per cent

of endemic plant species as threatened on 15 islands.

Human activities have been the major cause of species extinctions on islands in the past 50 000 years (Olson, 1989) through over-exploitation, habitat loss and introduced species. The relative importance of these factors in recorded extinctions varies according to the taxonomic group. Reid & Miller (1989) rated over-exploitation and introduced species as the most important causes in vertebrates, followed by habitat loss, whereas the World Conservation Monitoring Centre (1992) reported introduced animals and habitat loss to be the most important cause of animal extinctions, followed by over-exploitation. Both report substantial proportions of cases where the cause was unknown. Habitat loss is the most important cause of endangerment in all vertebrate taxa, except for reptiles where it is second to over-exploitation (Reid & Miller, 1989). The role of disease is not listed in these compilations. However, there is a growing suspicion that new and changed diseases represent a significant factor (Diamond, 1984; Dobson & May, 1986; O'Brien & Evermann, 1988; Flesness, 1989).

The reason for the susceptibility of island populations to extinction is controversial. The *coup de grâce* is usually delivered by stochastic factors, whether

**Table 1** Recorded extinctions, 1600 to present

| Taxa | Island | Mainland | Ocean | Total | Per cent island |
|------|--------|----------|-------|-------|-----------------|
| Mammals* | 34 | 24 | — | 58 | 59 |
| Birds* | 104 | 11 | — | 115 | 90 |
| Reptiles† | 20 | 1 | 0 | 21 | 95 |
| Amphibians† | 0 | 2 | 0 | 2 | 0 |
| Fish† | 1 | 22 | 0 | 23 | 4 |
| Molluscs* | 151 | 40 | — | 191 | 79 |
| Invertebrates† | 48 | 49 | 1 | 98 | 49 |
| Vascular plants† | 139 | 245 | 0 | 384 | 36 |

*From World Conservation Monitoring Centre (1992).
†From Reid & Miller (1989).

**Table 2** Endangered and vulnerable species (from Reid & Miller, 1989)

| Taxa | Island | Mainland | Ocean | Total | Per cent island |
|------|--------|----------|-------|-------|-----------------|
| Mammals | 48 | 159 | 9 | 216 | 22 |
| Birds | 87 | 91 | 0 | 178 | 49 |
| Reptiles | 21 | 41 | 6 | 68 | 31 |
| Amphibians | 0 | 14 | — | 14 | 0 |
| Fish | 21 | 443 | 0 | 464 | 5 |
| Invertebrates | 338 | 371 | 2 | 711 | 48 |
| Vascular plants | 2706 | 3985 | 0 | 6691 | 40 |

demographic, environmental, catastrophic, or genetic. Pimm (1991) and other ecologists stress the susceptibility of small island populations to demographic and environmental stochasticity. However, the susceptibility of island populations is predicted on genetic grounds (Frankham, 1995a). Oceanic island populations are expected to lose genetic variation at foundation (as few as a single individual in self-fertilizing species, or a pair in nonselfing species). Both oceanic and land-bridge islands should lose genetic variation after foundation as they typically have lower population sizes than mainland populations.

Genetic variation is the raw material for evolutionary change (Frankel & Soulé, 1981). Genetic variation allows populations to evolve in response to environmental change, whether that be new/changed diseases, parasites, predators and competitors, or greenhouse warming, ozone layer depletions, or other results of pollution. Pre-existing genetic variation is critical for short-term evolutionary change (Ayala, 1965; R. Frankham, E. Lowe, M. E. Montgomery, L. M. Woodworth, & D. A. Briscoe, unpublished data) as the waiting times for new favourable mutations are high unless population sizes are very large. The IUCN (World Conservation

Union) has recognized genetic diversity as one of three levels of biological diversity requiring conservation (McNeely et al., 1990).

Genetic variation on islands is determined by the net effects of loss at foundation, subsequent loss caused by finite population size since foundation, and gains arising from secondary immigration and new mutations (Jaenike, 1973). Natural selection influences the loss of genetic variation; selection for a favourable allele will increase rate of loss, whereas heterozygote advantage may slow it.

A single population size bottleneck is predicted to reduce heterozygosity and evolutionary potential by $1/2N_e$ where $N_e$ is the effective size of the bottleneck generation (James, 1971). For example, if an oceanic island population is founded from a single pair, heterozygosity is expected to be immediately reduced by 25 per cent. Populations that have been subjected to bottlenecks usually have reduced allozyme variation (see Leberg, 1992; Hartl & Pucek, 1994) and quantitative genetic variation (Robertson, 1966; James, 1971; Frankham, 1980; Franklin, 1980; Brakefield & Saccheri, 1994). Conversely, Bryant et al. (1986) and López-Fanjul & Villaverde (1989) reported higher quantitative genetic variation for characters related to fitness in bottlenecked popula-

tions. However, bottlenecked populations show reduced evolutionary potential (R. Frankham, P. R. England, K. E. L. Lees & D. A. Briscoe, unpublished data).

Heterozygosity for neutral alleles is expected to show an approximately exponential decay with generations in finite populations, as described by eqn 1

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

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). A feature of this relationship is that the variance in heterozygosity is expected to increase in small populations, such that the relationship can be obscured unless there are many genetic markers and many replicates.

A correlation between heterozygosity and effective population size is also 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, i.e. when the selection coefficient drops below $1/2N_e$ (Wright, 1931; Kimura, 1983). Selection on individual alleles detected by electrophoresis or DNA sequence is generally weak, so they will be subject to genetic drift unless population sizes are very large (Robertson, 1962; Kimura, 1983; Ohta, 1992; Satta *et al.*, 1994).

The predicted relationship between genetic variation and effective population size given in eqn 1 has been verified for allozyme genetic variation in experimental populations of *Drosophila* (M. E. Montgomery, R. K. Nurthen, L. M. Woodworth, D. A. Briscoe & R. Frankham, in preparation). Further, there are clear associations between population size and genetic variation in wildlife, both within and among species (reviewed by Frankham, 1996). For example, Soulé (1976) observed a correlation of 0.70 between allozyme heterozygosity and the logarithm of population size for animal species, explaining $\approx 1/2$ of the variation in heterozygosity.

Differences between island populations and main-

land ones are expected to be greater when the number of founders is smallest, when the population size differences are greatest, and when the immigration rates are lowest. Differences should be greater for small rather than large islands, for species with lower dispersal rates, and for distant rather than near islands (Jaenike, 1973). Reversal of the difference is expected when mainland populations are derived from island populations (e.g. after glaciation), and where island populations are larger than mainland populations.

Endemic island species have no mainland counterparts, yet they represent the oldest and most differentiated island populations. According to eqn 1, they would be expected to have proportionately lower genetic variation than island species with mainland representatives as their time since foundation from a mainland population will typically be greater than for nonendemic island populations.

Surprisingly, the evidence on genetic variation in island populations is equivocal. Selander & Johnson (1973) and Selander (1976) indicated there were differences, whereas Nevo (1978) reported that island populations of vertebrates had lower levels of genetic variation than mainland populations, but invertebrates did not show a significant difference. Conversely, the most recent comprehensive review by Nevo *et al.* (1984) found no significant difference for either group, though there was a trend in the predicted direction. Kilpatrick (1981) and Berry (1986) concluded that there were differences in mammals, while Boag (1988) concluded that island and mainland bird species do not differ. All these compilations were based on a small number of studies. Given the importance of the issue to the understanding of the susceptibility of island populations to extinction, it is critical that this issue be resolved.

The hypothesis that genetic factors contribute to the higher extinction rate of island populations predicts that island populations of sexually reproducing species will have, on average, lower levels of genetic variation than comparable mainland populations. Further, endemic island populations should have lower genetic variation than nonendemic island populations. The objective of this study was to test these hypotheses by reviewing and analysing published evidence.

## Collection and analyses of data

Data were obtained from a literature survey of publications where comparisons were made of genetic variation in mainland and island populations

of the same species, usually with the same loci surveyed. Literature was surveyed by checking all relevant previous reviews and the papers they referred to, by performing a keyword search of Biological Abstracts on CD ROM 1992–95, and by checking references that those papers made to other relevant studies. Data from all relevant studies were analysed using sign tests (see below). Marine species were excluded as island populations belong to the same continuous habitat over which they often disperse widely (Stepien & Rosenblatt, 1991; Fevolden, 1992). All data were on independent populations, apart from those for *Peromyscus polionotus* where the same two island populations were studied by Selander *et al.* (1971), Garten (1976) and Brewer *et al.* (1990). The mean of the three studies was used in the sign tests (heterozygosities of 3.33 and 6.97 per cent for island populations vs. 6.98 per cent for mainland). The data of Bock & McCracken (1988) on island populations of green iguanas from Gatun Lake were not included as the island populations were not isolated from the surrounding mainland population; animals from nearby mainland populations nest annually on the islands. The data of Wendel *et al.* (1992) on island vs. mainland populations of cotton (*Gossypium hirsutum*) were not analysed as its distribution is believed to be strongly influenced by human colonization and trade. Johnson & Selander (1971) reported an overall figure of 2.3 per cent heterozygosity for two island populations of *Dipodomys compactus*, with no individual details of sample sizes. The Mustang Island population was monomorphic. One of two populations on Padre Island was monomorphic, whereas the other Padre Island population was polymorphic for one of 18 loci, with two alleles at frequencies of 0.33 and 0.67 (heterozygosity = 2.46 per cent). A heterozygosity of 1.23 per cent was attributed to Padre Island (mean of 0.00 and 2.46 per cent). Only pooled data for several islands were reported for *Drosophila nebulosa* and *D. tropicalis* (Powell, 1975) so these were each treated as one island for the purposes of sign tests.

The null hypothesis is that island populations do not differ from mainland populations or have more variation, and the alternative hypothesis is that island populations have less genetic variation than comparable mainland populations. Consequently, one-tailed $\chi^2$ sign tests were used. Statistical analyses were performed on average heterozygosity values. Preference was given to using gene diversity (expected Hardy–Weinberg heterozygosity) as this is least affected by sample size. Where this was not available observed heterozygosity was used in analy-

ses. Data where both the mainland and the island populations had no genetic variation are included in Table 3, but were not used in the sign test as they are not informative.

Two sign tests were performed on the allozyme data for nonendemic populations, one where every island population was compared against the mean of its corresponding mainland populations, and a second where the mean of islands was compared with the mean of mainland populations for the same study. The latter test covers the possibility that there was migration to one island, and the other island populations were derived from that population. A Kruskal–Wallis test was used to determine whether taxa differed in the ratio of island to mainland heterozygosities. As ratios are not normally distributed, nonparametric statistics were used to compare them throughout this study. Statistical analyses were performed using the MINITAB statistical package release 7. The ratios of heterozygosities for island: mainland populations of the different taxa were obtained by calculating mean heterozygosities for islands and mainland populations of each taxa and then computing the ratio of these.

Similar comparisons were made of genetic variation in endemic island species and the most related mainland species or group that was available. The data of Johnson *et al.* (1989) on Hawaiian honeycreepers were based on very small sample sizes for both island and mainland species, though 36 loci were typed. Further, there was uncertainty regarding the appropriate mainland species to use for comparisons. Taxonomic data presented in the paper indicated that the family Emberizidae was the appropriate mainland group, so this was used. Analyses were also performed using the mean of the families Emberizidae and Fringillidae as the mainland group. Only pooled data for the two island populations of the endemic *Peromyscus sejugis* were reported, so these data have been treated as a single point for sign tests. Avantazi *et al.* (1994) describe two endemic species of mites on the Canary Islands, but only one is reported here as their taxonomic separation is doubtful; they shared the same alleles at 14 allozyme loci and frequencies were similar at the one polymorphic locus. For the endemic plants in the genus *Crepidiastrum*, the 'mainland' species for comparison come from the much larger main Japanese islands (Ito & Ono, 1990).

Comparisons of the ratio of heterozygosity in island:mainland populations were carried out for endemic vs. nonendemic species for the full data set, and for different taxa using Mann–Whitney nonparametric tests.

**Table 3** Allozyme genetic variation in island (Is) and mainland (M) populations, characterized as gene diversity ($H_e$ percentage), observed heterozygosity ($H_o$ percentage), allelic diversity ($A$) and percentage of loci polymorphic ($P$)

| Species | Is vs. M | $H_e$ | $H_o$ | $A$ | $P$ | M > Is: M < Is* | Reference |
|---|---|---|---|---|---|---|---|
| Mammals | | | | | | 82:20 | |
| *Alces alces* | Is† | | 2.6 | | 8.6 | 1:1 | Ryman *et al.* (1980) |
| | M | | 2.0 | | 9.8 | | |
| *Canis lupus* | Is | 3.9 | 4.0 | 1.08 | 8.0 | 1:0 | Wayne *et al.* (1991b) |
| | M | 8.7 | 6.1 | 1.20 | 20.0 | | |
| *Cervus elaphurus atlanticus* | Is | | 0.0 | | 0.0 | — | Gyllensten *et al.* (1983) |
| | M | | 0.0 | | 0.0 | | |
| *Cervus elaphurus scoticus* | Is | | 2.6 | | 14.3 | 1:0 | Gyllensten *et al.* (1983) |
| | M | | 3.3 | | 13.1 | | |
| *Lemur macaco* | Is | 3.4 | 3.3 | 1.25 | 25.0 | 1:0 | Arnaud *et al.* (1992) |
| | M | 7.0 | 3.3 | 1.33 | 33.3 | | |
| *Macaca fascicularis* | Is | 5.2 | | | 22.7 | 7:0 | Kondo *et al.* (1993) |
| | M | 9.9 | | | 40.2 | | |
| *Macaca fuscata* | Is | 1.4 | | 1.05 | 3.6 | 1:1 | Nozawa *et al.* (1975) |
| | M | 1.8 | | 1.15 | 12.9 | | |
| *Macaca fuscata* | Is | 0.5 | | | 3.1 | 1:0 | Nozawa *et al.* (1991) |
| | M | 2.3 | | | 14.6 | | |
| *Macrotus waterhousii* | Is | 3.0 | 4.0 | 1.19 | 4.8 | 0:1 | Greenbaum & Baker (1976) |
| | M | 2.7 | 2.1 | 1.16 | 7.9 | | |
| *Mastomys erytholeucus* | Is | 9.0 | 6.0 | 1.2 | 20.0 | 1:0 | Duplantier *et al.* (1990) |
| | M | 24.6 | 16.2 | 1.42 | 39.4 | | |
| *Mastomys huberti* | Is | 10.0 | 7.0 | 1.25 | 20.0 | 1:0 | Duplantier *et al.* (1990) |
| | M | 24.4 | 16.2 | 1.58 | 48.0 | | |
| *Melomys cervinipes* | Is† | 1.0 | | 1.08 | 8.3 | 1:0 | Leung *et al.* (1993) |
| | M | 5.1 | | 1.21 | 20.8 | | |
| *Mus musculus* | Is | | 3.6 | 1.20 | 14.5 | 17:2 | Berry & Peters (1977) |
| | M | | 7.4 | 1.33 | 30.2 | | |
| *Mus musculus* | Is | | 7.7 | 1.33 | 36.4 | 0:1 | Berry *et al.* (1978) |
| | M | | 7.4 | 1.33 | 34.9 | | |
| *Mus musculus* | Is | | 3.4 | 1.07 | 7.7 | 1:0 | Berry *et al.* (1979) |
| | M | | 7.4 | 1.33 | 30.2 | | |
| *Mus musculus* | Is | | 13.0 | | 38.9 | 0:3 | Berry *et al.* (1981) |
| | M | | 8.2 | | 27.2 | | |
| *Mus musculus* | Is | 9.4 | | 1.33 | 25.4 | 2:3 | Navajas y Navarro & |
| | M | 8.8 | | 1.3 | 27.0 | | Britton-Davidian (1989) |
| *Panthera leo leo* | Crater | | 2.2 | 1.12 | 10.0 | 1:0 | Packer *et al.* (1991) |
| | M | | 3.3 | 1.22 | 17.5 | | |
| *Panthera pardus* | Is | | 1.4 | | 4.0 | 1:0 | Miththapala *et al.* (1991) |
| | M | | 3.1 | | 10.0 | | |
| *Perameles gunii* | Is | 0.0 | 0.0 | 1.0 | 0.0 | — | Sherwin *et al.* (1991) |
| | M | 0.0 | 0.0 | 1.0 | 0.0 | | |
| *Peromyscus eremicus* | Is | | 1.3 | | 8.6 | 2:0 | Avise *et al.* (1974a) |
| | M | | 4.0 | | 11.6 | | |
| *Peromyscus gossypinus* | Is | | 9.9 | 1.7 | 41.3 | 3:3 | Boone *et al.* (1993) |
| | M | | 9.9 | 1.7 | 38.9 | | |
| *Peromyscus leucopus* | Is | | 6.8 | | 16.7 | 3:0 | Browne (1977) |
| | M | | 8.0 | | 22.6 | | |
| *Peromyscus maniculatus* | Is | | 6.6 | 1.37 | 29.0 | 7:1 | Gill (1980) |
| | M | | 8.3 | 1.64 | 43.0 | | |
| *Peromyscus maniculatus* | Is | | 4.2 | | 16.7 | 6:0 | Aquadro & Kilpatrick (1981) |
| | M | | 9.6 | | 27.6 | | |

**Table 3** *Continued*

| Species | Is vs. M | $H_e$ | $H_o$ | $A$ | $P$ | M > Is: M < Is* | Reference |
|---|---|---|---|---|---|---|---|
| *Peromyscus polionotus* | Is | 4.9 | | | | — | Selander *et al.* (1971) |
| | M | 6.3 | | | | | |
| *Peromyscus polionotus* | Is | | 5.9 | | | — | Garten (1976) |
| | M | | 5.2 | | | | |
| *Peromyscus polionotus* | Is | 4.6 | 3.6 | 1.12 | 11.5 | 2:0 | Brewer *et al.* (1990) |
| | M | 9.4 | 8.6 | 1.35 | 27.5 | | |
| *Rattus fuscipes* | Is | | 1.0 | 1.03 | 3.1 | 10:0 | Schmitt (1978) |
| | M | | 5.3 | 1.18 | 17.9 | | |
| *Rattus rattus* | Is | | 2.7 | | 10.0 | 5:3 | Patton *et al.* (1975) |
| | M | | 3.1 | | 8.1 | | |
| *Sigmodon hispidus* | Is | | 2.1 | 1.05 | 4.5 | 1:0 | Johnson & Selander (1972) |
| | M | | 2.2 | 1.09 | 8.6 | | |
| *Sorex cinereus* | Is | 5.6 | 5.4 | 1.22 | 12.9 | 4:1 | Stewart & Baker (1992) |
| | M | 7.9 | 7.8 | 1.43 | 15.6 | | |
| *Spermophilus spilosoma* | Is | | 0.9 | | 3.4 | 1:0 | Cothran *et al.* (1977) |
| | M | | 9.0 | | 30.1 | | |
| Birds | | | | | | 21:6 | |
| *Aplonis cantoroides* | Is | 0.9 | 1.1 | 1.06 | 5.6 | 3:0 | Corbin *et al.* (1974) |
| | M | 2.6 | 2.1 | 1.06 | 5.6 | | |
| *Aplonis metallica* | Is | 4.1 | 4.0 | 1.19 | 11.1 | 4:1 | Corbin *et al.* (1974) |
| | M | 4.9 | 4.9 | 1.22 | 11.1 | | |
| *Callipepla californica* | Is | 2.9 | 2.2 | 1.16 | 13.5 | 1:0 | Zink *et al.* (1987) |
| | M | 4.0 | 3.4 | 1.26 | 18.9 | | |
| *Empidonax difficilis* | Is | 3.4 | 3.7 | 1.12 | 9.8 | 1:0 | Johnson & Marten (1988) |
| | M | 5.6 | 5.4 | 1.29 | 22.6 | | |
| *Fringilla coelebs* | Is | 4.3 | | 1.21 | 18.7 | 9:5 | Baker *et al.* (1990) |
| | M | 5.2 | | 1.34 | 24.3 | | |
| *Lagopus lagopus* | Is | | 6.9 | | 20.3 | 3:0 | Gyllensten *et al.* (1985) |
| | M | | 8.0 | | 26.0 | | |
| Reptiles | | | | | | 20:6 | |
| *Anolis carolinensis* | Is | | 6.0 | | 17.0 | 0:1 | Webster *et al.* (1972) |
| | M | | 5.7 | | 13.9 | | |
| *Lacerta sicula* | Is | | 4.4 | | 16.8 | 4:0 | Gorman *et al.* (1975) |
| | M | | 9.0 | | 36.3 | | |
| *Trachydosaurus rugosus* | Is | 12.3 | 11.9 | 1.33 | 29.5 | 7:0 | Sarre *et al.* (1990) |
| | M | 16.1 | 14.3 | 1.62 | 36.1 | | |
| *Uta stansburiana* | Is | | 4.9 | | 26.2 | 9:5 | Soulé & Yang (1973) |
| | M | | 5.3 | | 28.7 | | McKinney *et al.* (1972) |
| Fish | | | | | | 3:0 | |
| *Astyanax mexicanus* | Cave | | 3.6 | 1.22 | 13.7 | 3:0 | Avise & Selander (1972) |
| | Surface | | 11.2 | 2.13 | 37.3 | | |
| Amphibians | | | | | | 2:0 | |
| *Bufo terrestris americanus* | Is | | Is < M§ | | | | Abramoff *et al.* (1964) |
| | M | | | | | | |
| *Bufo viridis* | Is | | 2.9 | 1.12 | 12.0 | 1:0 | Dessauer *et al.* (1975) |
| | M | | 13.3 | 1.65 | 42.3 | | |
| *Bufo woodhousii fowleri* | Is | 1.1 | | 1.14 | 14.3 | 1:0 | Hranitz *et al.* (1993) |
| | M | 3.0 | | 1.14 | 14.3 | | |
| Molluscs | | | | | | 2:0 | |
| *Cerion bendalli* | Is | | 4.8 | | 14.3 | 2:0 | Woodruff (1975) |
| | M | | 5.4 | | 19.0 | | |

**Table 3** *Continued*

| Species | Is vs. M | $H_e$ | $H_o$ | A | P | M > Is: M < Is* | Reference |
|---|---|---|---|---|---|---|---|
| Insects | | | | | | 23:4 | |
| *Drosophila equinoxialis caribbensis* | Is | | 17.1 | | 45.1 | 5:0 | Ayala *et al.* (1974) |
| | M | | 22.2 | | 60.9 | | |
| *Drosophila immigrans* | Is | | 11.5 | 2.24 | 70.6 | 0:1 | Steiner *et al.* (1976) |
| | M | | 9.3 | 1.82 | 52.9 | | |
| *Drosophila nebulosa* | Is | 17.0 | | | | 1:0 | Powell (1975) |
| | M | 18.8 | | | | | |
| *Drosophila simulans* | Is | | 7.3 | 1.46 | 36.6 | 2:0 | Steiner *et al.* (1976) |
| | M | | 16.2 | 2.17 | 55.6 | | |
| *Drosophila subobscura* | Is | 14.8 | | | | 4:1 | Cabrera *et al.* (1980) |
| | M | 18.3 | | | | | |
| *Drosophila tropicalis* | Is | 16.7 | | | | 1:0 | Powell (1975) |
| | M | 19.8 | | | | | |
| *Drosophila willistoni* | Is | | 16.2 | | 48.8 | 5:1 | Ayala *et al.* (1971) |
| | M | | 18.4 | | 54.2 | | |
| *Philaenus spumarius* | Is | | 6.2 | 1.52 | 35.7 | 5:1 | Saura *et al.* (1973) |
| | M | | 8.7 | 1.86 | 50.0 | | |
| Plants | | | | | | 12:1 | |
| *Atherosperma moschatum* | Is | 26.1 | 10.2 | 1.83 | 62.8 | 2:0 | Shapcott (1994) |
| | M | 28.6 | 8.1 | 2.24 | 78.0 | | |
| *Campanula punctata* | Is | | 4.3 | 1.30 | 26.4 | 6:0 | Inoue & Kawahara (1990) |
| | M | | 11.7 | 1.70 | 46.8 | | |
| *Cryptomeria japonica* | M‡ | 17.8 | 15.3 | 2.38 | 47.4 | — | Tsumura & Ohba (1993) |
| | Is | 19.5 | 18.6 | 2.60 | 47.6 | | |
| *Eichhornia paniculata* | Is | 3.0 | 2.0 | 1.07 | 7.6 | 1:0 | Glover & Barrett (1987) |
| | M | 9.0 | 7.8 | 1.27 | 23.8 | | |
| *Pinus banksiana* | Is† | 15.2 | 16.4 | 2.4 | 59.0 | 2:0 | Gauthier *et al.* (1992) |
| | M | 16.4 | 17.9 | 2.2 | 61.4 | | |
| *Pinus resinosa* | Is | 0.0 | 0.0 | 1.0 | 0.0 | — | Mosseler *et al.* (1991) |
| | M | 0.0 | 0.0 | 1.0 | 0.0 | | |
| *Pinus torreyana* | Is | 0.0 | 0.0 | 1.0 | 0.0 | — | Ledig & Conkle (1983) |
| | M | 0.0 | 0.0 | 1.0 | 0.0 | | |
| *Quercus petraea* | Is | | 39.8 | 3.09 | | 0:1 | Zanetto & Kremer (1995) |
| | M | | 38.0 | 3.22 | | | |
| *Turnera ulmifolia* | Is | 4.0 | 7.0 | 1.20 | 20.0 | 1:0 | Barrett & Husband (1989) |
| | M | 12.0 | 11.0 | 1.51 | 46.0 | | |
| Overall | | | | | | 165:37 | |

*Ratio of cases where mainland populations have higher vs. lower genetic variation than island populations, based on $H_e$, or $H_o$.

†Islands in lakes.

‡island population larger than mainland, and source for it after last glacial.

§Quantitative data not reported.

## Results

### Nonendemic species

Comparisons of genetic variation in island and mainland populations of the same species are given in Table 3. In a highly significant majority of cases (165:37) mainland populations had higher heterozygosities than island populations of the same species ($\chi_1^2 = 81.1$, $P < 0.00005$), the mean reduction being 29 per cent. Allelic diversity and percentage polymorphism also showed higher genetic variation of mainland than island populations. Mammals, birds, reptiles, insects and plants all showed significantly higher levels of genetic variation in mainland than island populations. Other groups showed similar trends, but had few data. If studies are only counted

**Table 4** Genetic and phenotypic variation in island (Is) and mainland (M) populations. Genetic variation was measured using DNA fingerprints, RAPDs, RFLPs, microsatellites and mitochondrial DNA

| Species | Island | Mainland | M > Is: M < Is | Reference |
|---|---|---|---|---|
| DNA fingerprints, RAPDs and microsatellites | | | | |
| Mammals | | | 9:0 | |
| Canis lupus* | 28.5 | 68.5 | 1:0 | Wayne et al. (1991b) |
| Perameles gunii* | 24.4 | 38.8 | 1:0 | Robinson et al. (1993) |
| Urocyon littoralis* | 12.0 | 52.9 | 6:0 | Wayne et al. (1991a) |
| Ursus americanus ‡ | 36.0 | 79.2 | 1:0 | Paetkau & Strobeck (1994) |
| Insects | | | 3:0 | |
| Drosophila subobscura § | 0.00278 | 0.00562 | 1:0 | Rozas & Aguadé (1991) |
| Nicrophorus americanus † | 96.0 | 92.0 | 1:0 | Kozol et al. (1994) |
| Nicrophorus orbicollis † | 79.5 | 77.1 | 1:0 | Kozol et al. (1994) |
| Mitochondrial DNA | | | | |
| Mammals | | | 16:0 | |
| Canis lupus ¶ | 1 | 9 | 1:0 | Wayne et al. (1991b) |
| Perameles gunii ** | 0.50 | 0.61 | 1:0 | Robinson (1995) |
| Peromyscus maniculatus ** | 0.20 | 0.79 | 8:0 | Ashley & Wills (1987) |
| Urocyon littoralis ** | 0.027 | 0.162 | 6:0 | Wayne et al. (1991a) |
| Insects | | | 1:0 | |
| Drosophila sechellia ** | 0.00036 | 0.0020†† | 1:0 | Cariou et al. (1990) |
| Drosophila simulans | Is < M‡‡ | | | Hale & Singh (1991) |
| Phenotypic variation | | | 24:0 | |
| Reptiles | | | | |
| Urocyon littoralis | 0.016 | 0.022 | 6:0 | Wayne et al. (1991a) |
| Uta stansburiana | 7.16 | 8.83 | 18:0 | Soulé (1972) |

*Average percent difference for DNA fingerprints.
†Percentage of band sharing for RAPDs.
‡Microsatellites heterozygosity.
§RFLP nucleotide diversity.
¶Number of mt DNA haplotypes.
**Nucleotide diversity.
††*Drosophila melanogaster*.
‡‡Quantitative data not reported.

once, 48 of 57 comparisons showed higher genetic variation in mainland than island populations with one tie ($\chi_1^2 = 28.1$, $P < 0.00005$). Nuclear DNA variability (DNA fingerprint, RAPDs and microsatellites) was lower in island populations than in mainland populations in all 12 comparisons ($\chi_1^2 = 12.0$, $P = 0.00025$; Table 4). Mitochondrial DNA nucleotide diversity was lower in island populations than in mainland populations (Table 4) in all 17 comparisons ($\chi_1^2 = 17.0$, $P < 0.00005$). The phenotypic coefficient of variation was higher in mainland populations than in island populations (Table 4) in all 24 comparisons ($\chi_1^2 = 24.0$, $P < 0.00005$).

Taxa did not differ significantly in the reduction in heterozygosity (Kruskal–Wallis $H = 13.76$, d.f. = 7, $P = 0.057$; Table 5). However, species capable

**Table 5** Ratios of heterozygosities in island populations to mainland populations ($H_{Is}/H_M$) in different taxa for nonendemic species and for endemic island species compared to related mainland species, and the sample sizes ($N$)

| Taxon | Nonendemics | | Endemics | |
|---|---|---|---|---|
| | $H_{Is}/H_M$ | $N$ | $H_{Is}/H_M$ | $N$ |
| Mammals | 0.65 | 102 | 0.20 | 10 |
| Birds | 0.79 | 27 | 0.37 | 9 |
| Reptiles | 0.78 | 26 | | |
| Fish | 0.32 | 3 | | |
| Amphibians | 0.24 | 2 | | |
| Molluscs | 0.88 | 2 | | |
| Insects | 0.79 | 27 | 0.83 | 8 |
| Arachnids | | | 0.47 | 1 |
| Plants | 0.71 | 13 | 0.54 | 10 |

**Table 6** Allozyme heterozygosity of endemic island (Is) species as compared to related mainland (M) species

| Island species Mainland species | | Heterozygosity | M > Is: M < Is | Reference |
|---|---|---|---|---|
| **Mammals** | | | 10:0 | |
| Dipodomys compactus | Is | 0.6 | 1:0 | Johnson & Selander (1971) |
| Dipodomys | M | 2.1 | | |
| Macaca fuscata | Is | 3.2 | 1:0 | Nozawa et al. (1991) |
| Macaca mulatta | M | 7.4 | | |
| Microtus breweri | Is | 0.7 | 1:0 | Kohn & Tamarin (1978) |
| Microtus pennsylvanicus | M | 6.0 | | |
| Peromyscus eva | Is | 0.0 | 1:0 | Avise et al. (1974a) |
| Haplomys | M | 3.0 | | |
| Peromyscus diskeyi | Is | 0.0 | 1:0 | Avise et al. (1974a) |
| Haplomys | M | 3.0 | | |
| Peromyscus guardia | Is | 1.4 | 1:0 | Avise et al. (1974a) |
| Haplomys | M | 3.0 | | |
| Peromyscus interparietalis | Is | 0.0 | 1:0 | Avise et al. (1974a) |
| Haplomys | M | 3.0 | | |
| Peromyscus sejugis | Is | 1.7 | 1:0 | Avise et al. (1974a, 1979), |
| maniculatis species group | M | 8.1 | | Selander et al. (1971), Kilpatrick (1981) |
| Peromyscus stephani | Is | 0.0 | 1:0 | Avise et al. (1974a,b), |
| boylii species group | M | 3.2 | | Kilpatrick & Zimmerman (1975) |
| Urocyon littoralis | Is | 2.0 | 1:0 | Wayne et al. (1991a) |
| Urocyon cinereoargenteus | M | 9.7 | | |
| **Birds** | | | 9:0 | |
| Hemignathus parvus | Is | 1.4 | 1:0 | Johnson et al. (1989) |
| Family Emberizidae | M | 5.6 | | |
| Hemignathus virens* | Is | 4.8 | 1:0 | Johnson et al. (1989) |
| Himatione sanguinea* | Is | 2.0 | 1:0 | Johnson et al. (1989) |
| Loxioides bailleui* | Is | 0.0 | 1:0 | Johnson et al. (1989) |
| Loxops coccineus* | Is | 0.0 | 1:0 | Johnson et al. (1989) |
| Oreomystis bairdi* | Is | 2.8 | 1:0 | Johnson et al. (1989) |
| Paroreomyza montana* | Is | 4.9 | 1:0 | Johnson et al. (1989) |
| Telespiza cantans* | Is | 0.7 | 1:0 | Johnson et al. (1989) |
| Vestiaria coccinea* | Is | 2.0 | 1:0 | Johnson et al. (1989) |
| **Insects** | | | 5:3 | |
| Drosophila adiostola | Is | 14.0 | 1:0 | Ayala (1975) |
| Drosophila willistoni group | M | 20.2 | | Powell (1975) |
| Drosophila crassifemur† | Is | 20.3 | 0:1 | Ayala (1975) |
| Drosophila dolichotarisi† | Is | 13.8 | 1:0 | Ayala (1975) |
| Drosophila nigella† | Is | 15.0 | 1:0 | Ayala (1975) |
| Drosophila nigra† | Is | 16.0 | 1:0 | Ayala (1975) |
| Drosophila planitibia† | Is | 23.6 | 0:1 | Ayala (1975) |
| Drosophila sechellia | Is | 2.7 | 1:0 | Cariou et al. (1990) |
| Drosophila melanogaster | M | 11.7 | | |
| Drosophila truncipenna† | Is | 22.4 | 0:1 | Ayala (1975) |
| **Arachnids** | | | 1:0 | |
| Steganacarus (S.) tenerifensis | Is | 2.6 | 1:0 | Avanzati et al. (1994) |
| Steganacarus (S.) magnus & S. (S.) hirsutus | M | 5.6 | | |

**Table 6** *Continued*

| Island species<br>Mainland species | | Heterozygosity | M > Is:<br>M < Is | Reference |
|---|---|---|---|---|
| Plants | | | 9:1 | |
| *Crepidiastrum ameristophyllum* | Is | 5.1 | 1:0 | Ito & Ono (1990) |
| *Crepidiastrum & Youngia* sp. | M | 8.2 | | |
| *Crepidiastrum grandicollum* | Is | 2.0 | 1:0 | Ito & Ono (1990) |
| *Crepidiastrum & Youngia* sp. | M | 8.2 | | |
| *Crepidiastrum linguaefolium* | Is | 2.0 | 1:0 | Ito & Ono (1990) |
| *Crepidiastrum & Youngia* sp. | M | 8.2 | | |
| *Galvezia leucantha* | Is | 1.1 | 1:0 | Elisens (1992) |
| *Galvezia fruticosa* | M | 6.8 | | |
| *Gossypium darwinii* | Is | 3.2 | 1:0 | Wendel & Percy (1990) |
| *Gossypium barbadense* | M | 6.7 | | Percy & Wendel (1990) |
| *Gossypium klotzschianum* | Is | 3.4 | 1:0 | Wendel & Percival (1990) |
| *Gossypium davidsonii* | M | 8.7 | | |
| *Gossypium tomentosum* | Is | 3.3 | 1:0 | DeJoode & Wendel (1992) |
| *Gossypium hirsutum* | M | 10.8 | | Wendel *et al.* (1992) |
| *Hosta jonesii* | Is | 27.3 | 0:1 | Chung (1994) |
| *Hosta capitata* | M | 15.3 | | |
| *Rhaphithamnus venusta* | Is | 2.8 | 1:0 | Crawford *et al.* (1993) |
| *Rhaphithamnus spinosus* | M | 10.3 | | |
| *Solanum fernandezianum* | Is | 0.0 | 1:0 | Spooner *et al.* (1992) |
| *S. etuberosum & S. brevidens* | M | 10.3 | | |
| Overall | | | 34:4 | |

*The mainland comparison was family Emberizidae as for *Hemignathus parvus* above.

†The mainland comparison was with the *Drosophila willistoni* group, as for *Drosophila adiostola* above.

of flight (bats, birds and insects) showed proportionately less reduction in heterozygosity than those that cannot fly (Kruskal–Wallis $H = 6.4$, d.f. $= 1$, $P = 0.006$).

### Endemic species

Insular endemic species showed lower genetic variation than related mainland species in 34 of 38 cases (Table 6; $\chi_1^2 = 23.7$, $P < 0.00005$). Taxa differed significantly in the reduction in heterozygosity (Kruskal–Wallis $H = 13.6$, d.f. $= 4$, $P = 0.009$). The proportionate reduction was greatest in mammals, intermediate in birds, arachnids and plants, and least in insects (Table 5).

### Comparison of endemic and nonendemic species

The ratio of allozyme genetic variation in island/mainland for endemic species was proportionately lower than that for nonendemic populations in taxa combined (Mann–Whitney $W = 25\,920.5$, $P < 0.00005$), mammals (Mann–Whitney $W = 6106$, $P = 0.00025$) and birds (Mann–Whitney $W = 578$,

$P = 0.0022$) and plants showed a similar trend (Mann–Whitney $W = 175$, $P = 0.13$); conversely, insects showed no evidence of such a difference (Table 5). The difference in birds remained significant when the mean of all potential mainland relatives was used for comparisons ($W = 565$, $P = 0.009$).

### Discussion

The major findings of this study are that a significant majority of island populations have lower levels of genetic variation than corresponding mainland populations, and that insular endemic species show proportionately lower genetic variation than nonendemic species. The former conclusion is based on allozymes, mtDNA, and nuclear DNA, though most evidence was for allozymes. Phenotypic variation was lower in island than mainland populations, so quantitative genetic variation is probably lower in island populations. Further, inversion polymorphism is lower in island than continental populations (Ayala & Campbell, 1974). DeJoode & Wendel (1992) reported that allozyme heterozygosity in over 60 insular endemic plant taxa was 43 per cent of that

in plants generally, or 67 per cent of that in all endemic (mostly mainland) plants. The equivocal nature of previous conclusions (see Introduction) can be attributed to small sample sizes.

In a similar vein, introduced populations typically have lower levels of genetic variation than native ones within several species of lizards (Taylor & Gorman, 1975; Gorman et al., 1978; Capula, 1994), land snails (Selander & Kaufman, 1973; Johnson, 1988), insects (Bryant et al., 1981; Gasperi et al., 1991) and plants (Schwaegerle & Schaal, 1979; Clegg & Brown, 1983; Barrett & Husband, 1989; Novak & Mack, 1993). Stone & Sunnucks (1993) found a pattern of reducing genetic variation with founder effects as a gall wasp spread across Europe.

Differences between island and mainland populations are predicted to be greater for small than large islands, for species with lower dispersal rates, and for distant than near islands (Jaenike, 1973). There is evidence to support each of these predictions. Genetic variation is correlated with island size (Frankham, 1996). Species with lower dispersal ability have been shown to have greater differences from analyses within this paper. Effects of distance from the mainland or a large source population have been detected in lizards (Soulé & Yang, 1973; Gorman et al., 1975) and in several species of mammals (Kilpatrick, 1981; Schmitt et al., 1995).

Why do some island populations have more genetic variation than mainland populations? Chance, high migration rates, and separate migrations from differentiated mainland populations can all cause this. Notably, a number of island populations of house mice have more genetic variation than mainland populations. House mice have excellent dispersal ability, as indicated by the number of new worldwide locations they have colonized. Further, several subspecies exist and Japanese populations are known to involve mixtures of them (Bonhomme et al., 1989). Pacific island populations on major trade routes (such as on Hawaii) are likely to have had introductions from Europe, Asia, North and South America. Other species where island populations have greater variation than mainland populations are often characterized by high dispersal ability [bat (Macrotus) Greenbaum & Baker, 1976; moose Ryman et al., 1980; oak (Quercus petraea) Zanneto & Kremer, 1995]. The plant Cryptomeria japonica is a particularly informative exception (Tsumura & Ohba, 1993). The island population acted as the refuge during a glacial period, and the smaller mainland population was derived from it. As predicted, the island population has higher genetic variation than the mainland population. Further, the

endemic island plant Hosta jonesii, that has a higher population size than the mainland H. capitata, has more genetic variation (Chung, 1994). The only other endemics that had higher genetic variation than mainland populations were all Hawaiian Drosophila. These have particularly high levels of genetic variation, especially as they are considered to suffer bottlenecks each time they migrate to a new island and speciate (Carson, 1970; Giddings et al., 1989). The scenario of a single inseminated female founding populations on new islands seems improbable in the light of the allozyme data.

There are four genetic factors that can contribute to higher extinction rates of island compared with mainland populations, namely inbreeding depression, loss of genetic variation, accumulation of mildly deleterious mutations, and genetic adaptations to island environments (flightlessness, limited ability to avoid predators and diseases). The last of these is widely acknowledged as a reason for the extinction proneness of island endemic species (Carlquist, 1974; Myers, 1979; Soulé, 1983; Temple, 1986; Vitousek, 1988; Atkinson, 1989; World Conservation Monitoring Centre, 1992). The evidence herein shows that insular populations, especially endemic species, have their evolutionary potential seriously compromised. Consequently, they are expected to be have limited ability to adapt genetically to environmental change, whether that be newly introduced diseases, global climate change, or introduced predators, or competitors. The susceptibility of Hawaiian birds to introduced avian malaria (Warner, 1968) may be an example of this compromised evolutionary potential. Several genetic mechanisms to resist malaria are known in humans (Allison, 1956; Cavalli-Sforza & Bodmer, 1971; Ruwende et al., 1995). On genetic grounds, endemic island species are predicted to have higher extinction rates than nonendemic island populations. This has been documented for New Zealand land birds (McDowall, 1969), and for reptiles (Case et al., 1992). It probably applies to most other taxa, but I am unaware of data on comparative extinction risks for them. Inbreeding depression increases the risk of extinction (Soulé, 1980; Frankham, 1995b), but is rarely mentioned as a cause of high extinction rates of island populations. This issue is worthy of detailed consideration. Arguments about whether demographic, environmental or genetic stochasticity cause extinctions are misguided. Genetic threats to island populations will interact with other threats to increase the risk of extinction of island populations.

In conclusion, an overwhelming majority of island populations have lower genetic variation than their

mainland counterparts, with endemic island species being proportionately lower than nonendemic species. Consequently, the hypothesis that genetic factors contribute to the higher extinction rate of island than mainland populations cannot be rejected.

## Acknowledgements

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