

A remnant population of the Floreana mockingbird on Champion island, Galápagos

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Abstract

Champion and Gardner are the only two satellite islands of Floreana in the Galápagos archipelago that support populations of the Floreana mockingbird, *Nesomimus trifasciatus*. The population on the much larger island of Floreana became extinct approximately 125 years ago. We studied the Champion population in every year from 1980 to 1991. Since the island is small (9.4 ha) we determined the demographic stability of the population by repeated censusing of the whole population. The number of breeding adults varied from 16 to 24 with a mean of ~ 20 . Using a standard population genetics formula we calculate that the Champion population has lost half of the original level of selectively neutral heterozygosity since presumed immigration from Floreana ceased more than a century ago. The short-term future of the Champion population is likely to be secure providing that goats and rats are not introduced, as these have caused much devastation on Floreana and probably resulted in the extinction of the mockingbird population there. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

It is now conventional wisdom that populations are becoming increasingly fragmented and the fragments, being generally small, are in danger of extinction. The two major sources of hazards a small population faces are genetic and environmental (Lande, 1988). Through random processes, small populations accumulate deleterious mutations (Lynch et al., 1995), lose genetic variation faster than larger ones and become increasingly inbred. In many cases this leads to a decline in average fitness. As a result, small populations may be incapable of adapting to changing environmental circumstances. Those circumstances may change too rapidly to permit evolutionary change. Moreover if a population occupies a small area all members of the population are subject to the same environmental change. Demographic stochasticity, for example random fluctuations in offspring sex ratio, adds to its vulnerability. Thus small popula-

tions are of particular concern to conservation biologists (Mace and Lande, 1991).

While these ideas are generally accepted in principle there is much debate on just how vulnerable small populations in nature really are (Caughley, 1994). Long-term studies of natural populations are necessary to empirically determine the risks of extinction (e.g. Saccheri et al., 1998). We report here the results of a 12-year study of a small population of birds that has been isolated from its parent population for more than a century.

The Floreana mockingbird, *Nesomimus trifasciatus*, is one of four allopatric, congeneric, species in the Galápagos (Swarth, 1931; Abbott and Abbott, 1978; Curry, 1989). The population on the large island of Floreana became extinct some time after a visit in 1868 by the scientist A. Habel, having been apparently common in the year (1835) of Darwin's visit when the first specimens were collected (Curry, 1986). The species is now represented by populations on two small satellite islands, Champion and Gardner-by-Floreana (Fig. 1). The combined populations were believed by Harris (1973) to number no more than 150 individuals. Apart from this, little was known of their size and status prior

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to 1980 when we began a long-term field study and monitoring program of the population on the very small island of Champion (9.4 ha). The population was chosen because it was small, potentially inbred and vulnerable to extinction, yet had persisted in isolation for a hundred years or more without immigration from the main island of Floreana less than one km away; Gardner, approximately 14 km to the south, is an unlikely source of immigrants of these relatively sedentary birds.

The goal of our study was to determine the size of the population and its variation, and to make an assessment of the long-term prospects of the population in the face of known or suspected hazards. We present the demographic data in the Results and use them in the Discussion to calculate the loss of selectively neutral heterozygosity.

2. Methods

Champion is a low tuff cone with eroded flanks of a central lava crater forming cliffs up to 30 m high. It is a circular island, ~400 m in diameter, 46 m in maximum elevation, and located less than one km from the north-east coast of Floreana. Vegetation consists of large cacti (*Opuntia megasperma*) interspersed with arid scrub dominated by low *Croton scouleri*, *Cordia lutea*, and *Parkinsonia aculeata*, and several species of plants in the herb layer.

On a 17-day visit in August 1980 all mockingbirds on the island were banded (by PRG). Observations and banding were continued every year for the next 10 years. RLC observed the population on this islet during brief visits (1–7 days) in January and May 1981, January and May 1982, and March and May 1983, and conducted intensive study during the following periods: 24

December 1983–14 January 1984, 26 January–16 February 1984, and 15–26 March 1984. Later brief (1 day) visits were made in May 1984, January and May 1985, June 1986, July 1987, February 1988, February 1989, March 1990 and March 1991 for the purpose of monitoring the populations and banding new birds. In most years 95–100% of the birds were banded. The proportion banded was at its lowest, 20%, in the final year.

Mockingbirds were captured using wire cage traps mainly, and occasionally mist nets. Less than 10% were banded as nestlings. All were marked with one or two colored plastic bands and, after 1981, a numbered aluminum band. The sex of many birds was determined by wing length, verified where possible by breeding observations, as explained in Curry (1989). Territories were mapped (e.g. Fig. 2) and group composition determined by observation according to criteria discussed in Curry (1988a). All vegetated habitat on Champion was continuously occupied (see also Curry, 1989).

Thirty two adults were measured on Champion in August 1980 and compared with measurements of thirty three adults of the related species *N. parvulus* on Genovesa in the preceding month. All measurements were made by one of us (PRG) and have been described elsewhere (Grant, 1981). The full set of measurements are body mass (weight) in grams, wing length, tarsus length, and three beak measurements, length, depth (height) and width, all in millimeters. Morphological variation in the two populations was compared in univariate analyses. Squared coefficients of variation were compared by two-tailed *F* tests (Lewontin, 1966).

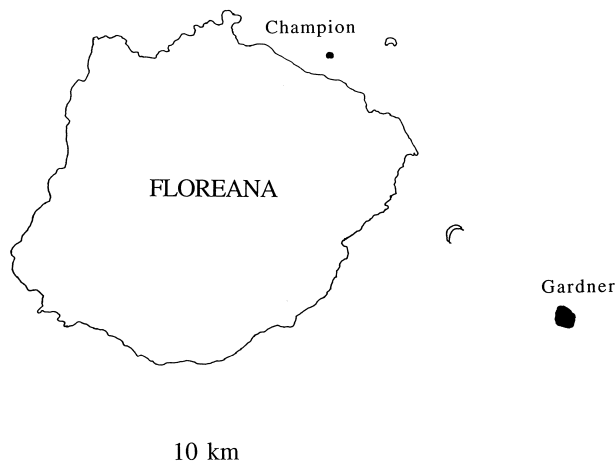


Fig. 1. Map of Champion and Gardner islands, satellites of Floreana. Floreana was formerly Charles island, and is officially Santa María.

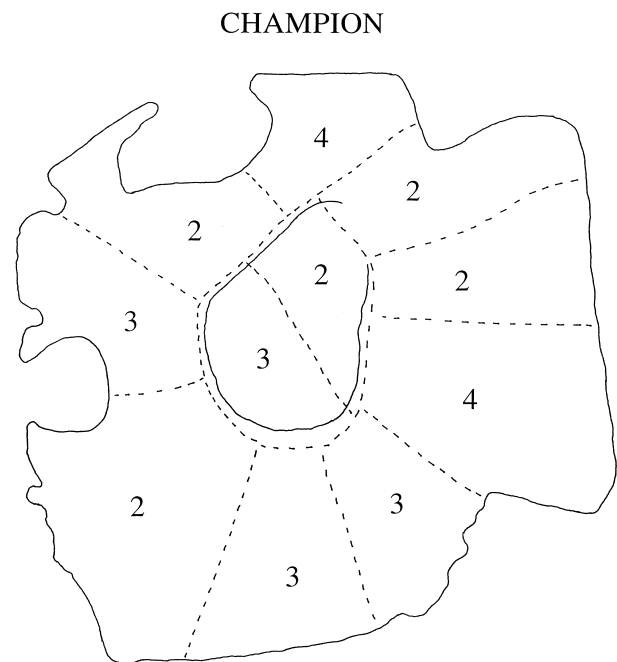


Fig. 2. Map of territories and adult group sizes in 1980 (see also Curry, 1989).

3. Results

3.1. Numbers

Champion was inhabited by between 24 and 53 mockingbirds in the years 1980–91. Density of adults ranged from 2.1 to 4.9 adults/ha. These values are comparable to densities of *N. parvulus* on Genovesa, lower than some local densities of *N. macdonaldi* on Española, but higher than those of *N. melanotis* on San Cristóbal (Curry, 1987, 1989; Curry and Grant, 1990).

Mockingbirds occurred in groups varying from an average of 2.4 ± 0.52 (SD) ($N=8$), range 2–3, in 1990, to a maximum of 4.5 ± 0.73 ($N=10$), range 2–7, in 1984. The number of territories varied from eight in 1990 to 12 in 1981 and 1991, with a mean of 10.4 and a coefficient of variation of 13.86%. The number of breeders, approximately twice the number of territories, varied from 16 to 24 (Fig. 3). The number of non-breeding adult members of the groups varied much more, from three in 1991 to 23 in 1988, with a mean of 12.5 and a coefficient of variation of 53.95%.

Annual survival of adults varied from 0.178 (females, 1986–87) to 1.000 (males, 1987–88) with a mean for sexes combined of 0.81 ± 0.16 (SD). One individual, hatched in 1981, lived to a minimum of nine years. Three individuals were apparently missing from the island for one year and re-sighted the next.

3.2. Behavior

On Champion, as on Genovesa, territories were tightly packed together. In 1980 we saw no “flick-fighting” and very little aggressive behaviour associated with territorial defence that is so conspicuous in the other three species (Grant and Grant, 1979; Curry and Grant, 1990). However, low-intensity flick-fights were observed during the more detailed observations made in 1984, and rarely in other years (e.g. 1991 but not in 1990). Within groups individuals displayed typical dominant–

subordinate aggressive behavior, with old birds being dominant (Grant, 1983; Curry, 1989).

Helping behavior at nests was observed frequently, as in *N. parvulus* on Genovesa (Curry, 1988a,b, 1989). Fifteen different birds helped at one or more of the nine nests observed on Champion between 1981 and 1984. All helpers helped known full siblings or suspected full or half siblings. No instances of close inbreeding were observed, although the chances of detecting it were low because the parents of most breeders were not known. According to behavioral evidence close inbreeding occurs on Genovesa (Grant, 1983; Curry and Grant, 1990).

3.3. Morphology

Mockingbirds are larger on Champion than on Genovesa, less so in beak dimensions than in wing and tarsus length (Table 1). Champion birds vary less than Genovesa birds in all dimensions, but not in mass (Table 1). We combined measurements of males and females in each sample by adding to the female measurements the difference between the male and female means for each trait. For the combined samples the difference in variation in bill length is highly significant ($F=3.33$, $N_1=33$, $N_2=32$, $P<0.001$ two-tailed), with Genovesa birds being the more variable. Differences in the other dimensions were not significant ($P>0.1$ in all cases).

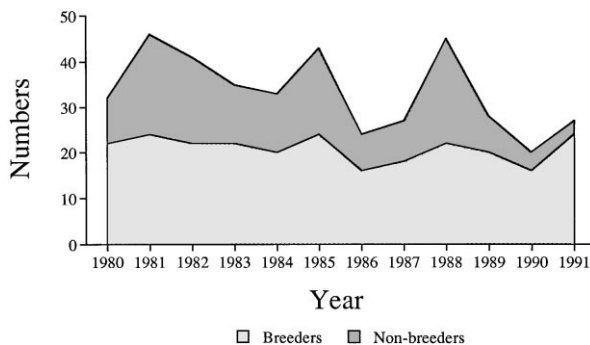


Fig. 3. Annual variation in number of breeders (i.e. twice the number of territories) and number of non-breeders (excluding juveniles).

Table 1
Morphological characteristics of Champion and Genovesa mockingbirds^a

	CHAMPION			GENOVESA		
	Mean	SE	CV	Mean	SE	CV
	Males ($N=13$)			Males ($N=18$)		
Mass	65.31	1.25	6.908	56.67	0.54	4.138
Wing length	125.00	0.49	1.424	117.83	0.43	1.547
Tarsus length	39.49	0.28	2.349	34.73	0.21	2.637
Bill length	20.71	0.09	1.533	20.34	0.16	3.253
Bill depth	5.96	0.04	2.425	5.50	0.04	3.300
Bill width	5.58	0.06	3.719	5.22	0.04	3.492
	Females ($N=19$)			Females ($N=15$)		
Mass	59.60	0.76	5.590	50.20	0.64	4.963
Wing length	117.58	0.34	1.250	110.13	0.48	1.677
Tarsus length	37.69	0.16	1.850	33.45	0.16	1.832
Bill length	20.13	0.08	1.759	19.57	0.14	2.748
Bill depth	5.66	0.03	2.371	5.16	0.04	3.090
Bill width	5.39	0.04	3.381	4.97	0.04	3.457

^a Mass is in grams and dimensions are in millimeters. SE = standard error; CV = coefficient of variation.

4. Discussion

The population of mockingbirds on Champion would appear to be prone to extinction. Not only is this population very small, its environment is subject to strong annual fluctuations in rainfall and primary and secondary production. A 13 year study (1978–90) of the related *N. parvulus* on Genovesa island has shown how environmental variation affects mockingbird demography (Curry and Grant, 1989, 1991). Under El Niño conditions of abundant and prolonged rainfall (1982–83 and 1987) birds breed several times with elevated clutch sizes and produce a large number of fledglings. Under the contrasting drought (La Niña) conditions birds do not breed and adult mortality increases. Our study of mockingbirds on Champion is not as detailed, yet it shows the same pattern of elevated populations in years following extensive breeding (but not elevated clutch sizes), and higher adult mortality in drought years such as 1988 and 1989. Despite these manifest effects of environmental variation the size of the breeding population on Champion remained relatively stable at about 10 pairs.

The territorial, breeding and social system is an important factor contributing to relative stability. Limited habitat is responsible for the small number of territories, and all habitat is occupied by territories. Young birds help adults to rear offspring before they themselves breed. They stay on territory and either breed there or disperse to another territory and become a breeder (Curry 1988a,b, 1989). There is little marginal (coastal) habitat in which a non-territorial bird can forage and find enough food to sustain itself. Therefore the size of the population is larger than twice the number of territories only as a result of tolerance of non-breeders by breeders. The fraction of non-breeders varies annually much more than the fraction of breeders.

A second reason why the population is extinction prone is that, being small and isolated, it is likely to lose genetic variation (e.g. see Baker et al., 1990; Mundy et al., 1997a; Bouzat et al., 1998). Given its location close to Floreana, and the suitability of habitat on the adjacent coast of Floreana, it is reasonable to believe that the Champion population was formerly connected to the Floreana population by occasional immigration and gene flow. That connection was broken when the Floreana population became extinct. We assume that the only other population on Gardner island is too far away to be a source of immigrants. Therefore the Champion population has been isolated from gene flow for the past 100–125 years. We base this estimate on records from Floreana. The last specimen was collected on Floreana by Kinberg in 1852 (Sundevall, 1871), and the birds were last seen by a scientist (Habel) in 1868 (Salvin, 1876). They were searched for and not found in 1888, and therefore probably became extinct in the last

quarter of the nineteenth century, or perhaps even earlier (Curry, 1986).

Using data from the population of *N. parvulus* on Genovesa (Curry and Grant, 1989) and two, better known, populations of Darwin's finches on Daphne Major island (Grant and Grant, 1992) with similar demographic properties to the population on Champion, we estimate the generation length of Floreana mockingbirds to be between four and 5 years. Thus the Champion population has been isolated for at least 20–30 generations. Over this time period we would predict that the population has become genetically depauperate since the last century as a result of permanently small numbers of breeders, inbreeding, drift, and the absence of genetic input from immigration.

The loss of genetic variation can be expressed more quantitatively. The reduction in heterozygosity at selectively neutral loci is expected to be a function of population size (N) and time in generations (t), and to occur at a rate of $(1 - 1/[2N_e + 1])^t$, according to a standard formula from population genetics (Crow, 1986); N_e refers to the genetically effective population size. With an assumed stable population size of 20 breeders, monogamy, an equal sex ratio and a Poisson distribution of offspring per family, so that $N_e = N$, the population is expected to lose 39% of its heterozygosity in 20 generations, or 52% in 30 generations. This assumes random mating and no replenishment of genetic variation by mutation. Experience with other bird populations (Grant and Grant, 1992) suggests that $N_e \ll N$, therefore the rate of loss heterozygosity is in reality likely to be much higher.

Comparable values for the loss of genetic variation in the only other population of this species on Gardner are 18 and 26%. These estimates are obtained by assuming the population to be similarly stable but at a size 4 to 5 times greater than on Champion, i.e. a maximum of 100 breeders. On two separate 1-day visits (21 August 1980 and 14 March 1991) to Gardner we estimated the population size to be at least four times greater (>200 birds) than the Champion population size. However, on two other visits in 1984 (February 16 and April 2) our estimates were closer to 3 times the size of the Champion population. Harris (1973) gives a figure of 150 individuals for the populations on Champion and Gardner combined; therefore 2–3 times more on Gardner than on Champion. If this lower figure of 150 is accepted the estimated loss of genetic variation in the Gardner population will be greater than the estimated loss of 18–26% given above. The number of breeding groups and the degree of population stability on Gardner are not known.

Simple predictions from the preceding theoretical reasoning are (1) selectively neutral genetic variation should be lower in the Champion population than in the Gardner populations, and (2) both populations should

have less genetic variation than populations of related species on larger islands such as *N. parvulus* on Genovesa, *N. melanotis* on San Cristóbal and *N. macdonaldi* on Española. From the estimated rates of loss in the two populations it should be possible to crudely estimate the original standing variation in the Floreana population.

These predictions will be tested with microsatellite DNA loci (cf. Mundy et al., 1997a). Already a preliminary analysis with minisatellite DNA data has been carried out, and it provides support for prediction (2). Gergel (1991) used the Jeffrey's probe on blood samples from 14 mockingbirds of unknown relatedness from Champion, seven mockingbirds (*N. parvulus*) from Genovesa that were not closely related and two large ground finches (*Geospiza magnirostris*) from Daphne. All 14 of the samples from Champion had identical banding patterns, no two samples from Genovesa were identical, and both sets differed from the banding patterns of the two finch samples. Resolution of the patterns was not clear enough for a quantitative comparison, but was clear enough to justify a tentative conclusion: the observations are consistent with the hypothesis that the Champion population of mockingbirds, unlike the one on Genovesa, is genetically depauperate as a result of inbreeding and drift.

The consequences of inbreeding are difficult to gauge. In theory, it should lead to a purging of strongly deleterious recessive alleles in homozygous state from a small population (Meffe and Carroll, 1994). The population may then persist for some time, even at very low numbers and reduced genetic variation (e.g. Butler and Merton, 1992; Ardern and Lambert, 1997; Ardern et al., 1997; Mundy et al., 1997b), although it will continue to lose mildly deleterious alleles by selection unless they are fixed through drift (van Noordwijk, 1994; Vrijenhoek, 1994). The Champion population may have already lost the most deleterious alleles. We observed no signs of developmental abnormalities. The study was not sufficiently detailed to detect possible inbreeding depression in the form of reduced hatching success of eggs or reduced survival of adults attributable to genetic constitution when under environmental stress (e.g. Keller et al., 1994). We found a reduced level of phenotypic variation in beak length in comparison with *N. parvulus* on Genovesa, a large and outbred population in which nevertheless inbreeding does occur (Grant, 1983; Curry and Grant, 1990). Reduced phenotypic variation may reflect reduced genetic variation, although other explanations involving uncontrolled sources of environmental variation (during growth, and later abrasion) cannot be excluded.

Small populations are vulnerable to disease organisms and predators to which they have not been previously exposed. A loss of genetic variation might make them especially susceptible to epizootics. One observation suggests that this state of relative defenselessness has

not yet been reached. Pox virus is presumed to have been brought to the Galápagos last century when chickens were introduced. Pox was strongly suspected of being the cause of increased mortality during the 1982–83 El Niño event because symptoms of infection were seen on Champion similar to those observed on Genovesa (Curry and Grant, 1989; see also Vargas, 1987). However, this did not offset the prolonged and successful breeding in 1983. Moreover the effects of pox on both adult and juvenile survival were more severe in the Genovesa population (Curry and Grant, 1989).

The population does not exist in a predator-free environment. Known or potential predators on the island are resident snakes (*Alsophis biserialis*) and night-herons (*Nyctanassa violacea*), and visiting short-eared owls (*Asio flammeus*), lava herons (*Butorides sundevalli*) and possibly Galápagos hawks (*Buteo galapagoensis*). Introduced mammals are not known from the island. We did not witness any predation event, and the only signs of predation we encountered were the remains of a single mockingbird in one out of 129 owl pellets examined in 1980 by K. T. Grant (pers. comm.). Nevertheless the fate of the mockingbird population on Floreana illustrates how vulnerable the much smaller populations on Champion and Gardner must be. Extinction has been attributed to (a) human hunting (Rothschild and Hartert, 1899), (b) predation by dogs or cats (Swarth, 1931), (c) disappearance of *Opuntia megasperma*, a favored place to nest and a source of food, caused by goats (Steadman, 1986) or, more plausibly, (d) predation at the nest by introduced black rats, *Rattus rattus* (Curry, 1986). Whatever the particular reason or combination of reasons, human interference is at the core, as on islands elsewhere (Mayer and Chipley, 1992; Pimm et al., 1994; Steadman, 1995).

We conclude that as long as Champion and Gardner remain free of goats, rats and new diseases the populations of mockingbirds appear to be secure. Fluctuations in natural environmental conditions, although strong, are not sufficient to imperil the populations in the short-term. These conclusions need to be assessed with a more detailed analysis of demography through computer modelling (Curry and Grant, in preparation). Over the long-term the populations may not persist if (a) the climate changes and droughts become more frequent, and (b) continuing loss of genetic variation has deleterious effects on individual fitnesses. For these reasons, and because they can be considered a model of fragmented populations, they deserve to be monitored and investigated further, preferably on an annual basis.

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References

- Abbott, I., Abbott, L.K., 1978. Multivariate study of morphometric variation in Galápagos and Ecuadorean mockingbirds. *Condor* 80, 302–308.
- Ardern, S.L., Lambert, D.M., 1997. Is the black robin in genetic peril? *Molecular Ecology* 6, 21–28.
- Ardern, S.L., Lambert, D.M., Rodrigo, A.G., McLean, I.G., 1997. The effects of population bottlenecks on multilocus DNA variation in Robins. *Journal of Heredity* 88, 179–186.
- Baker, A.J., Dennison, M.D., Lynch, A., Le Grand, G., 1990. Genetic divergence in peripherally isolated populations of chaffinches in the Atlantic Islands. *Evolution* 44, 981–999.
- Bouzat, J.L., Lewin, H.A., Paige, K.N., 1998. The ghost of genetic diversity past: historical DNA analysis of the Greater Prairie Chicken. *American Naturalist* 152, 1–6.
- Butler, D., Merton, D., 1992. *The Black Robin: saving the world's most endangered bird*. Oxford University Press, Auckland, New Zealand.
- Caughley, G.C., 1994. Directions in conservation biology. *Journal of Animal Ecology* 63, 215–244.
- Crow, J.L., 1986. *Basic concepts in population, quantitative, and evolutionary genetics*. W. H. Freeman and Company, New York.
- Curry, R.L., 1986. Whatever happened to the Floreana Mockingbird? *Noticias de Galápagos* 43, 13–15.
- Curry, R.L., 1987. Evolution and ecology of cooperative breeding in Galapagos mockingbirds (*Nesomimus* spp.). Unpublished Ph.D. thesis, University of Michigan.
- Curry, R.L., 1988a. Group structure, within-group conflict, and reproductive tactics in cooperatively-breeding Galápagos Mockingbirds. *Nesomimus parvulus*. *Animal Behaviour* 36, 1708–1728.
- Curry, R.L., 1988b. Influence of kinship on helping behavior of Galápagos Mockingbirds. *Behavioral Ecology and Sociobiology* 22, 141–152.
- Curry, R.L., 1989. Geographic variation in social organization of Galápagos Mockingbirds: ecological correlates of group territoriality and cooperative breeding. *Behavioral Ecology and Sociobiology* 23, 141–152.
- Curry, R.L., Grant, P.R., 1989. Demography of the cooperatively breeding Galapagos mockingbird, *Nesomimus parvulus*, in a climatically variable environment. *Journal of Animal Ecology* 58, 441–463.
- Curry, R.L., Grant, P.R., 1990. Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds*. Long-term studies of ecology and behavior. Cambridge University Press, Cambridge, pp. 291–331.
- Curry, R.L., Grant, P.R., 1991. Impact of climatic variation on Galápagos mockingbird social organization. Proceedings of the XX International Ornithological Congress, Canterbury, NZ, 1990, pp. 1333–1341.
- Gergel, J.R., 1991. Towards developing a methodology for the determination of paternity in Darwin's Finches (*Geospiza*). Unpublished BA thesis, Princeton University.
- Grant, N., 1983. The breeding and behaviour of mockingbirds on the Galapagos. *Noticias de Galápagos* 37, 28–31.
- Grant, P.R., 1981. Patterns of growth in Darwin's Finches. *Proceedings of the Royal Society of London B* 212, 403–432.
- Grant, P.R., Grant, B.R., 1992. Demography and the genetically effective size of two populations of Darwin's Finches on Isla Daphne Major. *Galápagos. Ecology* 73, 776–784.
- Grant, P.R., Grant, N., 1979. Breeding and feeding of Galápagos mockingbirds, *Nesomimus parvulus*. *Auk* 96, 723–736.
- Harris, M.P., 1973. The Galápagos avifauna. *Condor* 75, 265–278.
- Keller, L.F., Arcese, P., Smith, J.N.M., Hochachka, W.M., Stearns, S.C., 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 372, 356–357.
- Lande, R., 1988. Genetics and demography in biological conservation. *Science* 241, 1455–1460.
- Lewontin, R.C., 1966. On the measurement of relative variability. *Systematic Zoology* 15, 141–143.
- Lynch, M., Conery, J., Bürger, R., 1995. Mutation accumulation and the extinction of small populations. *American Naturalist* 146, 489–518.
- Mace, G.M., Lande, R., 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5, 148–157.
- Mayer, G.C., Chipley, R.M., 1992. Turnover in the avifauna of Guana Island, British Virgin Islands. *Journal of Animal Ecology* 61, 561–566.
- Meffe, G.K., Carroll, C.R., 1994. *Principles of Conservation Biology*. Sinauer, Sunderland, MA.
- Mundy, N.I., Winchell, C.S., Burr, T., Woodruff, D.S., 1997a. Microsatellite variation and microevolution in the critically endangered San Clemente Island loggerhead shrike (*Lanius ludovicianus mearnsi*). *Proceedings of the Royal Society of London B* 264, 869–875.
- Mundy, N.I., Winchell, C.S., Woodruff, D.S., 1997b. Genetic differences between the endangered San Clemente Island loggerhead shrike *Lanius ludovicianus mearnsi* and two neighbouring subspecies demonstrated by mt DNA control region and cytochrome b sequence variation. *Molecular Ecology* 6, 29–37.
- Pimm, S.L., Moulton, M.P., Justice, L.J., 1994. Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society of London B* 344, 27–33.
- Rothschild, W., Hartert, E., 1899. A review of the ornithology of the Galapagos Islands, with notes on the Webster-Harris expedition. *Novitates Zoologicae* 6, 85–205.
- Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., Hanski, I., 1998. Inbreeding and extinction in a butterfly population. *Nature* 392, 491–494.
- Salvin, O., 1876. On the avifauna of the Galapagos archipelago. *Transactions of the Zoological Society of London* 9, 447–510.
- Steadman, D.W., 1986. Holocene vertebrate fossils from Isla Floreana, Galapagos. *Smithsonian Contributions in Zoology* No. 413, 1–103.
- Steadman, D.W., 1995. Pleistocene extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* 267, 1123–1131.
- Sundevall, C.J., 1871. On birds from the Galapagos Islands. *Proceedings of the Zoological Society of London*, pp. 124–129.
- Swarth, H., 1931. The avifauna of the Galapagos Islands. *Occasional Papers of the California Academy of Science* 18, 5–299.
- van Noordwijk, A.J., 1994. The interaction of inbreeding depression and environmental stochasticity in the risk of extinction of small populations. In: Loeschcke, V., Tomiuk, J., Jain, S.K. (Eds.), *Conservation Genetics*. Birkhäuser, Basel, pp. 131–146.
- Vargas, H., 1987. Frequency and effect of pox-like lesions in Galapagos mockingbirds. *Journal of Field Ornithology* 58, 101–102.
- Vrijenhoek, R.C., 1994. Genetic diversity and fitness in small populations. In: Loeschcke, V., Tomiuk, J., Jain, S.K. (Eds.), *Conservation Genetics*. Birkhäuser, Basel, pp. 37–53.