

Selection against inbred song sparrows during a natural population bottleneck

Lukas F. Keller*, Peter Arcese*, James N. M. Smith†, Wesley M. Hochachka† & Stephen C. Stearns‡

* Department of Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, Wisconsin 53706, USA

† Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4, Canada

‡ Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

THE genetic and demographic consequences of population subdivision have received considerable attention from conservation biologists. In particular, losses of genetic variability and reduced viability and fecundity due to inbreeding (inbreeding depression) are of concern¹⁻³. Studies of domestic, laboratory^{4,5} and zoo populations^{2,6,7} have shown inbreeding depression in a variety of traits related to fitness. Consequently, inbreeding depression is widely accepted as a fact. Recently, however, the relative impact of inbreeding on the viability of natural populations has been questioned⁸⁻¹⁰. Work on the cheetah (*Acinonyx jubatus*), for example, has emphasized the overwhelming importance of environmental factors on mortality in the wild^{9,10}. Here we report that song sparrows (*Melospiza melodia*) that survived a severe population bottleneck were a non-random subset of the pre-crash population with respect to inbreeding, and that natural selection favoured outbred individuals. Thus, inbreeding depression was expressed in the face of an environmental challenge. Such challenges are also likely to be faced by inbred populations of endangered species. We suggest that environmental and genetic effects on survival may interact and, as a consequence, that their effects on individuals and populations should not be considered independently.

Although inbreeding has been reported for several wild vertebrates¹¹, the few detailed studies of inbreeding done in the wild are equivocal¹²⁻¹⁶. This could be explained by historical differences in the size and structure of populations. For example, purging of deleterious, recessive alleles from the genome is often put forward as a potentially positive effect resulting from periods of intense inbreeding following a severe bottleneck^{5,17}. Other work, however, suggests that even given severe bottlenecks, it may be difficult or impossible to eliminate detrimental mutations with individually small deleterious effects^{18,20}. We studied the resident population of song sparrows on Mandarte Island, British Columbia, from 1975 to 1990²¹. During this period the breeding density of the population fluctuated by 18-fold because of two major crashes in population size (Fig. 1). Both crashes occurred outside the breeding season, in 1979-1980 (9 females and 18 males surviving, corresponding to 18% of the adult population) and in 1988-1989 (4 females and 7 males surviving, corresponding to 11% of the adult population). Earlier accounts from Mandarte also report catastrophic mortality among adult song sparrows in 1962²². The 1962 and 1989 crashes were coincident with severe winter weather^{22,23}. The cause of the crash in 1980 is unknown. Immigration rates on Mandarte are low in ecological terms (16 immigrants in 16 years), but they are probably high enough to lead to near-panmixia in genetic terms⁵. There was no increased immigration after crashes²⁴.

Inbreeding coefficients were estimated on the basis of the pedigree (Fig. 1). Because their accuracy depends largely on the number of generations of known matings²⁵, for 1980, only five years after the initiation of our study, we underestimated the true inbreeding coefficients. Because of this, and a coincidental

TABLE 1 Mean inbreeding coefficient of adults and juveniles before and after the 1989 crash

| | Adults | Juveniles |
|--------------|----------------------|-----------------------|
| Before crash | 0.0189 <i>n</i> = 74 | 0.0363 <i>n</i> = 132 |
| After crash | 0.0025 <i>n</i> = 7 | 0.0156 <i>n</i> = 3 |

n, Numbers of individuals with known grandparents in the sample.

gap in data collection (Fig. 1), we did not consider survival over the 1980 crash in detail.

During both the 1980 and 1989 crashes, the mean inbreeding coefficient in the breeding population was lower in the season after the crash than in the previous season (Fig. 1). This suggests that selection favoured birds that were relatively less inbred. To test this hypothesis, we compared the inbreeding coefficients of birds that survived the 1989 crash to those of birds that did not survive. As expected, we found that the average inbreeding coefficient was significantly lower among the birds that survived

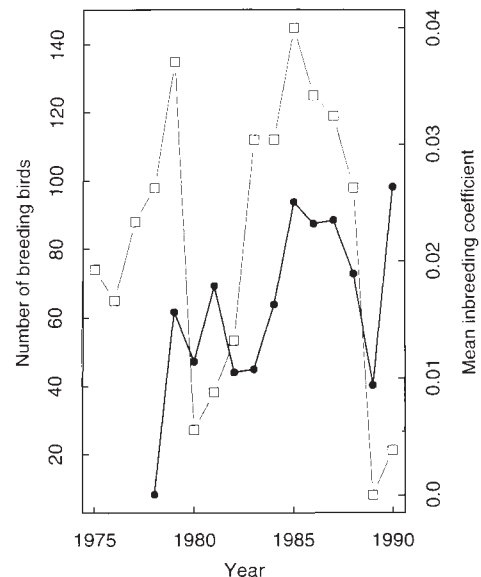


FIG. 1 The size of the song sparrow population breeding on Mandarte Island from 1975-1990 (squares) and the mean inbreeding coefficient of the population (circles). Because all individuals were colour-banded, survival was readily estimated²¹ and in 99.5% of 1,574 breeding attempts the putative parents were identified by detailed observations of pairing, mating and parental behaviour. Extra-pair paternity may have occurred, but several lines of evidence suggest it was rare²⁸. Continuous records of breeding success and adult and juvenile survival (except in 1980) allowed construction of a pedigree and the calculation of inbreeding coefficients. These were estimated using PEDSYS, a Pedigree Data Management System, provided by the Southwest Foundation for Biomedical Research, San Antonio, Texas, using the algorithm described in²⁹. We only used individuals whose grandparents were known to accommodate different depths of the pedigree due to founders and immigrants. This gave the following sample sizes for the calculations of mean *f* from 1978-1990: 9, 48, 11, 7, 12, 41, 52, 91, 93, 92, 74, 7 and 15. Incomplete data for 1980 led to a gap in the pedigree and resulted in low sample sizes of birds with known grandparents in 1981 and 1982. This contributed to lower mean inbreeding coefficients in these years. For 1975-1977 there were no breeding birds where all grandparents were known. Inbreeding coefficients are given relative to the founder population in 1975, assuming that all adults in 1975 and all subsequent immigrants had inbreeding coefficients of zero. The effects of this assumption on our analysis of the 1989 crash are small, because of the 11 intervening generations since the start of the study and the low level of immigration.

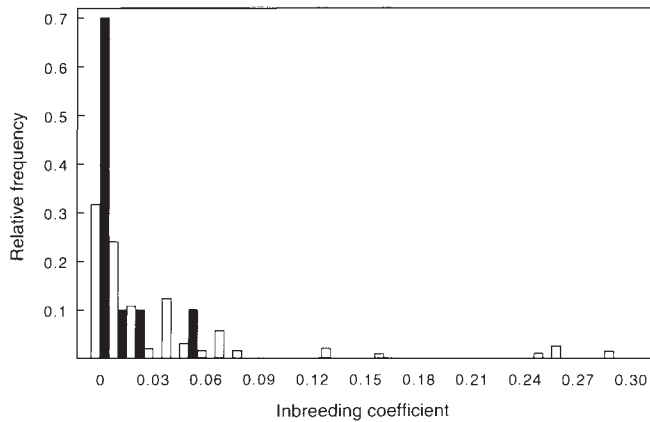


FIG. 2 The distribution of inbreeding coefficients of the birds that did not survive the crash (white bars) and of the survivors (black bars). The mean f of the birds that died equalled 0.0312 (s.d. = 0.059, $n = 196$), that of the survivors equalled 0.0065 (s.d. = 0.015, $n = 10$). The difference in the means of the two distributions was 0.0247 (two-tailed Mann-Whitney U -test, $Z = -2.24$, $P = 0.025$). The comparison was based on all adults and nestlings banded in 1988. Twelve birds survived the crash, but one was an immigrant and another had unknown maternal grandparents. Only eight of the survivors bred in 1989. Adult and juvenile birds were combined because of the small sample of survivors.

the crash than among birds that did not survive (Fig. 2). Only three of the survivors were inbred at all, two of which had low inbreeding coefficients ($f = 0.002$ and $f = 0.016$).

In a closed population, juveniles are expected to be more inbred on average than their parents. Hence differential mortality between juveniles and adults might be a confounding factor in our analysis, because juveniles typically survive less well than adults in our study population²¹. However, we found that the mean inbreeding coefficient was lower after the crash both among adults and juveniles (Table 1). This suggests that selection acted both against adults and juveniles, but the small number of survivors precluded a powerful test of this hypothesis. Nevertheless, our findings indicate that inbreeding depression occurred during a period of severe environmental stress. As a consequence of selection against inbred individuals, the mean inbreeding coefficient in the population was lower in the year following the bottleneck.

Our results show that inbreeding can affect survival in the wild. Given that the Mandarte population has undergone at least three population bottlenecks in the last three decades, our results also suggest that serial bottlenecks did not purge the genetic load sufficiently to alleviate the negative effects of inbreeding. Alternatively, immigration may be sufficient to re-establish deleterious alleles purged from the population during bottlenecks⁵. Finally, although genetic considerations should not be overemphasized^{9,26}, our results support the idea that genetic effects should not be considered independently of environmental effects²⁶. Our study shows that even in circumstances where most mortality can be attributed to environmental causes, genetic factors may still affect which individuals survive. In fact, inbreeding depression may be most pronounced exactly when individuals are environmentally stressed²⁷. This emphasizes the need to integrate demography and population genetics in studies in natural environments. □

Received 12 July; accepted 7 October 1994.

- O'Brien, S. J. *et al.* *Science* **227**, 1428–1434 (1985).
- Proc. Workshop on Genetic Management of Captive Populations *Zoo Biol.* **5**, 81–238 (1986).
- Wilmsen Thornhill, N. *The Natural History of Inbreeding and Outbreeding* (Univ. Chicago Press, Chicago, 1993).
- Wright, S. *Evolution and the Genetics of Populations Vol. 3: Experimental Results and Evolutionary Deductions* (Univ. Chicago Press, Chicago, 1977).
- Falconer, D. S. *Introduction to Quantitative Genetics* 3rd edn (Longman, London, 1989).

- Ralls, K., Brugger, K. & Ballou, J. *Science* **206**, 1101–1103 (1979).
- Lacy, R. C., Petric, A. & Warneke, M. in *The Natural History of Inbreeding and Outbreeding* (ed. Wilmsen Thornhill, N.) 352–374 (Univ. of Chicago Press, Chicago, 1993).
- Harcourt, S. *Nature* **354**, 10 (1991).
- Caro, T. M. & Laurenson, M. K. *Science* **263**, 485–486 (1994).
- Caughy, G. *J. anim. Ecol.* **63**, 215–244 (1994).
- Ralls, K., Harvey, P. H. & Lyles, A. M. in *Conservation Biology, the Science of Scarcity and Diversity* (ed. Soule, M. E.) 35–56 (Sinauer, Sunderland, MA, 1986).
- Greenwood, P. J., Harvey, P. H. & Perrins, C. M. *Nature* **271**, 52–54 (1978).
- van Noordwijk, A. J. & Scharloo, W. *Evolution* **35**, 674–688 (1981).
- Bulger, J. & Hamilton, W. J. III *Anim. Behav.* **36**, 574–578 (1986).
- Gibbs, H. L. & Grant, P. *Evolution* **43**, 1273–1284 (1989).
- Hoogland, J. *Am. Nat.* **139**, 591–602 (1992).
- Templeton, A. R. in *Mammalian Dispersal Patterns: the Effect of Social Structure on Population Genetics* (eds Chepko-Sade, B. D. & Halpin, Z. T.) 257–272 (Univ. Chicago Press, Chicago, 1987).
- Lande, R. & Schemske, D. W. *Evolution* **39**, 24–40 (1985).
- Charlesworth, D. & Charlesworth, B. A. *Rev. Ecol. Syst.* **18**, 237–268 (1987).
- Barrett, S. C. H. & Charlesworth, D. *Nature* **352**, 522–524 (1991).
- Arcese, P., Smith, J. N. M., Hochachka, W. M., Rogers, C. M. & Ludwig, D. *Ecology* **73**, 805–822 (1992).
- Tomba, F. S. *Auk* **88**, 753–759 (1971).
- Rogers, C. M. *et al.* *Ornis Scand.* **22**, 387–395 (1991).
- Smith, J. N. M., Arcese, P., Hochachka, W. M., Cassidy, A. L. E. V. & Rogers, C. M. *Acta XX Congr. Int. Ornith.* 1514–1521 (1991).
- MacCluer, J. W. *et al.* *J. Hered.* **74**, 394–399 (1983).
- Lande, R. *Science* **241**, 1455–1460 (1988).
- Hoffmann, A. A. & Parsons, P. A. *Evolutionary Genetics and Environmental Stress* (Oxford Univ. Press, Oxford, 1991).
- Smith, J. N. M. & Arcese, P. *Am. Nat.* **133**, 830–845 (1989).
- Boyce, A. J. *J. Hered.* **74**, 400–404 (1983).

ACKNOWLEDGEMENTS. We thank all who collected data in the field, particularly A. Cassidy and C. Rogers. Discussions with J. Baylis, J. Crow, C. Denniston, M. Hatch, W. Karasov, C. Keller, A. Lotem, A. J. van Noordwijk, S. Temple and D. Waller improved the paper. The Tsawout and Tseycum Indian bands kindly allowed us to work on their island. The Southwest Foundation for Biomedical Research provided PEDSYS and L. Freeman-Shade helped us to use it. A. Thomas provided and helped with PEDPACK. Funds were provided by the Swiss Priority Programme Environment/Biodiversity of the Swiss National Foundation, the Natural Sciences and Engineering Research Council of Canada, the Graduate School of the University of Wisconsin-Madison and the Roche Research Foundation. P.A. was supported by post-doctoral fellowships from NATO-NSF and NSERC.

Non-spatial extinction following lesions of the parietal lobe in humans

Glyn W. Humphreys*, Cristina Romani*, Andrew Olson*, M. Jane Riddoch* & John Duncan†

* Cognitive Science Research Centre, School of Psychology, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK
† MRC Applied Psychology Unit, 15 Chaucer Road, Cambridge CB2 2EF, UK

EFFICIENT behaviour in the visual environment requires selection between stimuli competing for control of action. Many current models of selection are spatial: relevant objects are chosen by attending to their locations^{1–3}. The unilateral stimulus extinction observed following lesions of the parietal lobe provides evidence for spatial selection⁴. Such patients may identify a single stimulus presented in their contralesional field, but can fail to detect the same stimulus when a competing stimulus is shown simultaneously on the ipsilesional side⁵. Here we demonstrate that extinction need not be spatial in nature, but may be determined by characteristics of the objects to be selected. In two patients with parietal lobe lesions and poor spatial localization, pictures extinguished words and closed shapes extinguished open shapes. This object-based extinction indicates the existence of biases within non-spatial selection mechanisms which are independent of biases produced by spatial selection mechanisms. We suggest that selection of objects for action requires that the 'winners' produced by the independent competitive biases for selection are bound together within distinct neural areas concerned with object properties and space.

We tested two patients: G.K., who suffered two strokes which resulted in lesions of the right occipito-parietal region and the left temporo-parietal region, and J.F., who suffered anoxia lead-