## Conservation biology

## 'Ghost' alleles of the Mauritius kestrel

he population of Mauritius kestrels is thought to have recovered from a single wild breeding pair in 19741, when its prospects were considered to be hopeless, to over 200 pairs today<sup>2</sup>. Here we evaluate the loss of genetic variation that resulted from this bottleneck by typing 12 microsatellite DNA loci in museum skins up to 170 years old and from modern kestrels. We find that ancestral variation was remarkably high and comparable to continental kestrel species. This shows that the unexpected resilience of the population could not have been due either to benefits contributed by an undetected remnant population or to reduction of the inbreeding genetic load by a history of small population size<sup>3</sup>.

Following the widespread use of pesticides in 1940-60<sup>2</sup>, the Mauritius kestrel population was for a long time smaller than the 50 individuals recommended as the minimum for viability4 (Fig. 1a). An intensive conservation programme between 1983 and 1993 led to a recovery to 400-500 birds5. Historical and post-bottleneck genotypes of Mauritius kestrels at one microsatellite locus show some of the 'ghost' alleles lost through the bottleneck (Fig. 1b). Across all loci, allelic diversity fell by 55%, and heterozygosity by 57% (Table 1). This reduction is broadly in line with the value of 0.48 expected from estimates of population size through the bottleneck<sup>6</sup> (Fig. 1a).

Differences in genetic variation can be measured more precisely from estimates of effective population size,  $N_e$ . These take into account variation in genetic diversity among loci, small sample size and missing data. The likelihood of the genotypes observed at each locus was calculated as a function of  $N_i\mu_i$ , where  $N_i$  is population size and  $\mu_i$  is the locus-specific mutation rate, which we parametrized as the differences from their means  $(N_i = \overline{N} + \Delta N_i, \overline{\mu}_i = \mu +$  $\Delta \mu_i$ ).  $\Delta N_i$  and  $\Delta \mu_i$  were estimated using the Metropolis–Hastings algorithm<sup>7</sup>.

Endemic island species show high rates

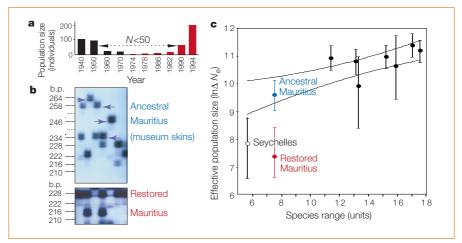


Figure 1 The genetic diversity of the ancestral population of Mauritius kestrels is similar to those of continental populations. a, Known population size across the bottleneck; records from Mauritius naturalists (black bars) and the Mauritius Wildlife Foundation (red bars); data calculated at 4-year intervals. b. Hexanucleotide microsatellite genotypes of Mauritius kestrel museum skins (top) include a mixture of alleles unique to the ancestral population (arrows) and those found in the restored population (bottom). c, The relationship between estimates of effective population size and species range. The 95% confidence limits are shown for the linear regression through all species, excluding the restored Mauritius (red) and Seychelles (white) population. Points show modal  $\Delta N_e$  values estimated using the likelihood function for the k-alleles model; error bars show the 95% credible interval.

variation<sup>9</sup>. Is this low genetic diversity a cause or a consequence of their vulnerability? The relationship between our estimates of relative  $N_e$  (Table 1) and species range (current population size) shows that the ancestral  $N_e$  of the Mauritius kestrel lies within the range extrapolated from continental populations (Fig. 1c). However, both the restored Mauritius and Seychelles populations are clearly outliers. The much higher ancestral N<sub>e</sub> on Mauritius suggests that the current low level of genetic diversity is a consequence of a recent population crisis.

Unlike some other species<sup>10</sup>, the kestrel population has recovered without the addition of new genetic variation. The kestrel population's resilience may be because its productivity was only weakly affected by the bottleneck. Laboratory studies of bottlenecked species show that the effects on productivity range from negligible to severe, and that populations may or may not recover from these in later generations<sup>1</sup>

Comparison with other tropical falcons suggests that there has been some reduction in the fitness of the Mauritius kestrel<sup>5</sup>. There is also evidence of an improvement

comparisons can only be made with the 5 years since intensive management has ceased, but productivity was consistently higher in each of these  $(P=0.5^5<0.05)$ , averaging 1.1 fledglings per nest (31% increase). The recovery need not be a genetic response: growing populations can show surprising behavioural plasticity in colonizing habitat outside the native forest<sup>5</sup>.

The high ancestral level of genetic variation in the Mauritius kestrel shows that the loss of variation associated with the arrival of humans on Mauritius and the Seychelles is without recent precedent. More encouraging is that a population can recover from a bottleneck, even after a dramatic loss in genetic variation. This may help endangered island endemics stake a claim for finite conservation resources.

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Table 1 Genetic diversity of kestrel populations				
Population	Sample size (2N)	Mean number of alleles	Heterozygosity*	Estimate of $log_e\Delta N_i$
Mauritius (restored)	150*	1.41	0.10	7.38
Mauritius (ancestral)	52	3.10	0.23	9.60
Seychelles	8	1.25	0.12	7.84
European	20	5.50	0.68†	11.2
Canary Islands	16	4.41	0.64†	10.92
South African	20	5.00	0.63†	10.96
Greater kestrel	20	4.50	0.59†	10.8
Lesser kestrel	16	5.41	0.70†	11.36

\*Methods for maximum likelihood estimates of heterozygosity and data on a further 225 individuals (including methods and genotypes for all populations) are available at http://www.qmw.ac.uk/~ugbt112/programs/Mauritius\_kestrel/

 $\dagger$ Significantly different from restored Mauritius population (Edwards likelihood ratio criterion, P < 0.01).