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The success of a soft-release reintroduction of the flightless Aldabra rail (*Dryolimnas [cuvieri] aldabranus*) on Aldabra Atoll, Seychelles

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Abstract

Humans and introduced mammalian predators have caused local extinctions and range reductions in the rallid genus *Dryolimnas* (endemic to western Indian Ocean islands); today two subspecies survive, one on Madagascar and one on three islands (ca. 8000 birds) of Aldabra Atoll. Domestic cats (*Felis catus*) still occur on Aldabra and their presence poses a significant potential threat to the rails. Reintroduction to cat-free islands would significantly improve their conservation status. In 1999, 20 rails were captured and brought to now cat-free Picard Island (the third largest island of Aldabra Atoll). Two rails died in captivity but all 18 remaining birds were released and survived beyond the first breeding season. Eight pairs had bonded and bred successfully within 2 months of release, producing a minimum of 13 chicks. Eleven monitored pairs produced 20 chicks in 2000/2001, with 1-year-old birds breeding successfully. Average chick production was significantly higher in the reintroduced population than in the source population in both breeding seasons. The reintroduced population at the end of the 2001 breeding season was at least 51, an increase of 283% in 18 months. Around 20 pairs are expected to attempt breeding on Picard in the third season after reintroduction, with excellent prospects for continued, exponential population growth in the medium-term. The soft-release reintroduction protocol allowed monitoring of individual birds' health before release into the wild. This is believed to have played a crucial role in the success of the reintroduction by allowing individuals to acclimatise and providing additional energetic reserves for the period between release and self-sufficiency. A soft-release is recommended as the conservative and precautionary method of choice for avian reintroductions and translocations.

1. Introduction

The rallid genus *Dryolimnas* is endemic to western Indian Ocean islands (Benson, 1967; Taylor and van Perlo, 1998). Representatives occurred on the Aldabra Group (Aldabra and Cosmoledo atolls and Astove and Assumption islands), as well as on Madagascar, Réunion and Mauritius (Rand, 1936; Rountree et al., 1952; Benson, 1967; Cowles, 1987; Mourer-Chauviré et al., 1999). *D. augusti* from Réunion is extinct and *D. [cuvieri] cuvieri* is locally extinct on Mauritius (Cowles, 1987; Mourer-Chauviré et al., 1999). *D. [c.] cuvieri* is volant and a common endemic on Madagascar (Taylor and van Perlo, 1998; Sinclair and Langrand, 1998). The flightless subspecies *D. [c.] abbotti* became extinct on Astove, Cosmoledo and Assumption between 1905 and 1937 (Nicoll, 1906; Vesey-FitzGerald, 1940). *D. [c.] aldabranus* is flightless and endemic to Aldabra Atoll [Benson, 1967; Wanless, in press (a)].

The world range of the Aldabra rail (*D. [c.] aldabranus*), before this project began, was restricted to Polymnie, Malabar and Île aux Cèdres (Benson and Penny, 1971; Collar, 1993; Taylor and van Perlo, 1998). The only reliable estimate of the populations was made in the 1970s, when Malabar was estimated to support ca. 8000, Polymnie ca. 270 and Île aux Cèdres ca. 80 rails (Huxley, 1982). Based on recent surveys, using comparable methodology, there has been no substantial change in any of the populations since then (Hambler et al., 1993; R. Wanless, unpublished data).

Domestic cats (*Felis catus*) were established on Aldabra as early as 1892 (Abbott, 1893). Although cats have

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never been documented killing rails, their disjunct distributions strongly suggests that cats were responsible for local extinctions of rails, including the populations on Picard and Grande Terre (Benson and Penny, 1971; Hambler et al., 1993). Cats have been seen on Malabar and Picard, but have only been consistently recorded from Grande Terre (Stoddart, 1971a; Hambler et al., 1993). They were never explicitly targeted for removal from Picard, nevertheless they have not been seen since pet cats were removed in the 1970s and are therefore considered locally extinct (L. Chong Seng, in litt.).

The range contraction experienced by the rail has been cause for concern for some time (Collar, 1993; Hambler et al., 1993; Taylor and van Perlo, 1998). Although the remaining populations are numerically healthy, their very restricted range leaves them vulnerable to catastrophic events, both extrinsic (e.g. cyclones) and intrinsic (e.g. disease). The possibility exists that cats from Grande Terre could disperse to and become established on any of the other islands. Cats on Malabar would almost certainly cause the demise of 95% of the world population of *D. [c.] aldabranus*.

There are essentially no ecological/environmental differences between Picard and Malabar islands. Their geographic proximity and positions have ensured that their geology and local climates are very similar. There are no broad-scale differences in vegetation cover (Gibson and Phillipson, 1983). There are no detectable differences in leaf-litter and soil invertebrate communities, primary prey of rails on Aldabra (Penny and Diamond, 1971; Spaull, 1979; this study). These similarities vitiate the possibility of Picard being ecologically unsuitable for rails. Picard has no domestic cats, no significant, human-mediated changes and no human exploitation of rails. Hence it was assumed to be as well-suited to rails as it was when rails were abundant there (Abbott, 1893).

Given the above, the guidelines set out by the IUCN (1996) for reintroductions were met and sound conservation and scientific rationales existed for undertaking a reintroduction. We follow the IUCN definition of reintroduction as an "attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct" (IUCN, 1996). The term "translocation" is used as an overarching descriptor for moving populations of animals, including reintroductions. It was decided that a limited, experimental reintroduction, followed by intensive monitoring, would not endanger existing populations and would best reveal the potential to establish a viable population of rails on Picard Island.

2. Methods

2.1. Study area

Aldabra Atoll (9°24′ S, 46°20′ E) lies 400 km north of Madagascar and 1100 km southwest of the granitic Seychelles. It is a large (34×14.5 km), slightly raised coral platform with a land surface area of ca. 155 km^2 (Stoddart et al., 1971). It comprises four large islands and numerous smaller islets (Fig. 1), which form a land rim around a substantial, shallow lagoon (almost 30 km across) and fringed by an intact reef (Stoddart et al., 1971).

2.2. Reintroduction

Rails were only taken from Malabar, to ensure that no mixing of (possibly) distinct genetic stocks occurred. We attempted to ensure a broad representation of the Malabar population's variability by taking half the birds from the extreme eastern end (Gionnet) and half from the extreme western end (Passe Houareau) of the island.

The wet northwestern monsoons start in December and initiate breeding in most of the landbirds of Aldabra, including the rails (Benson and Penny, 1971; Stoddart, 1971b; Penny and Diamond, 1971, this study).

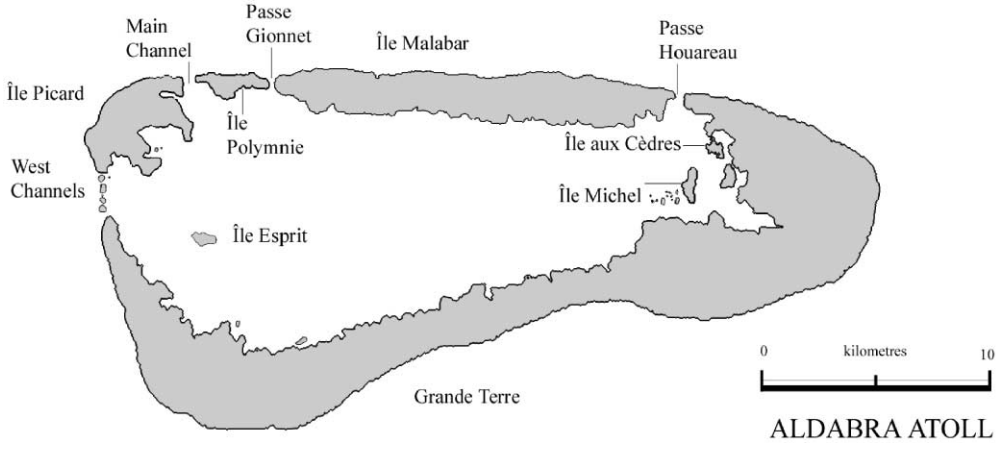

Fig. 1. Aldabra Atoll, Seychelles.

Rails were located on Malabar using taped audio-cassette recordings of territorial-defence/pair-bonding calls (Huxley and Wilkinson, 1977). The birds were captured in late October and early November, when pair-bonding and its concomitant vocalisations are obvious but no breeding activity has begun. The methods employed to attract rails normally resulted in two birds arriving. If no aggressive interactions were observed it was assumed they were a territory-holding pair and were immediately trapped using hand-operated swing-door traps and fresh crab bait.

Once trapped, rails were immediately weighed using a 500 g Salter spring balance. Blood for genetic analyses was collected from a puncture to the brachial vein and stored in EDTA buffer. Each bird was banded with a numbered metal band on the right tarsus and a plastic band engraved with a unique alpha-numeric code on the left tarsus.

Pairs of rails were kept in holding crates ca. 75×40×45 cm. Rails trapped at Gionnet were transported daily to Picard. The 3 m tidal range and ca. 30 km transfer distance made it impossible for this to be done for birds captured at Passe Houareau, which were kept in holding crates for up to three nights (Farrow and Brander, 1971).

The release was designed as a soft-release (sensu Bright and Morris, 1994; Snyder et al., 1994; Letty et al., 2000). Five 30 m^2 enclosures were constructed adjacent to good quality habitat, to acclimatise rails to Picard. They were given shelter, fresh water and fed twice daily with a variety of food. Scavenging crabs *Coenobita* spp. and *Birgus latro* and rats (*Rattus rattus*) gained access to the enclosures and consumed unknown amounts of the rails' food, preventing an assessment of their daily food intake. Adult rails are not vulnerable to predation from rats on Aldabra [Wanless, in press (b)]. Rails were recaptured in their enclosures at irregular intervals (to avoid undue stress) and weighed. They were kept in captivity until they became habituated to being fed and appeared to be in good health. Weight-changes over time were expressed as percentage deviation from mass at capture. A smoothing curve (least-squares distance-weighted regression) was fitted to the data using StatSoft (2000).

The first group of birds (from Gionnet) was kept in captivity for 14 days, then weighed and released. The second group (from Passe Houareau) gained weight sufficiently fast to permit their release after only 6 days in captivity (this may also have been a suitable period for the first group). Rails were released between 2 and 12 November. The morning of release, birds were fed but the doors to the enclosures were left open, allowing them to leave at will. We continued to feed birds that remained in or around cages. Individuals were closely observed and reproduction was monitored until April 2000, and again between December 2000 and April 2001.

Chick production was defined as the number of chicks reared *to independence*. The number of chicks produced in 1999/2000 (the first breeding season) was estimated using the Petersen method corrected for bias, with Poisson 95% Confidence Intervals (Krebs, 1998). Inter- and intra-island differences in mean chick production were tested for significance using Mann–Whitney *U*-tests.

2.3. Microsatellite study

A microsatellite study was undertaken a posteriori to determine the distinctiveness of the populations on Malabar, Polymnie and Île aux Cèdres and assess the degree of genetic variation in the reintroduced individuals, to ascertain how much of the total variation these birds represented. Approximately 100 μl of blood was collected from individuals from Picard (25), Malabar (25), Polymnie (15) and Île aux Cèdres (8). Total DNA was extracted by standard proteinase K digestion (Sambrook et al., 1989). Radioactive PCRs were performed in 10 μl reaction volumes following O'Ryan et al. (1998).

A panel of microsatellite loci from a variety of bird species was tested on the Aldabra rail, including primers from the chicken (*Gallus gallus*; Cheng, personal communication), Tasmanian moorhen (*Gallinula mortierii*; J. Buchanan, personal communication), cranes (*Grus* spp; K. Jones, personal communication), Scottish crossbill (*Loxia scotia*; Piertney et al., 1999) and the blue tit (*Parus caeruleus*; Dawson et al., 2000). Of the 30 loci tested, only one (TM18 from Tasmanian moorhen) produced an informative polymorphic product. Although based on a single primer, subsequent analysis showed interesting trends. Genetic variation was quantified using average number of alleles per locus (A), observed heterozygosity (H_o) and Hardy–Weinberg expected heterozygosities (H_e; Nei, 1973), using the Biosys-1 package (Swofford and Selander, 1981). Hardy–Weinberg exact probabilities were calculated using the Markov chain method (Guo and Thompson, 1992) implemented in GENEPOP (version 3.2a; Raymond and Rousset, 1995). Levels of population differentiation were calculated using F-statistics from the programme FSTAT (version 2.8; Weir and Cockerham, 1984; Goudet, 1995) and σ estimates from R_{st}Calc (Goodman, 1997), based on Slatkin's (1995) R_{st}, with both small and unequal sample sizes accounted for in the R_{st} calculation.

3. Results

3.1. Reintroduction

Ten rails were captured at Gionnet on 19 and 20 October and 10 at Passe Houareau on 4 and 5 November.

Both individuals of a "pair" died shortly after being transported to Picard. A post-mortem revealed that both birds were male—contrary to evidence in the field being based on bill-colour (see Penny and Diamond, 1971). In retrospect, most of their time together was probably spent fighting one another to the point of exhaustion and death. The larger individual had considerable fat reserves at death, militating against starvation as a cause of death. Subsequently, we discovered that a female had also been incorrectly sexed. Thus 18 birds (90%) survived to be released, of which 10 were female and eight were male.

Birds lost weight during transit, and steadily increased weight whilst in enclosures (Fig. 2). All but two birds were released weighing more than they did at capture; neither exception was substantially underweight. At release, one male weighed almost 145% of its mass at capture (mean increase at release was 12%, $n=18$).

There was a 100% post-release survival at the end of the 1999/2000 season. In 2000/2001 only 17 adults (94%) were retrapped (i.e. positively identified). The mate of the missing bird was seen once in December 2000 and this pair is thought to have established a new territory in an inaccessible part of the island. There were no other significant changes in territory between the two breeding seasons and mate fidelity was probably 100% ($n=8$ pairs) in 2000/2001. All pairs established territories close to their enclosures, and three individuals that remained near the enclosures were gradually weaned of supplementary food over 2 months.

All chick mortality (30%) on Picard occurred in the first 3 weeks after hatching; all chicks that survived beyond that age survived to be captured, banded and retrapped.

Aldabra rails undergo a post-breeding moult, which commences after young have left the natal territory in the case of successful breeding (RMW, unpublished data). No monitored pairs deviated from this pattern in 1999/2000, including the seven monitored pairs on Picard. An eighth pair was only found at the end of the season, having just started moulting. They are thus assumed to have bred successfully. Thirteen chicks were banded in 1999/2000, and eight were retrapped in 2000/2001. It is likely that chicks that were not retrapped were alive but had moved beyond the detectable range covered by the existing path network. The Petersen mark-recapture method (closed population) produced an estimate of 15.5 (95% CI = 7.1–32.3) chicks produced 1999/2000.

Eight of the 18 reintroduced birds were male (ergo eight pairs). This female-biased skew was exacerbated by the production of nine female and four male chicks in 1999/2000. This limited the number of pairs in 2000/2001 to 12, of which 11 were closely monitored (Table 3), including three pairings of first-year birds and a reintroduced female with a first-year male. Fourteen chicks were reared in the first round of nesting. Six pairs are known to have laid second clutches and another six chicks were probably produced. At least two pairs attempted third clutches, though both apparently failed (G. Esparon, in litt.). Total chick production in 2000/2001 was at least 20. Given that at least two pairs were not monitored (Table 3), we consider the estimate of 33 chicks produced in the two seasons on Picard to be conservative. Assuming the six birds not seen in the

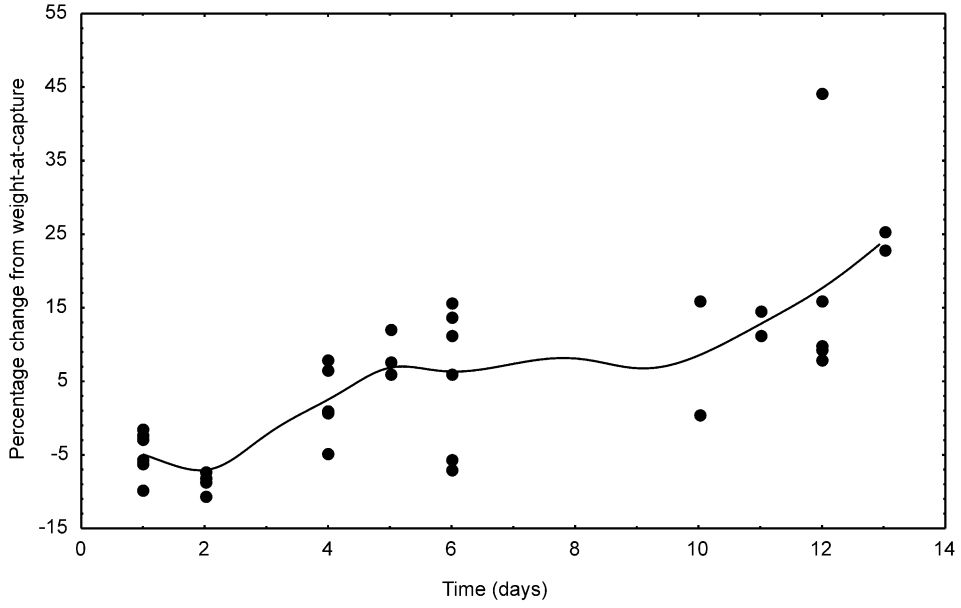

Fig. 2. Weight changes of captive Aldabra rails *Dryolimnas [cuvieri] aldabranus* expressed as a percentage difference from weight at capture. All ($n=20$) except three birds were weighed twice.

second season were alive but not within detectable range, the minimum number of rails on Picard at the end of breeding in 2001 was 51, an increase of 283% in 18 months. The number of pairs attempting to breed on Picard in the third season after reintroduction is expected to be in the region of 20, with excellent prospects for continued, exponential population growth in the medium term.

Mean chick production on Malabar was lower in 1999/2000 than in 2000/2001 (0.3 vs. 0.9 chicks/pair, Table 3), however small sample sizes make it impossible to assess the significance of this difference ($U=25$, $P>0.1$). No Malabar pairs are known to have attempted multiple clutches. By contrast, the reintroduced birds produced 1.6–2.0 chicks per pair in both seasons and successful repeat clutches were recorded. The marginally lower mean chick production in 2000/2001 results mostly from inexperienced first-year pairs' attempts to breed; three out of four attempts failed (including one second clutch). Combining data from both seasons, Picard pairs had mean chick production three times higher than Malabar pairs ($U=67.5$, $P=0.001$).

3.2. Microsatllite study

Locus TM18 was successfully amplified in 73 individuals and six alleles were identified. When treated as a single population, Aldabra rails had an observed heterozygosity of 0.528, which differed significantly from that expected under Hardy–Weinberg assumptions (Table 1). When treated separately, the Île aux Cèdres population displayed the highest heterozygosity ($H_o=0.75$) and Polymnie the lowest ($H_o=0.40$). H_o was significantly lower than expected for the Picard subset. Malabar and Picard showed the highest allelic diversity, with six and five alleles, respectively, while Polymnie had four and Île aux Cèdres only three (Table 1, Fig. 3). The Malabar and Picard populations show very similar allele distributions as would be expected given that the Picard birds are a subset of the larger population on Malabar. Polymnie and Île aux Cèdres, however, show several differences in both allele frequency and allele distribution. Only half of the Malabar population's alleles are found in the Île aux Cèdres population. In addition, the latter is characterised by a high frequency of allele 5, which does not reach a frequency greater than 0.1 in other populations.

Differences in the observed allele frequencies give a preliminary indication of population structuring, corroborated by both F_{st} and R_{st} values (Table 2). Pairwise population differentiation trends were similar using both estimates, with the exception of the σ estimates for Île aux Cèdres. The Malabar/Picard comparisons revealed essentially no differentiation, whereas Polymnie and Île aux Cèdres showed high levels of differentiation both with respect to each other and to Malabar and Picard. The relatively high degree of differentiation between Île aux Cèdres and Malabar/Picard suggested by F_{st} contrasts with the σ estimates, which suggest little differentiation. This could be an artefact of the way in which the σ estimate is calculated.

4. Discussion

The Aldabra rail is typical of many island birds in its behaviour towards novel stimuli such as humans—it is curious and inquisitive or "ecologically naïve" (sensu Quammen, 1996). It shows no fear of humans, which it does not recognise as potential predators. A negative aspect of this trait is an inability to recognise domestic cats as predators. For two reasons, this trait also made rails an ideal species on which to conduct a reintroduction experiment. First, it contributed to their rapid adjustment to being trapped, handled, held in captivity, released, followed and retrapped, all without any indications of lasting distress (behavioural, physiological or other). Second, rails were easy to retrap repeatedly, facilitating monitoring activities.

The single variable microsatellite locus gives limited insight into the genetic structuring of the populations. Levels of diversity and heterozygosity in all populations were relatively high, despite the difference between H_o and H_e in the Picard population. The largest population (Malabar) displayed the highest levels of diversity.

Table 1
Heterozygosity values observed (H_o) and expected (H_e) under Hardy–Weinberg equilibrium in the four populations of Aldabra rails *Dryolimnas [cuvieri] aldabranus*, based on locus TM18

	Picard	Malabar	Polymnie	Île aux Cèdres	Overall population
H_o	0.46	0.60	0.40	0.75	0.53
H_e	0.59*	0.66	0.34	0.55	0.68*
n	25	25	15	8	73
Na	5	6	4	3	6

Na = number of alleles found in that population.
* $P<0.05$.

Table 2
Pairwise population differentiation from a single microsatellite locus for Aldabra rails *Dryolimnas [cuvieri] aldabranus*

	Picard	Malabar	Polymnie	Île aux Cèdres
Picard	–	0.007	0.532*	−0.050
Malabar	−0.014	–	0.403*	−0.030
Polymnie	0.342	0.249	–	0.337
Île aux Cèdres	0.303	0.228	0.237	–

F_{st} values below the diagonal and σ values above the diagonal
* $P<0.05$.

Initial results suggest that the reintroduced population has retained a large proportion of the variation present in the parent population (five out of six alleles). This is supported by low pairwise estimates of F_{st} and R_{st} between Malabar and Picard. We tentatively suggest that the growing Picard population is likely to be genetically healthy, at least in relation to the other populations.

Aldabra rails are flightless and weak, reticent swimmers (R. Wanless, personal observation) and the islands on which they occur are separated by 10s or hundreds of metres of very strongly flowing water (Farrow and Brander, 1971). They are unlikely to have crossed such formidable barriers to dispersal since becoming flightless, thus preventing inter-island gene flow and possibly causing some degree of population structuring. From the microsatellite data there does appear to be some differentiation between Polymnie, Île aux Cèdres and Malabar rails. Thus, the precautionary step of using only a single source population for the reintroduction was appropriate. Additional analysis of other microsatellite loci is required to determine the full extent of this suggested differentiation. This is important for the management of individual populations as well as for future reintroductions to other islands.

The discrepancy in mean chick production on Malabar over the two seasons (Table 3) probably reflects environmental conditions. The first season was an exceptionally dry year: rainfall was low, late and episodic (Betts, 2000). The second season experienced prolonged, sustained and above-average rainfall (G. Esparon, personal communication). Interestingly, reproduction in Picard birds was not affected by rainfall. The significantly higher mean chick production on Picard suggests that a vacant niche existed here and that the reintroduced birds have increased their reproductive output in response to competitive release.

Weight-loss occurred between capture and release into acclimatisation enclosures. Fig. 3 implies that longer than three days in close confines could have had serious ramifications for the survival of captive rails. The acclimatisation period served to improve the rails' post-capture body condition, and, more crucially, it more than compensated for weight-loss during capture and transit. Had the rails not acclimatised and improved body condition they would have entered their new environment in a state of physiological stress. Under these circumstances it is likely that post-release survival and reproductive success would be compromised (Black et al., 1994; Sharp, 1996). The soft-release

Table 3
The number of Aldabra rails *Dryolimnas [cuvieri] aldabranus* monitored and their chick production in the first two breeding seasons after reintroduction to Picard Island, with comparative chick production data for the source population on Malabar Island

Island	1999/2000			2000/2001		
	Known pairs	Monitored pairs	Chicks produced	Known pairs	Monitored pairs	Chicks produced
Picard	8	7	13	12	11	20
Malabar	–	10	3	–	9	8

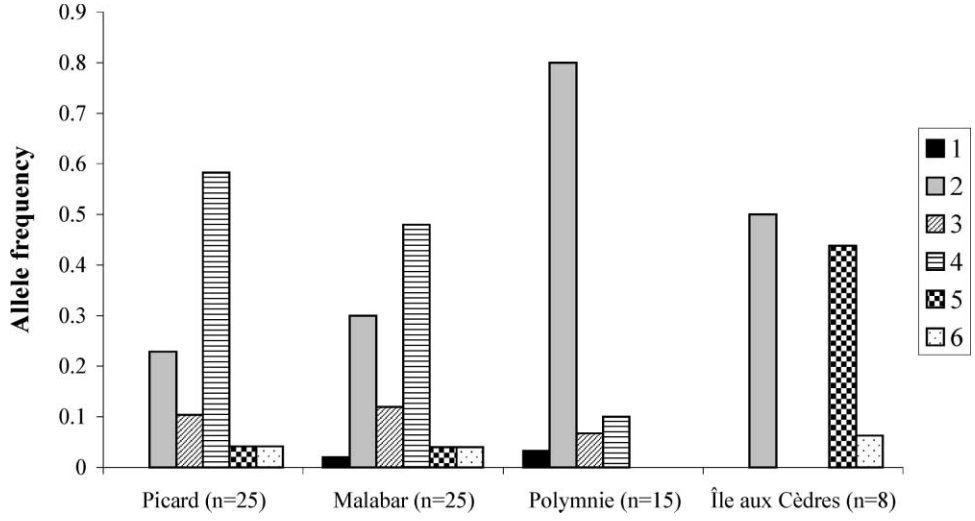

Fig. 3. Allele frequency distributions for the six alleles at locus TM18 in each of the four populations of Aldabra rails *Dryolimnas [cuvieri] aldabranus*.

protocol provided additional energetic reserves for the period between release and self-sufficiency in the new environment and this may have been instrumental in the 100% post-release survival.

The primary function of a soft-release is to acclimatise animals to their new environment (Bright and Morris, 1994; Snyder et al., 1994; Letty et al., 2000). Secondarily, however, it allows monitoring of behaviour and condition (weight-changes in this study), to ensure that animals are not manifestly stressed (either in behaviour or condition) when released into their new environment. Several studies assessing translocation successes have not taken cognisance of the release method (e.g. Griffith et al., 1989; Snyder et al., 1994; Wolf et al., 1996, 1998). However, other studies (e.g. Bright and Morris, 1994; Biggins et al., 1998) found that soft-releases resulted in better survival than did hard-releases. We cannot say whether a hard-release would have resulted in any substantial differences in the ultimate success of this reintroduction. An experimental approach is required to make direct comparisons between hard- and soft-release designs for birds (Bright and Morris, 1994); the cost and effort of the latter is considerable compared with the former. If criteria can be found to predict when soft-release is important and when a hard-release would suffice, the benefit to future reintroductions would be substantial.

The speed with which reintroduced rails adjusted to Picard, the success with which they bred and their genetic integrity obviates any demographic or genetic needs for supplementary reintroductions (see Armstrong and Ewen, 2001). While some authors have correctly argued that moving larger numbers of animals increases the likelihood of success (e.g. Griffith et al., 1989; Wolf et al., 1996,1998; Armstrong and Ewen, 2001), results of this study show that carefully managed programmes involving small numbers of birds can be highly successful. Although hard-releases may be appropriate in some cases (e.g. Komdeur, 1994), we recommend a soft-release as the conservative and precautionary method of choice for avian translocations.

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References

Abbott, W.L., 1893. Notes on the natural history of Aldabra, Assumption and Gloriosa Islands, Indian Ocean. Proceedings of the United States National Museum 16, 759–764.

Armstrong, D.P., Ewen, J.G., 2001. Assessing the value of follow-up translocations: a case study using New Zealand robins. Biological Conservation 101, 239–247.

Benson, C.W., 1967. The birds of Aldabra and their status. Atoll Research Bulletin 118, 63–111.

Benson, C.W., Penny, M.J., 1971. The land birds of Aldabra. Philosophical Transactions of the Royal Society, London B 260, 529–548.

Betts, M., 2000. Research Officer's Annual Report June 1999–July 2000. Unpublished Report to Seychelles Island Foundation, 96 pp.

Biggins, D.E., Godbey, J.L., Hanebury, L.R., Luce, B., Marinari, P.E., Matchett, M.R., Vargas, A., 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. Journal of Wildlife Management 62, 643–653.

Black, J.M., Marshall, A.P., Gilburn, A., Santos, N., Hoshide, H., Medeiros, J., Mello, J., Hodges, C.N., Katahira, L., 1994. Survival, movements, and breeding of released Hawaiian Geese: An assessment of the reintroduction program. J. Wildl. Manag. 61, 1161–1173.

Bright, P.W., Morris, P.A., 1994. Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. Journal of Applied Ecology 31, 699–708.

Collar, N.J., 1993. The conservation status in 1982 of the Aldabra white-throated rail *Dryolimnas cuvieri aldabranus*. Bird Conservation International 3, 299–305.

Cowles, G.S., 1987. The fossil record. In: Diamond, A.W. (Ed.), Studies of Mascarene Island Birds. Cambridge University Press, Cambridge, pp. 90–100.

Dawson, D.A., Hanotte, O., Greig, C., Stewart, I.R.K., Burke, T., 2000. Polymorphic microsatellites in the blue tit, *Parus caeruleus*, and their cross-species utility in twenty song-bird families. Molecular Ecology 9, 1941–1944.

Farrow, G.E., Brander, K.M., 1971. Tidal studies on Aldabra. Philosophical Transactions of the Royal Society, London B 260, 93–121.

Gibson, C.W.D., Phillipson, J., 1983. The vegetation of Aldabra atoll: preliminary analysis and explanation of the vegetation map. Philosophical Transactions of the Royal Society, London B 302, 201–235.

Goodman, S.J., 1997. RstCalc: a collection of computer programmes for calculating estimates of genetic differentiation from microsatellite data and determining their significance. Molecular Ecology 6, 881–885.

Goudet, J., 1995. FSTAT version 1.2, a computer programme to calculate F-statistics. Journal of Heredity 86, 485–486.

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. Science 245, 477–480.

Guo, S.W., Thompson, E.A., 1992. Performing the exact test of Hardy–Weinberg proportion for multiple alleles. Biometrics 48, 361–372.

Hambler, C., Newing, J.M., Hambler, K., 1993. Population monitoring for the flightless rail *Dryolimnas cuvieri aldabranus*. Bird Conservation International 3, 307–318.

Huxley, C.R., 1982. Unpublished typescript on the Aldabra rail.

Huxley, C.R., Wilkinson, R., 1977. Vocalisations of the Aldabra white-throated rail *Dryolimnas cuvieri aldabranus*. Proceedings of the Royal Society B 197, 315–331.

IUCN, 1996. IUCN/SSC Guidelines for Re-introductions. Available from http://iucn.org/themes/ssc/pubs/policy/reinte.htm.

Komdeur, J., 1994. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousine. Biological Conservation 67, 143–152.

Krebs, C.J., 1998. Ecological Methodology, second ed. Addison Wesley Longman, Menlo Park, CA.

Letty, J., Marchandeau, S., Clobert, J., Aubineau, J., 2000. Improving translocation success; an experimental study of anti-stress treatment and release method for wild rabbits. Animal Conservation 3, 211–219.

Mourer-Chauviré, C., Bour, R., Ribes, S., Moutou, F., 1999. The avifauna of Réunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. In: Olson, S.L. (Ed.), Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, DC, 4–7 June 1996. Smithsonian Institution Press, Washington, DC, pp. 1–38.

Nei, M., 1973. Analysis of gene diversity in sub-divided populations. Proceedings of the National Academy of Science, USA 70, 3321–3323.

Nicoll, M.J., 1906. On the birds collected and observed during the voyage of the "Valhalla", R.Y.S., from November 1905 to May 1906. Ibis 6, 666–712.

O'Ryan, C., Harley, E.H., Bruford, M.W., Beaumont, M., Wayne, R.K., Cherry, M.I., 1998. Microsatellite analysis of genetic diversity in fragmented South African buffalo populations. Animal Conservation 1, 85–94.

Penny, M.J., Diamond, A.W., 1971. The white-throated rail, *Dryolimnas cuvieri* on Aldabra. Philosophical Transactions of the Royal Society, London B 260, 529–548.

Piertney, S.B., Marquiss, M., Summers, R., 1999. Characterisation of tetranucleotide microsatellites in the Scottish Crossbill (*Loxia scotia*). Molecular Ecology 4, 493–498.

Quammen, D., 1996. The Song of the Dodo. Hutchinson, London.

Rand, A.L., 1936. The distribution and habits of Madagascar birds. Bulletin of the American Museum of Natural History 72, 143–499.

Raymond, M., Rousset, F., 1995. GENEPOP (version 1.2): Population genetic software for exact tests and Ecumericism. Journal of Hereditary 3, 248–249.

Rountree, R.R.G., Guérin, R., Pelte, S., Vinson, J., 1952. Catalogue of the birds of Mauritius. Mauritius Institute Bulletin 3, 155–217.

Sambrook, J., Fritsch, E.F., Maniatis, T., 1989. Molecular Cloning: a Laboratory Manual, second ed. Cold Spring Harbor Laboratory Press, New York.

Sharp, B.E., 1996. Post release survival of oiled, cleaned seabirds in North America. Ibis 138, 222–228.

Sinclair, I., Langrand, O., 1998. Birds of the Indian Ocean Islands. Struik, Cape Town.

Slatkin, M., 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics 139, 457–462.

Snyder, N.F.R., Koenig, S.E., Koschmann, J., Snyder, H.A., Johnson, T.B., 1994. Thick-billed parrot releases in Arizona. Condor 96, 845–862.

Spaull, V.W., 1979. Distribution of soil and litter arthropods on Aldabra Atoll. Philosophical Transactions of the Royal Society. London B 286, 109–117.

StatSoft, 2000. STATISTICA for Windows. Tulsa, USA.

Stoddart, D.R., 1971a. Settlement, development and conservation of Aldabra. Philosophical Transactions of the Royal Society, London B 260, 611–628.

Stoddart, D.R., 1971b. Rainfall on Indian Ocean coral islands. Atoll Research Bulletin 147, 1–21.

Stoddart, D.R., Taylor, J.D., Fosberg, F.R., Farrow, G.E., 1971. Geomorphology of Aldabra Atoll. Philosophical Transactions of the Royal Society, London B 260, 31–65.

Swofford, D.L., Selander, R.B., 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity 72, 281–283.

Taylor, B., van Perlo, B., 1998. Rails: A Guide to the Rails, Crakes, Gallinules and Coots of the World. Pica Press, Sussex.

Vesey-FitzGerald, D., 1940. The birds of the Seychelles. I. The endemic birds. Ibis 4, 480–489.

Wanless, R.M., in press (a). Can the flightless Aldabra Rail *Dryolimnas cuvieri aldabranus* actually fly? Atoll Research Bulletin.

Wanless, R.M., in press (b). Flightless Aldabra Rail *Dryolimnas cuvieri aldabranus* kills Black Rat *Rattus rattus*. Ostrich.

Weir, B.S., Cockerham, C.C., 1984. Estimating F-statistics for the analysis of population structure. Evolution 38, 1358–1370.

Wolf, C.M., Griffith, B., Reed, C., Temple, S., 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10, 1142–1154.

Wolf, C.M., Garland, T., Griffith, B., 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological Conservation 86, 243–255.