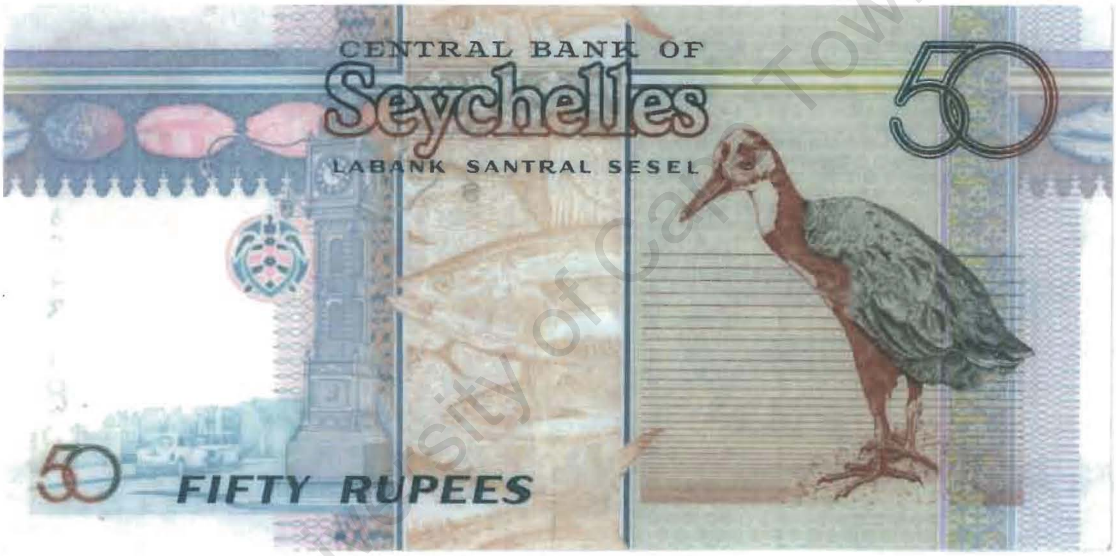
The reintroduction of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to Picard Island, Aldabra Atoll

by

Ross McLeod Wanless



Thesis submitted for the degree of Master of Science (Ornithology)

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"Aldabra is one of the wonders of the world. It is so because the rest of the world is so far away from it. This isolation has given it animals and plants that make it unique. It has the largest population of giant tortoises in the world...[and] is the home of the only remaining flightless bird of the Indian Ocean...Other islands in the Indian Ocean once had similar marvels. There were giant tortoises on Madagascar and on the Comoro Islands. They are gone now. There were flightless birds on Mauritius and Réunion. They too have gone. All were destroyed unthinkingly and carelessly by human beings."

Sir David Attenborough (1995)

"I am told that rails swarm upon the Cosmoledo Atoll and on Astove, about sixty miles eastward from Aldabra. I fear they are doomed to early extinction on Aldabra from the wild cats which will eventually reach the other islands of the group or be introduced from Grande Terre."

Dr. W.L. Abbott
[Cited in Ridgway 1895]

"I have to say the [Aldabra] rail is the most ridiculous bird I've seen..."

Justin Gerlach (2000)

To my late wife, Janet Wanless, who gave more than the reckoning thereof to the completion of the project. And, of course, to the Tyomityos: long may they live!

DECLARATION

This thesis describes original research undertaken towards a Master of Science degree at the Percy FitzPatrick Institute (University of Cape Town), and none of it has been submitted, in any form, towards a degree at any other university. I submit it as my own endeavour, and have acknowledged all assistance received in achieving this end.

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Cover picture: Republic of Seychelles R50 note, illustrating the Aldabra Rail

Drawings and sketches by Gabby Raaff

Abstract

Wanless, R.M. 2002. The reintroduction of the Aldabra rail *Dryolimnas cuvieri aldabranus* to Picard Island, Aldabra Atoll. MSc thesis, Percy FitzPatrick Institute, University of Cape Town.

The rallid genus *Dryolimnas* is endemic to western Indian Ocean islands. Formerly widespread, it is now restricted to Aldabra Atoll (the Aldabra Rail *D. cuvieri aldabranus*) and Madagascar (the White-throated Rail *D. c. cuvieri*). Before this project began, the Aldabra Rail was restricted to Polymnie, Malabar and Île aux Cèdres, having been extirpated from Grande Terre and Picard by Domestic Cats *Felis catus* (still found on Grande Terre) and humans. In 1999, following IUCN guidelines, I captured 20 Aldabra Rails and brought them to now Cat-free Picard. Two Rails died in captivity, an indirect result of incorrect sexing based on a published field sexing method; a subsequent genetic sexing technique confirmed the unreliability of sexing Aldabra Rails in the field. All 18 remaining birds were released on Picard and survived beyond the first breeding season. Eight pairs had bonded and successfully reared a minimum of 13 chicks within five months of release. Eleven monitored pairs reared 20 chicks in 2000/2001, with one-year-old birds breeding successfully. Average chick production was significantly higher on Picard than on Malabar in both breeding seasons. The Picard population at the end of the 2000/2001 breeding season was at least 51, an increase of 283% in 18 months. There are excellent prospects for continued, exponential population growth until the population reaches carrying capacity (*ca* 1000 pairs), predicted to be between 2007 and 2009. Limited genetic data suggest some population structure between extant populations, and the Picard population is genetically healthy relative to that of Malabar. There has been no substantial change in the Aldabra Rail population since the 1960s. However, I have revised an earlier population estimate downwards to *ca* 3500 pairs. I also estimate the floating population on Malabar was around 1700 Rails in early 2000. A population model of the Malabar Rails predicts a likely minimum annual adult survival rate of 85 %, with a fluctuating floater population. It also shows the population to be very robust to the removal of territorial birds for other proposed reintroductions, but highly vulnerable to the establishment of a predator. The soft release protocol (including a period of acclimatisation before release and supplementary feeding, as required, after release) is believed to have played a crucial role in the success of the reintroduction by allowing individuals to acclimatise and providing an energetic cushion between release and self-sufficiency. A soft release is recommended as the conservative and precautionary method of choice for avian reintroductions and translocations.

General acknowledgements

My supervisor, Phil Hockey, is thanked first and foremost for providing me with the opportunity to do this project. He also graciously accommodated some rather unusual requests and was unstinting in his support (financial, logistical and intellectual) of my work. He provided very intuitive conceptual guidance in Cape Town, before either of us had ever seen an Aldabra rail. Phil, together with the FitzPatrick administrative staff, also went beyond the call of duty in facilitating my oft-demanding logistical requirements. Phil's tight writing style and ecological acumen and sagacity have kept my penchant for florally descriptive meanderings (mostly) in check. His style is indelibly etched on these pages and on my writing style in general. I have declined to repeatedly acknowledge his comments at the end of each chapter. Phil, together with Peter Ryan, Morne du Plessis and John Cooper, are thanked for their gentle yet frank appraisals of my earlier attempts at writing, and I owe such scientific writing abilities as I may have, largely to them. John Cooper kindly and expeditiously reviewed all the chapters; his comments and insights greatly improved their quality.

My late wife, Janet Wanless, provided assistance in the field and great personal support during 1999 and 2000. I acknowledge her great personal sacrifices and the countless ways in which she contributed to the success of the project. My parents David and Joy Wanless, and my mother-in-law Barbara Young, were constants in times of great change, and are responsible for keeping me together, body and soul, through all that has come to pass since Jan and I embarked on the enterprise of which this thesis is the culmination.

The Seychelles Islands Foundation (SIF) Scientific sub-Committee approved my project proposal. The staff of SIF collectively formed a superb, if at times somewhat unorthodox, organisational backbone of support to this project, and my seeing it though to its current state is in no small measure their success. I especially thank Lindsay Chong Seng (SIF Executive Director), Michael Betts (Warden and Research Officer of Aldabra, 1999/2000) and Guy Esparon (Warden of Aldabra, 2000/2001) for their support of me personally and their rôles in facilitating this project.

The staff of Aldabra provided excellent and professional logistical support, notably Michael Betts, Guy Esparon, Tony and Murielle Jupiter, Brian Betsy and Phillip Baccus, who collectively assisted with almost every aspect of this project. Rachel Wiseman was an excellent field assistant and an even better friend at an extremely difficult time of my life. Richard White kept great company and was also superb in the field; he made singular contributions to Aldabra besides his work with the rails. Jeanne Mortimer also assisted in the field.

The initial field season (1999/2000) and all the genetic analyses were funded by the Dutch Trust Fund. Olivier Langrand facilitated my successful application to Conservation International and the Center for Applied Biodiversity Sciences, who funded the 2000/2001 season of follow-up monitoring. SIF also made significant financial and logistical contributions to this project. I received financial support for the first two years of my Masters degree from the National Research Foundation (NRF), and I especially thank the NRF for graciously permitting a top-up bursary (from project funds), in excess of their annual limit for Masters students. The University of Cape Town (UCT) also provided logistical support and financial assistance to me in the form of a scholarship in my third year. The FitzPatrick Institute awarded me the Gordon Sprigg Scholarship in 1999.

Much reference is made in this thesis to an unpublished typescript by Huxley (1982) that describes three seasons of research on the rails of Aldabra in the 1970s. I was able to locate a copy of this document (with great difficulty) only after the reintroduction, but it has proven valuable nonetheless. Although Huxley and I differ in many interpretations, the document was a source of inspiration, pointing me along interesting avenues of research.

Gabby Raaff did the various line drawings and sketches that illustrate and decorate this thesis. Christian Teleki kindly provided maps and Verna Love selflessly gave of her time and expertise to help reformat them. My colleagues at the Fitz are thanked for their boundless enthusiasm for this project, and for often reminding me how lucky I was to have this opportunity. And last, but not least, Andrea Angel, who has assisted me during the final stages of the write-up, more than she or anyone else could imagine. Thank you, one and all.

Introduction and overview

Introduction

The rallid genus *Dryolimnas* is endemic to western Indian Ocean islands. Formerly widespread, representatives are now restricted to parts of Aldabra Atoll (the Aldabra Rail *D. cuvieri aldabranus*) and Madagscar (the White-throated Rail *D. c. cuvieri*)(Benson 1967, Taylor & van Perlo 1998). Before this project began, the Aldabra Rail was restricted to Polymnie, Malabar and Île aux Cèdres, having been extirpated from Grande Terre and Picard by Domestic Cats *Felis catus* (still found on Grande Terre) and humans (Benson & Penny 1971, Collar 1993, Taylor & van Perlo 1998, Chapter 1). 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, Chapter 4). However, I have revised the total population estimate downwards to *ca* 3500 *pairs* (Chapter 4).

Following the guidelines for reintroductions set out by the World Conservation Union (Appendix 3), I conducted a limited, experimental reintroduction of the Aldabra Rail to Picard Island in late 1999, followed by intensive monitoring for the next two breeding seasons.

I attempted to ensure a broad representation of the source (Malabar) population's heterogeneity in the reintroduced population by taking ten birds from the extreme eastern end and ten from the extreme western end of Malabar. Both individuals of a putative pair died shortly after being transported to Picard – a post mortem revealed that they were both male. Later, I used a genetic sexing technique to confirm suspicions that the published method for sexing Aldabra Rails in the field was unreliable (Penny & Diamond 1971, Chapter 4). Thus 18 Aldabra Rails were brought to Picard, of which eight were male and ten were female (Chapter 2).

Enclosures were constructed abutting good quality habitat to acclimatise Rails to Picard. They were kept captive until they appeared accustomed to their new environment and were in good body condition (Chapter 2). The release was designed as a soft release, the primary function of which is to acclimatise animals to their new environment (Bright & 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. 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 (Chapter 2). Had they not acclimatised and improved body condition they could have entered their new environment in a state of physiological stress. Under such circumstances it is likely that post-release survival and reproductive success would be compromised (Black *et al.* 1994). The soft release protocol provided an energetic cushion between release and self-sufficiency in the new environment. This was probably instrumental in ensuring the high survival immediately after release (Chapter 3).

The reintroduced birds had a 100% post-release survival at the end of the 1999/2000 season and 94% survival in the 2000/2001 season, with no confirmed mortality (Chapter 3). All eight reintroduced males paired with reintroduced females, and the seven pairs that were monitored reared at least 13 chicks to independence in 1999/2000. The initial sex-ratio skew at reintroduction was exacerbated by the production of nine female and four male offspring in 1999/2000. This limited the number of possible pairs in 2000/2001 to 12, of which 11 were closely monitored, including three pairings of first-year birds. Fourteen chicks were reared to independence in the first round of nesting. Six pairs laid second clutches and these produced at least another six chicks, total chick production in 2000/2001 was thus at least 20. Given that at least one pair was not monitored in both seasons, the estimate of 33 chicks produced in the two seasons on Picard is conservative. The minimum number of Rails on Picard at the end of the breeding season in 2001 was 51, an increase of 283% in 18 months. Combining data from both seasons, Picard pairs had mean chick production three times higher than pairs on Malabar, the source population. This suggests that a vacant niche existed on Picard and that the reintroduced birds have increased their reproductive output in response to competitive release. 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. The positive changes in survival and reproductive traits observed in reintroduced birds, relative to birds from the source population, can be ascribed largely to the excellent quality habitat on Picard.

Aldabra Rails were taken only from Malabar (the largest population) to ensure that no mixing of (possibly) distinct genetic stocks occurred (Chapter 2).

Chapter 4 details a microsatellite study, undertaken *a posteriori*, to determine the distinctiveness of the three original populations and assess the degree of genetic variation in the reintroduced individuals. Only one locus produced an informative, polymorphic product. Nevertheless, subsequent analysis showed interesting trends. Rails from Malabar and Picard had the highest allelic diversity, with six and five alleles respectively, while Polymnie had four alleles and Île aux Cèdres only three. The Malabar and Picard populations showed very similar allele distributions as would be expected given that the Picard Rails are a subset of the larger population on Malabar. Polymnie and Île aux Cèdres, however, showed several differences in both allele frequency and allele distribution, suggesting some degree of population structuring. Thus, the precautionary step of using only a single source population for the reintroduction was appropriate. The growing Picard population is likely to be genetically healthy, at least in relation to the other populations.

The speed with which reintroduced Aldabra Rails adjusted to Picard, the success with which they bred and their genetic integrity obviates any demographic or genetic need for supplementary reintroductions (see Armstrong & 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, Lloyd & Powlesland 1994), I recommended a soft release as the conservative and precautionary method of choice for avian translocations.

Overview

This thesis is primarily devoted to describing a trial reintroduction of 20 Aldabra Rails from Malabar to Picard, within Aldabra Atoll. Key questions that I address, and the chapters that deal with them, are:

1. Was Picard suitable for reintroducing Aldabra Rails? **Chapter 2**
2. What methods were most appropriate for this reintroduction, and what implications does this study have for translocations (including reintroductions) in general? **Chapters 2 & 3**
3. How did the Aldabra Rails respond to reintroduction, and why? **Chapter 3**
4. What constitutes an objective set of criteria that can adequately describe a range of potential outcomes for translocations in general and this reintroduction in particular? **Chapter 3**
5. What aspects of the Aldabra Rail's demography and population biology were discovered during this study, and how can this information be used to enhance the conservation status of the Aldabra Rail? **Chapters 2 & 4**

CHAPTER OUTLINE

Chapter 1: provides a description of Aldabra, and discusses the current and historical distribution of Aldabra Rail, and some of the likely factors underlying the observed distribution.

Chapter 2: documents the methods employed in effecting the reintroduction of the Aldabra Rail to Picard Island, and the results up to and including the release of 18 birds.

Chapter 3: assesses the results of two seasons of post-release monitoring of the reintroduced Aldabra Rails on Picard, within the context of a theoretical framework for objectively assessing the outcome of a reintroduction. I place my findings in a broader conservation context and make some recommendations about general reintroduction methods based on the findings in this chapter.

Chapter 4: reviews census methods used to estimate Aldabra Rail densities on Aldabra and provides a current population estimate. I use some simple computer simulations to model the dynamics of the Malabar population. I also use a modified model to predict the rate of increase in the reintroduced Picard population. Lastly, I describe attempts to analyse the genetic structure of the three extant Rail populations and the reintroduced population.

Appendix 1: describes several aspects of the biology and ecology of the Aldabra Rail that were previously unknown or unpublished, including a comprehensive, illustrated description of their displays and postures.

Appendix 2: details an investigation I made into the actual and theoretical capacity for flight in the Aldabra Rail. This is of some relevance to the project: if the Aldabra Rail were found to be volant, it might have tried and failed to colonise Picard naturally. The implications of this take on added significance in the light of the investigation into the genetic structure of the extant populations on Aldabra, as the source population is not geographically closest to Picard.

Appendix 3: is a copy of a document that I have cited several times in the thesis. The document is published (by the IUCN) on the Internet, and gives definitions and guidelines for reintroductions. I followed these guidelines closely before and during the reintroduction.

Appendix 4: is a banding scheldule for all Aldabra

Rails banded during the coarse of this project. It includes the sex of individuals (where known) and the most recent retrap data. Reference is made throughout this thesis to the data in this appendix.

KEY FINDINGS

- the environment of Picard was as well-suited to Aldabra Rails as it was before their local extinction
- The soft release protocol was probably instrumental in ensuring a 100% survival during acclimatisation and immediately after release; good quality habitat ensured high post-release survival and a significantly higher mean chick production on Picard than on Malabar
- The speed with which reintroduced Rails adjusted to Picard, the success with which they bred and their genetic integrity obviates any demographic or genetic need for supplementary reintroductions
- The Picard population is likely to experience exponential growth until *ca* 2007
- Soft-releases should be viewed as the method of choice for avian translocations (including reintroductions)
- Future reintroductions of the Aldabra Rail to other nearby atolls and islands are highly desirable, and the Malabar population would be entirely resilient to the removal of the numbers of breeding pairs required for a full-scale reintroduction.

INTRODUCTION

PHYSICAL DESCRIPTION OF ALDABRA

Aldabra Atoll (9° 24' S, 46° 20' E) lies 400 km N of Madagascar and 1100 km SW of Mahe, the main island of the granitic Seychelles (Figure 1.1). It is a large (34 km by 14.5 km), slightly raised coral platform with a land surface area of approximately 155 km^2 (Stoddart *et al.* 1971; Taylor *et al.* 1979). It comprises four large islands - Grande Terre, Malabar, Picard and Polymnie - which form a land rim around a substantial, shallow lagoon (almost 30 km across) (Figure 1.2). The lagoon is dotted with numerous smaller islets (up to *ca* 50 ha) and the atoll is fringed by an intact reef (Stoddart *et al.* 1971; Taylor *et al.* 1979). The lagoon is strongly tidal, experiencing two tides daily and a spring-tide maximum range of *ca* 2.7 m (Farrow & Brander, 1971). Aldabra is part of an archipelago, referred to as the Aldabra Group, comprising Aldabra and Cosmoledo atolls and Astove and Assumption islands.

Aldabra is the coraline tip of a of volcanic seamount, rising from depths of 4 000 - 4 500 m in the Somali Basin (Stoddart *et al.* 1971). Subsidence has placed Aldabra's volcanic base well below the present sea level, while the raising and lowering of sea-levels has exposed marine (predominantly fossilised coral) limestone surface rocks (Stoddart *et al.* 1971). Fryer (1911) described the surface features of Aldabra, introducing the local terms *champignon* for the heavily dissected, deeply pitted and solution-fretted rock, and *platin* for the extensive areas of relatively flat, smooth rock. This dichotomous classification is an oversimplification, but is useful nonetheless (Stoddart *et al.* 1971). Champignon is almost certainly derived from the Creole term for the mushroom-shaped islets that typically consist of the pitted rock and are so abundant on Aldabra.

Aldabra was completely submerged during the last interglacial, around 140-120 ka B.P. (ka: 1000 years, B.P.: Before Present), when the sea surface around Aldabra was *ca* 10 m above its present level (Thomson & Walton 1972). It re-emerged around 100 ka B.P. and reached an estimated maximum height of around 120 m a.s.l. during the Wisconsin glacial maxim *ca* 17 ka B.P. (Taylor *et al.* 1979). At this point its land area measured *ca* 400 km^2, more than double the present area. A subsequent rise in sea level resulted in the breaching of the land rim in four places, and consequent filling of the lagoon, around 5 ka B.P.. There has been no substantial geological change since then, with the exception of the widening and deep incising of existing channels between the lagoon and open sea. The current maximum land-elevation (excluding dunes) is 8 m a.s.l., at Île Esprit (Stoddart *et al.* 1971).

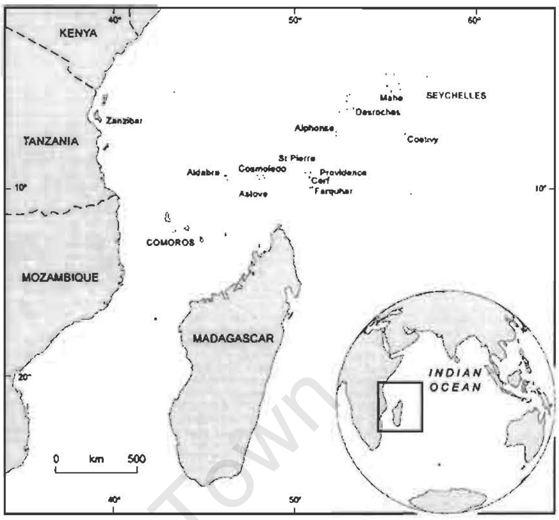

Figure 1.1. Map of the western Indian Ocean showing Aldabra Atoll's location, NW of northern Madagascar

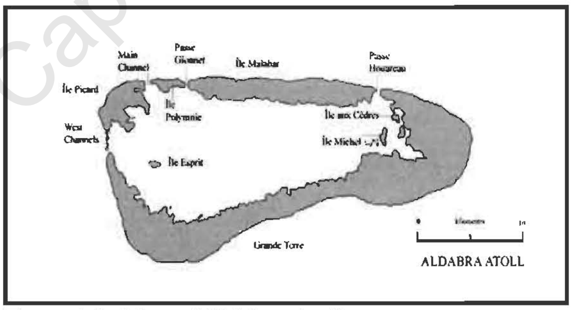

Figure 1.2. Map of Aldabra Atoll

HISTORICAL BACKGROUND

Human impacts on Aldabra

Aldabra was certainly visited by pre-European seafarers, although they left little visible evidence (Stoddart 1971a). Aldabra appears, under various pseudonyms, on Portuguese charts from as early as 1517 (Stoddart 1971a). Early European voyagers occasionally visited Aldabra, starting with the *Charles* and *Elisabeth* in 1742, but its situation away from major shipping lanes combined with lack of fresh water discouraged settlement (Stoddart 1971a). Its more recent human history is one of exploitation and very near biological disasters.

The establishment of a settlement in the granitic Seychelles in the 18th Century saw the advent of frequent, artisanal fishing trips to Aldabra (Stoddart 1971a). These sorties made extensive use of marine turtles, tortoises and probably other land animals, for food. They may also have been responsible for the introduction of the Black (or Ship) Rat *Rattus rattus*, and the Domestic Cat *Felis catus*.

The leasing of Aldabra for exploitation of its natural resources began in 1888, while under the aegis of Britain's Colonial Mauritius administration. The decision to tender a commercial lease created considerable public outcry. This included a letter to the colonial administration from eminent biologists of the day, including Charles Darwin, expressing particular concern over the conservation of the last extant population of the region's giant tortoises, the Aldabra Giant Tortoise *Dipsochelys dussumieri* (Stoddart 1971a). A lease was granted without legislated protection for the tortoises (Stoddart 1971a). Attempts were made to cultivate Cotton *Ricius communis*, Sisal *Agave sisalana* and Coconuts *Cocos nucifera*, with only the latter proving marginally viable (Stoddart 1971a). At the start of the 20th Century, plans were made to mine phosphates, a fate that befell all of the other islands of the Aldabra Group. Fortunately, Aldabra's coral limestone contains only low-grade phosphate deposits (Skerret & Mole 1995); had this not been the case Aldabra could well have become as ecologically devastated as nearby Assumption Island.

The British Government took a sinister interest in Aldabra early in the 1960s, embarking on a covert operation to assess Aldabra's suitability as a military base. Britain transferred Aldabra into the British Indian Ocean Territory (B.I.O.T.) in 1965, preparatory to building the base (Stoddart 1971a). Public outrage, spearheaded by the British Royal Society, resulted in a campaign that became known as "the Aldabra Affair" (Skerret & Mole 1995). The military agenda was eventually dropped, but the Royal Society maintained a strong interest in Aldabra. Early in the 1970s a research station was built and the atoll's lease was formally handed over to the Royal Society in 1976. At the same time Aldabra was returned from the B.I.O.T. to the Seychelles, which gained independence in that year.

In 1979 a Presidential Decree created a statutory body, the Seychelles Island Foundation (SIF), to administer Aldabra (Beaver & Gerlach 1998). The Royal Society donated all the buildings and equipment of the research station to SIF in 1980 (D. Stoddart pers. comm.). In 1981 Aldabra was designated a Special Reserve under Seychelles law (Order S/I 86/1981) and was declared a UNESCO World Heritage Site in 1982, in recognition of its outstanding natural beauty and to conserve it in perpetuity (Skerret & Mole 1995).

FLORA AND FAUNA

Habitat types

Aldabra's vegetation is a unique example of raised coral vegetation that remains largely free of human transformation, and is strongly influenced by a reptilian herbivore, the Giant Tortoise (Gibson & Phillipson 1983). *Casuarina equistefolia* groves on the seaward rim, and stands of mangroves (*Rhizophora* sp., *Bruguieria* sp. and *Ceriops* sp.) fringing the lagoon are, with few exceptions, the only trees – the rest of the atoll is a remarkably uniform landscape with vegetation height seldom exceeding four metres. Where the land is close to saline groundwater, vegetation is dominated by the shrub *Pemphis acidula*, which usually grows in dense, monotypic canopy stands with a low diversity of understorey plants. Other researchers (e.g. Huxley 1982) have found it useful to divide mixed scrub vegetation (i.e. non-*Pemphis* dominated) dichotomously into "open" mixed-scrub and "dense" mixed-scrub, the former characterised by large areas of bare rock or grass cover, the latter being mostly closed-canopy. Of the 176 flowering plants native to Aldabra, *ca* 40 are endemic to either Aldabra or to the Aldabra Group. The scale and topographical heterogeneity of Aldabra have given rise to a relatively high diversity of plant communities and assemblages for a coral atoll (Gibson & Phillipson 1983). Yet, despite this species diversity and complexity of vegetation patterns, all extant endemic landbirds have been observed in all habitat types, differing only in their usage of habitat types and in relative abundances around the atoll (R. Wanless unpubl. data).

Reptiles

The Giant Tortoise is perhaps Aldabra's most renowned resident, being the last representative of a taxon that was once spread across the entire region (Coe & Swingland 1984). Subsistence and commercial exploitation is believed to have rendered all other giant tortoise species in the region extinct by the mid 19th Century (Coe & Swingland 1984), and very nearly exterminated the Aldabran population (Stoddart 1971a). It continues to serve as a flagship species for the conservation of the atoll. Two species of marine turtle nest on beaches on Aldabra: the Green Turtle *Chelonia mydas* and Hawksbill Turtle *Eretmochelys imbricata* (Frazier 1984). Both were, like the tortoise, heavily exploited and in urgent need of conservation (Frazier 1984), but more recently have benefited from the protection of Aldabra (Mortimer 1988). Other reptiles found on Aldabra are the House Gecko *Hemidactylus mercatorius*, Bouton's Skink *Cryptoblepharus boutonii* and an endemic subspecies of Abbott's Day Gecko *Phelsuma abbotti abbotti* (Cheke 1984).

Seabirds

Aldabra has ten species of breeding seabirds (Diamond & Penny 1971) and is of both regional and global importance for several of these. It hosts possibly the largest population of Red-tailed

Tropicbirds *Phaethon rubicauda* and the second largest colony of frigatebirds in the world (*Fregata ariel* and *F. minor*) (Reville 1983, Stoddart 1984). The Red-footed Booby *Sula sula* breeds there in greater numbers than anywhere else in the region. Regionally it is important as one of two breeding localities for Black-naped Terns *Sterna sumatrana* and Caspian Terns *Hydroprogne caspia* and there are significant numbers of breeding White-tailed Tropicbirds *P. lepturus* (Stoddart 1984, Diamond & Prŷs-Jones 1986, Wanless & White in press).

Shorebirds and waterbirds

Aldabra is of little significance for the 15 species of migrant shorebirds recorded there, with the exception of the Crab Plover *Dromas ardeola*, which winters in significant numbers (Feare & Watson 1984, Betts 2000). Five species of the family Ardeidae breed on Aldabra. The Madagascar Squacco Heron is known to breed only on Aldabra and Madagascar (Hancock & Kushlan 1984). Aldabra is the only atoll and one of only two oceanic breeding sites for the Greater Flamingo *Phoenicopterus ruber* (Benson & Penny 1971, Rainbolt *et al.* 1997)

Landbirds

Fifteen species of landbirds (including the sacred ibis *Threskiornis aethiopica abbotti* in this definition) have bred on Aldabra in historical times (Benson & Penny 1971). The endemic Aldabra Brush Warbler *Nesillas aldabranus* became extinct between 1983 and 1986 (Hambler *et al.* 1985, Roberts 1987). The Barn Owl *Tyto alba* became locally extinct for unknown reasons some time in the 1960s (Benson & Penny 1971). Aldabra has a single remaining endemic bird species, the Aldabra Drongo *Dicrurus aldabranus* (Benson & Penny 1971). Of the remaining 12 species, only the Pied Crow *Corvus albus* has not been described as a distinct subspecies. All endemic forms except the Comoro Blue Pigeon *Alectroenas sganzini minor* have Madagascan affinities (Benson & Penny 1971). The Aldabra Rail is flightless, unlike its close relative from Madagascar, and its taxonomic status is in need of review. It is the last flightless bird of the tropical western Indian Ocean islands.

Introduced mammals

The Black Rat became established on Aldabra before historical records were kept. It is ubiquitous and abundant throughout most of the atoll. Its semi-arboreal habits mean that both ground- and tree-nesting species are vulnerable to predation (Racey & Nicoll 1984). The subspecies found on Aldabra is *frugivorous*, a race with a mostly vegetarian diet (Racey & Nicoll 1984). Evidence of Rat predation has been found on even quite distant islets in the lagoon, where it depredates eggs and nestlings of seabirds and shorebirds (pers. obs.). The impact of Rats on the ecology of Aldabra has never been quantified, although they are known to impact heavily the nesting success of all the endemic passerine species (Frith 1976, R. Wanless unpubl. data). Control at present is limited to trapping around the station.

Feral Cats were first recorded on Aldabra in 1890, but may have colonised before then (Abbott 1893). They have been recorded from Malabar and Picard islands, but have only been consistently recorded from Grande Terre (Stoddart 1971a, Huxley 1982, Hambler *et al.* 1993). This pattern has never been properly explained, but is possibly a function of water availability: only the latter island has standing fresh water year-round (Stoddart 1971a) and is thus able to support a population of Cats through the long, dry monsoon. This might explain the current absence of Cats from Picard. They were never explicitly targeted for removal, but nonetheless have not been seen since pet Cats were removed in the 1970s (L. Chong-Seng *in litt.*).

Goats *Capra hircus* were brought to Aldabra in 1890 (Stoddart 1971a). By 1971 they had colonised the whole atoll (barring lagoonal islets). An eradication programme removed Goats from all other islands but had not completely eradicated them from Grande Terre when the programme ended in 1997 (M. Bergeson *in litt.*). Currently, their numbers appear to be increasing (Betts 2000).

THE ALDABRA RAIL

The Aldabra Rail is a medium-sized rail (tail to bill length 29-33 cm, n = 3). It has a slender build, with long, fairly slender neck, bill, legs and feet. Its wings are somewhat reduced and do not protrude beyond the body when at rest (Appendix 2). They are seldom used and when closed, they blend with the rest of the plumage to give the impression of lacking wings entirely. The Aldabra Rail's body is also quite slender, an impression that is emphasised by the noticeable reduction of the breast musculature (Appendix 2), and thus the overall impression is of a small, but graceful bird.

The Aldabra Rail is an inquisitive, curious bird. Adults show little fear of humans and, after initially investigating an approaching human, will generally ignore observers and continue with regular activities (Penny & Diamond 1971, pers. obs.). The species' inquisitiveness was exploited to locate birds and their tolerance of human proximity allowed observations of birds to be made with relative ease. This enabled me to document much of their ecology, behaviour and biology, previously unknown or unpublished.

Figure 1.3. Adult Aldabra Rail. Note strong contrast between white throat-patch and surrounding plumage.

Figure 1.4. Adult Aldabra Rail showing upper body plumage. The bird is performing the Nest Defence Display (Appendix 1)

Figure 1.5. Adult Aldabra Rail foraging. Note the white undertail and barring on lower belly. Also note the lack of breast musculature.

Figure 1.6. Juvenile Aldabra Rail. Note overall dull appearance vs that of adult (Figs 1.4 & 1.5).

Figure 1.7. Aldabra Rail chick (3 days old). Note the white egg-tooth at the tip of the bill and otherwise entirely black appearance.

Plumages

Adult Aldabra Rails from Malabar and Polymnie have rich, dark, red-brown feathering on the face, cheeks, crown, nape, neck, lower throat, breast and upper belly (Figure 1.3). This coloration in adults from Île aux Cèdres is noticeably duller, paler and with pink tones. In all adults, the white throat-patch contrasts strongly with the dark surrounding colour (Figure 1.3). The mantle, back, upperwing coverts, rump, uppertail, mid-belly and flanks are a dark, olive-green colour (Figure 1.4), with adults from Île aux Cèdres being slightly duller, with suggestion of more yellow on the dorsal feathering. The shafts and central portions of the back, scapular and tertial feathers are dark, giving the back a streaked appearance. The upper flanks and lower belly are grey-brown with fine, white barring, as are the underwing coverts. Flight feathers are dull grey-brown. Undertail coverts are white (Figure 1.5). The iris is dark brown. The bill is long and slender, tapering to a sharp point. It is black from tip to near the base, where it has a variably pink or red colour. The colour extends about a third of the length of the bill, but is restricted to the lower half of the upper mandible. Legs are dark brown.

Juvenile plumage resembles that of adults but is very much duller, lacking the strong contrast in upper and lower body coloration (Figure 1.6). The upperparts, belly and flanks are dull olive-brown. The back is streaked with black as in adults. The olive-brown also extends patchily onto the neck and crown. The face, nape, neck, lower throat, breast and belly are mostly grey-brown, with a pale pink-brown wash on the throat and breast. The belly lacks the white barring of adults. The throat patch is smaller, poorly defined and flecked with the pale pink-brown colour of the throat and breast, giving it a dull appearance. The iris is pale green-brown but gradually changes to the dark brown of adults. The bill is black and the pinkish-red colour (present in adults) is considerably less obvious. Juveniles undergo a complete moult in their first year, achieving adult plumage regardless of whether they are paired or not. I have no details of this moult, excepting that as no juvenile birds were seen in August, I assume that they moult into adult plumage between May and July in their first year.

Newly hatched chicks are thickly covered in black down, and all bare parts are also black (Figure 1.7), except for the white egg-tooth, which is lost after about a week. When parents give a danger signal (the "mpclick" call of Huxley & Wilkinson (1977)) to downy chicks, the chicks immediately run to the nearest dark place, such as under the aerial roots of a *Pandanus* bush or a deep solution hole. It is extremely difficult to see black, downy chicks that are concealed in this way. Similar behaviour has been observed in other rallids and precocial species only distantly related to rallids, e.g. African Black Oystercatcher *Haematopus moquini* and Black-naped Terns *Sterna sumatrana* (Baker & Hockey 1984, Taylor & van Perlo 1998, pers. obs). The precise timing of the emergence of juvenile feathers is not known. However, primary feathers begin to emerge from their sheaths at about two weeks and at three weeks juvenile contour feathers are present, often with a stripy appearance from the black down extending from the face down the sides of the throat.

Range reduction of Dryolimnas

The rallid genus *Dryolimnas* is endemic to the tropical western Indian Ocean islands (Benson 1967, Taylor and van Perlo 1998). Representatives occurred on the Aldabra Group, 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. The White-throated Rail *D. cuvieri cuvieri* is locally extinct on Mauritius but is common on Madagascar (and is able to fly) (Cowles 1987, Taylor & van Perlo 1998, Sinclair & Langrand 1998). The flightless subspecies *D. c. abbotti* became extinct on Astove, Cosmoledo and Assumption between 1905 and 1937 (Nicoll 1906, Vesey-FitzGerald 1940). The Aldabra Rail *D. c. aldabranus* is the only surviving flightless representative of the genus and is endemic to Aldabra (Benson 1967, Appendix 2).

Box 1.1. Classification and taxonomy of the Aldabra Rail
This classification follows Sibly & Ahlquist (1990). Details of the type specimen and taxonomic notes are taken from Taylor & van Perlo (1998).
Class: Aves
  Order: Guiformes
    Suborder: Ralli
      Superfamily: Ralloidea
        Family: Rallidea
          Genus: *Dryolimnas*
            Species: *cuvieri*
              Subspecies: *aldabranus* (Ridgway 1894)
Holotype: *Rallus cuvieri* Pucheran, 1845, (Mauritius).
Synonyms: *Rallus/Eulabiornis gularus; Dryolimnas aldabranus; Rougetius aldabranus; Rallus/Calamodromas bernieri; Canirallus kioloides/cuvieri*
Alternative names: White-throated Rail, Aldabra White-throated Rail; *Tyomityo* (Seychellois Creole)

Historical records of the distribution of the Aldabra Rail are equivocal. There remains some doubt as to whether they ever inhabited the largest of the islands, Grande Terre (Ridgway 1895, Gaymer 1967, Collar 1993). Abbott (in Ridgway 1895) found them to be common throughout the atoll with the exception of Grande Terre, explaining their absence there in 1892 as being due to feral Cats ("... excepting Grande Terre, where it has been exterminated by the cats, which run wild there."). The first documented introduction of Cats to Aldabra was in 1890. Huxley (1982) questioned whether this could have led to local extinction of the Rail by 1892 (Ridgway 1895). However, the presence of Cats on Grande Terre from prior, unrecorded introductions cannot be ruled out. Indeed, without invoking predation by Cats, the absence of Aldbra Rails from Grande Terre is anomalous. Grande Terre makes up around 80% of Aldabra's land area, and its vegetation is suitable for Aldabra Rails. That this genus successfully colonised Mauritius, Rèunion and all the islands of the Aldabra Group including all the islands and several islets on Aldabra Atoll *except* Grande Terre, is highly unlikely.

There are considerable morphological differences between birds on Île aux Cèdres and those on either Malabar or Polymnie, strongly suggesting that they were not translocated in historical times (*contra* Huxley 1982). It is quite plausible that they are a relict population, separated from Grande Terre when the lagoon filled. If, on the other hand, Île aux Cèdres was colonised by Rails, colonists would most likely have originated from Grande Terre. The next closest source is Malabar, which is over two kilometres distant. Aldabra Rails are incapable of flight (Appendix 2) and are reluctant swimmers (Huxley 1982, pers. obs.). In crossing the lagoon from Malabar, they would have had to overcome strong currents and abundant sharks and predatory fish, and have done so in sufficient numbers to establish a persistent population on a small island. By contrast, Rails colonising from Grande Terre would only have had to cross a few tens of metres of relatively calm, shallow water, with several islets and rocks exposed at low tide to serve as staging-posts. This suggests that the Île aux Cèdres population represents the closest living representative of an undescribed and extinct Grande Terre form of the Aldabra Rail

Huxley (1982) suggested that historical records of Aldabra Rails on Picard refer to birds translocated by Seychellois labourers. This is unsubstantiated, and apparently contradicts the more plausible interpretation of Abbott (in Ridgway 1895), who was the first person to document the distribution of the Rail on Aldabra. Abbott states that Rails are "very common on all the islets of the Aldabra group, abounding on even the smallest, which do not contain more than half an acre..." (Ridgway 1895, p 528). Furthermore, a sub-fossil portion of a metatarsal bone typical of *Dryolimnas* from Picard shows that they occurred there between 100 and 15 ka B.P (Harrison & Walker 1978, Taylor *et al.* 1979). These lines of evidence strongly suggest that Rails were naturally ubiquitous on Aldabra before the arrival of humans and the introduction of Cats. I conclude that Aldabra Rails occurred naturally on Picard. Their subsequent extermination there is most likely the result of predation by both humans and Cats.

The world range of the Aldabra Rail before this project began was confined to Polymnie, Malabar and Île aux Cèdres (Huxley 1982, Collar 1993, Taylor & von Perlo 1998). The only reliable estimate of the populations was made in 1974, when Malabar was estimated to support *ca* 8000, Polymnie *ca* 270 and Île aux Cèdres *ca* 80 Rails (Huxley 1982, Collar 1993, but see Chapter 4). Survey methods comparable to those that produced these estimates reveal no substantial changes in any of the populations since 1974 (Hambler *et al.* 1993, Chapter 4).

The "Picard rail"

During the 1990s a single Aldabra Rail was present around the station on Picard. How it came to be there is not documented. What follows is a description pieced together from several personal communications, often of quite divergent opinion. It seems that around 1992, Tony Morel, incumbent warden on Aldabra, captured at least one but possibly a pair of Rails on Malabar and released them on Picard. Whatever the reason, their release on Picard was unauthorised, unsupervised and undocumented. At some stage one of the two birds died, from unknown causes. I captured the surviving bird on 18 October 1999, placed a metal and an alpha-numerically coded plastic band on it and released it on the "Inland Coccid Transect" at Middle Camp, on 3 November 1999. It was retrapped near the point of release in May 2001.

REINTRODUCTION

The regional range-contraction experienced by the Rail, from all the islands in the Aldabra Group and probably all those of Aldabra Atoll, to two islands and one islet on Aldabra Atoll, has been cause for concern for some time (Collar 1993, Hambler *et al.* 1993, Skerret 1999, Taylor & von Perlo 1998). Whereas the remaining populations are numerically healthy, their limited distribution leaves them vulnerable to catastrophic events, both extrinsic (e.g. cyclones) and intrinsic (e.g. disease). Because feral Cats still survive on Grande Terre (pers. obs.) the possibility exists that they could establish themselves on Malabar. They have succeeded in dispersing to Malabar at least once (Huxley 1982) but never became established. Should Cats become established on Malabar they would almost certainly cause the demise of the largest extant population of Aldabra Rails (Hambler *et al.* 1993, Chapter 4). Calls have been made to establish captive breeding populations of the Rails and to investigate reintroducing then to rehabilitated parts of their former range (e.g. Hambler *et al.* 1993, Taylor & von Perlo 1998).

The Aldabra Management Plan (Beaver & Gerlach 1998) established a zoning policy for the atoll that specifically restricts unaccompanied shore visits by tourists to Picard. In practice, however, demand from visitors to see "the last flightless bird of the Indian Ocean islands" places pressure on tour operators and island wardens to allow access to Malabar (pers. obs.). This led to calls from members of the board of SIF for Rails to be reintroduced to Picard, essentially to curtail visits to areas of the atoll zoned off-limits to tourists (L. Chong Seng, *in litt.*).

Cats, the most probable cause of extinction of Rails from Picard, are no longer found there (L. Chong Seng *in litt.*, M. Bergeson *in litt.*, pers. obs.). There is apparently no other factor rendering Picard unsuitable for the establishment of a new Aldabra Rail population (Chapter 2) — the survival of the "Picard rail" providing further evidence of the island's suitability for Rails. It was decided that Picard represents the most suitable habit presently available for re-establishing a population of Aldabra Rails.

Given the above, the guidelines set out by the World Conservation Union for reintroductions (Appendix 2) were met and sound conservation and scientific rationales existed for undertaking a reintroduction. SIF approached Prof. Phil Hockey to conduct a feasibility study with a view to undertaking a reintroduction of Rails to Picard (Chong-Seng *in litt.*). We decided that a limited, experimental reintroduction would not endanger existing populations and would best reveal the potential to establish a viable population on Picard (Hockey & Wanless *in litt.* to L. Chong-Seng).

ACKNOWLEDGEMENTS

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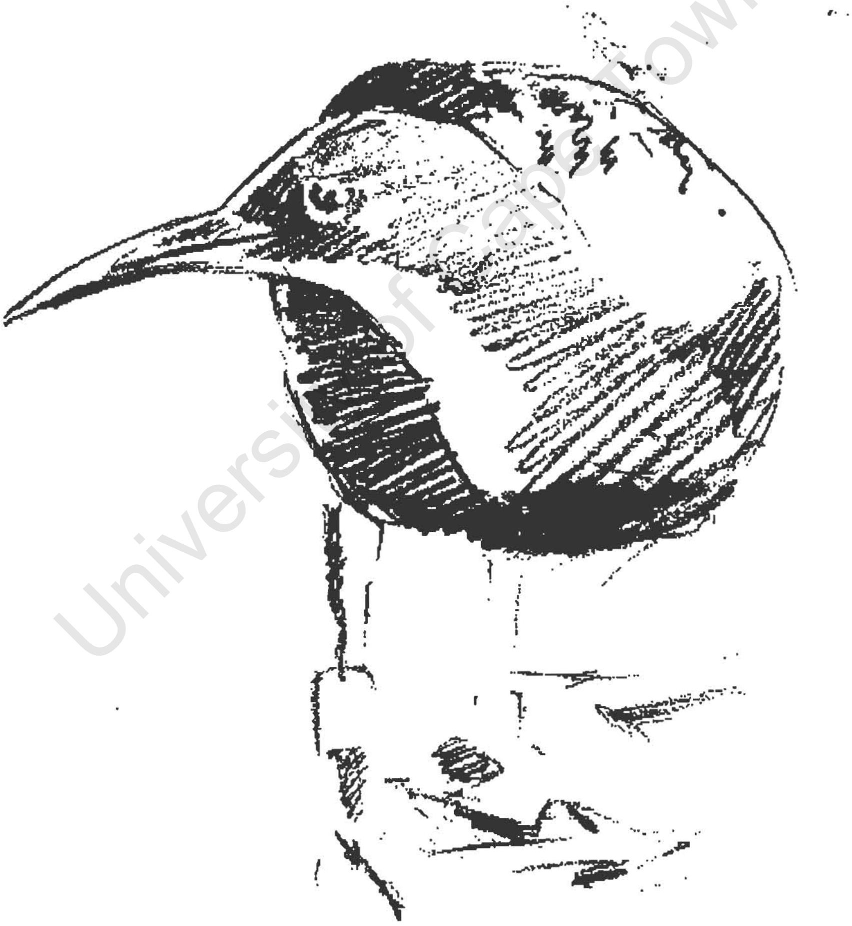

The "soft release" reintroduction of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to Picard Island

INTRODUCTION

The Aldabra Rail *Dryolimnas cuvieri aldabranus* has experienced substantial range-contraction in the 19th and 20th Centuries, as a result of human activities (Chapter 1). Most authorities agree that Domestic Cats *Felis catus* are responsible for the absence of Aldabra Rails on Picard and Grande Terre (Hambler *et al.* 1993, Chapter 1). Domestic Cats are no longer on the former but are still present on the latter. According to World Conservation Union (IUCN) criteria, this range-contraction qualified the Aldabra Rail for reintroduction (Appendix 3).

Reintroduction (often referred to the wider literature under the banner of "translocation") is increasingly used as a tool in conservation (Griffith *et al.*1989, Bright & Morris 1994, Cade & Temple 1994, Wolf *et al.*1996, 1998, Maxwell & Jamieson 1997, Pierre 1999, Engelhardt *et al.* 2000, Letty *et al.* 2000, Osterman *et al.* 2001). The IUCN has published a set of guidelines for moving (translocating, reintroducing, etc) animals (Appendix 3). These procedures were closely followed before and during the reintroduction described below.

I follow the IUCN definition of reintroduction, which is defined 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" (Appendix 3). The same source defines translocation, a term widely used with reference to moving populations of wild animals, as the "deliberate and mediated movement of wild individuals or populations from one part of their range to another". These definitions are confusing, as they are not necessarily mutually exclusive. The latter does not explicitly state that movement is within a species *current* range. The former definition describes the situation of the Aldabra Rails, if one accepts that Picard represents a discrete part of their range, from which they became extinct (Chapter 1). The latter definition, although frequently used as an over-arching term for moving animals in wider literature (e.g. Griffith *et al.* 1989, Wolf *et al.* 1996, Letty *et al.* 2000), is not applicable to this study.

Three areas of concern were identified *a priori* as possible problems that could affect the successful reintroduction of Aldabra Rails to Picard. First, the presence of Cats, or continued human predation, both responsible for local extinction on Picard (Chapter 1). Second, major differences in habitat type or leaf-litter and soil invertebrate communities between Picard and Malabar, resulting in local conditions to which Aldabra Rails from Malabar were not adapted. Third, niche expansion by other species on Picard in the absence of Aldabra Rails, resulting in competition. I qualitatively assessed the likelihood of various factors negatively impacting the reintroduction using literature reviews (including unpublished data from monitoring efforts, housed in the Aldabra Library), discussions with long-term staff and associates of Aldabra and personal observations of conditions on Picard.

The literature reviewed (summarised in Stoddart 1979) suggests that Domestic Cats have probably never been independent of humans on Picard, unlike on Grande Terre. Cats closely associate with turtle-nesting beaches on the latter (turtle monitoring data, Aldabra library). In recent times no Cats have been reported from the turtle-nesting beaches or anywhere else on Picard (Chapter 1). I assumed that Picard was free of Cats and thus suitable for Rail reintroductions in this respect (Chapter 1). The staff compliment on Aldabra is currently at a minimum compared with levels when Aldabra was exploited on commercial lease (Stoddart 1979). Rangers, managers and support staff for the research station are now the only residents (typically 12-15 individuals at any given time). I considered the likelihood of and potential for human predation of the reintroduced Rails negligible.

A desktop study of ecological/environmental conditions on Picard and Malabar revealed essentially no differences. Their geographic proximity and positions have ensured that their geology and local climates (which can differ substantially across the 34 km length of Aldabra) are very similar (Stoddart 1983). There are no major differences in vegetation cover, with the exception of the western end of Malabar being more densely vegetated. Gibson & Phillipson (1983) found that Picard had the highest plant species-richness of any island on the atoll. Newberry & Hill (1981) were unable to detect any classifiable differences in the predominant "mixed scrub" vegetation of the whole atoll. Further, Spaull (1979) found no intra-habitat structure to the distribution of terrestrial invertebrates across Aldabra. The impact of human settlement on Picard is confined to a small area around the research station, and the vast proportion of Picard's environment is essentially pristine (Gibson & Phillipson 1983, pers. obs.).

Aldabra Rails are generalist ground-foragers, with a very inquisitive nature that promotes an eclectic diet (Penny & Diamond 1971, Appendix 1). The majority of their foraging time is spent searching through leaf-litter, although the relative importance that larger, more occasional food sources such as reptiles, crabs, eggs, etc. contribute to their diet is unknown (Appendix 2). The Aldabra Rail's niche may overlap to a limited extent with other Aldabran species that prey predominantly on invertebrates, most notably the Madagascar Coucal *Centropus toulou insularis* (predominantly arboreal) and the Sacred Ibis *Threskiorins aethiopica abbotti* (predominantly intertidal) (Frith 1977). However, numbers and behaviour of both species suggested that neither had expanded its niche in the absence of Aldabra Rails on Picard (Benson & Penny 1971, pers. obs.).

Black (or Ship) Rats *Rattus rattus* are common all over Aldabra. There are several accounts of Aldabra Rails interacting with Black Rats (e.g. Frith 1977), all of which ended with Rails successfully defending nests or food against Rats. Aldabra Rails in captivity on Aldabra even killed an adult Black Rat that entered their enclosure (Wanless *in press*). Aldabra Rails have persisted on Malabar, Polymnie and Île aux Cèdres in the presence of high Rat densities. I therefore assumed that the Rats on Picard would have no impact on reintroduced Rails.

Thus, Picard had no Domestic Cats, no significant, human-mediated changes to the environment and no human exploitation of Aldabra Rails. It also had no other apparent biological/ecological obstacles to a successful reintroduction. Hence it was assumed to be as well-suited to Aldabra Rails as it was when they were abundant there (Abbott, 1893). The pre-conditions set out by IUCN (Appendix 3) had been met, and heeding calls for conservation action to be taken (e.g. Hambler *et al* 1993), I undertook a limited reintroduction of Aldabra Rails to Picard in 1999.

METHODS

The reintroduction was designed as a "soft release" (*sensu* Bright and Morris 1994, Snyder *et al.* 1994, Letty *et al.* 2000). In general, a soft release requires that animals are housed in "acclimatisation enclosures" after capture. The enclosures should be in or near good quality habitat. Captivity should continue at least until animals can regain lost condition. It may be desirable to release animals only when they have gained energetic reserves sufficient to see them through a reasonable period after release and before self-sufficiency. At release, the doors to cages are left open for individuals to leave at will. Any individuals that remain in or near the cages are fed, while efforts are made to wean them off supplementary food. In contrast, a hard release requires that animals are simply captured, transported to their new environment and released, without any acclimatisation, supplementary feeding or other measures to mitigate the impact of the move.

To ensure that no mixing of (possibly) distinct genetic stocks occurred, Aldabra Rails were taken only from Malabar. A second reason for this decision was that Malabar is host to an order of magnitude more Rails than Polymnie, and two orders more than Île aux Cèdres (Huxley 1982, Collar 1993, Chapter 4). I considered that moving 20 birds in a trial reintroduction would have no measurable effect on the Malabar population (estimated at 3500 pairs – Chapter 4). However, should a second or supplementary reintroduction be needed, this consideration takes on greater significance (but see Chapter 4). Without *a priori* knowledge of population structure or heterogeneity (Chapter 4), I attempted to ensure a broad representation of the Malabar population's genetic variability in the Picard birds by taking half from the extreme eastern end and half from the extreme western end of the island.

Trapping

Aldabra Rails were located along four existing paths (two at each locale) at the eastern (Middle Camp/Passe Houareau) and western (Gionnet) ends of Malabar ("Coastal" and "Inland" transects at Gionnet and "Inland Coccid" and "Inland Traverse" transects at Middle Camp). To locate birds, taped recordings of the Aldabra Rails' territorial-defence/pair-bonding calls were played on a Sony TCM 40DV cassette recorder (Huxley & Wilkinson 1977).

The traps used to catch rails (Figure 2.1) consisted of a steel frame 70 cm x 30 cm x 30 cm, covered with black, nylon, 10%-shade netting (ALLNET® "Hailguard"). The trap door was slightly longer and narrower than the entrance and was hinged at the top. I found that a hand-held trap-line, consisting of a length of fine-gauge nylon twine tied to the base of the trap-door and threaded through the roof of the trap, was the most reliable release mechanism.

A length of nylon twine (bait-line) was tied to bait, either Rock Crab *Grapsus* sp. or Mangrove Crab *Cardisoma* sp.. The carapace was removed to provide Rails with easy access to soft, edible parts of the crab. The other end of the bait-line was threaded through the rear of the trap, so that the bait could be pulled deep inside the trap.

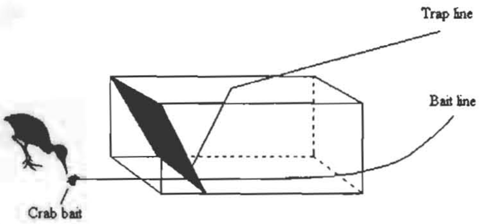

Figure 2.1. Trap used to catch rails on Aldabra. Solid black area represents the hinged, closed trap-door.

When an Aldabra Rail was located, the trap was placed on relatively flat ground and the crab and bait-line tossed towards it; this invariably elicited an immediate and positive response from naïve birds, which would run to investigate the bait. The person trapping stood two to three metres behind the trap and used the bait-line to lure birds into the trap. This was achieved by slowly drawing the bait into the back of the trap while allowing Rails to pull tidbits from the crab. As soon as a bird entered the trap far enough that the door would not strike it when dropped, the trap-line was released. The trap-door would swing closed, capturing the bird. Because the length of the trap-door was greater than the height of the trap, when released it came to rest flush with the sides and at an angle (Figure 2.1) and thus could not be pushed open from the inside

The breeding season on Aldabra is fairly tightly constrained for most landbirds, including the Aldabra Rail (Benson & Penny 1971). Typically, the wet monsoon, which defines the breeding season, begins in late November (Farrow 1971, Stoddard 1971b). Aldabra Rails were captured in October, before the breeding season began. The timing was deliberate, as pair-bonding and its concomitant vocalisations were considerably more obvious in October than earlier in the year. The methods employed to attract Aldabra Rails usually resulted in two birds arriving. If no aggressive interactions were observed it was assumed they were a territory-holding pair and both were trapped.

Handling

Once trapped, birds were immediately weighed using a 500 g Salter spring balance, standard measurements were taken and blood was collected for genetic analyses (Chapter 4). Blood was collected by wiping the underwing with alcohol and removing a few underwing coverts to expose the brachial vein, which was then punctured with a gauge 27 needle. Blood was drawn into a heparinised capillary tube that was emptied into a screw-cap Eppendorf tube sealed with a rubber o-ring and primed with the tissue-buffer Ethylene diametritetraacetic acid (EDTA). Birds were banded with 7.5 mm metal SAFRING bands on the right tarsus and plastic bands engraved with highly visible alpha-numeric codes on the left tarsus (Appendix 4). Two colour schemes were used for adults, with black lettering on yellow reserved for birds to be taken to Picard.

Birds were carried in thin cotton bags from the field to camp. Pairs of birds were kept in plastic crates approximately 75 cm x 40 cm x 45 cm. Birds trapped at Gionnet were transported daily to Picard Island. The 3 m tidal range and the *ca* 30 km transfer distance made it impossible for this to be done for birds captured at Middle Camp (Farrow & Brander, 1971). Middle Camp birds were transported to Picard only when all five pairs had been trapped (three days).

Captivity

Five 30 m^2 aviaries were constructed to house pairs of Aldabra Rails. They were provided with fresh and sea water and a loose pile of palm fronds for shelter. Captive birds were fed morning and evening with a variety of food, including cooked rice, canned tuna, scrambled egg, cooked and raw fish and fresh crab. The most frequently used food, which also seemed to be preferred by all the captive Rails, was fresh crab (*Grapsus* sp. and *Cardisoma* sp.). Uneaten food was removed after 24 hours, and water was replaced every second or third day.

Aldabra Rails could not be weighed every second day, as had been planned, as it was apparent that regular handling would be unduly stressful to them. They were recaptured and weighed at irregular intervals. They were held in captivity until they became habituated to being fed, were eating regularly and *appeared* to be in good health. Weight-changes over time were expressed as percentage deviation from weight at capture (Figure 2.2). A smoothing curve (least-squares distance-weighted regression) was fitted to the data using STATISTICA®, to draw attention to the initial decrease and subsequent increase in weight (Statsoft 2000).

Release

On the day of release, food was brought to the enclosures, but the doors were left open for the birds to leave at will. Any individuals that remained in or around the enclosures after release were fed, but gradually weaned of supplementary food.

RESULTS

Trapping

Naïve Aldabra Rails proved easy to trap. Ten birds were captured at Gionnet on 19 and 20 October and ten at Middle Camp between 4 and 6 November. However, both individuals of a "pair" from Middle Camp died shortly after being transported to Picard. A post-mortem revealed that both birds were male - contrary to evidence in the field (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, I discovered that a female had also been incorrectly sexed (Chapter 4). Thus 18 birds (90%) survived to be released, of which ten were female and eight were male.

Captivity

Captive birds settled in to their enclosures very quickly, although some seemed reluctant to eat at first. It was impossible to quantify how much food was eaten because Hermit Crabs *Coenobita* sp. gained constant access to the enclosures, and Black Rats and Robber Crabs *Birgus latro* occasionally gained access, consuming unknown quantities of the rails' food. I recaptured and weighed birds in the enclosures at night to minimise the likelihood of them associating humans with stressful experiences. The first group of birds was kept captive for 14 days. I found that the second group gained weight sufficiently fast to be released after just six days: this may have been an appropriate period for the first group. The unequal duration of confinement for the two groups resulted in an incomplete record of weight changes (Figure 2.2). Nevertheless, these data indicate a decrease in weight over the first three days after capture (i.e. during transit), and a steady weight increase whilst in enclosures. All but two birds were released weighing more than they did at capture; neither exception was substantially underweight. At release, one exceptional male (YA8) weighed almost 145% of its mass at capture. This cannot be ascribed to its monopolising food resources at the expense of its mate (YA7), as the latter also showed an above-average increase: 16% more than its mass at capture (mean increase at release 12%, n=18).

Release

All the Aldabra Rails left their enclosures within a day of release. However, some pairs did not leave together, which may have contributed to the breaking of some pair bonds (Chapter 3). After the first release, one pair (YA7 & YA8) remained in the vicinity of the enclosures and responded immediately to the distinctive whistle I used to announce the arrival of food. A third individual from the second group (Y13) responded in the same way. I continued to feed all three individuals, gradually weaning them by reducing meal sizes and decreasing the frequency of feeding from twice a day to every third day. Supplementary feeding ended two months after release. By this time YA7 & YA8 had shifted their core territory (Chapter 3) and were probably travelling several hundred metres for the supplementary food. Y13 had also paired with Y17, who did not respond to the food-whistle.

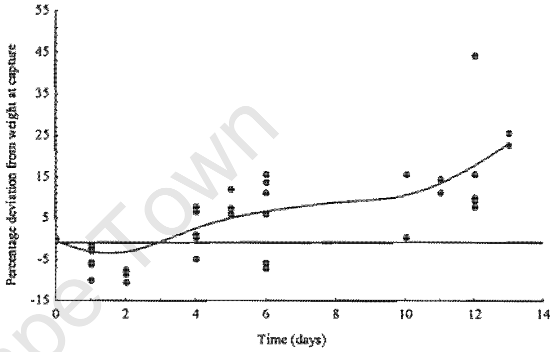

Figure 2.2. Weight changes of captive Aldabra Rails expressed as a percentage difference from weight at capture. All except three birds were weighed twice (n=20).

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 cannot have evolved to recognise as a potential predator. A corollary of this trait is an inability to recognise cats as predators. Although Domestic Cats have never been documented killing Aldabra Rails, their disjunct distributions strongly suggests that Cats are responsible for the Aldabra Rail's extinction on all the islands in the region where the former became established, including local extinctions on Picard and Grande Terre (Benson & Penny 1971, Hambler *et al.* 1993, Chapter 1). For two reasons this trait also made Aldabra 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, then released, followed and retrapped, all without any indications of lasting distress (behavioural, physiological or other). Second, Aldabra Rails were easy to locate repeatedly, facilitating monitoring activities.

The naïveté of Aldabra Rails notwithstanding, they vigorously defend their nests against all intruders (Appendix 1). This is in contrast to many island birds, such as seabirds, which have not evolved, or have lost, nest-defence instincts (Moors & Atkinson 1984). The retention of this strong instinct can be explained by the presence of several native nest-predators on Aldabra, including the aptly named Robber Crab, Madagascar Kestrel *Falco newtoni aldabrensis* and the Madagascar Coucal, all egg-predators (Gaymer 1967, Benson & Penny 1971, Haig 1984, R. Wanless unpubl. data). This must have contributed to the Aldabra Rail's persistence in the presence of high densities of the introduced Black Rat, another generalist egg-predator that is ubiquitous throughout the range of the Rails (Frith 1976, Chapter 1). The Rails are unlikely to have had and retained an evolved defensive response to Rats in the absence of other nest-predators. Thus I believe their survival as a ground-nesting species in the presence of high Rat densities can probably be ascribed to the presence of native nest predators.

Several factors conspired to cause the death of the two birds that died in captivity; these could have been avoided in retrospect. First and foremost, they were incorrectly sexed. Penny & Diamond (1971) report being able to sex birds reliably, based on the colour of the base of the bill, being deep, dull red in males and bright pink in females (Chapter 4). They cite observations of pairs copulating, with red-billed birds mounting pink-billed birds, as evidence that the technique is reliable. However, it is now known that both members of a pair will mount during pseudo-copulatory, pair-bonding behaviour and during coitus (Huxley 1982; Appendix 1). Other individuals were also incorrectly sexed in the field (Chapter 4) and this could easily have resulted in more deaths in captivity. It is now clear that sexing in the field should be undertaken with caution. Second, the incorrectly-sexed pair was captured at the start of a three-day trapping expedition at Middle Camp, which meant they spent longer than any other birds in the close confines of the plastic crates. Third, their behaviour could not readily be observed in the plastic crates. Wire mesh crates for transport would allow observations of birds confined together, which would reduce the risk of two males fighting to death.

Changes in the weight of Aldabra Rails during captivity raises several points of interest. The initial decrease occurred during the period that birds were kept in crates; weight-gain commenced as soon as they were placed in aviaries. Figure 2.1 implies that any longer than three days in such close confines could have serious ramifications for the survival of captive Aldabra Rails. Weight-gain in captivity is difficult to interpret in any depth, as it was impossible to determine how much food individuals ate. Patrikeev (1995, in Taylor & van Perlo 1998) describes adults of another rallid, the Common Coot *Fulica atra*, becoming so fat after migration that 70-80% of the population cannot fly when chased (see Appendix 2). The enormous weight-gain shown by YA8 is evidence that Aldabra Rails are also capable of substantial mass gain. This is probably an important physiological adaptation to the harsh environmental conditions on Aldabra that benefited the reintroduction by promoting weight-gain.

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). Temporary caging allows monitoring of behaviour. This ensures that animals are not manifestly stressed 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. I cannot say whether a hard release would have resulted in a substantial difference 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 are considerable when 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 avian reintroductions would be substantial.

I argue that the acclimatisation period served a second, vital function: it allowed individuals to improve body condition prior to release. This meant that at release, birds were all in as good or better condition than when they were captured. All birds lost condition (i.e. body weight) in the period between capture and confinement in acclimatisation enclosures. Had birds not been allowed to acclimatise and improve condition they could have entered their new environment in a state of mild physiological stress and lowered body condition. It is likely that, under the latter circumstances, their post-release survival and reproductive success would have been compromised (Black *et al.* 1994, Chapter 3). However, the benefit of caging is not necessarily be universal or unequivocal. For example, caging flying birds, even for relatively short periods, may reduce flying stamina or ability, and thereby reduce their chances of survival after release (e.g. White *et al.* 2000).

In conclusion, the protocol designed for the reintroduction of the Aldabra Rail from Malabar to Picard proved, with one exception (incorrect sexing), entirely satisfactory. This is of importance for future supplementary reintroductions to Picard or reintroductions of Aldabra Rails elsewhere. I recommend that Aldabra Rails be kept in close confines for as short a period as possible. Caution is urged when attempting to sex rails in the field. Unless the sex of both members of a putative pair is totally unequivocal, birds should not be kept in captivity together. Monitoring an index of body condition (changes in body weight from weight at capture in this study) is essential in ensuring that individuals have acclimatised to their new surroundings and have overcome the energetic costs of being captured, moved and held in captivity. Measuring weight changes relative to weight at capture is an objective means of assessing when individuals are ready for release.

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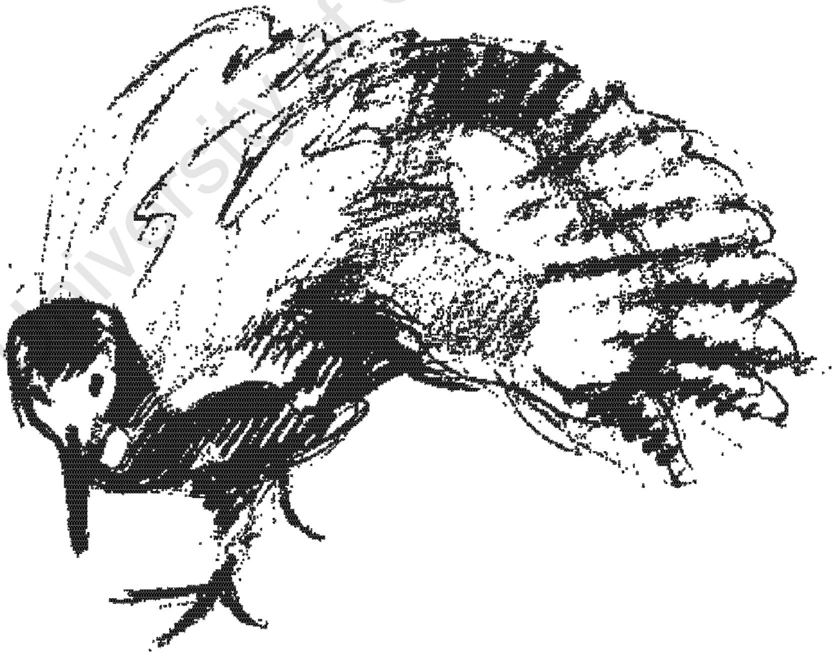


Responses of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to reintroduction

INTRODUCTION

Translocations (including reintroductions) are an increasingly popular technique for conserving endangered species (Griffith *et al.*1989, Bright & Morris 1994, Cade & Temple 1994, Wolf *et al.*1996, 1998, Maxwell & Jamieson 1997, Pierre 1999, Engelhardt *et al.* 2000, Letty *et al.* 2000, Osterman *et al.* 2001). Few studies have critically examined translocation methodology and its role in success or failure; also, outcomes of translocations are often not evaluated or published. Three reviews have shown generally low successes for mammal and bird translocations, with around half ending in failure (Griffith *et al.*1989, Wolf *et al.*1996, Fischer & Lindenmayer 2000). These statistics possibly underestimate the true failure rate, as failures are less likely to be reported. In general, success is positively correlated with the number of translocated individuals (Griffith *et al.*1989, Wolf *et al.*1996, Engelhardt *et al.* 1999, Fischer & Lindenmayer 2000). Other factors found to have significant impacts on success or failure include moving into core historical range (versus extra-range introductions or translocations into marginal habitat) and habitat quality (Wolf *et al.*1996, Miller *et al.* 1999). A lack of follow-up monitoring has been identified as a major shortcoming of translocations, as it precludes a definitive analysis of the success or failure of the work (Short *et al.* 1992, Miller *et al.* 1999).

Given the low success of reintroductions, I generated a hierarchy of scenarios *a priori*, from worst to best, to predict possible responses of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to reintroduction. These scenarios also represent an objective set of criteria by which to measure the outcome of this, and other, vertebrate translocations (Sarrazin & Barbault

1. Low survival in captivity.
2. Low post-release survival.
3. High adult survival but no breeding attempted.
4. Breeding attempted but fledging success zero or very low.
5. Fledging successful but low juvenile survival.
6. Juveniles recruit into the breeding population and the population grows.
7. Higher reproductive success than from source

There are no descriptions of previous Rail reintroductions on Aldabra, although the lone Rail on Picard (Chapter 1) and passing references elsewhere (Snow 1976, Anon undated) is evidence that Aldabra Rails have previously survived being moved and held in captivity. From these inferences, combined with their naïveté, I hypothesised that Aldabra Rails would not be unduly stressed by the reintroduction and that Picard could probably support a viable population. A conservative hypothesis was that the stress ofhe reintroduction, coupled with the Aldabra Rails being in unfamiliar territory, would cause pair bonds to break. Neither the duration or stability of pair bonds, nor the length of the courtship period was known prior to the reintroduction.

The Allee principle predicts that where individuals occur at very low densities, they become less likely or unable to locate mates, lowering reproductive success and threatening the viability of small populations (Sutherland 1996). Because the trial reintroduction involved the release of so few birds (18) into such a substantial area (Picard is *ca* 7 km^2), the Allee effect could not be ruled out *a priori*. However, I hypothesised that failure to breed in the first year after release would not necessarily be indicative of failure of the reintroduction. The medium-term impacts of the reintroduction on both individuals (i.e. lost body condition, stress-induced hormonal imbalances, etc.) and the group (Allee effect, sub-optimal habitat) could be counteracted by competitive release (from conspecifics at higher densities on Malabar), supplementary feeding after release or a supplementary reintroduction involving substantially more individuals.

The aim of the reintroduction of a limited number of individuals was to assess the likelihood of success of a full-scale reintroduction, envisaged at some future date. I took the conservative view that the trial reintroduction would to conform to Scenario 3 or 4 in the first year. I further hypothesised that by supplementing the reintroduced population, within a few years the reintroduction would conform to Scenario 6, and possibly Scenario 7. Here I report on aspects of the life history (survival and reproduction) and behaviour of Aldabra Rails in response to reintroduction. I define the outcome of the reintroduction in relation to the above scenarios.

METHODS

See Chapter 2 for a detailed discussion of the methods of the reintroduction and the performance of the birds up to release. Briefly, 18 (ostensibly paired) adult Aldabra Rails were taken from the large population on Malabar and released on Picard. The reintroduction followed a soft release protocol (*sensu* Bright & Morris 1994, Snyder *et al.* 1994, Letty *et al.* 2000). Further, birds were released into a large area of good quality habitat. At release they were not exhibiting unusual behaviour and were at least as heavy as when they were first captured. I monitored their dispersal, survival, behaviour and reproductive success over the next two breeding seasons (1999/2000 and 2000/2001). I made a comparative study of Aldabra Rails at two sites on Malabar (Gionnet and Middle Camp).

Survival, dispersal and territoriality

All Aldabra Rails on Picard were individually colour-banded and were retrapped (i.e. a positive visual identification) for monitoring purposes whenever possible (see Appendix 4). Each pair of Aldabra Rails gives a daily, pre-dawn duet that is very loud and can be heard over several hundred metres (Huxley & Wilkinson 1977, Wilkinson & Huxley 1979). This behaviour was exploited to locate their roost site. If birds could not be found whilst duetting, they were called up using playback tapes of their territorial song. Territories could not be accurately mapped for two reasons. First, they were established in dense vegetation and broken terrain which prevented birds from being followed for any length of time. Second, territorial behaviour of reintroduced birds was reduced, and aggressive encounters were much less frequent than on Malabar. Territory sizes on Picard were thus estimated based on observed ranges of known pairs, and mapped relative to the position of the two paths and open, unvegetated areas (Figure 3.1). Core territory is loosely defined as the area in which pairs spent most of their time outside the chick-rearing phase, where they built nests and where they roosted.

Foraging and diet

Attempts were made to quantify the foraging behaviour of Aldabra Rails, to see if there were any differences in the amount of time spent foraging, in prey capture rates, in the effort expended in finding food or in prey species diversity between Picard and Malabar birds. Focal birds were watched for one minute, the number of food items taken in that time counted, and, where possible, prey size relative to bill length was estimated. Opportunistic sightings of Aldabra Rails foraging were recorded.

Reproduction

Pairs of Aldabra Rails on Picard were located and followed in both the 1999/2000 and 2000/2001 breeding seasons, to find nests or chicks. Nests were monitored daily until hatching in the second breeding season. For personal reasons I was unable to monitor reproduction during the nesting and early chick-rearing stages in the first breeding season after reintroduction (1999/2000). I left Aldabra on 4 January and returned on 14 February 2000, by which time I could find no pairs still incubating. Family groups were periodically relocated after hatching. When chicks had most of their juvenile plumage they were trapped and banded. Despite being in their natal territories for at least another two weeks, chicks in nearly complete juvenile plumage are capable of foraging independently. At this stage I considered them to have been reared to independence. I define chick production as the number of chicks reared *to independence*. Inter- and intra-island differences in mean chick production were tested for significance using Mann-Whitney U-tests.

Logistical difficulties prevented long field trips to Malabar, resulting in less intensive monitoring of birds in the comparative study. In February 2000 (during the chick-rearing stage), known pairs along the Gionnet "Inland" transect were located. They either had chicks or had started primary moult (evidence of failed breeding (R. Wanless unpubl. data)). Nests found on Malabar in 2000/2001 were checked periodically from discovery until chicks were old enough to be classed as independent. From these data I estimated chick production for Malabar for the both seasons. Differences in chick production between islands were tested for significance using Mann-Whitney U-tests.

RESULTS

Foraging and diet

The diet of Aldabra Rails included flower petals, berries, terrestrial vertebrates and even fairly large terrestrial crabs (Penny & Diamond 1971, Huxley 1982, this study). However, the great majority of their foraging time is spent searching for invertebrates among leaf litter and in soil; numerically, these prey make up most of the diet (Appendix 1). Aldabra Rails on Picard spent most of their foraging time in mixed dense or *Pemphis* scrub. Similarly, Huxley (1982) found the greatest density of Aldabra Rails on Malabar in the densest vegetation. Following birds in dense scrub is exceptionally difficult. When they are foraging, they move almost constantly, stopping only to probe litter or soil before moving on. Consequently, they were frequently obscured by rocks and bushes, and were often facing away from the observer. Birds could not even be accurately observed for one minute on a regular basis, so attempts to quantify food intake rates, prey capture rates or meal sizes were abandoned. Huxley (1982) also abandoned attempts to quantify rail foraging and diet, having encountered identical obstacles. Consequently, no quantitative comparisons in foraging behaviour, prey-capture rates or prey species diversity between Picard and Malabar birds can be made. However, from watching Rails foraging for many hours all over Aldabra, I never gained the impression that Picard was in any way unsuitable or deficient in food for them. Other results (see below) strongly support this observation.

Dispersal and territoriality

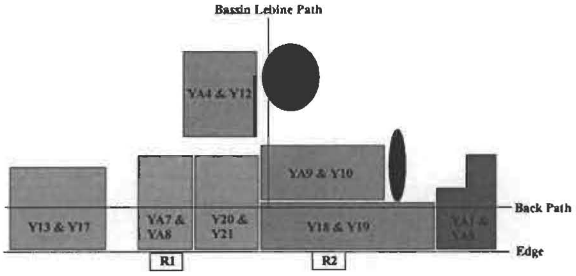
The release site on Picard was on the boundary between dense mixed-scrub (to the south and east) and open mixed-scrub (to the north and west), including the northern end of the research station and mixed *Casuarina*/Coconut groves. Reintroduced birds dispersed over a relatively small area to the south and east of their enclosures. Pairs began to form and establish territories within days or weeks after release. Fortuitously, all eight possible pairs (see Chapter 2) established territories in the vicinity of their release site, in an area of roughly 1 km^2, and within earshot of the two paths in the area. Territory sizes in dense mixed-scrub on Picard were markedly larger than in the same habitat on Malabar (*ca* 3-4 ha versus *ca* 0.7 ha respectively).

In 1999/2000, two pairs (YA7 & YA8 and Y20 & Y21) established new territories when breeding, moving their core territory from moderately dense mixed-scrub interspersed with *Casuarina*, into very dense mixed-scrub and dense *Pemphis* scrub. Both moves caused other pairs to shift their territories in response (Figures 3.1a and 3.1b). Two pairs (YA1 & YA5 and Y18 & Y19) increased their foraging range during the chick-rearing stage. In each case this shift was into unoccupied areas of dense mixed-scrub that contained extensive tracts of *Pemphis* scrub. All pairs except Y13 & Y17 showed a strong preference for *Pemphis* scrub when foraging with chicks. Y13 & Y17 established the largest territory in the least dense habitat of any pair, and it contained no substantial *Pemphis* stands. Nevertheless, the habitat was still classified as dense mixed-scrub.

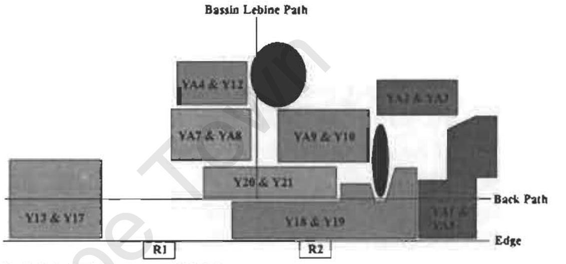
Both Picard and Malabar pairs showed high territory fidelity across years. Only one of eight pairs (YA4 & Y12, Figure 3.1b) is believed to have shifted territory on Picard in 2000/2001. They could not be found in the 2000/2001 season (absent from Figure 3.1c). Similarly, one pair on Malabar could not be located in 2000/2001, out of six pairs where both members were banded. With one exception, new pairs on Picard (one previously unpaired, reintroduced female and seven offspring from the 1999/2000 season) established territories in unoccupied areas adjacent to existing territories in 2000/2001 (Figures 3.1b and 3.1c). The exception was B49 & B58, whose territory overlapped with part of that of an established pair's (YA1 & YA5). I witnessed frequent territorial disputes in a particular area, which seemed to mark the boundary or buffer zone between territories. There was not always a clear winner in these disputes, although YA1 & YA5 were not seen beyond the new boundary. Without exception, new territories were established in very dense mixed-scrub with substantial tracts of *Pemphis*.

Post-release survival

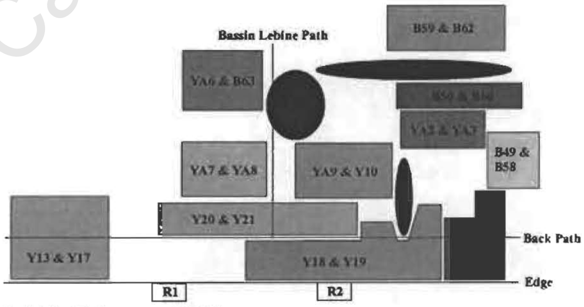
Aldabra Rails were released before the start of the breeding season in 1999, weighing the same or more than they did at capture (Chapter 2). There was a 100% post-release survival at the end of the 1999/2000 season and at least 95% survival in December 2000, with no confirmed mortalities.



3.1(a). November 1999



3.1(b). February 2000



3.1(c). February 2001

Figure 3.1. Territories of Aldabra Rails on Picard in (a) November 1999, (b) February 2000 and (c) February 2001. Territories are not drawn to scale and represent estimates of relative position, relative size and approximate shape. The solid black areas are open, unvegetated areas that Aldabra Rails never utilise. R1 and R2 are the approximate positions of the enclosures from which birds were released. The edge is the boundary between natural vegetation and the lawns or plantations around the research station.

Mate fidelity

An erroneous sexing skewed the sex ratio of the reintroduced birds 10:8 in favour of females (Chapter 2). This may have contributed to the number of "divorces" that occurred after release. Equally, although the other males and females were correctly sexed, they may not have been pair-bonded prior to capture. Of the eight reintroduced "pairs", four remained paired and four divorced and formed pairs with new partners. Birds were released in two stages and were handled and housed slightly differently (Chapter 2), but this did not affect the divorce rate: two pairs from each group remained paired and two divorced. Within nine days of release, a new pairing (YA1 with YA5) was discovered. Other pairs were discovered before then but were birds, originally caught together, that had remained together. Thus the courtship period remains unknown, but can be less than nine days.

None of the three potential divorces in 2000/2001 could be confirmed. On Picard, seven of the eight pairs from 1999/2000 were confirmed to have remained intact, as were four of six banded pairs on Malabar. Two of the three presumed divorces in 2000/2001 are just as likely to have moved from the area, as opposed to divorced. One member of the third pair was not retrapped in 2000/2001, the other member had paired with a banded floater. I thus have no evidence of any natural divorce. Even if these uncertain pairs are treated as divorces, Aldabra Rails showed a minimum of 80 % annual mate fidelity (n = 14 pairs), and possibly pair for life. This result contrasts with the relatively high rate of divorce around the time of release. Aldabra Rails in general seem to show relatively high mate fidelity, and this trait was not disrupted after release (Appendix 1).

Reproductive behaviour

Aldabra Rails undergo a post-breeding moult. Floaters and unsuccessful breeders begin primary moult early in the breeding season, whereas moult commences after young have left the natal territory in the case of successful breeders (data not presented). No monitored pairs deviated from this pattern in 1999/2000, including the seven monitored pairs on Picard. An eighth pair (YA2 & YA3) was only found on Picard at the end of the season. They had just started primary moult, and I thus assumed that they had bred successfully.

Eight of the 18 reintroduced birds were male (ergo eight pairs). This sex-ratio 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 (Tables 3.1 & 3.2), 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 reared. At least two pairs attempted third clutches, though both failed (G. Esparon, *in litt.*). No Malabar pairs are known to have attempted multiple broods in this study. In a three-year study, Huxley (1982) reported two pairs raising second broods (sample sizes not given). Total chick production on Picard in 2000/2001 was at least 20. Given that at least two pairs were not monitored (Table 3.2), I consider the estimate of 33 chicks produced in the two seasons on Picard to be conservative. Assuming that the six birds not seen in the second season were alive but not within detectable range, the minimum number of Aldabra 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 (Chapter 4).

Mean chick production on Malabar was lower in 1999/2000 than in 2000/2001 (0.3 vs 0.89 chicks/pair, Table 3.2), however small sample sizes, pseudo-replication and non-independence of samples make it impossible to assess the significance of this difference. By contrast, the reintroduced birds produced an estimated 1.8-2.0 chicks per pair in both seasons. 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).

Juvenile survival, recruitment and chick production

Thirteen juvenile birds from 1999/2000 were banded on Picard, of which nine were retrapped in 2000/2001 (Appendix 4). Survival from independence to 12 months old was thus at least 70%. Seven one-year-old birds formed pairs and attempted to breed in 2000/2001; the remainder (six individuals) were all females, which could not have paired. It is likely that the four juveniles not retrapped were alive but had moved beyond the detectable range covered by the existing path network. Unpaired birds are known to range very widely (Appendix 1) and they were most probably wandering around Picard in search of (non-existent) mates, making the likelihood of retrapping them very low.

Two pairings of one-year-olds failed (Table 3.1). B50 & B60s attempt failed at the egg stage. The nest of B49 & B58 was never found, but they hatched two chicks. Their breeding ended in failure when both chicks went missing while still quite small. A third pairing of one-year-olds, B59 & B62, successfully raised three chicks in their first breeding attempt. For all clutches where size was known, this was the only one to have experienced no mortality between laying and rearing to independence. Their second clutch, however, failed at the egg stage. The seventh one-year-old to breed, B63, had paired with a previously unpaired female (YA6). They reared a single chick in their first brood and from their behaviour I suspect that they laid a second clutch, although this was never found.

Table 3.1. Two seasons of reproductive data of Aldabra Rails on Picard. Chicks are listed on the same row as their parents; chicks not alongside pairs are of unknown parentage. Clutch sizes in parentheses indicate minimum estimates based on known numbers of chicks hatched (but not necessarily reared to independence). Dashes indicate missing data.

	1999/2000 season			**2000/2001 season**				
	Known pairs	**First clutch**	**Chicks fledged**	**Known pairs**	**First clutch**	**Chicks fledged**	**Second Clutch**	**Chicks fledged**
	YAI & YA5	(2)	B50 & B51	YAI & YA5	4	B64 & B65	4	B79, B80 & B81
	YA2 & YA3	-	-	YA2 & YA3	(1)	1[b]	4	1[d]
	YA4 & Y12	(3)	-	YA4 & Y12	-	-		
	YA7 & YA8	(1)	B53	YA7 & YA8	4	B77	4	0
	YA9 & Y10	(2)	1[a]	YA9 & Y10	3	B67 & B70	2	1[d]
	Y13 & Y17	(1)	B57	Y13 & Y17	3	B74 & B75		
	Y18 & Y19	3	B55 & B56	Y18 & Y19	4	1[c]	2	1[d]
	Y20 & Y21	(1)	B52	Y20 & Y21	4	B76		
			B49	YA6/B63	(1)	1[b]		
			B58	B50/B60	2	0		
			B59	B49/B58	(2)	0		
			B60	B59/B62	3	B71, B72 & B73	2	0
			B62			B78		
			B63					
Total	8 pairs	13 eggs	13 chicks	12 pairs	31 eggs	14 chicks	18 eggs	6 chicks

[a] Chick left natal territory before capture, and is probably one of B49 – B63
[b] Chicks left natal territory before capture; either could be B78
[c] Not banded as its leg was broken (unknown cause) before capture
[d] Chicks were too young to band, but probably reached independence (Appendix 1)

Table 3.2. The number of Aldabra Rails monitored on Picard and Malabar islands and their chick production in the first two breeding seasons after reintroduction to Picard.

	1999/2000 season			**2000/2001 season**		
Island	**Monitored pairs**	**Chicks produced**	**Mean chick production/pair**	**Monitored pairs**	**Chicks produced**	**Mean chick production/pair**
Picard	7	13	1.86	11	20	1.82
Malabar	10	3	0.3	9	8	0.89

DISCUSSION

Ideal despotic distribution (IDD) predicts that birds will occupy the best quality territories first (Fretwell & Lucas 1970, Brooke 1979, Møller 1982, Sutherland 1996). Spaull (1979) found that dense mixed-scrub vegetation had the highest density of litter and therefore the highest density of invertebrate fauna. This habitat should be the best quality foraging habitat. The Rails' post-release dispersal conformed broadly to theoretical predictions, as all pairs established territories in dense mixed-scrub. However, YA7 & YA8, Y20 & Y21 and Y13 & Y17 showed a relatively trivial deviation from the IDD predictions at first, by establishing territories in less-dense habitat (although it was classified as dense mixed-scrub). The two former pairs then moved and established new territories in very dense habitat. Y13 & Y17 apparently compensated for a lack of very dense scrub in their territory by exploiting a very large area. The pattern of dispersal (restricted to the vicinity of the release site) strongly suggests that pairs did not prospect widely before choosing territories, but chose the first good quality habitat that was not already occupied. The Rails were released into a novel environment and thus had no prior experience of the quality of available territories. Furthermore, being flightless, they were handicapped in assessing territory quality over a large area. I interpret their territorial selection as being "good enough" rather than "the best possible". The pattern of establishment for the four new pairs in 2000/2001 is more in line with IDD predictions. Given that unpaired birds roam widely before establishing territories (Appendix 1), one-year-old birds are expected to have a good knowledge of where the best available habitat is. I predict that new pairs will continue to establish in dense mixed-scrub with abundant *Pemphis*. I further predict that they are unlikely to displace resident pairs through aggressive interactions until the Picard population approaches carrying capacity (Chapter 4).

Territorial expansions on Picard during chick-rearing in 1999/2000 were all into areas of very dense, predominantly *Pemphis* scrub. The apparent preference for dense stands of *Pemphis* scrub during the chick rearing phase is unexpected in the light of Spaull's (1979) finding, that *Pemphis* scrub has a slightly lower invertebrate density than mixed dense scrub. This finding suggests that dense mixed-scrub and dense *Pemphis* scrub have different, possibly complimentary, values as foraging grounds. Alternatively, because *Pemphis* scrub is invariably on heavily eroded, fretted and pitted champignon substrata, the physical nature of the substratum concentrates litter (and therefore food) into discrete pits, that can be systematically searched. Dense *Pemphis* scrub was heavily utilised by most pairs during chick rearing. Thus it may be easier for parents in *Pemphis* scrub to a) find food for chicks and b) teach chicks how to forage. A case in point is Y18 & Y19, who in both breeding seasons frequently skirted the borders of two other territories with their chicks (a demonstrably risky behaviour) and crossed open terrain (which they are generally very reluctant to do) to access an unoccupied tract of *Pemphis* scrub (Figures 3.1a & 3.1b). This pair's original/core territory was in good quality mixed dense scrub, but had no dense *Pemphis* scrub.

Aldabra Rails rarely reacted to taped vocalisations during the breeding season, although they will attack visible intruders (Chapter 4, Appendix 1). The former behaviour is assumed to be adaptive: by remaining inconspicuous, nests and chicks are hidden and protected from aggressive intruders. On several occasions, trespassing adults were seen to attack chicks *in the chick's natal territory*. The primary reason for infanticide in Aldabra Rails is almost certainly to reduce potential competition; adult Aldabra Rails will achieve both direct and indirect fitness benefits from infanticide. Firstly, Kluiver (1966) showed that when a population is regulated by density-dependent factors, as is the case on Malabar (Chapter 4), adult survival is affected by juvenile survival. Higher juvenile survival means greater competition for limited resources and an increased likelihood of adult starvation. Secondly, juvenile survival is generally much lower than adult survival. By killing other pairs' offspring, Aldabra Rails are indirectly investing in the survival of both themselves and their offspring.

I now describe more fully the seven predictive scenarios, presented in the Introduction, as they relate to this reintroduction. As they also represent objective criteria to assess the outcome of a reintroduction, I also define the outcome of this reintroduction.

Scenario 1: Aldabra Rails may not respond well to being trapped, handled or confined. Some may die before release, resulting in low survival in captivity. This could arise from the stresses inherent in being captured, or could arise from being kept in close confines for protracted periods. By implication, survivors would be released in poor condition and their post-release survival is also expected to be low (Letty *et al.* 2000). The dangers inherent to small founder populations would be magnified, and the reintroduction is expected to fail (Frankham 1995).

Scenario 2: The stress of being released into an unfamiliar environment, possibly combined with high physiological costs of being in captivity, could result in low post-release survival, poor reproductive success and a failed reintroduction (Letty *et al.* 2000).

Scenario 3: Aldabra Rails may survive the reintroduction and adjust to the new environment. However, despite high adult survival, birds may have lost body condition before release or experience poor environmental conditions in the new habitat. The resultant proximal energetic constraints would prevent birds from attempting to breed or result in greatly reduced reproductive effort (Clout & Craig 1994, Armstrong & Ewen 2001). Alternatively, hormonal imbalances arising from the reintroduction may temporarily change, reduce or eliminate reproductive behaviour. A further potentially complicating factor could be the Allee effect: even a relatively large number of individuals being released on Picard may not be sufficient to overcome the Allee effect. Intensive monitoring in the medium-term is required to assess the causes of low survival or low reproductive success, and determine the feasibility of a full-scale reintroduction.

Scenario 4: The same factors affecting Scenario 3 might operate at reduced intensity, only partially or on a proportion of individuals. This would result in very low or zero fledging success. Should territories be established in sub-optimal habitat, parents may spend too much time foraging for themselves, compromising time available for incubating eggs, or brooding or provisioning chicks. This could affect hatching success, fledging success and chick quality through starvation or malnutrition, as well as increasing the probability of eggs or chick being depredated. Reintroducing more Rails, possibly with supplementary feeding, might assist in the establishment of a viable population by giving more individuals more time to adapt to local conditions.

Scenario 5: Reintroduced birds breed successfully. The resultant high fledging success would not necessarily translate into good juvenile survival if juveniles failed to survive in marginal or sub-optimal habitats. Alternatively, low parental investment might produce poor quality offspring. These offspring are predicted to have reduced foraging skills, have lower body condition and energetic reserves, have poorer inter- and intraspecific competitive abilities for shared resources and more be more prone to disease. Medium-term monitoring of juvenile survival and recruitment would be required to assess the viability of a population on Picard.

Scenario 6: Any negative effects of reintroduction on individuals or the group would be temporary. Pairs would breed successfully, juvenile survival would be high and juveniles would recruit into the breeding population. The trial reintroduction would be a success, but low genetic heterogeneity or allelic diversity (relative to the source population) may require intervention on the form of a supplementary reintroduction.

Scenario 7: The reintroduced birds would establish territories in ideal habitat, and there would be no confounding factors. The growing population would experience a higher reproductive success compared with the stable parent population, as the former experiences competitive release whereas the latter is regulated by density dependant factors. The trial reintroduction would be successful and no further action, besides low-intensity monitoring, would be required.

The reintroduction conformed partially to Scenario 1 in that two birds died in captivity (through incorrect sexing, Chapter 2). However, the relatively rapid pair-formation that occurred either during captivity or shortly after release meant that the effect of incorrect pair identification was minimal, and had no impact on the outcome of the reintroduction. Aldabra Rails are extremely inquisitive and the methods used to attract and capture them at the start of the reintroduction (Chapter 2) may have attracted floaters or birds from neighbouring territories. Aggressive responses by territorial birds towards intruders may be superseded by their interest in humans, the taped vocalisations or in other methods used to attract them. Thus field observations used to judge pairing, namely the absence of aggression between two birds in close proximity that appeared to have dimorphic characters associated with the two sexes, may have been unreliable. I cannot say with any confidence that any were actually paired before capture.

Contrary to the predictions of Scenario 2, the energetic costs of being held in captivity were outweighed by the benefits of being fed *ad libitum*, and birds were released in good body condition. Any costs arising from being in a novel environment were obviated by the acclimatisation period and the benefits of competitive release. Therefore the reintroduction did not conform to Scenario 2.

The Allee effect, or the potential inability of the rails to find one another after release, was a source of concern before release. Had reintroduced birds failed to form pairs, the reintroduction would have conformed to Scenario 3. However, their loud, penetrating vocalisations, whether as duets or single songs, served to keep birds in auditory contact. Their flightlessness also limited their dispersal capabilities, and the observed dispersal pattern after release meant that pairs remained within vocal contact of at least one other pair. The fact that they were released directly into good quality habitat vitiated a need for them to range widely in search of good foraging areas (Griffith *et al.* 1989, Black *et al.* 1997, Wolf *et al.* 1996, Miller *et al.* 1999, Ostermann *et al.* 2001). These results both facilitated monitoring and ensured that the reintroduction did not conform to Scenario 3.

Environmental conditions at release (especially habitat quality) have been shown to be a significant factor in determining the outcome of a reintroduction (Griffith *et al.* 1989, Black *et al.* 1997, Wolf *et al.* 1996, Miller *et al.* 1999, Ostermann *et al.* 2001). Picard once supported a viable population of Aldabra Rails (Abbott 1893). From a habitat perspective it is virtually pristine, and thus is still well suited to Rails (Chapter 2). On a proximal scale, the habitat around the two release sites on Picard was ideal for Aldabra Rails, namely dense mixed-scrub. Aldabra Rails showed an unexpected predilection for dense *Pemphis* scrub, and there were also extensive tracts of this near the release sites. Thus the reintroduction was unlikely to fail due to a lack of good quality habitat. This ruled out the reintroduction conforming to Scenarios 4 or 5.

Having excluded scenarios 1-5, the outcome of the reintroduction must therefore conform to either Scenario 6 or 7. I now present several lines of evidence, which together argue that the reintroduction to Picard was the most successful outcome possible.

There were no sources of extrinsic mortality of Aldabra Rails peculiar to Picard (Chapter 1). This, combined with low densities that make costly and potentially lethal intra-specific competitive interactions less likely (see Appendix 1), probably elevated adult survival above that expected in a population regulated by density-dependent factors such as Malabar (e.g. Komdeur *et al.* 1995, Chapter 4).

Reproduction in Aldabra Rails on Malabar seems constrained by density-dependent factors, as shown by the low mean chick production compared with Picard pairs. Mean chick production on Picard was significantly higher than on Malabar in both seasons. The low densities of Aldabra Rails *per se* and their large territories made the likelihood of infanticide on Picard small. I propose that the quality of habitat on Picard explains much of the dispersal and the reproductive behaviour of the Rails. The large territories in good quality habitat on Picard enabled pairs to achieve breeding condition earlier (data not presented), and probably assisted in maintaining relatively good body condition throughout the breeding season. This would have allowed them to increase reproductive effort by raising second broods, and even attempting (previously unrecorded) third clutches. The net result was significantly higher mean chick production than on Malabar.

I have assumed that the high chick production on Picard equates to the production of good quality offspring (as manifest in the high juvenile survival and recruitment). I have argued above that one should not necessarily interpret failure to retrap unpaired birds as those birds having died. For these reasons, and given that the Picard population is increasing, juvenile survival on Picard is expected to be equivalent to adult survival, i.e. very high.

The likelihood of one-year-old birds on Malabar successfully competing with older floaters for vacant territories is probably very low. However, during a translocation of the Seychelles Warbler *Acrocephalus sechellensis*, Komdeur *et al.* (1995) found that when released from the constraints of habitat saturation, one-year-old birds paired and bred successfully. I too found this to be the case on Picard. Seven of the 13 one-year-old Aldabra Rails on Picard had paired and bred in 2000/2001 season. The age at first breeding for this species was previously unknown. The five other one-year-old birds on Picard could not pair, as they were all females (Chapter 4).

The changes I observed in life-history traits on Picard (high adult survival, higher mean chick production, increased reproductive effort, high juvenile survival and the successful recruitment of one-year-old birds into the breeding population) is not surprising. Komdeur *et al.* (1995) observed very similar changes in a comparable transfer experiment of the Seychelles Warbler. These factors combine to make the reintroduction conform to Scenario 7. As this scenario describes the best possible outcome, I conclude that the reintroduction was highly successful.

The speed with which reintroduced Rails adjusted to Picard and the success with which they bred obviates any demographic need for supplementary reintroductions (see also Armstrong & Ewen 2001). Failure to remove or mitigate the original cause(s) of extinction or decline is likely to result in a failed translocation (e.g. Priddel & Wheeler 1994). I concur with the findings of others, that after the cause of extirpation has been removed, habitat quality is probably the most crucial factor determining the outcome of translocations (e.g. Griffith *et al.* 1989, Fischer & Lindenmayer 2000). Although 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 & Ewen 2001), results of this study show that carefully managed programmes involving small numbers of birds can be highly successful (see Chapter 4 for a discussion on the genetic implications). The results described in this chapter and those of Chapter 2 together show that the soft release protocol I employed made a significant contribution to the success of this project. Although hard releases may be appropriate at times (e.g. Komdeur 1994, Lloyd & Powlesland 1994), I recommend a soft release protocol as the conservative and precautionary method of choice for avian translocations (including reintroductions).

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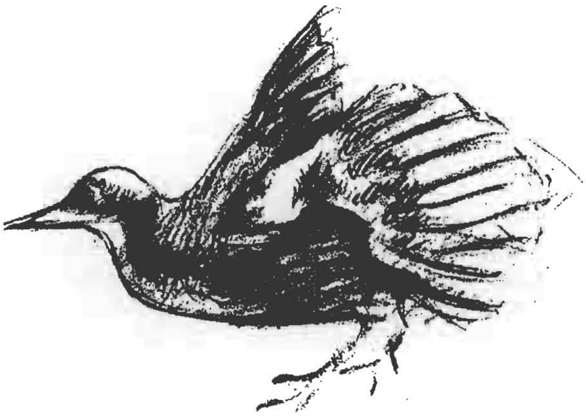


Aspects of the demography and population biology of the Aldabra Rail *Dryolimnas cuvieri aldabranus*

INTRODUCTION

The historical distribution of the genus *Dryolimnas* and the range contraction of the Aldabra Rail *Dryolimnas cuvieri aldabranus* on Aldabra are reviewed in the introductory chapter. Here I restrict discussion to the extant and reintroduced populations on Aldabra Atoll. To summarise; before November 1999 the Rails were restricted to the islands of Malabar and Polymnie, and the small lagoon islet of Île aux Cèdres. In 1999 Aldabra Rail were reintroduced to Picard.

Two published methods have been used to estimate the number of breeding/territory-holding Rails on Aldabra. The first study was conducted in the mid 1970s. Arising from that was an unpublished typescript in which a method for censusing Aldabra Rails was described and a population estimate produced (Huxley 1982). Collar (1993) published the population estimate. I located the typescript and produced a population estimate for 1999, based on Huxley's methods. A second method was used to verify the findings of Huxley's (*op. cit.*) methodology and to compare with historical records (Hambler *et al.* 1993). Hereafter they are referred to as the Huxley and Hambler methods respectively. The latter method is a means of rapid population assessment, rather than estimating actual numbers (Hambler *et al.* 1993).

Neither the Huxley nor Hambler method is designed to count non-breeding adults (hereafter termed "floaters"), and there has been no previous attempt to census this portion of the population, or understand their role in population dynamics. Also, several other aspects of the Aldabra Rails' demography, such as adult survival rates, longevity and site fidelity had not been investigated before this study (and remain poorly understood). The two seasons I spent studying the biology and ecology of the Rails are insufficient to make reliable estimates of some of these parameters. I attempt to compensate partially for lacking or inadequate data by modelling the Rail population on Malabar. The two objectives in modelling the Malabar population were firstly to estimate a likely annual adult mortality (or alternatively: annual adult survival estimate) for territory-holding birds and for floaters. Secondly, given a reasonably robust and biologically meaningful model, I sought to determine the effects of removing adult birds from Malabar. This was simulated as an annual harvest of birds by cats (the most likely predator to colonise Malabar) but the results apply equally to intentional harvesting of birds for other purposes, e.g. a full-scale reintroduction to other islands of the Aldabra Group. A subsidiary objective of the model was to use the parameters of the Malabar model to estimate the period of expansion that the Picard population is likely to undergo.

Exactly when rails colonised Aldabra is not known, but it was almost certainly before the atoll's separation into discrete islands. Taylor *et al.* (1979) estimate that around the Wisconsin glacial maxim, *ca* 17 ka B.P., Aldabra stood about 120 m a.s.l.. This represents a considerably larger target for avian colonisers than present-day Aldabra (8 m a.s.l.), especially for a weakly volant species. I speculate that the Rail colonised Aldabra from Madagascar (probably via Assumption Island) around this time (Benson 1967, Benson & Penny 1971). This is supported by the discovery of a sub-fossil rail bone on Picard, from at least 15 ka B.P. (Harrison & Walker 1978, Taylor *et al.* 1979). The land rim of Aldabra was breached around 5 ka B.P., creating the lagoon and separate islands present today (Taylor *et al.* 1979). The propensity for rallids to become flightless on predator-free islands is well documented (Taylor & van Perlo 1998). If the Aldabra Rail colonised Aldabra *ca* 17 ka B.P., it probably lost the ability to fly before the breaching of the land rim 13 ka later. Given these assumptions, the extant Rail populations on Aldabra have been isolated from one another for around 5 ka, sufficient time for them to have experienced genetic drift and to thus show some level of population structure.

The reintroduction to Picard was originally intended as a trial reintroduction, hence the small number of birds (18) involved (Chapter 2). Most reviews or studies of reintroduction methods have found that the chance of successful translocation is positively correlated with the number of individuals moved (e.g. Griffith *et al.* 1989, Wolf *et al.* 1996,1998, Armstrong & Ewen, 2001). There are two management implications arising from having a small founder population. First, if the Malabar population has a high degree of variability, 18 founder birds on Picard would probably not represent that variability adequately, and the Picard population might suffer problems such as inbreeding depression, founder effects or low resistance to disease (Miller & Hedrick 1993, Frankham 1995). Second, if there was no significant difference between the three populations, then it might be desirable to increase the Picard populations heterogeneity by reintroducing birds from Polymnie or Île aux Cèdres.

Despite many publications emanating from research at Aldabra (Stoddart 1997), surprisingly few aspects of the biology, ecology or demographics of the endemic birds of Aldabra have been studied, including the Aldabra Rail. In this chapter, I describe attempts to address three areas of the population biology of the Aldabra Rail. First, I use census data to make a current population estimate and to assess historical changes in the population. Second, I use population models to gain insight into some of the parameters regulating the dynamics of the relatively stable, and apparently saturated, Malabar population. I then modify the Malabar model to predict the growth of the reintroduced Picard population. Third, I determine the sex of Aldabra Rails using a genetic sexing technique, and review the accuracy of a published field sexing method (Penny & Diamond 1971). Fourth, in an attempt to quantify the degree of population structure between the four populations, I analyse genetic variation at microsatellite loci. Finally, I investigate the genetic integrity of the reintroduced (Picard) population relative to the parent population on Malabar.

METHODS

Population estimates

Huxley (1982) calculated the density of Aldabra Rails in open scrub habitat on Malabar by banding every bird in a defined area of open mixed-scrub and mapping their territories. He also made linear transects through the same area and through dense scrub, and from these calibrated a linear transect census method and extrapolated the number of Rails in each habitat. I used the same census technique along the same transects to assess any changes in density between 1976 and 2000. I also banded Rails along the Gionnet Inland transect in the 1999/2000 breeding season. I monitored pairs of Rails and determined how many territories this transect intersected. I also used banding and retrap rates of non-territorial birds as a very crude measure of the density of floaters per territory.

The total area of each habitat type on each island (including Picard) was calculated from a 1:25 000 habitat map of Aldabra (Republic of Seychelles 1978). Habitats were traced from the map and superimposed on grid paper. The area was then calculated by counting the number of 1 cm^2 blocks that were more than 50% covered.

Census methods

HUXLEY METHOD

Recordings of Rail song were played at full volume using a Sanyo M1100C cassette player. Songs were played continuously for up to 5 minutes at 50 m interval markers along fixed transects. Birds seen or heard were recorded, but only visual records were used to estimate territory occupancy. Surveys started around 8 am in late May.

HAMBLER METHOD

This gave a rough measure of Rail density. The number of territories along a transect was calculated based on both visual and vocal responses. Each transect was divided into 50 m sections. Each section was scored as '–' if there was no response for that section and '+' if there was a positive response, i.e. territorial birds came to investigate the "intruder" or gave the territorial defence song (Appendix 1). These results were compared with published results, to assess broad population trends. Huxley's (1982) method rather than that described by Hambler *et al.* (1993) was used to evoke responses from birds along transects.

Population modelling

Malabar model

I created a simple, deterministic model of the Malabar Rail population using Stella® software (Figure 4.1). The Rail population was modelled as two "stocks": Breeders (representing territorial adults capable of reproducing) and Floaters (representing non-territorial adults that do not breed). The population was simulated over 100 years at one year intervals. All outputs were rounded to the nearest integer. Box 4.1 describes the settings and parameters of the model.

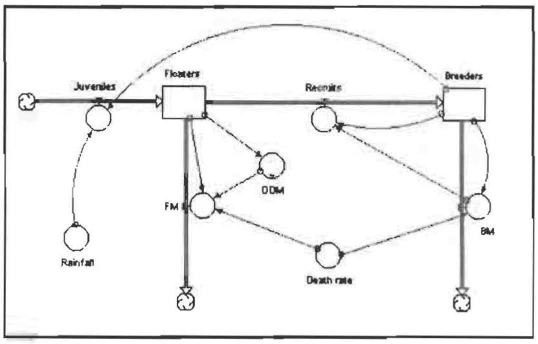


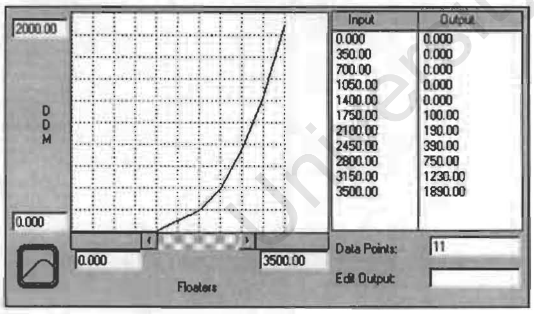
Figure 4.1. Stella® model of the Aldabra Rail population of Malabar Island. BM = Breeder Mortality, FM = Floater Mortality, DDM = Density Dependent Mortality. Boxes represent stocks and tubes with open arrows represent flow paths and directionality of flow of individuals between stocks. Clouds represent gains or losses of stock to the system. Free-floating circles represent variables, with solid arrows denoting the inputs to and outputs of variables. Circles attached to flows are flow regulators.

The equations describing the model are:

Breeders:
Breeders(t) = Breeders(t - dt) + (R - BM)*dt
where
R = 7000 - (Breeders - BM)
BM = Breeders*DR

Floaters:
Floaters(t) = Floaters(t - dt) + (J - R - FM)*dt
where
J = (Breeders/2)*Rainfall
Recruits = 7000 - (Breeders - BM)
FM = (Floaters*DR) + DDM

BOX 4.1. Converters, regulators and initial settings
Rainfall = Random(0.3,0.8,1)
DR = Random(0.15,0.05,1) + 0.1
R = Recruits, the number of floaters that recruit into the breeding population
J = Juveniles, the number of chicks reared to independence in a given year
DR = Death Rate, the percentage of each stock that dies in a given year
BM = Breeder Mortality, the number of breeders that die in a given year
FM = Floater Mortality, the number of floaters that die in a given year
DDM = Density Dependent Mortality, which is described by a graphical relationship between the number of Floaters and the number of Floaters that die (Figure 4.2).
Initial Breeders = 7000
Initial Floaters = 1700



Input	Output
0.000	0.000
350.00	0.000
700.00	0.000
1050.00	0.000
1400.00	0.000
1750.00	100.00
2100.00	190.00
2450.00	390.00
2800.00	750.00
3150.00	1230.00
3500.00	1890.00

Data Points: 11

Figure 4.2. Graphical relationship between the number of Floaters (x-axis and "Input") and DDM (y-axis and "Output") used in a Stella ® model of the Aldabra Rail population on Malabar. As Floaters increases above 1700 individuals, density dependent mortality increases

There are several assumptions underlying the model. First, rough population estimates spanning several decades show no measurable changes in the number of breeding birds (Hambler *et al.* 1993, this study). Therefore I used an estimate of 7000 territorial birds and did not allow for any environmentally induced fluctuation in this number. The number of territories is likely to change between "good" and "bad" years, as low rainfall may make marginal habitat unsuitable for breeding and force increases in territory size. However, given the crudeness of the population estimates and the population's long-term stability, this is unlikely to have any significant effect on the model, and was ignored for the sake of simplicity. I assumed that any territorial vacancy was immediately filled as Floaters recruit to become Breeders. However, the flow is unidirectional, i.e. Breeders cannot become Floaters. Therefore, the number of Breeders in the model is buffered by Floaters, and remains constant, unless there are no Floaters to replenish (recruit into) the stock of Breeders. The initial number of Floaters was set at a conservative 1700, based on a very rough estimate at the end of a period of low rainfall. I used rainfall as a surrogate for all environmental variability. This is linked directly to the reproductive rate, i.e. the number of offspring produced (J) annually is contingent upon the Rainfall output and the number of Breeders. Rainfall was linked indirectly to DR, which determines the annual mortality of Breeders and Floaters (BM & FM respectively).

The converter "Rainfall" was a stochastic variable. It produced a repeatable string of random numbers evenly distributed between 0.3 and 0.8. These values represent a conservative estimate of chick production rates for a low rainfall year (0.3 chicks per pair) and a high rainfall year (0.8 chicks per pair) (Chapter 3). The same string of random numbers was repeated with each simulation, making sensitivity analyses more comparable. The number of breeding pairs (Breeders/2) multiplied by Rainfall gave annual juvenile production (J). The converter DR consisted of two components: extrinsic (or environmentally determined) and intrinsic mortality. Extrinsic mortality used the same *relative* string of random numbers as was generated in Rainfall, but in an inverse relationship with Rainfall and across a different range (between 0.15 and 0.05). Therefore a low Rainfall output corresponded to an equivalently high DR output, e.g. in a dry year juvenile production (J) was low and mortality (DR) was equivalently high. The intrinsic component of mortality (senescence, disease, etc.), for both BM and FM was set at 0.1, so the average DR output (both extrinsic and intrinsic mortality) was 0.2 (± 0.5, SD 0.03), in other words a 20% annual mortality. However, FM was also influenced by DDM, which simulated the effect of density dependent mortality: the number of individuals that die was positively linked to the number of Floaters, with DDM increasing FM when Floaters ≥ 1700 (Figure 4.2).

Sensitivity analyses

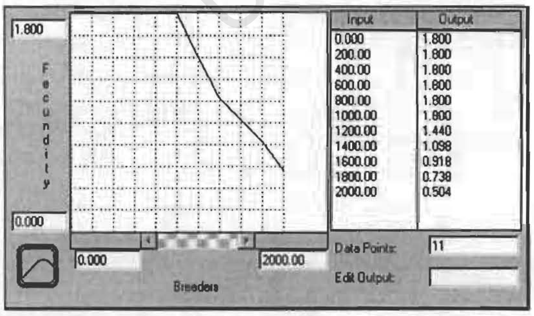
The robustness of the model to changes in Rainfall was tested using three different rainfall regimes (very low, low and high rainfall). I did this by skewing the distribution of the randomly generated numbers. This was repeated with a range of reduced BM figures.

To test the model's sensitivity to DR, I de-coupled DR and Rainfall and ran five simulations with DR set at fixed levels between 0.2 and 0.3. Rainfall still determined J.

I linked a converter to FM and BM to model the impact of an alien predator, such as cats. I assumed that each cat would kill two Rails per week, taking Floaters and Breeders in proportion to their relative abundance. The number of cats was held constant in each simulation, and simulations were run with the number of cats ranging from six to 14. The impact of cats was also tested on a model with BM set at 70% of the DR (i.e. 14% annual mortality).

Picard model

I modified the Malabar model to predict the growth rate of the Picard population. I removed Rainfall from the Picard model because chick production on Picard was independent of environmental conditions in the two seasons after reintroduction (Chpater 3). I changed DR to be an evenly-distributed string of random numbers between 0.15 and 0.3, equating to annual mortality rates of 15% - 30%. As the population approached the projected carrying capacity (*ca* 1000 territories), I expected fecundity to decrease from the 1.8 chicks per pair observed on Picard at low population density, to the 0.55 chicks per pair that was the average production in the Malabar model. To model this effect I added the converter Fecundity, a graphical function that decreased fecundity as the number of Breeders approached 2000 (Figure 4.3). I ignored the effect of a skewed sex ratio (Chapters 2 & 3).



Input	Output
0.000	1.800
200.00	1.800
400.00	1.800
600.00	1.800
800.00	1.800
1000.00	1.800
1200.00	1.440
1400.00	1.098
1600.00	0.918
1800.00	0.738
2000.00	0.504

Data Points: 11

Edit Output:

Figure 4.3. Graphical relationship between the number of Breeders (x-axis and "Input") and Fecundity (y-axis and "Output") used in a Stella ® model of the reintroduced Aldabra Rail population on Picard. Fecundity tends towards 0.5 as the number of Breeders approaches 2000

Equations describing the model are the same as for the Malabar model, excepting the removal of the Rainfall converter and:

Juveniles = (Breeders/2)*Fecundity

Initial Breeders = 18
Initial Floaters = 0

Genetic sexing and population structure

Two genetic analyses were conducted *a posteriori*, using blood samples collected from Rails from all three extant populations and from the reintroduced Rails on Picard. I used a universal genetic sexing technique to verify the sex of individuals (Box 4.2). I used microsatellite data to investigate 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. Secondarily I analysed the genetic structure of the four populations to assess whether it would be beneficial to the small Picard population to mix stocks from all three islands, or if the genetic variation and heterogeneity of the Malabar Rails was sufficiently well represented in the reintroduced Rails to ensure their genetic integrity. Blood for genetic analyses was collected from a puncture to the brachial vein and stored in EDTA buffer (Chapter 2). Approximately 100µl 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).

Microsatellite Study

Twenty DNA samples were amplified at each locus to test for polymorphic product. A positive Chicken *Gallus gallus* DNA control was included during the testing of the Chicken primers. The PCR amplification conditions were as follows: the forward primer of each primer set was end-labelled with gamma ^{32}P - ATP (O'Ryan *et al.* 1998). PCR was then performed in 10µl reaction volumes at the following reaction conditions: 25pM of reverse primer, 5mM dNTPs, 1.5mM $MgCl_2$ and 0.5U *Taq* polymerase (Bioline). Cycling parameters for PCR amplifications were as follows: a one minute denaturing step at 94°C, one minute at the annealing temperature (46°C to 62°C to maximise the specificity of the hybridisation) and a 45 second extension step at 72°C. The amplified product was then electrophoresed on a 6% denaturing polyacrylamide gel. Genotypes were scored from the autoradiographs and allele lengths (in base pairs) determined using a sequenced size ladder of M13 ssDNA.

A panel of microsatellite loci from a variety of bird species was tested on the Aldabra

Rail, including primers from the Chicken (H. Cheng, pers. comm.), Tasmanian Moorhen *Gallinula mortierii* (J. Buchanan, pers. comm.), cranes *Grus* spp. (K. Jones, pers. comm.), Scottish Crossbill *Loxia scotia* (Piertney *et al.* 1999) and the Blue Tit *Parus caeruleus* (Dawson *et al.* 2000). 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 & Selander 1981). Hardy-Weinberg exact probabilities were calculated using the Markov chain method (Guo & Thompson 1992) implemented in GENEPOP (version 3.2a) (Raymond & Rousset 1995). Levels of population differentiation were calculated using F-statistics from the programme FSTAT (version 2.8) (Weir & Cockerham 1984, Goudet 1995). Estimates of σ were calculated from R_{st}Calc (Goodman 1997), based on Slatkin's (1995) R_{st}, with both small and unequal sample sizes accounted for in the calculation of R_{st}.

RESULTS

Population estimates

Both the Huxley and Hambler methods suffer from an inadequate representation of habitats in the transect array, and there is a high variability in results from short transects. Ideally, a transect should cross between 30 and 50 territories, rather than the 10 to 15 of established transects.

Huxley method

The average diameter of each territory in 2001 was very similar at Gionnet (67 m) and Middle Camp (76 m) (Table 4.1). These are the same as Huxley's (1982) estimate of a new territory every 70 m. The encounter rate on Polymnie was lower, with a pair every 112 m. However, much of the transect through dense scrub runs along the coast, halving the probability of encountering Rail territories for that section. Also, significant lengths of the transect run through *Casuarina* woodland, Mangroves stands or completely open habitat, in which Rail territories are very seldom found. Together, these sources of bias probably explain the apparently larger territories on Polymnie. Huxley (1982) also reported lower densities on Polymnie (Table 4.2). He made direct counts of the Rails on Polymnie in a defined area that included both open and dense scrub. He did not, however, quantify the relative amounts of different habitat and used an average density in his calculation of 1.42 Rails/ha. His method of estimating the Île aux Cèdres population was also inconsistent with the methods used for Malabar. There is no obvious reason why Rail densities should be significantly lower on either Polymnie or Île aux Cèdres and I have therefore assumed that they equate with those on Malabar, in the same habitat. I used the same density estimates for all populations and extrapolated from habitat-area calculations of my own.

Hambler method

This method of population monitoring is less sophisticated than the Huxley method. Nevertheless, it can reveal broad trends, especially when comparisons span decades. Results (Table 4.3) indicate that there has been no detectable change in Rail densities on Malabar since 1983.

Table 4.1. Results of Aldabra Rail censuses using the Huxley method, in May 2001. The number of adults encountered is not always equivalent to the number of territories as both members of a pair may respond to playback

Transect Location	Transect length	Adults encountered	Territories	Average diameter of territory
Gionnet	400	11	6	67
Middle Camp	650	15	9	72
Polymnie	800	7	7	114

Table 4.2: Summary results of Rail censuses on Malabar in March/April 1975 and 1976 (Huxley 1982). Results from all transects (no data given) and both years were combined (Huxley *op. cit.*)

Habitat type	Total length sampled (m)	Territories	Average diameter of territory
Open mixed-scrub with *Casuarina*	1200	10	120
Dense mixed-scrub	1600	23	70
Dense *Pemphis* scrub	2700	31	87

Table 4.3: Percentage of 50 m sections of linear transects that intersect Aldabra Rail territories Malabar. Data from 1983-88 are taken from Hambler et al. (1993)

Year	Gionnet	Middle Camp
2001	100	77
1988	92	93
1986	77	73
1983	77	93

I identified nine Aldabra Rail territories along a 500m transect at Gionnet (100 m longer than that used for the censuses). However, two territories, one at either end of the transect, barely intersected the transect. Excluding these two territories, and based on known, mostly ringed pairs, a 500 m section of path through dense scrub should intersect seven territories, equating to a territory every 71 m. This was virtually identical to Huxley's finding of a territory every 70 m (Table 4.2). Hambler *et al.* (1993) had almost identical results in a similar study made in 1988 at Middle Camp. These results are also broadly comparable to earlier studies, and I thus conclude that there has been no significant change in Rail densities since 1967 (Penny & Diamond 1971, Huxley 1982, Hambler 1993, this study).

The congruence of the findings of this study with those of Huxley (1982) and Hambler *et al.* (1993) allows me to calculate the Aldabra Rail population with confidence. Huxley calculated a density of 3 Rails/ha in dense scrub and 1.5 Rails/ha in open mixed-scrub. However, his estimates of the areas of the different habitats on each island have discrepancies, and he does not state how they were derived. I thus used my own estimates of area to re-estimate the Rail populations.

Table 4.4 shows the areas of dense scrub and open mixed-scrub vegetation on the four islands where the Rails occur. These areas differ from those used by Huxley (1982) and this population estimate is slightly lower. Given the relatively low resolution of the census techniques, the estimate of *ca* 7000 territorial Rails is approximate; the actual number of territorial adults at the end of the breeding season probably lies between 6000 and 8000. There is almost certainly some measure of annual variation in territory numbers, and territory sizes probably vary in response to rainfall, but the magnitude of these fluctuations is not known.

Table 4.4. Area in hectares of each major vegetation type on the four islands where Aldabra Rails occur. The number of territorial Rails is calculated at 3 Rails/ha in dense scrub and 1.5 Rails/ha in open mixed-scrub.

Island	Dense scrub (ha)	Rails	Open mixed-scrub (ha)	Rails	Total Rails	Huxley's (1982) estimates
Malabar	1925	5775	362	543	6318	7708
Polymnie	125	375	69	107	482	270
Île aux Cèdres	50	150	0	0	150	80
Current total					6950	8058
Picard	590	1770	110	170	1940	-
Projected total					8890	-

The population estimate for Picard (*ca* 1000 pairs) is a prediction based on the assumption that Rail densities there will be the same as those on Malabar. I estimate that Picard can support around 1000 territories. Thus, when the Picard population reaches carrying capacity it will add *ca* 2000 breeding birds to the population, i.e. there will be between 8000 and 10000 territorial Rails on Aldabra, an increase of nearly 30% above the current population.

Floaters

I banded 17 adult Rails along the Gionnet transect in 1999 and 2000 (Appendix 4). Of these, seven were floaters. Some floaters appeared to be semi-resident (i.e. ranged over a limited area and were retrapped close to where they had been banded), whereas others were presumably itinerant because they were not seen again after banding. From retraps I estimate that there were around 3.5 floaters per 500 m of transect, or roughly one floater per two territories. Given an estimate of 3500 territories on Malabar, I estimate there were *ca* 1700 floaters in the 1999/2000 breeding season.

However, the banding and retrapping was done during a very dry period, and floater numbers are predicted to be higher in years of average rainfall and a lot higher in wet years.

Population models

Malabar model

The Malabar population model maintained a stable breeding population and a fluctuating floater population when rainfall was set to produce an average of 0.55 juveniles per pair per year and a mean annual mortality of 20% (Table 4.5). The mean number of Floaters was close to the estimated 1700 (mean 1642), but showed considerable fluctuations (range = 3406, CV = 0.53) and consistently fell to zero after three successive dry years. Furthermore, this model was very sensitive to increases in DR and to dry rainfall regimes. The model became significantly more robust when I reduced BM from 20% to 14% and left FM unchanged. The number of Floaters increased concomitantly (mean = 2265) and never fell to zero, because fewer Floaters recruited into the breeding population annually. However, FM increased (mean = 36.7%) due to the increased effect of DDM, and fluctuations in the number of Floaters were lower (range = 3041, CV = 0.34). Therefore, I used both 14% and 20% annual BM for other simulations and sensitivity analyses. The mean number of floaters from this model is more than 30% higher than the 1700 estimated using trap-retrap data.

For the sake of brevity and readability I have only presented the most informative results of the various sensitivity analyses.

DR sensitivity analyses

DR was de-coupled from Rainfall, and set at one of five levels for each simulation:
Low: L = 0.2, or 20% annual mortality
Medium-low: ML = 0.225, or 22.5% annual mortality
Medium: M = 0.25, or 25% annual mortality
Medium-high: MH = 0.275, or 27.5% annual mortality
High: H = 0.3, or 30% annual mortality

In the first set of sensitivity analyses, BM was set at 100% of the DR. The stock of Breeders occasionally fell below carrying capacity even with a Medium DR setting. Breeders fluctuated considerably at a Medium-high DR setting and was tending towards complete collapse at a High DR setting (Figure 4.4). The number of Floaters was also very unstable at this BM setting, and only when DR was set at Low did the Floater numbers remain constantly above zero (Figure 4.5). At the High DR setting, the Floaters fell to zero immediately and never recovered. However, in the second set of sensitivity analyses, with the lower BM, the Breeders never fell below carrying capacity. Also at the lower BM rate, the number of Floaters never fell to zero even at the High DR settings (DR = 0.3, or 30% FM mortality and 21% BM) (Figure 4.6).

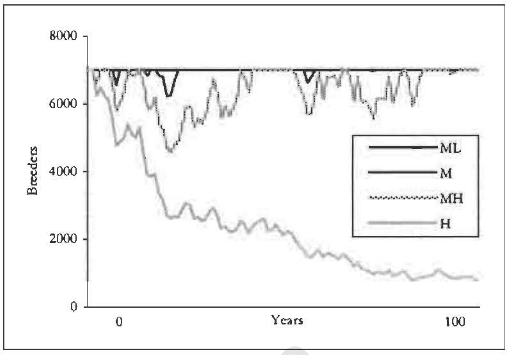


Figure 4.4. Changes to the numbers of Breeders in the DR sensitivity analyses for the Aldabra Rail population model for Malabar; each simulation was run for 100 years. BM was set at 100% of DR. DR settings: ML = 0.225, M = 0.25, MH = 0.275, H = 0.3. Results of the simulation with DR set at 0.2 are not shown for purposes of readability.

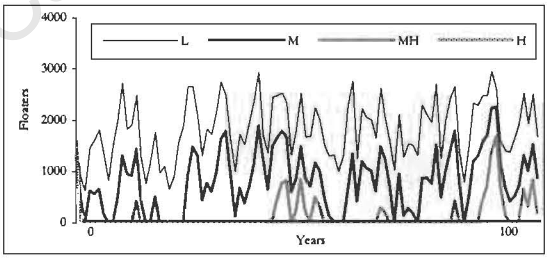


Figure 4.5. Changes to the numbers of Floaters in the DR sensitivity analyses for the Aldabra Rail population model for Malabar; each simulation was run for 100 years. BM was set at 100% of DR. DR settings: L = 0.2, M = 0.25, MH = 0.275, H = 0.3. Results of simulation with ML DR setting (0.225) are not shown for purposes of readability, but lie between L and M.

Rainfall sensitivity analyses

The results of the Malabar population model's sensitivity to different rainfall regimes under 20% (or 100% of DR) and 14% (or 70% of DR) annual BM settings are shown in Table 4.5. When BM was set at 100% of the DR, a low Rainfall (mean = 0.45) resulted in the stock of Floaters falling to zero almost immediately and essentially remaining at that level (mean = 4, CV = 7.82). Under very low Rainfall (mean = 0.4), the stock of Floaters also fell immediately to zero, but more importantly, the Breeders decreased steadily to a minimum of 160 at

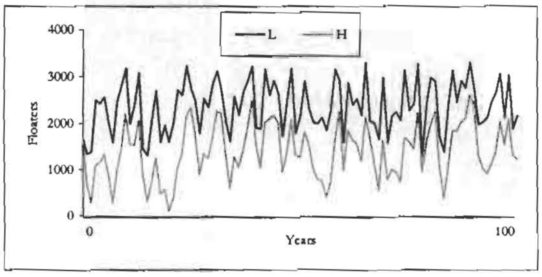


Figure 4.6. Changes to the numbers of Floaters in the DR sensitivity analyses for the Aldabra Rail population model for Malabar; each simulation was run for 100 years. BM was set at 70% of DR. DR settings: L = 0.2, H = 0.3. Results of other simulations are not shown for purposes of readability, but lie between those that are shown.

year 100, and the population would thus have become extinct within a few more years. By contrast, the Malabar model with the BM set at 70% of the DR was far less sensitive to low-rainfall scenarios. Even at the very low Rainfall setting, the stock of Breeders remained at or around carrying capacity and the stock of Floaters averaged 915 (CV = 0.72).

Table 4.5. Summary statistics of the sensitivity analysis of the Malabar population model of the Aldabra Rail. Three annual rainfall scenarios (normal, low and very low) are modelled with two mean annual mortality rates for territorial Rails: 20% (1) and 14% (2). Each simulation was run for 100 years

Rainfall	Breeders	Floaters	BM	FM	Rainfall
Normal (1)					
Mean	7000	1651	1387	573	0.56
CV	0.00	0.53	0.15	0.95	0.26
Max	7000	3406	1750	2422	0.80
Min	7000	0	1050	0	0.30
Normal (2)					
Mean	7000	2265	971	983	0.56
CV	0.00	0.34	0.15	0.75	0.26
Max	7000	3670	1225	2768	0.80
Min	7000	628	735	124	0.30
Low (1)					
Mean	5004	4	1131	5	0.45
CV	0.17	7.82	0.25	10.00	0.29
Max	7000	1700	1876	541	0.80
Min	3620	0	657	0	0.30
Low (2)					
Mean	7000	1478	1096	469	0.45
CV	0	0.47	0.13	0.91	0.29
Max	7000	3551	1313	2551	0.80
Min	7000	245	824	58	0.30
V. Low (1)					
Mean	1441	3	365	5	0.40
CV	1.13	10.00	1.18	10.00	0.31
Max	7000	1700	1876	541	0.80
Min	160	0	38	0	0.30
V. Low (2)					
Mean	6982	915	1153	262	0.40
CV	0.01	0.72	0.12	1.04	0.31
Max	7000	3076	1313	1720	0.80
Min	6585	0	824	0	0.30

Table 4.6. Predicted population growth rate of Aldabra Rails on Picard Island after reintroduction.

Year	Breeders	Increase	Breeder mortality	Juvenile production
0	18	-	-	16
1	31	13	3	28
2	54	23	5	49
3	89	30	14	80
4	150	60	19	135
5	251	101	34	226
6	431	180	46	388
7	751	320	68	676
8	1238	487	189	851
9	1777	539	312	674
10	1935	158	516	561
11	2000	65	402	504

Cat predation

When cat predation was included in the Malabar model with BM set at 100% of DR, the stock of Breeders crashed very quickly. Even with just six cats (harvesting 624 Rails per year), the Floater population regularly fell to zero, and the Breeders regularly dropped below 7000. With 8 cats, the Rail population became extinct within about 60 years, and with 10 cats it became extinct within just 30 years. Even when the model was re-run to incorporate density-dependent fecundity, this had no ultimate effect on whether or not the population crashed. When the BM was reduced to 14%, the number of Breeders remained at carrying capacity with up to 12 cats and only fell to zero when the cat population was increased to 14.

Picard model

The reintroduced population is predicted to reach saturation between eight and ten years after reintroduction (Table 4.6). The estimates for the first two years compare very closely with observed Rail numbers (Chapter 3).

BOX 4.2. Genetic sexing

The published method for sexing birds in the field (Penny & Diamond 1971) proved to be unreliable after two birds died in captivity, and I felt it necessary to verify the sex of the reintroduced birds (Chapter 2). Furthermore, it is not possible to sex chicks or juveniles visually.

Total DNA was extracted from nucleated red blood cells by proteinase K digestion (0.1mg/ml) at 65^{0}C for 1 hour in lysis buffer (50mM Tris-HCL pH 7.5; 400mM NaCl; 5mM EDTA pH 7.4; 0.5% SDS), followed by precipitation of DNA in the presence of 2M ammoniumacetate after addition of 2 volumes of 100% ethanol (Sambrook *et al.* 1989). The resulting DNA pellets were air dried and resuspended in 100 µl TE, pH 8. The genomic DNA was then diluted to a final concentration of between 10 and 50ng/µl for Polymerase Chain Reaction (PCR) amplifications.

Primers 2550F and 2718R (Fridolfsson and Ellegren 1999) were used in the amplification reaction. Females were identified by the presence of 2 bands (approximately 120 bp apart) and males were identified by a single band, as visualised by ethidium bromide staining on an agarose gel (Fridolfsson and Ellegren *op cit.*). PCR blanks and positive controls were included in all PCR amplifications to ensure the reliability of the reactions.

The known population on Picard at the end of the second breeding season was 51 individuals. At least 4 chicks from the second season were too small to be banded and have blood collected. Of the 47 birds for which data were available, 28 were female and 19 were male (Appendix 4). Ten of the 18 reintroduced Rails (YA1-Y21) were female and eight were male. The sex ratio of known-sex chicks from the first breeding season (B49-B63) was also biased 9:4 in favour of females. The ratio of known-sex chicks (B64-B81) from the second season was equal (8 females: 8 males). These results indicate that the sex ratio is likely to have a slight female bias for some time, but as the population grows it will become less significant.

I compared the results of genetic sexing with the accuracy with which these birds were sexed in the field using the criteria of Penny & Diamond (1971). Of the 58 adults for which I identified a sex (some were specified "Uncertain"), 47 (81%) were correct and 11 were incorrect. There was no bias in the error: I incorrectly sexed six males as females, and five females as males. Thus the Rails can be correctly sexed in the field with only about 80% accuracy.

The death of two Rails in captivity, and the subsequent post-mortem revealed that the published method for sexing Aldabra Rails in the field was not reliable. This impression was strengthened by the failure of two birds to form pairs (they proved to be both female), and a pairing of two birds that I had initially sexed as males. The unreliability of the characters used to sex Aldabra Rails in the field was unequivocally confirmed by the results of the genetic sexing method (*contra* Penny & Diamond 1971). The low accuracy (80%) that I achieved is brought more sharply into focus when one considers that all of the incorrectly sexed birds were in the hand at the time of sexing and could be closely examined. I thus conclude that Aldabra Rails cannot be reliably sexed in the field or in the hand using mensural or morphological characters, unless there are obvious size differences between unequivocally paired birds, females being, on average, smaller than males (Penny & Diamond 1971, personal data, not presented).

Microsatellite study

Of the more than 150 loci tested, only one (TM18 from Tasmanian Moorhen) produced an informative polymorphic product. Although based on a single primer, subsequent analyses showed interesting trends.

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 4.7). When treated separately, the Île aux Cèdres population had 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 had the highest allelic diversity, with six and five alleles respectively, while Polymnie had four and Île aux Cèdres only three (Table 4.7, Figure 4.7). The Malabar and Picard populations had 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, showed 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.

Table 4.7. Heterozygosity values observed (H_o) and expected (H_e) under Hardy-Weinberg equilibrium in the four populations of Aldabra Rails, 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 4.8. Pairwise population differentiation from a single microsatellite locus for Aldabra Rails. F_{st} values appear below the diagonal and σ values above the diagonal

	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	-

* $p < 0.05$

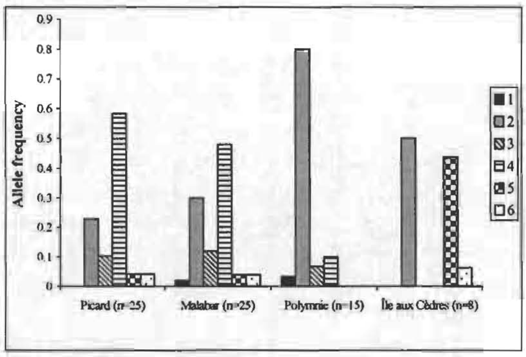


Figure 4.7. Allele frequency distributions for the six alleles at locus TM18 in each of the four populations of Aldabra Rails

Differences in the observed allele frequencies give a preliminary indication of population structuring, corroborated by both F_{st} and R_{st} values (Table 4.8). 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, as suggested by F_{st}, contrasts with the σ estimates that suggest little differentiation. This could be an artefact of the way in which the σ estimate is calculated.

DISCUSSION

The two methods of population estimation exploit different aspects of the Rails' biology. The Huxley method relies on their habit of directly confronting persistent intruders, and thus attracts territorial birds to the observer using tape playback. The Hambler method relies on paired Rails' vocal response to an intruder's vocalisations. Rails that are attracted to the observer but do not call are not counted in the latter method. I found Rails' responses to playback (either vocal or coming to investigate) highly variable and dependent on the time of day, recent exposure to playback tapes (measured in weeks) and particularly the period of the year. Responses during the breeding season were wholly unreliable, and results (not presented here) of monitoring during the dry, non-breeding season show a marked decrease in responses.

I believe that both census methods are flawed. The Huxley method may underestimate the number of territories, as the reliability of birds coming to confront an intruder has not been tested. Conversely, non-territorial birds, which do not respond to playback, may be in the vicinity of the 50 m markers during playback, or may be attracted to the presence of humans out of curiosity (Appendix 1). This method cannot always distinguish between territorial and non-territorial birds and thus introduces another source of error, one that probably overestimates the number of territories. The net result of these conflicting biases is unknown. The Hambler method may underestimate Rails for similar reasons. Furthermore, if two (or more) territories happen to fall within a single section (e.g. the path forms the territorial boundary), the section will be scored as a single positive, and not account for the second territory. Another source of negative bias occurs when territorial birds happen to be close to the observer when playback begins. These birds typically come to investigate and often search for the "intruder" rather than responding vocally, especially if their mate is not in the vicinity. The Hambler method is therefore subject to greater bias than the Huxley method.

The two census methods are relatively crude, but conditions on Aldabra make counting birds difficult (Chapter 2), and results of both methods are in broad agreement. Using the corrected area estimates and the comparable density estimates, a new, slightly lower but essentially similar population estimate for the Rails, of around 7000 breeding birds, reveals no changes in the populations since they were first estimated. I recommend censusing shortly before the start of breeding and at the end of the breeding season, when juveniles have left the natal territory. In this period, pair-bonding activities and territorial behaviour are strong, and responses to playback are more reliable (Huxley 1982, this study).

Population models

Many of the data I used in the Stella® models are relatively crude, and based on a few, small samples. For example, field work was conducted over just two breeding seasons. While I was fortunate in that the first breeding season was very dry and the second was very wet, enabling me to make a very rough estimate of the relationship between chick production and rainfall, it is unlikely that they represent either extreme in annual chick production. The models would be greatly improved if a) rainfall and chick production figures could be correlated; b) there were adequate data to estimate the mean number of floaters; and c) temporal fluctuations in both territorial and floater populations could be correlated with environmental variables. Nevertheless, population dynamics on small, predator-free islands are simple and lend themselves to uncomplicated modelling. I believe that the results of this modelling exercise, if treated with due caution, provide reasonably accurate estimates of some unknown parameters, give guidelines for future conservation efforts and are useful in pointing out directions for further research.

The model and the sensitivity analyses showed that an average annual mortality of 14% of territorial birds (Breeders in the model) is probably the upper limit. Any higher than this and the population as a whole, but particularly the floaters, became unrealistically sensitive to relatively minor perturbations. Thus I do not expect mean annual mortality of territorial birds to exceed 14%, and it is probably less than that. In other words, annual survival for territorial birds is likely to be at least 85% or higher. The model shows that floaters are key to the maintenance of a stable breeding population, but also that they experience a very high annual mortality: the lower the mortality of breeders, the higher the mortality of floaters.

The Malabar model suggests that the Rail population can withstand a relatively large harvest without any significant impact on the number of breeders. For example, if a full-scale reintroduction of the Rails to another island were to be undertaken, Malabar could comfortably withstand the removal of 100 pairs (200 individuals, < 3% of the breeding population) in a single year. The sensitivity analysis suggests that this would be true even after several years of below-average rainfall. The floater population is big enough to absorb such a removal, even if such a removal was repeated indefinitely. However, the model also shows that if cats established themselves, it would be disastrous once the cat population reached the point where more than about 30 adult Rails were killed per week. This scenario could become a reality relatively quickly, and the Rails would almost certainly be driven to local extinction. There are several other similarly naïve species of endemic birds as well as other sources of food on the islands that support Rails (evidenced by the persistence of Domestic Cats *Felis catus* on Rail-free Grande Terre). These other prey species could sustain a growing predator population, vitiating the notion that predators could not hunt a naïve, flightless prey species such as the Aldabra Rail to extinction.

The exponential growth predicted by the Picard model rests on the assumption that first year birds are capable of breeding, as was observed in this study (Chapter 3), and thus, while territories remain unfilled, there is no floater population. Although first year pairs produced fewer chicks per pair than older pairs, the small samples sizes preclude a definitive analysis of this. I thus did not factor a reduced fecundity for first-year birds into the Picard model, but urge caution in relying too heavily on the predictions as a consequence. I strongly recommend that intensive monitoring activities be conducted from 2007 onwards, to track the final stages of population growth and to study the effects of increasing breeding densities (with concomitant decreases in territory size) on reproductive behaviour and success.

Microsatellite study

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. Initial results suggest that the reintroduced population has retained a large proportion of the variation present in the parent population (5 of 6 alleles). This is supported by low pairwise estimates of F_{st} and R_{st} between Malabar and Picard. I 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 (pers. obs.) and the islands on which they occur are separated by tens 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. However, 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.

It would be of great scientific and conservation interest if other polymorphic loci of the Aldabra Rails could be amplified. The suggested differentiation between the three original populations needs to be confirmed, especially as there are noticeable morphological differences between birds from Île aux Cèdres and the other islands (Appendix 1). Should significant genetic differences be found, there would be a strong case for moving birds from Île aux Cèdres to another predator-free island that once supported Rails of the genus *Dryolimnas*. The main limitation to this is the small size of the Île aux Cèdres population. This could be overcome by effecting a staged reintroduction, with a lagoon islet such as Île Michel (which formerly had Rails) on Aldabra being used to host a temporary population of birds from Île aux Cèdres.

The rate at which the reintroduced Rail population on Picard is growing, coupled with their genetic integrity, obviates any demographic or genetic needs for supplementary reintroductions (see Armstrong and Ewen, 2001, Chapter 3). Results of the modelling and genetic studies suggest that the Picard population, short of some unforeseen catastrophe, is likely to continue to grow exponentially until *ca* 2007. The genetic analyses also suggest that carefully managed programmes involving small numbers of birds can be highly successful.

The existing populations of the last flightless bird of the tropical Indian Ocean islands appear to be both numerically and genetically healthy. However, the persistence of Domestic Cats on Aldabra remains a source of concern.

The protocol for monitoring breeding Rails now in place on Aldabra should continue because its results are needed to validate predictions in Table 4.6. However, models show that the floater population is the most sensitive to environmental fluctuations and other perturbations. I therefore recommend that this portion of the population also be monitored. This is only practicable through the continuation of the banding and retrapping programme that started with this study. Although it would be difficult to detect accurately changes in floater numbers, they would serve as an early warning of threats to the breeding population.

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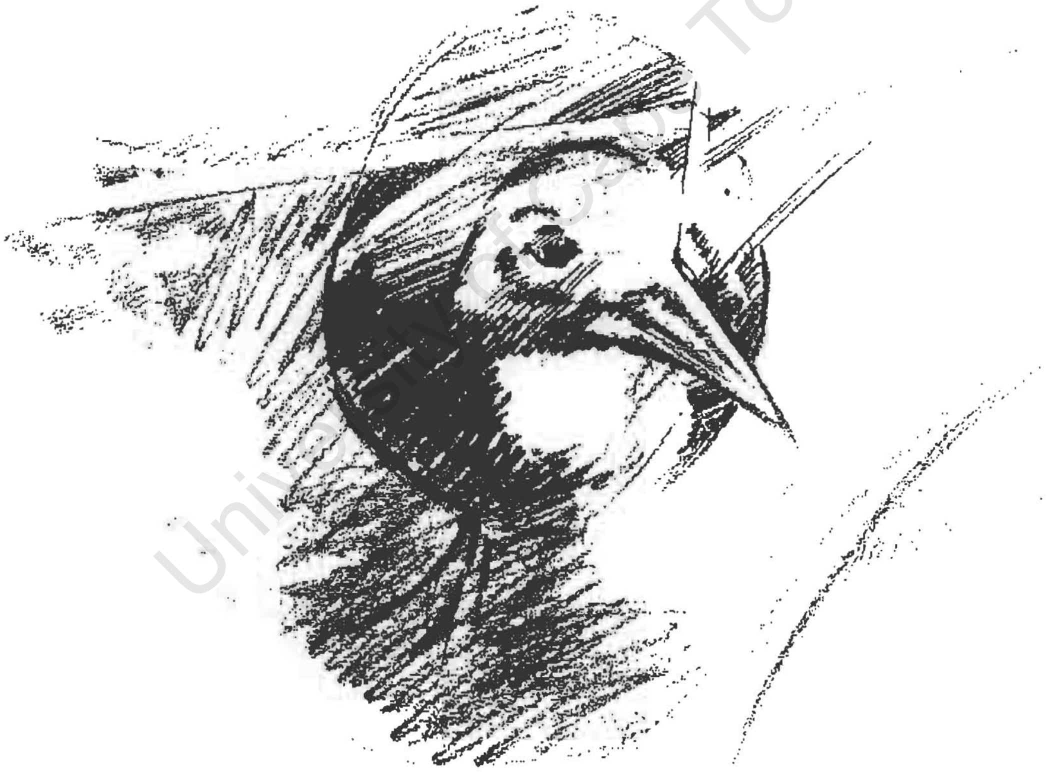


Aspects of the biology, behaviour and ecology of the Aldabra Rail *Dryolimnas cuvieri aldabranus*

Introduction

The first ecological study of the Aldabra Rail was conducted between 1973 and 1976, but most of the findings have languished in an unpublished typescript (Huxley 1982). I located the typescript in June 2000, after completing the reintroduction of Rails to Picard. I received permission to use the results reported in the unpublished document (C. Huxley *in litt.*), many of which confirm the findings of this study. However, Huxley and I differ considerably on many of our interpretations of Rail behaviour. Furthermore, Huxley based many of his interpretations of Rail behaviour on the assumption that they could be reliably sexed in the field (see Penny & Diamond 1971). However, this study has shown conclusively that Aldabra Rails cannot always be correctly sexed on either physical characters or behaviour (Chapter 4). A retrospective analysis of observations of banded birds of known sex lent greater confidence to my understanding of Rail behaviour, especially in the context of reproduction.

General ecology

Aldabra Rails are diurnal, becoming active at first light, usually half an hour before dawn. Paired birds roost close to one another (< *ca* 10 m) but are not known to roost together. When they awake they immediately give a duet. This is frequently echoed by awaking pairs nearby, in a domino effect. Individuals may remain at their roost site for a few minutes after duetting, before venturing out and making visual contact with their mate. They forage very actively for the first three hours of the day, but thereafter activity decreases, with more and more time spent resting, sleeping and preening as midday approaches. They are relatively inactive during the early afternoon, unless it is cool or overcast. Activity increases again in the latter part of the afternoon. They move quite quickly to the roost site in the late afternoon, foraging intermittently as they commute and timing their arrival at the roost site to coincide with the end of twilight. Typically, they give a duet before roosting. They generally roost on the ground, under the cover of a bush, under tree roots or in a crevice, and show fairly high roost-site fidelity. Occasionally, individuals sing or pairs duet long after nightfall and well before first light – neither the cause nor function of this behaviour is known.

Aldabra Rails utilise all vegetation types on the islands on which they occur. They forage in mangrove swamps but must vacate them twice daily because the swamps are inundated with the high tide (Penny & Diamond 1971, this study). They prefer dense vegetation, and are found there in the highest concentrations (Chapter 3). They are very seldom seen in monospecific stands of *Casuarina equistefolia*, probably reflecting a paucity of invertebrate prey (Spaull 1979). *Casuarina* stands are generally found along seaward-facing strips of coast near the channels, and do not account for a significant area on Aldabra. Where territories include large tracts of open mixed scrub or unvegetated areas, Aldabra Rails spend most of their time in the denser areas and always seem reluctant to venture into open spaces (Penny & Diamond 1971, this study). The terrain on Aldabra is dichotomously classified into *champignon* and *platin* (Chapter 1). The former supports denser vegetation by virtue of the many cracks, fissures and solution pits that allow soil to accumulate and thereby support vegetation. Similarly, *champignon* promotes the collection of leaf litter and thus supports a high density of leaf litter and soil invertebrates. Consequently, Rails spend most of their time on heavily dissected, fretted *champignon* substrata, in the densest vegetation.

Aldabra Rails forage in a diversity of habitats, exploiting a wide range of foods, including berries, flowers, intertidal invertebrates, organic jetsam on beaches, turtle and tortoise eggs and hatchlings, skinks and geckos, terrestrial crabs, carrion and kitchen scraps (Penny & Diamond 1971, Frith 1977, Huxley 1982, Chapter 3). However, the vast majority of their time is spent foraging in leaf litter and soils. Leaf-litter and soil invertebrates numerically dominate their diet (pers. obs). Their foraging strategy involves rapidly picking up large clumps of litter with their beak and discarding them with a quick flick of the head. When soil has been exposed it is probed with the long, pointed bill. The Rails will often pause before removing litter and then stab at or target a point, having apparently listened for and located prey. When an area has been cleared of litter, they insert their bill below the soil and pump it rapidly, like a piston. They seem to target the bases of bushes and solution holes in rocks filled with soil and litter (Penny & Diamond 1971, this study). They will often wash food items if water is nearby. The size of prey items was, in the majority of cases, too small to estimate. No identifiable remains were ever found in faecal samples; a single regurgitated sample contained very finely crushed arthropod exoskeleton(s) and eighteen tiny land-snail shells. The latter might have been ingested as grit.

When caught, geckos or skinks are held in the bill, the head is rapidly flicked from side to side and the prey is beaten against the ground or a branch. Small crabs are killed in the same manner, but large individuals are killed by rapid, powerful blows with the sharp bill, aimed between the eyes. Crab exoskeletons and hermit crab shells are broken open by placing them on the ground and repeatedly hammering them from vertically above with the sharp bill. Flesh is removed by pulling or rapidly shaking the head. The feet are never used to scratch in litter or manipulate food. Aldabra Rails were occasionally seen with damaged, broken or missing legs, but all such afflicted individuals appeared to be quite capable of foraging and even reproducing successfully.

Reproduction

Aldabra Rails are strictly monogamous and territorial (Benson 1967, Gaymer 1967, Huxley 1982, this study). Sexes share incubation and chick-provisioning duties more-or-less equally (Gaymer 1967, Huxley 1982, this study). There is no evidence of co-operative breeding, and young are always expelled from the natal territory aged between about eight and ten weeks, once they have attained full juvenile plumage. In these respects the breeding biology of Aldabra Rails is similar to most other rallids (Taylor & Van Perlo 1998). Both sexes defend the territory, although pairs often tolerate itinerant individuals or singletons; such birds are not known to be related to the pair. Penny & Diamond (1971) argue that territories are not necessarily contiguous, but conform to a "neighbourhood" system, where core territories are defended but communal foraging areas exist. Neither Huxley (1982) nor I found any evidence of this, and the tolerance of semi-resident floaters is presumably responsible for this misinterpretation by Penny & Diamond (1971).

Neither Huxley (1982) nor I recorded extra-pair copulations. However, a pair at Middle Camp, WA3 (female) and WA5 (male) had some interesting interactions with a third, unringed individual. WA3 & WA5 were trapped together in 1999 and were thus a well-established pair at the start of the breeding season in December 2000. WA5 was frequently aggressive towards WA3 (see *Intra-pair aggression displays* below), although they also often duetted. Both seemed quite tolerant of an unringed individual, which was frequently seen close by. On a few occasions WA3 was seen with the unringed bird and once stood next to it and they duetted. WA5 responded to the duet immediately (by singing), but did not move towards the other two. Shortly after the duet, WA5 attacked WA3 (but was never seen attacking the unringed bird). The next visit to Middle Camp was in January 2001, when WA3 and WA5 were attending a nest together and there was no sign of the unringed bird, which had presumably been expelled from the territory. Penny & Diamond (1971) also record a remarkably similar set of interactions, including an unringed bird copulating with a member of a ringed pair.

Courtship behaviour prior to pair-formation has never been knowingly observed. It is possible Aldabra Rails don't have any, but very few rails lack any courtship display (B. Taylor pers. comm.). Pair bonding activities include a greeting display, duetting, allopreening, copulation, "courtship feeding" by the male to the female and numerous vocalisations that are given in a variety of circumstances and serve to confirm the bonds (Huxley & Wilkinson 1977). Pair bonding activities increase in frequency in October and peak when females are receptive (usually in mid to late December). During chick rearing, duetting is noticeably reduced and other pair bonding behaviour is seldom seen. However, these activities increase again before second clutches are laid. In all my observations, laying of second clutches was timed such that the first brood was expelled shortly before the second clutch was due to hatch. Huxley (1982), however, recorded two second clutches, both of which hatched before offspring from the first brood had been expelled. At the end of the breeding season, pair-bonding activities again become more evident, but decrease as the dry season progresses.

Nesting

Prospecting for a nest site begins in late November or early December and is done by both sexes. The male, however, is responsible for most of the building. Two or more nests may be built, and material is often placed in a number of potential sites before one is selected and concerted building starts. Once a site has been selected, one or both birds will stand on or near the site and give a series of low, groaning "*crreaaaak*" calls (described as "*mp yeah*" by Huxley & Wilkinson (1977)). During the prospecting and building stages, males frequently collect nesting material while foraging, carry it a few paces and then drop it. Eight out of 23 active nests were built on the ground; the other 15 were in low shrubs, *Pandanus tectorius* bushes or natural cavities in trees. Elevated nests ranged from barely elevated to 160 cm above ground (mean = 80 cm, n = 14). They were always concealed to varying degrees, and pairs were secretive while nest-building, relative to their typically unconcerned behaviour. When building, the male gathers a beak full of dead material from nearby and places it on the nest site. The bill is then used to push the material into place, and the body and legs force a depression in the middle of the pile. No effort is made to weave material, although the constant adding by males, and placing and billing by both adults ultimately results in some measure of consolidation. Males often add nest material throughout the incubation period.

Aldabra Rails use a wide diversity of dead plant material (usually the dominant litter of the area) in nest construction. Nest length was measured on the longest axis across the centre of the cup, width was measured across the centre of the cup at right angles to the length measurement and depth was measured vertically from the deepest part of the nest to level with the rim of the cup. All measurements were made to the nearest 0.5 cm using a tape measure or ruler. Nests are almost always constrained in some way by the nature of the nest site (i.e. the shape of the fork in a tree, dimensions of the crevice, etc.) and are thus difficult to characterise. Nevertheless, most nests are quite large structures, typically around 26 cm long, 22 cm wide and 12 cm deep (Table 1). The cup is usually deep enough that only the head of an incubating adult protrudes. The dull, olive-green back, streaked with black, camouflages birds on the nest remarkably well. Some nests, however, have almost no added material and are simply natural depressions under a shrub that have been sparsely lined with dry grasses or *Casuarina* needles.

Table 1. Total nest and nest cup dimensions of Aldabra Rails. N = 9

	Length (cm)		**Width (cm)**		**Depth (cm)**	
	Total	**Cup**	**Total**	**Cup**	**Total**	**Cup**
Mean	26.0	14.9	22.1	13.4	11.6	4.8
SD	3.3	2.2	3.5	2.7	6.1	2.4
Max	31	18	25	18	18	10
Min	20	11	17	10	3.5	3

Pairs occasionally use brooding nests. These are built on the ground under shelter, and are simple constructions consisting of a thin layer of dry material with a shallow cup. They are used to brood downy chicks, probably only for a few days after hatching.

Eggs

Eggs were measured to the nearest 0.1 mm using vernier callipers and weighed to the nearest 0.5 g using a 100 g Pesola spring balance. However, many egg-weight measurements were taken from eggs of unknown age and the results must thus be treated with caution (Table 2). Eggs are variable in shape, but most are elliptical or biconical. The moderately glossy, off-white shell is covered in maroon-brown speckling and has a finely granulated surface (Bendire 1894, this study). The density of speckling is greatest at the rounded end, and many speckles appear clouded or adumbrated, which gives the speckling a multi-toned appearance.

Table 2. Dimensions of eggs from 14 clutches (including repeat clutches) of the Aldabra Rail (n = 39 eggs).

	Length (mm)	**Width (mm)**	**Mass (g)**
Mean	43.3	30.6	21.4
SD	1.2	1.1	2.1
Max	45.8	32.6	25.5
Min	40.9	27.4	16

Table 3. Summary of nesting success of Aldabra Rails in the 2000/2001 breeding season. Dashes indicate missing data, where too few visits were made to Malabar nests to permit estimates of success. Statistics for Picard include six second clutches. They exclude two third clutches that I did not see and were only reported to me (G. Esparon *in litt.*).

	Picard	Malabar
Complete clutches	15	6
Total eggs laid	46	14
Mean clutch size	3.1	2.3
Maximum clutch size	4	3
Minimum clutch size	2	1
Modal clutch size	4	3
Hatching success (%)	59	-
Fledging success (%)	43	36
% hatchlings fledged	74	-

Reproductive effort

Average clutch size was estimated from nests that were visited at least twice during the breeding season and that did not vary - i.e. are assumed to have been complete clutches. Where nests were not found but newly hatched chicks were seen, the clutch size was assumed to be the same as the number of chicks seen (i.e. a minimum estimate). Clutches ranged from one to four eggs. Clutch sizes differed between Picard and Malabar, probably as a result of competitive release for the reintroduced population on Picard. No single-egg clutches have been found on Picard, and there were six four-egg clutches out of 17 clutches (including repeat clutches). By contrast, two of six nests on Malabar contained only one egg and no four-egg clutches were ever found, nor have any pairs on Malabar been seen with more than three chicks (T. Jupiter pers. comm., this study). Too few nests were found to test for significance. Of the 46 eggs from 15 complete clutches in 2000/2001 on Picard, 23 (50%) did not hatch through infertility (8), presumed depredation (7), being broken before hatching (3) or unknown causes (5)

Six pairs on Picard attempted second clutches following successful first clutches (Chapter 3). Of these, four re-used nests from the first clutch and two built new nests. One nest on Malabar is believed to have been re-used by the same pair over two breeding seasons. Two pairs on Picard laid third clutches in 2000/2001, both re-using nests for the third time, although both of these failed at the egg stage (G. Esparon pers. comm.). Huxley (1982) recorded only two second clutches following successful first clutches on Malabar (sample size not given). One pair on Malabar built a new nest and relaid immediately after their first nest was depredated; I found no other repeat clutches on Malabar. Two pairs of first-year birds on Picard did not relay after their first attempts failed.

Timing

Breeding is closely tied to the start of the rains and the concomitant increase in invertebrate densities (which constitute the bulk of the Rail's diet) (Penny & Diamond 1971). Laying thus usually commences in late November and can continue into April. For most pairs, laying closely follows the arrival of the rains. However, pairs in good condition may hatch their first brood before the onset of rains, especially if rains are late. In the 2000/2001 breeding season on Picard, laying of first clutches was concentrated around the end of December and early January. Eggs are laid at intervals of between one and four days, typically every other day. Incubation lasts between 19 and 23 days (n = 5 nests, mode = 22 days) and, based on hatching intervals, usually starts when the last egg is laid. Incubation shifts were watched on three occasions, totalling more than 28 hours of diurnal observations (Table 4). Y13 & Y17 were watched continuously during daylight on two days, between 7.30 am and 7.30 pm. B59 & B63 were watched once, between 8 am and 2 pm. Both sexes incubate, with the female doing the bulk of incubation during the morning. From watching incubation shifts and checking nests daily each afternoon, it seems that the male does the bulk of the incubating in the afternoon. The male also incubates at night (Huxley 1982, Table 4). Diurnal incubation shifts last between 10 and 200 minutes. The hatching interval is 0-3 days, synchrony being the norm. Chicks are sub-precocial, sometimes leaving the nest within a few hours of hatching, and always within 3 days. The female eats the shells of hatched eggs, but infertile eggs are abandoned in the nest. When infertile or slow-developing eggs are being incubated, newly hatched chicks may leave the nest for periods, always in the care of a parent.

Chicks

Once the nest is permanently abandoned, parents adopt one of two caring and provisioning strategies. They usually divide the brood between themselves and forage independently. The second strategy is to leave chicks well concealed, forage alone, and return to the chicks with food. When the former strategy is employed, young chicks remain close to the adults for around two weeks, frequently tripping them up as they scurry under the body of a walking adult. Downy chicks often make a continuous, high-pitched "*peepeepeepee*" call while following foraging adults. Daily foraging ranges increase as chicks are able to walk further but, unless the roost site is changed, adults and chicks return to the same roost site at the end of each day. Chicks increasingly explore and investigate things for themselves until about 4 weeks old, by which time they are proficient at foraging for themselves. However, parents continue to feed, or capture food for, chicks until they are between six and eight weeks old. At around eight weeks, when chicks are in full juvenile plumage, parents decrease their provisioning rate and also become aggressive towards juveniles. Aggressive interactions become increasingly violent and frequent until offspring leave the natal territory (eight to ten weeks). Juveniles and unpaired adults range quite widely, and possibly only establish a territory after finding a mate.

Table 4. Incubation shifts (in minutes) of two pairs of Aldabra Rails on Picard in the 2000/2001 breeding season. A cumulative total of 28 hours was spent observing diurnal incubation shifts on three days. Note: no average shift length for last set of observations.

	Incubation shifts (minutes)	
Pair	Female	Male
Y13 (F) & Y17 (M)	73	56
	83	30
	57	25
	58	34
	53	180
Average shift length	**65**	**65**
Sub-total	**324**	**325**
Y13 (F) & Y17 (M)	218	30
	48	65
	17	46
	73	86
	10	62
	65	
Average shift length	**72**	**58**
Sub-total	**431**	**289**
B62 (F) & B59 (M)	198	42
	123	
Sub-total	**321**	**42**
Total	**1076**	**656**
Total observation time	1732	
% total time spent incubating	62	38

Aberrant plumages

Juvenile Aldabra Rails undergo a moult into adult plumage in their first year, between May and July (Chapter 1). However, on 21 December 2000 on Picard, I captured and banded (B60) a fully-grown male Aldabra Rail still in juvenile plumage. This was unusual, as there are no other records of Rails in juvenile plumage at this time of the year. B60's juvenile plumage seemed fresh, and the wear on the primaries was comparable to that of other birds of the same age. This suggests that it had undergone a pre-breeding moult but for some reason retained juvenile plumage. It was paired with another first-year bird (in adult plumage), and they laid a two-egg clutch. The eggs disappeared before they were due to hatch (presumed depredated) and the pair did not relay.

A banded Aldabra Rail had a diffuse, white patch on its breast when captured. This patch had disappeared by the following year, presumably having been a once-off, leucistic aberration in moult that was lost in the subsequent moult. There are no records of partial or complete albinism in this species.

Displays and postures

A variety of displays and postures are used by adult Aldabra Rails, usually in territorial or sexual contexts (see also Penny & Diamond (1971)). For a comprehensive treatment of Aldabra Rail vocalisations see Huxley & Wilkinson (1977) and Wilkinson & Huxley (1979) – I have not repeated data on vocalisations. Two prominent features carry particular significance in these ritualised behaviours. The white throat patch and white undertail coverts contrast strongly with the darker plumage of the rest of the bird, and also stand out against the darkly shaded surroundings of the understorey that Rails frequent. The following descriptions are taken from detailed notes made in the field and from photographs of Aldabra Rails in various displays and postures.

Relaxed Posture Figure 1(a)

This posture is used when resting, foraging and commuting. Neither the throat patch nor the undertail coverts is displayed. When standing, the neck is usually bent or retracted with the head pointing horizontally or down, thus hiding the throat patch. The tail is flicked with each step, but the undertail coverts are not fanned. There are no vocalisations associated with this posture. An exception is during the early breeding and pre-egg-laying period. Pairs stay very close together (usually within sight, always within earshot), give the '*mpclick*' call (*sensu* Huxley & Wilkinson 1977) continuously and may partially fan the undertail coverts.

Sleeping

The head and neck are pulled right in and the bill is held horizontally. The head is not tucked under the wing. Neither the throat patch nor undertail coverts are visible. Birds may stand on one leg with the other held against the body. The white eyelids of closed eyes are conspicuous.

Bathing
Aldabra Rails bathe twice a day or more, if fresh water is readily available. Bathing is done in shallow water and the head is dipped repeatedly under the water in a bobbing fashion, spilling water over the upperparts on each rise and wetting the underparts on each dip. The body feathers are raised and the wings are spread and splashed repeatedly. Feathers may be preened vigorously while the bird is in the water. After bathing, the feathers are vigorously shaken and preened again. A wet bird may sun itself, with the wings fanned horizontally. There are no records of alternative bathing activities (e.g. dust-bathing or bathing in the sea) during the dry season, when fresh water may be absent or insufficient for bathing.

Preening
When preening, the bird stands on both legs and adopts a variety of body and neck positions depending on the feathers being preened. The contour feathers are raised during preening, and after preening the bird shakes its body and then relaxes the feathers. Eyes are always shut during actual preening. Allopreening is initiated by gently pecking around the head area. It may be initiated by either sex and may also be directed at offspring. The individual being preened often has eyes half-shut and tilts its head up or at an angle to expose areas to be preened. The rest of the body is in the relaxed posture. Allopreening is usually done to the head and neck areas that individuals are not able to reach themselves. It often precedes other pair-bonding behaviour such as duetting and copulation.

Curious Posture Figure 1(b)
This is given when an Aldabra Rail encounters a novel stimulus such as humans and/or their equipment. The context of it is very similar to that of the Alert Posture, although the latter is used when a bird's attention is drawn to something further away, and is most often seen when territorial intruders are discovered. The neck is stretched and held on or close to the horizontal. The body is also horizontal and the head is often cocked at an angle. The neck is then often retracted and extended at a new angle. The legs may be in a half-crouch, as if ready to flee. The contour feathers are not raised. The bird may peck and pull at things, including clothing, shoes, fingers or toes, particularly if small, rapid movements are made that attract attention.

Alert Posture
This is used when a bird is in a similar state of arousal as for the Curious Posture, but is not restricted to investigating novel stimuli. It is very similar to the upright posture, only the undertail coverts are not displayed. In this posture, a bird holds its body very upright and its neck fully or partially stretched. The head is held horizontal, so the throat patch is partially obscured. The tail is kept pointing down and the coverts and contour feathers are not fanned. This posture probably evolved out of a need to see over a greater distance.

Territorial Defence Display Figure 1(c)
This display is given when another adult Aldabra Rail intrudes on a territory, or when a boundary is being disputed, and is different from the Nest Defence Display. The body is held horizontally and the neck pulled in. The head is horizontal, partially obscuring the throat patch. The tail is raised and coverts fully fanned. The contour feathers are all raised, greatly increasing the apparent size of the bird. Wings may be held slightly away from the body, with primary feathers partially splayed. Birds may approach each other and move from side to side, flicking the tail with each step. If neither protagonist retreats, they adopt the Upright Posture and typically a fight will ensue.

Upright Posture Figure 1(d)
This posture is used in a territorial defence context. The body position is very upright, and the neck is fully extended and held vertically. The head is horizontal, displaying the throat patch. The tail is held horizontal or pointing slightly downwards with coverts fully fanned. Contour feathers may be slightly raised. It is usually preceded by the Territorial Defence Display and followed by Chasing or Fighting. It is also used during Aggression Displays, by the aggressor.

Chasing
After the Upright Posture is given by one or both individuals, if one bird backs down it will be chased, if not, they will fight. The chasing bird holds its neck up and out and displays both the throat patch and the undertail coverts, whereas the fleeing bird hold the neck closer to the body and keeps the tail down, hiding the undertail coverts. Both birds flap their wings to assist in manoeuvring. Chasing is also used by adult birds when expelling their offspring from the natal territory, and is also used in a trespassing situation, against the young of other birds, either when young trespass into a neighbouring territory or when adults intrude into another pair's territory. The bird doing the chasing pursues and pecks the other bird vigorously; the latter runs away. In a trespassing situation the chick constantly gives a distress call. A parent of the young being attacked will usually run immediately towards the distress call and attack or chase the other adult.

Fighting
Birds circle each other or approach head-on in the Territorial Defence Stance. They then suddenly adopt the Upright Posture (fully displaying the throat patch) and attack, leaping and kicking each either simultaneously, while flapping their wings vigorously and aiming powerful blows with their bills. They may land on their feet and repeatedly circle and jump at each other, alternating between the Upright and Territorial Defence postures. Alternatively, they fall to the ground, facing each other while balancing on their tails and wings and kicking vigorously in typical rallid fashion. Fights are very vigorous and occasionally result in serious injury or death.

Bill Greeting Display Figure 1(e)
If paired birds have been foraging separately, they may greet one another when reunited by trotting towards the other with neck partially stretched and vertical and the head horizontal, displaying the throat patch. Both make soft, purring vocalisations and occasionally touch bills. Contour feathers are slightly raised and undertail coverts fanned, but the white throat patch is concealed by a low head position and retracted neck once birds meet. After greeting, birds may resume foraging, allopreen or duet.

Singing Posture Figure 1(f)
This is used by individuals either when singing singly or when duetting. It is often preceded by the Greeting Display if singing is done as a pair-bonding behaviour. When duetting, birds often run towards each other and stand very close, although the direction faced seems arbitrary. In the Singing Posture the bill is held slightly below the horizontal plane and the neck is stretched and angled forward and up. The body is angled slightly upwards and the legs are relatively wide apart and in a partial crouch. The song is of variable length, and after the Singing Posture birds usually adopt the Relaxed Posture. However, I never saw the roosting and waking duets, which are normally given from each individual's roosting site before it is light enough to see clearly. On one occasion, when I was close to roosting birds in the early morning, they duetted from their roosting sites. I found one of the roosts when the bird left it after the duet.

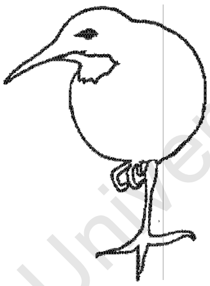
Copulation Figure 1(g,h,i & j)
A series of highly ritualised postures are used before, during and after coitus. I describe here a complete series of events. However, unless specified, any one or more of the elements described may be missing from any given event. The sequence of events is fixed with the exception of the initiation. Incomplete events may be due to the presence of observers, but I believe cloacal contact does not necessarily form part of the pair-bonding copulatory act, and when absent, the behaviour is referred to as Pseudo-copulation. Pseudo-copulation is frequently seen months before reproduction begins and after young have left the natal territory, and could be used in courtship. Copulation often follows duetting and is initiated in one of two ways. A bird may adopt the Approach Posture, moving towards its mate with the neck stretched vertically, body angled up (but not as much as in the Upright Posture), showing throat patch and undertail coverts. Alternatively, initiation of the sequence may begin when a bird faces away from its mate and performs the Invitation Display. This is present in every copulation sequence. In the Invitation Display the bird arches its neck and points the bill downwards at around 30°. The body is angled upwards and the bird waddles forward a few paces in a half crouch with its legs spread quite wide, slowing quickly to standstill. The tail points down, the undertail coverts are fanned and the wings are folded. The neck is arched, but is neither fully stretched nor retracted. The head and bill are held straight, pointing forwards and downwards at around 30°. If the mate does not ignore the Invitation Display, it adopts the Approach Posture and walks or trots towards the displaying bird. The approaching bird then mounts the inviting bird and crouches on the latter's back, its body almost horizontal, tarsi and feet touching the other bird's back, the head pointing down at 45°, the wings folded and the undertail coverts fully fanned. The mounted bird then raises its tail while still displaying the undertail coverts. Its head and neck position change repeatedly until it is dismounted, including the neck almost retracted, highly arched or straight (but never stretched), and the bill pointing vertically downwards, 30° forwards or even backwards. These changes in neck and bill postures are probably related to the practicalities of balance rather than having a specific contextual meaning. The mounting bird then treads on the other bird's back a few times. It then leans back, fluttering its wings for stability, and moves its tail under that of the inviting bird's to make cloacal contact, usually for no more than one or two seconds. It then dismounts and performs the Post-copulatory Display. In this display, the bird walks in a semi-circle around the front of its mate, who remains in the Invitation Display. The wings are fanned and contour feathers are raised, with the head held low and the neck neither fully stretched nor retracted, in the same way as in the Nest Defence Display. The Post-copulatory Display was described by Frith (1977), who conjectured that it was restricted to extra-pair copulations; this is not the case. Normally the entire copulation sequence is then repeated with roles reversed.

Nest defence displays Figure 1(k,l)

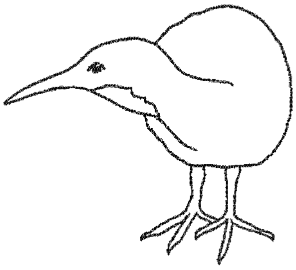
These are given to any intruder that approaches too close to the nest or chicks, except for crabs, which are vigorously pecked. For other intruders, birds rush towards the intruder in the Full Nest Defence Display (Figure 1(k)), with wings held fully opened, at right angles to the body and twisted downwards (i.e. with the feathers pointing upwards). The body is held low and horizontal and the head is kept close to the body, facing the intruder while obscuring the throat patch. The tail is held horizontally and the undertail coverts are fully fanned. The mantle and back feathers are slightly raised. The displaying bird stops about a metre from the intruder and walks to and fro in front of the intruder. It may also make very rapid attacks with a single, jabbing peck at the intruder. If the intruder does not advance towards the nest, the displaying bird may circle it. The intensity of the display decreases quite rapidly, and the bird may adopt the Partial Nest Defence Display Figure 1(l)), with both wings being partially folded or, more usually, the wing on the opposite side to the intruder completely folded. This is followed by a Staring Display identical to the Territorial Defence Display, except the contour feathers are completely raised and the displaying bird usually stands still and stares directly at the intruder; the contour feathers are gradually lowered as the display ends. If a mate is present and displaying, an incubating or brooding bird tends to stay on the nest until an intruder is very close. When the intruder gets too close, the bird will leave the nest in the Full Nest Defence Display, either charging at the intruder or moving off the side of the nest and displaying (possibly in an attempt to divert attention away from the nest). When an intruder attempts to raid the nest the bird that was incubating stands next to or over the nest and repeatedly rushes the intruder, making powerful, jabbing pecks and giving a loud, piercing squeal that is only ever heard in this context (see also Huxley & Wilkinson 1977). Birds often follow a retreating intruder, sometimes in the Partial Nest Defence Display. Birds occasionally stop mid-display to feed (Penny & Diamond 1971, this study).

Provisioning Posture

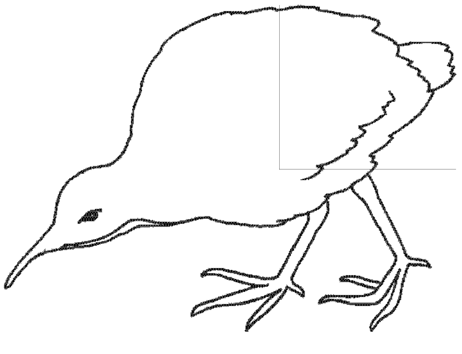
When "courtship feeding" or provisioning young, the Rail will approach the intended recipient, carrying the food item in the bill, and adopt the Provisioning Posture. It points its head vertically downwards so the bill almost touches the ground. The rest of its body is in the relaxed posture. This posture is maintained until the food item has been taken from the bill. If a chick drops food or struggles to handle it, the adult will pick it up repeatedly, sometimes breaking the item into smaller pieces. The chick usually approaches the adult in this posture from the side and underneath, small chicks even standing under the chest of the displaying bird.



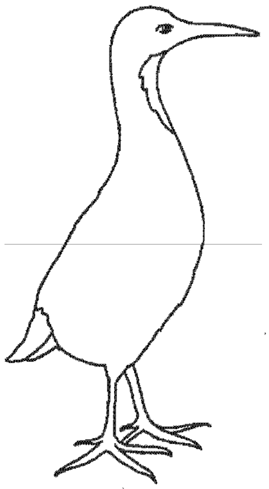
(a) Relaxed Posture



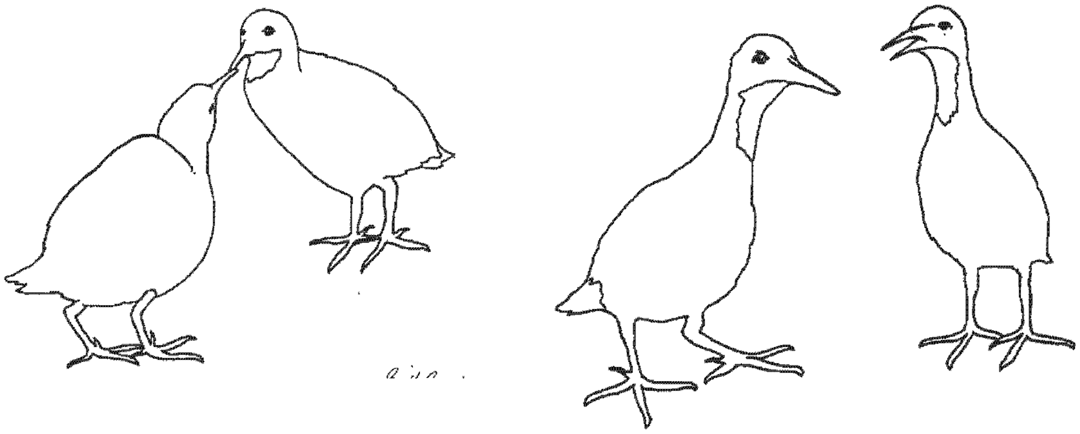
(b) Curious Posture



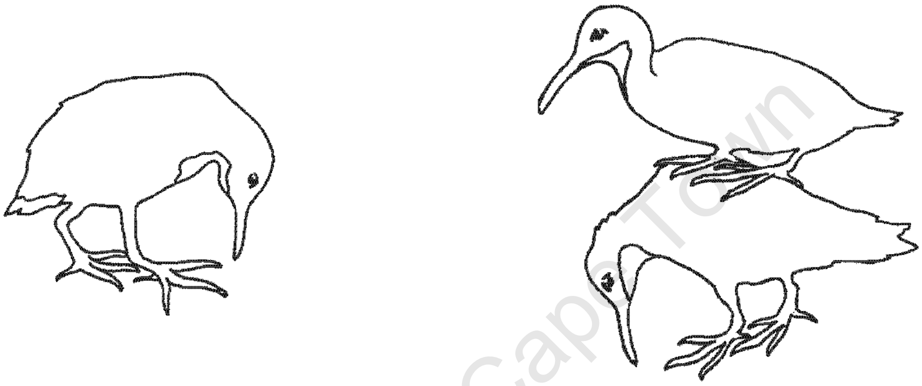
(c) Territorial Defence Display



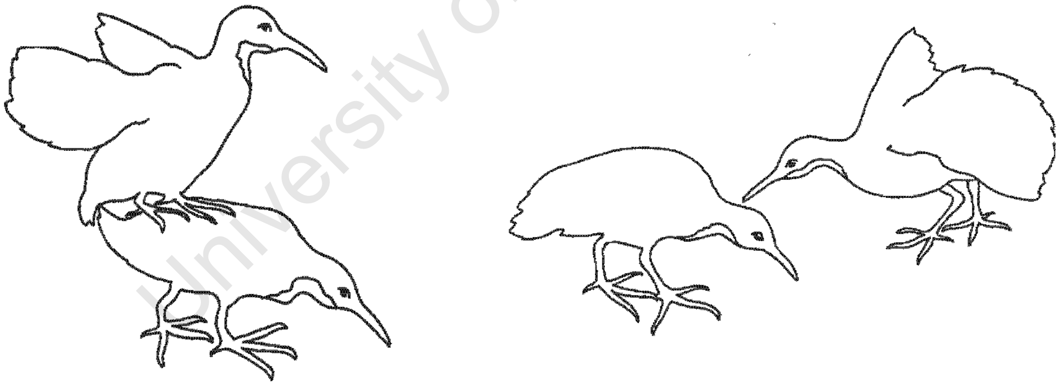
(d) Upright Posture



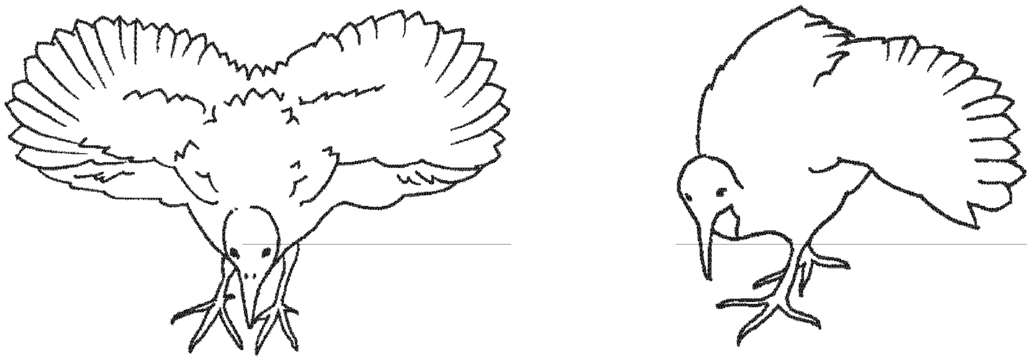
(e) Bill Greeting Display (f) Singing Posture



(g) Invitation Display (h) Mounting

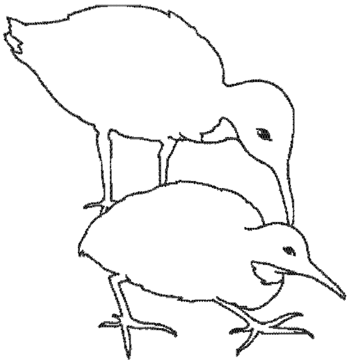


(i) Coitus (j) Post-copulatory Display



(k) Full Nest Defence Display (l) Partial Nest Defence Display

Figure 1 (continued)



(m) Aggressive and Submissive displays

Figure 1. Postures and displays of the Aldabra Rail, based on photographs and field observations (see text for details).

Aggressive and Submissive displays Figure 1(m)
This is distinct from the Territorial Defence Display, and differs from the positions described for fighting, as only one bird is aggressive in this instance. The Aggressive/Submissive displays form part of intra-pair behaviour and when adults expel young from the natal territory. When a bird performs the Aggressive Display, it adopts the Upright Posture while approaching another bird. It then stands over the other bird and leans forward when attacking. An attacking bird may also grab the other bird's head or neck in its bill or push the other bird with its chest. The bird being attacked either adopts a Submissive Posture or flees. In the Submissive Posture, a bird crouches on the ground with the neck retracted and the head pointing down and away from the aggressor, hiding the throat patch from the attacker. The tail is pointed down, no undertail coverts are visible, the wings are kept folded and the contour feathers are flattened. Outside the breeding season, I only observed intra-pair aggression arising from direct competition for food. During the breeding season it could be part of ritualised pair-bonding behaviour, or arise over squabbling for food. Where the sex of pairs in aggressive interactions was known, the aggressor was usually, but not exclusively, male. On one occasion, the female of a pair lost consciousness for about 20 minutes after being attacked by the male (M Betts pers. comm.).

Interactions with other species

Huxley (1979) describes a mutualistic relationship between Aldabra Rails and Aldabra Giant Tortoises *Dipsochelys dussumieri*. The Rails are alleged to glean flies, dead skin or ectoparasites from the Giant Tortoises, which in turn assist Rails by adopting a distinctive posture, exposing the full surface of skin for Rails to glean. This relationship, however, has never been seen by me or anyone else with whom I have worked or to whom I have spoken to about it. On the contrary, on several occasions I have seen Aldabra Rails foraging in the leaf litter less than a metre from Giant Tortoises, and never has either species shown the slightest interest in the other.

Aldabra Rails have an immediate fleeing response to the sudden appearance of a large bird. In one instance a Green-backed Heron *Butorides striatus* landed on top of a bush about two metres from a pair of Aldabra Rails with chicks. At the sound of the heron landing, both adults instinctively gave an alarm call and ran extremely quickly for cover. I have seen similar reactions to the sudden appearance of boobies and frigatebirds. This trait is shared with the majority of other rallid species (Taylor & van Perlo 1998, B. Taylor pers. comm.). Furthermore, the Aldabra Rails are very reluctant to venture into the open. Without recourse to raptor avoidance, this behaviour is difficult to explain. Although there are no extant, predatory birds on Aldabra large enough to kill adult Aldabra Rails, it is possible that some raptorial species either regularly visited Aldabra or were resident there in the past. It may also be that Aldabra Rails have retained this instinct from before they colonised Aldabra, as there are numerous raptor species on Madagascar that could prey on rails (Rand, 1936, Sinclair and Langrand 1998).

There are several species on Aldabra that exhibit predatory behaviour, some of which are considerably larger than Aldabra Rails. These include the massive, terrestrial Robber Crab *Birgus latro*, ~~Mangrove Crab *Cardisoma carniflex*,~~ Madagascar Kestrel *Falco newtoni*, Madagascar Coucal *Centropus toulou*, Pied Crow *Corvus albus*, and the introduced Black (or Ship) Rat *Rattus rattus* and Domestic Cat *Felis catus*. The presence of the aforementioned crabs and birds, all indigenous to Aldabra and known nest predators, has probably ensured the retention of strong nest defence instincts in Aldabra Rails (Benson 1967, Frith

1976, R. Wanless unpubl. data, this study). Of the species listed, only the Cat is a genuine predator of adult Aldabra Rails.

Aldabra Rails easily overcome Robber Crabs in competition for food and the latter have never been seen to pose a significant threat to Rail nests or chicks. Nevertheless, parents treat them as if they were nest predators, and peck them until they retreat. Large Mangrove Crabs (which are not restricted to mangroves, but found throughout terrestrial Aldabra) are similarly attacked, and occasionally killed for food.

I never witnessed Kestrels or Coucals interacting with Aldabra Rails. However, Madagascar Kestrels prey on adult and juvenile passerine species on Aldabra (R. Wanless unpubl. data), and may well take downy chicks of the Rail. Further, Huxley (1982) reports that the Rails will always attack Coucals, especially at the nest. I have also seen Coucals raiding nests of other species, including taking quite large squabs of the Aldabra Turtle Dove *Streptopelia picturata copingeri*. Pied Crows on Aldabra are opportunistic predators. Wanless and Jupiter (in press) report them killing adult Turtle Doves, but this occurred in unusual, human-mediated circumstances. Aldabra Rails have successfully defended nests and chicks against Pied Crows (pers. obs.). Aldabra Rails were occasionally seen harassing Turtle Doves during the breeding season, but the reasons for this are unclear. They do not compete for food, as the latter species is vegetarian, and the Turtle Dove is unlikely to pose any threat to Aldabra Rail chicks of any age. Aldabra Drongos *Dicrurus aldabranus* have occasionally been seen making aerial attacks on Aldabra Rails. The Rails always retreated when under attack, but these are unlikely to ever be more than a nuisance to Rails.

A few interactions have been noted between Aldabra Rails and Black Rats (Penny & Diamond 1971, Frith 1977, Huxley 1982, Wanless in press). With one exception, Black Rats retreated in the face of aggression from Aldabra Rails. The exception occurred when a pair of Aldabra Rails being held in captivity killed an adult Black Rat that entered their enclosure at night (Wanless in press). Aldabra Rails are very attentive parents, during both the incubation and rearing phases (see above). Black Rats probably steal eggs or take individual downy chicks opportunistically, but are unlikely to do so when parents are present. I conclude that Black Rats are not a significant predator of Aldabra Rail eggs or chicks and pose little or no threat to adult Aldabra Rails (Wanless in press).

In Chapter 1, I argue that Cats are largely responsible for the local extinction of Aldabra Rails on Aldabra. Two records of Aldabra Rail behaviour towards Cats strongly support that argument (Huxley 1982, Hambler *et al.* 1993). In both circumstances, Aldabra Rails adopted a Nest or Territory Defence Posture rather than flee. This leads me to conclude that Aldabra Rails do not have an appropriate (i.e. fleeing) response to Cats, and do not treat them as potential predators.

ACKNOWLEDGMENTS

Rachel Wiseman and Richard White helped locate and monitor chicks, and Richard White helped collect much of the data relating to Rail nests; he also made observations of their behaviour and interactions with other species. His patience in watching incubation-shifts, a monumentally boring and uncomfortable task, is greatly appreciated. Gabby Raaff produced the beautiful drawings that illustrate the various postures and displays. Some of the descriptive terminology I used to classify and describe the different postures and displays were originally used by Chris Huxley, and a few of his observations of their behaviour were new to me. Barry Taylor and John Cooper greatly improved an earlier draft of this chapter.

Can the Aldabra White-throated Rail *Dryolimnas cuvieri aldabranus* fly?

Wanless, R.M. in press. Can the Aldabra White-throated Rail *Dryolimnas cuvieri aldabranus* fly? *Atoll Research Bulletin.*

ABSTRACT

The Aldabra White-throated Rail *Dryolimnas cuvieri aldabranus*, endemic to Aldabra Atoll (Seychelles), has long been considered the last flightless bird of the western Indian Ocean islands. However, this study represents the first quantitative approach to determine the rail's capacity for sustained, level flight. Morphological, physiological and behavioral aspects are considered in determining its actual and theoretical capacity for flight. Wing loading calculations suggest that it can fly. All other evidence, most importantly the greatly reduced breast musculature, indicate flightlessness. The Aldabra Rail originated from Madagascar, where the nominate form is volant, but only weakly. The Aldabra Rail evolved as a ground forager in the absence of any adult predation, i.e. without any apparent need to fly. This, combined with energetic advantages to becoming flightless, has led to the Aldabra Rail losing its capacity for flight.

INTRODUCTION

Aldabra Atoll (9° 24' S, 46° 20' E) is home to the last flightless bird of the western Indian Ocean islands (Hambler *et al.* 1993): the Aldabra White-throated Rail (hereafter Aldabra Rail) *Dryolimnas cuvieri aldabranus*. It is currently classified a subspecies of the nominate form on Madagascar (Benson, 1967). A major difference between the two taxa is that the form on Madagascar can fly, whereas *aldabranus* is thought to be flightless (Taylor & van Perlo 1998).

The Aldabra Rail's ability to fly has been questioned since it was first studied. Abbott (in Ridgway 1895) describes them "flying at each other like game cocks". Frith (1977) more accurately describes this fighting behavior, making it clear that they leap at each other using their wings to assist them but certainly not flying. Abbott also states "that they are not absolutely flightless, but use their wings to assist them in leaping…" (Ridgway 1895). Benson (1967) considered the wings so short as to render them "virtually flightless". Penny & Diamond (1971) report flying abilities similar to those of the domestic chicken, qualified by describing flapping as used to assist in jumping, which presumably means they did not believed it capable of powered flight. While such observations are commonplace on Aldabra, there are no records of Aldabra Rails actually flying — defined here as sustained, level flight.

The Aldabra Rail's inability to fly has thus far been inferred from behavioral observations only (principally a lack of observations of birds flying), and there has been no quantitative approach to actually determine their capacity for flight. I here describe investigations made into their actual and theoretical capacity for flight using morphological, physiological and behavioral data.

METHODS

Wing-loading is the ratio between total wing area and body weight. Wing area was measured for 12 individuals by tracing the outline of the right wing in a notebook, superimposing this on grid paper and counting the number of squares more than half-covered by the wing. The resultant area was doubled for total wing area. Birds were weighed at capture using a 500 g Salter spring balance.

Two rails, trapped as part of a separate study, died in captivity. Their breast muscles (pectoralis and supracoracoideus) were completely excised when freshly dead. The tissue was weighed using a 50 g Pesola spring balance and compared against their body weight at capture.

The length of each primary feather was measured on both wings of four Aldabra Rails. This was done by inserting a ruler between the feathers until it was pressed gently against the skin of the wing, where the feather being measured exited the skin. The feather was then flattened against the ruler and measured. The lengths of all primaries on each wing were then summed and the percentage difference between summed values for right and left wings calculated.

Observations of Aldabra Rails were made in situations where flight would have been advantageous. These include catching birds by hand and, on one occasion, gently launching a bird about three meters up into the air. I carefully watched its behavior in the air and on landing.

RESULTS

Results of wing-loading calculations for Aldabra Rails (Table 1) are all well within theoretical limits for volant birds, with a mean of 0.62 g/cm² (± 0.08, n=12).

Aldabra Rails in the hand have noticeably small breast muscles. Dissection of two dead specimens corroborated this impression, showing very small breast muscles relative to total body weight (Table 2). Aldabra Rails handled throughout the year (both newly caught and retrapped individuals) show no perceptible change in breast musculature, thus a larger sample size of breast weights (necessarily destructive) is unlikely to produce substantially different results.

Table 1. Wing area, total mass at capture and wing loading of adult Aldabra Rails.

Total wing area (cm^2)	Mass (g)	Wing loading (g/cm^2)
354	230	0.65
294	180	0.61
230	185	0.80
272	185	0.68
322	215	0.67
258	161	0.62
340	205	0.60
246	152	0.62
350	182	0.52
242	157	0.65
276	144	0.52
306	165	0.53

Table 2. Weight of breast muscle, total mass at capture and percentage of total body weight that breast muscle constitutes for two Aldabra Rails.

Breast muscle (g)	Mass (g)	%
7.15	164	4.4
5.85	201	2.9

The fluctuating asymmetry in left and right primary feather lengths (Table 3) showed a consistent, unexpected bias towards longer primaries on the right wing. Further, the difference increased as primary length increased.

Table 3. Fluctuating asymmetry in cumulative right- and left-wing primary feather lengths of four Aldabra Rails.

Right Wing	Left Wing	% difference
735	716	2.7
728	716	1.7
791	757	4.5
761	734	3.7

Anecdotal evidence of Aldabra Rails being unable to fly is unequivocal. In the first incident, an Aldabra Rail was cornered on a rocky ledge overhanging open water. As it leaped, fluttering, past me, I lunged for it. I failed to catch it and instead accidentally knocked it off its path while it was in mid air. Despite its flapping, it did not gain any lift or appreciable forward movement. It could not correct its course and fell quite rapidly into the water below. It swam easily to the shore and clambered out. It was seen foraging nearby within two minutes.

A second incident occurred after I had succeeded in cornering an adult bird that never attempted to fly when I captured it by hand. After briefly examining it, I took it outside and released it by gently tossing it up and away (no more than three meters vertical or horizontal). It flapped vigorously, but appeared uncoordinated in the air. I do not believe its flapping contributed any lift at all. It sawed, rolled and pitched before landing quite heavily and awkwardly. It then ran off without any obvious difficulty and was seen several times in the same vicinity over the next two days.

The last incident occurred when a free-living Aldabra Rail was discovered entangled by a metal band on its right tarsus with a mat of long, human hair. How this came about is not known. The bird held its right leg in the air and did not use it at all. Two of us pursued it and caught it after about three minutes. It was able to hop, and by flapping its wings managed to move quite rapidly. On several occasions it leapt off rocks and fallen tree trunks. At no stage did it ever gain lift, nor did it attempt to fly. It appeared to be terrified and, I believe, would have flown if it could have.

DISCUSSION

A capacity for flight is determined by three main factors: wing loading, power (≈ relative volume of flight muscles) and flapping rate (Pennycuick 1975). Upon handling an Aldabra Rail it became apparent that calculating wing loading would be uninformative. Their wings are not substantially reduced (*contra* Benson 1967) and they have a wing loading that lies within theoretical limits for flight (Pennycuick 1975). They have, however, lost most of their breast musculature (this is very apparent when a bird is in the hand). Thus, they lack the power required for level flight, violating the second requirement for flight. The persistence of a large wing area, contrary to expectations of a flightless form, can be understood in the light of their nest- and chick-defense displays. In these displays wings are fanned and held vertically, which has the effect of greatly increasing the apparent size of the displaying bird (R. Wanless unpubl. data). Thus any selective pressure to evolve much smaller wings is counteracted. Asymmetry in flight organs may not compromise their efficacy in defensive displays, but would have a significant, detrimental effect in flight (Shykoff & Möller 1999, Cadee 2000).

The flight muscles of volant birds constitute around 15% of their body weight, with exceptions tending to be higher than this (Livezey & Humphrey 1986, Schmidt-Nielsen 1990). Those of the Aldabra Rail (Table 1) are considerably below the 15% average for volant birds. The bulk of flight muscles is simply too small for Aldabra Rails to engage in powered flight.

Aldabra Rails undergo an annual, simultaneous, post-breeding moult (Penny & Diamond 1971, R. Wanless unpubl. data) and are unequivocally flightless at this time. Further, the primary and secondary feathers are generally *extremely* abraded by the onset of moult (pers. obs.); it is difficult to imagine the tattered feathers being useful in flight.

The energetic advantages of becoming flightless are well known (McNab 1994, Feduccia 1996). Flight muscles are amongst the most energetically demanding organs in birds (Feduccia 1996). Reduction in the bulk of flight muscles may be adaptive (genetically based), or a result of under-development or atrophy through disuse. Whatever the cause, reduction results in a considerable energetic saving for birds that no longer need to fly. Further, powered flight *per se* demands a high metabolic rate; evolution of flightlessness allows concomitant evolution of a lowered metabolic rate, a trait common to several species of flightless rails (McNab 1994).

White-throated Rails on Madagascar (the source population for Aldabra Rails) are, at best, marginal flyers and were probably weakly volant at the time they colonized Aldabra (Benson 1967, Benson & Penny 1971, Taylor & van Perlo 1998). These birds could not have stored large amounts of fat while retaining an ability to fly due to the negative impact that this would have on wing-loading. Patrikeev (1995, in Taylor & van Perlo 1998) describes a population of Common Coot *Fulica atra* where adults become so fat after migration that 70-80% of the population cannot fly when chased. For all landbirds on Aldabra, reproduction is closely tied to the wet NW monsoon (Benson & Penny 1971). Variable timing and amount of rainfall means that in some years rains may be late and/or far below average (Farrow 1971, Betts 2000). An ability to store large reserves of energy (fat) at times of abundance would be advantageous in surviving the long, dry, SE monsoon and allow birds to achieve breeding condition early in the wet season. It would further serve as an energetic insurance policy, should rains be late or fail. The original impetus for Aldabra Rails becoming flightless may well have been storing fat as an adaptation to surviving periods of scarcity.

CONCLUSION

Aldabra Rails are ground foragers and in the absence of predation on adults, evolved on Aldabra without need to fly; even on Madagascar, where numerous predators exist, they seldom fly (Taylor & van Perlo 1998). There are numerous and considerable energetic advantages to becoming flightless, a condition to which rallids are predisposed (Taylor & van Perlo 1998). The complete absence of observations of the Aldabra Rail flying, especially in circumstances where flight would be highly advantageous, has led to a general belief that they are flightless. Their complete, simultaneous, post-breeding molt renders adults unequivocally flightless for a time without any adverse consequences. Further, flight feathers are not maintained and become extremely abraded, rendering them highly ineffective as organs for flight. While wing loading calculations suggest the Aldabra Rail could theoretically fly, the insubstantial bulk of flight muscles and asymmetry of their wings militates against this completely. I conclude that the Aldabra Rail cannot fly.

ACKNOWLEDGEMENTS

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IUCN/SSC Guidelines For Re-Introductions
Prepared by the SSC Re-introduction Specialist Group *
Approved by the 41st Meeting of the IUCN Council, Gland Switzerland, May 1995

INTRODUCTION

These policy guidelines have been drafted by the Re-introduction Specialist Group of the IUCN's Species Survival Commission (1), in response to the increasing occurrence of re-introduction projects worldwide, and consequently, to the growing need for specific policy guidelines to help ensure that the re-introductions achieve their intended conservation benefit, and do not cause adverse side-effects of greater impact. Although IUCN developed a Position Statement on the Translocation of Living Organisms in 1987, more detailed guidelines were felt to be essential in providing more comprehensive coverage of the various factors involved in re-introduction exercises.

These guidelines are intended to act as a guide for procedures useful to re-introduction programmes and do not represent an inflexible code of conduct. Many of the points are more relevant to re-introductions using captive-bred individuals than to translocations of wild species. Others are especially relevant to globally endangered species with limited numbers of founders. Each re-introduction proposal should be rigorously reviewed on its individual merits. It should be noted that re-introduction is always a very lengthy, complex and expensive process.

Re-introductions or translocations of species for short-term, sporting or commercial purposes - where there is no intention to establish a viable population - are a different issue and beyond the scope of these guidelines. These include fishing and hunting activities.

This document has been written to encompass the full range of plant and animal taxa and is therefore general. It will be regularly revised. Handbooks for re-introducing individual groups of animals and plants will be developed in future.

CONTEXT

The increasing number of re-introductions and translocations led to the establishment of the IUCN/SSC Species Survival Commission's Re-introduction Specialist Group. A priority of the Group has been to update IUCN's 1987 Position Statement on the Translocation of Living Organisms, in consultation with IUCN's other commissions.

It is important that the Guidelines are implemented in the context of IUCN's broader policies pertaining to biodiversity conservation and sustainable management of natural resources. The philosophy for environmental conservation and management of IUCN and other conservation bodies is stated in key documents such as "Caring for the Earth" and "Global Biodiversity Strategy" which cover the broad themes of the need for approaches with community involvement and participation in sustainable natural resource conservation, an overall enhanced quality of human life and the need to conserve and, where necessary, restore ecosystems. With regards to the latter, the re-introduction of a species is one specific instance of restoration where, in general, only this species is missing. Full restoration of an array of plant and animal species has rarely been tried to date.

Restoration of single species of plants and animals is becoming more frequent around the world. Some succeed, many fail. As this form of ecological management is increasingly common, it is a priority for the Species Survival Commission's Re-introduction Specialist Group to develop guidelines so that re-introductions are both justifiable and likely to succeed, and that the conservation world can learn from each initiative, whether successful or not. It is hoped that these Guidelines, based on extensive review of case - histories and wide consultation across a range of disciplines will introduce more rigour into the concepts, design, feasibility and implementation of re-introductions despite the wide diversity of species and conditions involved.

Thus the priority has been to develop guidelines that are of direct, practical assistance to those planning, approving or carrying out re-introductions. The primary audience of these guidelines is, therefore, the practitioners (usually managers or scientists), rather than decision makers in governments. Guidelines directed towards the latter group would inevitably have to go into greater depth on legal and policy issues.

1. DEFINITION OF TERMS

"Re-introduction": an attempt to establish a species(2) in an area which was once part of its historical range, but from which it has been extirpated or become extinct (3) ("Re-establishment" is a synonym, but implies that the re-introduction has been successful).

"Translocation": deliberate and mediated movement of wild individuals or populations from one part of their range to another.

"Re-inforcement/Supplementation": addition of individuals to an existing population of conspecifics.

"Conservation/Benign Introductions": an attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and eco-geographical area. This is a feasible conservation tool only when there is no remaining area left within a species' historic range.

2. AIMS AND OBJECTIVES OF RE-INTRODUCTION

a. Aims:

The principle aim of any re-introduction should be to establish a viable, free-ranging population in the wild, of a species, subspecies or race, which has become globally or locally extinct, or extirpated, in the wild. It should be re-introduced within the species' former natural habitat and range and should require minimal long-term management.

b. Objectives:

The objectives of a re-introduction may include: to enhance the long-term survival of a species; to re-establish a keystone species (in the ecological or cultural sense) in an ecosystem; to maintain and/or restore natural biodiversity; to provide long-term economic benefits to the local and/or nataional economy; to promote conservation awareness; or a combination of these.

3. MULTIDISCIPLINARY APPROACH

A re-introduction requires a multidisciplinary approach involving a team of persons drawn from a variety of backgrounds. As well as government personnel, they may include persons from governmental natural resource management agencies; non-governmental organisations; funding bodies; universities; veterinary institutions; zoos (and private animal breeders) and/or botanic gardens, with a full range of suitable expertise. Team leaders should be responsible for coordination between the various bodies and provision should be made for publicity and public education about the project.

4. PRE-PROJECT ACTIVITIES

4a. BIOLOGICAL

(i) Feasibility study and background research

- An assessment should be made of the taxonomic status of individuals to be re-introduced. They should preferably be of the same subspecies or race as those which were extirpated, unless adequate numbers are not available. An investigation of historical information about the loss and fate of individuals from the re-introduction area, as well as molecular genetic studies, should be undertaken in case of doubt as to individuals' taxonomic status. A study of genetic variation within and between populations of this and related taxa can also be helpful. Special care is needed when the population has long been extinct.
- Detailed studies should be made of the status and biology of wild populations(if they exist) to determine the species' critical needs. For animals, this would include descriptions of habitat preferences, intraspecific variation and adaptations to local ecological conditions, social behaviour, group composition, home range size, shelter and food requirements, foraging and feeding behaviour, predators and diseases. For migratory species, studies should include the potential migratory areas. For plants, it would include biotic and abiotic habitat requirements, dispersal mechanisms, reproductive biology, symbiotic relationships (e.g. with mycorrhizae, pollinators), insect pests and diseases. Overall, a firm knowledge of the natural history of the species in question is crucial to the entire re-introduction scheme.
- The species, if any, that has filled the void created by the loss of the species concerned, should be determined; an understanding of the effect the re-introduced species will have on the ecosystem is important for ascertaining the success of the re-introduced population.
- The build-up of the released population should be modelled under various sets of conditions, in order to specify the optimal number and composition of individuals to be released per year and the numbers of years necessary to promote establishment of a viable population.
- A Population and Habitat Viability Analysis will aid in identifying significant environmental and population variables and assessing their potential interactions, which would guide long-term population management.

(ii) Previous Re-introductions

- Thorough research into previous re-introductions of the same or similar species and wide-ranging contacts with persons having relevant expertise should be conducted prior to and while developing re-introduction protocol.

(iii) Choice of release site and type

- Site should be within the historic range of the species. For an initial re-inforcement there should be few remnant wild individuals. For a re-introduction, there should be no remnant population to prevent disease spread, social disruption and introduction of alien genes. In some circumstances, a re-introduction or re-inforcement may have to be made into an area which is fenced or otherwise delimited, but it should be within the species' former natural habitat and range.
- A conservation/ benign introduction should be undertaken only as a last resort when no opportunities for re-introduction into the original site or range exist and only when a significant contribution to the conservation of the species will result.
- The re-introduction area should have assured, long-term protection (whether formal or otherwise).

(iv) Evaluation of re-introduction site

- Availability of suitable habitat: re-introductions should only take place where the habitat and landscape requirements of the species are satisfied, and likely to be sustained for the for-seeable future. The possibility of natural habitat change since extirpation must be considered. Likewise, a change in the legal/ political or cultural environment since species extirpation needs to be ascertained and evaluated as a possible constraint. The area should have sufficient carrying capacity to sustain growth of the re-introduced population and support a viable (self-sustaining) population in the long run.
- Identification and elimination, or reduction to a sufficient level, of previous causes of decline: could include disease; over-hunting; over-collection; pollution; poisoning; competition with or predation by introduced species; habitat loss; adverse effects of earlier research or management programmes; competition with domestic livestock, which may be seasonal. Where the release site has undergone substantial degradation caused by human activity, a habitat restoration programme should be initiated before the re-introduction is carried out.

(v) Availability of suitable release stock

- It is desirable that source animals come from wild populations. If there is a choice of wild populations to supply founder stock for translocation, the source population should ideally be closely related genetically to the original native stock and show similar ecological characteristics (morphology, physiology, behaviour, habitat preference) to the original sub-population.
- Removal of individuals for re-introduction must not endanger the captive stock population or the wild source population. Stock must be guaranteed available on a regular and predictable basis, meeting specifications of the project protocol.
- Individuals should only be removed from a wild population after the effects of translocation on the donor population have been assessed, and after it is guaranteed that these effects will not be negative.
- If captive or artificially propagated stock is to be used, it must be from a population which has been soundly managed both demographically and genetically, according to the principles of contemporary conservation biology.
- Re-introductions should not be carried out merely because captive stocks exist, nor solely as a means of disposing of surplus stock.
- Prospective release stock, including stock that is a gift between governments, must be subjected to a thorough veterinary screening process before shipment from original source. Any animals found to be infected or which test positive for non-endemic or contagious pathogens with a potential impact on population levels, must be removed from the consignment, and the uninfected, negative remainder must be placed in strict quarantine for a suitable period before retest. If clear after retesting, the animals may be placed for shipment.
- Since infection with serious disease can be acquired during shipment, especially if this

is intercontinental, great care must be taken to minimize this risk.

- Stock must meet all health regulations prescribed by the veterinary authorities of the recipient country and adequate provisions must be made for quarantine if necessary.

(vi) Release of captive stock

- Most species of mammal and birds rely heavily on individual experience and learning as juveniles for their survival; they should be given the opportunity to acquire the necessary information to enable survival in the wild, through training in their captive environment; a captive bred individual's probability of survival should approximate that of a wild counterpart.
- Care should be taken to ensure that potentially dangerous captive bred animals (such as large carnivores or primates) are not so confident in the presence of humans that they might be a danger to local inhabitants and/or their livestock.

4b. SOCIO-ECONOMIC AND LEGAL REQUIREMENTS

- Re-introductions are generally long-term projects that require the commitment of long-term financial and political support.
- Socio-economic studies should be made to assess impacts, costs and benefits of the re-introduction programme to local human populations.
- A thorough assessment of attitudes of local people to the proposed project is necessary to ensure long term protection of the re-introduced population, especially if the cause of species' decline was due to human factors (e.g. over-hunting, over-collection, loss or alteration of habitat). The programme should be fully understood, accepted and supported by local communities.
- Where the security of the re-introduced population is at risk from human activities, measures should be taken to minimise these in the re-introduction area. If these measures are inadequate, the re-introduction should be abandoned or alternative release areas sought.
- The policy of the country to re-introductions and to the species concerned should be assessed. This might include checking existing provincial, national and international legislation and regulations, and provision of new measures and required permits as necessary.
- Re-introduction must take place with the full permission and involvement of all relevant government agencies of the recipient or host country. This is particularly important in re-introductions in border areas, or involving more than one state or when a re-introduced population can expand into other states, provinces or territories.
- If the species poses potential risk to life or property, these risks should be minimised and adequate provision made for compensation where necessary; where all other solutions fail, removal or destruction of the released individual should be considered. In the case of migratory/mobile species, provisions should be made for crossing of international/state boundaries.

5. PLANNING, PREPARATION AND RELEASE STAGES

- Approval of relevant government agencies and land owners, and coordination with national and international conservation organizations.
- Construction of a multidisciplinary team with access to expert technical advice for all phases of the programme.
- Identification of short- and long-term success indicators and prediction of programme duration, in context of agreed aims and objectives.
- Securing adequate funding for all programme phases.
- Design of pre- and post- release monitoring programme so that each re-introduction is a carefully designed experiment, with the capability to test methodology with scientifically collected data. Monitoring the health of individuals, as well as the survival, is important; intervention may be necessary if the situation proves unforseeably favourable.
- Appropriate health and genetic screening of release stock, including stock that is a gift between governments. Health screening of closely related species in the re-introduction area.
- If release stock is wild-caught, care must be taken to ensure that: a) the stock is free from infectious or contagious pathogens

and parasites before shipment and b) the stock will not be exposed to vectors of disease agents which may be present at the release site (and absent at the source site) and to which it may have no acquired immunity.

- If vaccination prior to release, against local endemic or epidemic diseases of wild stock or domestic livestock at the release site, is deemed appropriate, this must be carried out during the "Preparation Stage" so as to allow sufficient time for the development of the required immunity.
- Appropriate veterinary or horticultural measures as required to ensure health of released stock throughout the programme. This is to include adequate quarantine arrangements, especially where founder stock travels far or crosses international boundaries to the release site.
- Development of transport plans for delivery of stock to the country and site of re-introduction, with special emphasis on ways to minimize stress on the individuals during transport.
- Determination of release strategy (acclimatization of release stock to release area; behavioural training - including hunting and feeding; group composition, number, release patterns and techniques; timing).
- Establishment of policies on interventions (see below).
- Development of conservation education for long-term support; professional training of individuals involved in the long-term programme; public relations through the mass media and in local community; involvement where possible of local people in the programme.
- The welfare of animals for release is of paramount concern through all these stages.

6. POST-RELEASE ACTIVITIES

- Post release monitoring is required of all (or sample of) individuals. This most vital aspect may be by direct (e.g. tagging, telemetry) or indirect (e.g. spoor, informants) methods as suitable.
- Demographic, ecological and behavioural studies of released stock must be undertaken.
- Study of processes of long-term adaptation by individuals and the population.
- Collection and investigation of mortalities.
- Interventions (e.g. supplemental feeding; veterinary aid; horticultural aid) when necessary.
- Decisions for revision, rescheduling, or discontinuation of programme where necessary.
- Habitat protection or restoration to continue where necessary.
- Continuing public relations activities, including education and mass media coverage.
- Evaluation of cost-effectiveness and success of re- introduction techniques.
- Regular publications in scientific and popular literature.

Footnotes:

1 Guidelines for determining procedures for disposal of species confiscated in trade are being developed separately by IUCN.

2 The taxonomic unit referred to throughout the document is species; it may be a lower taxonomic unit (e.g. subspecies or race) as long as it can be unambiguously defined.

3 A taxon is extinct when there is no reasonable doubt that the last individual has died

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* The IUCN/SSC Re-introduction Specialist Group (RSG) is a disciplinary group (as opposed to most SSC Specialist Groups which deal with single taxonomic groups), covering a wide range of plant and animal species. The RSG has an extensive international network, a re-introduction projects database and re-introduction library. The RSG publishes a bi-annual newsletter RE-INTRODUCTION NEWS.

Banding schedule and retrap data for Aldabra Rails *Dryolimnas cuvieri aldabranus*

The data presented in Table A-4.1 are records of all Aldabra Rails *Dryolimnas cuvieri aldabranus* banded on Aldabra during the course of this project. Rails were banded with 7.5 mm metal SAFRING bands on the right tarsus and plastic bands engraved with highly visible alpha-numeric codes on the left tarsus. Yellow (Y) plastic bands were reserved for adult Rails moved to Picard. White (W) plastic bands were used for adults on Malabar and Polymnie. Blue plastic bands were reserved for chicks or juveniles. The age of adults at banding was unknown. However, WA6 is believed to have been brought to Picard as an adult in 1992 (Chapter 1). It was therefore at least 8 years old when banded and at least 10 years old when retrapped in October 2001. Sex was determined by genetic analysis (see Chapter 4) except for Y14 and Y15. These birds died in captivity (Chapter 2) and were sexed by dissection. Missing sex data, represented by dashes, indicates unsexed individuals (i.e. no usable genetic product could be obtained). The banding location for the reintroduced birds (YA1-Y21) is given as Picard, as this is where they now occur. However, YA1-Y10 were trapped and banded at Gionnet and Y12-Y21 were trapped and banded at Middle Camp (both on Malabar - see Chapter 2). Retrap data are the most recent month in which a positive visual identification of a banded individual was made. These data were taken from personal records, routine monitoring on Aldabra and incidental observations by staff on Aldabra. Dashes indicate that individuals were either not retrapped after banding or, in the case of chicks, not retrapped after leaving the natal territory.

Table A-4.1. Banding schedule for Aldabra Rails. The banding locations Malabar MC and Malabar G are Middle Camp and Gionnet respectively

Metal band	Plastic band	Banding date	Age at banding	Sex	Banding location	Retrap
677802	White A2	07/10/1999	Adult	M	Malabar MC	11/1999
677803	White A1	08/10/1999	Adult	M	Malabar MC	04/2001
677804	White A3	08/10/1999	Adult	F	Malabar MC	10/2001
677805	White A4	08/10/1999	Adult	M	Malabar MC	12/2002
677806	White A5	08/10/1999	Adult	M	Malabar MC	10/2001
677807	White A6	18/10/1999	8 years	M	Malabar MC	10/2001
677808	Yellow A1	19/10/1999	Adult	F	Picard	01/2002
677809	Yellow A2	19/10/1999	Adult	M	Picard	01/2002
677810	Yellow A3	19/10/1999	Adult	F	Picard	01/2002
677811	Yellow A4	19/10/1999	Adult	F	Picard	12/2000
677812	Yellow A5	20/10/1999	Adult	M	Picard	01/2002
677813	Yellow A6	20/10/1999	Adult	F	Picard	04/2001
677814	Yellow A7	20/10/1999	Adult	F	Picard	04/2001
677815	Yellow A8	20/10/1999	Adult	M	Picard	04/2001
677816	Yellow A9	20/10/1999	Adult	M	Picard	01/2002
677817	Yellow 10	20/10/1999	Adult	F	Picard	01/2002
677819	Yellow 12	04/11/1999	Adult	M	Picard	03/2000
677820	Yellow 13	04/11/1999	Adult	F	Picard	04/2001
677821	Yellow 14	04/11/1999	Adult	M	Picard	Died
677822	Yellow 15	04/11/1999	Adult	M	Picard	Died
677823	Yellow 16	05/11/1999	Adult	F	Picard	02/2001
677824	Yellow 17	05/11/1999	Adult	M	Picard	04/2001
677825	Yellow 18	05/11/1999	Adult	M	Picard	01/2002

Metal band	Plastic band	Banding date	Age at banding	Sex	Banding location	Retrap
677826	Yellow 19	05/11/1999	Adult	F	Picard	01/2002
677827	Yellow 20	05/11/1999	Adult	M	Picard	01/2002
677828	Yellow 21	05/11/1999	Adult	F	Picard	01/2002
677829	White A7	17/11/1999	Adult	F	Malabar G	06/2001
677830	White A8	17/11/1999	Adult	M	Malabar G	03/2000
677831	White A9	17/11/1999	Adult	M	Malabar G	03/2000
677832	White 10	17/11/1999	Adult	F	Malabar G	12/2000
677833	White 11	17/11/1999	Adult	M	Malabar G	05/2001
677834	White 12	17/11/1999	Adult	M	Malabar G	06/2001
677835	White 13	17/11/1999	Adult	F	Malabar G	03/2000
677836	White 14	17/11/1999	Adult	M	Malabar G	05/2001
677837	White 15	18/11/1999	Adult	F	Malabar G	08/2001
677838	White 16	18/11/1999	Adult	M	Malabar G	03/2000
677839	White 17	17/12/1999	Adult	F	Malabar G	10/2001
677840	No band	17/12/1999	Adult	F	Malabar G	12/2000
677841	White 19	17/12/1999	Adult	F	Malabar G	12/2000
677842	White 20	17/12/1999	Adult	F	Malabar G	-
677843	White 21	17/02/2000	Adult	M	Polymnie	-
677844	White 22	17/02/2000	Adult	F	Polymnie	03/2000
677845	White 23	18/02/2000	Adult	M	Polymnie	04/2001
677846	Blue A1	18/02/2000	Chick	-	Polymnie	-
677847	White 24	18/02/2000	Adult	M	Polymnie	-
677848	None	18/02/2000	Chick	-	Polymnie	-
677849	White 25	18/02/2000	Adult	F	Polymnie	07/2001
677850	White 26	18/02/2000	Adult	F	Polymnie	07/2001
677851	White 27	18/02/2000	Adult	M	Polymnie	08/2001
677852	White 28	18/02/2000	Adult	M	Polymnie	10/2001
677853	White 30	28/02/2000	Adult	F	Malabar MC	10/2001
677854	White 31	28/02/2000	Adult	M	Malabar MC	10/2001
677855	Blue A2	29/02/2000	Chick	-	Malabar MC	-
677856	Blue 50	02/03/2000	Chick	F	Picard	04/2001
677857	Blue 51	02/03/2000	Chick	F	Picard	12/2000
677858	Blue 52	04/03/2000	Chick	F	Picard	05/2001
677859	Blue 53	06/03/2000	Chick	F	Picard	-
677860	None	07/03/2000	Adult	F	Île aux Cèdres	-
677861	None	07/03/2000	Adult	M	Île aux Cèdres	-
677862	None	07/03/2000	Adult	M	Île aux Cèdres	-
677863	None	08/03/2000	Adult	M	Île aux Cèdres	-
677864	None	09/03/2000	Chick	F	Île aux Cèdres	-
677865	Blue 55	10/03/2000	Chick	F	Picard	-

Metal band	Plastic band	Banding date	Age at banding	Sex	Banding location	Retrap
677866	Blue 56	10/03/2000	Chick	F	Picard	-
677867	Blue A3	13/03/2000	Chick	F	Malabar G	-
677868	Blue A4	13/03/2000	Chick	M	Malabar G	-
677869	White 32	13/03/2000	Adult	F	Malabar G	-
677870	White 33	14/03/2000	Adult	F	Malabar G	06/2001
677871	White 34	15/03/2000	Adult	F	Malabar G	-
677872	Blue A5	15/03/2000	Chick	F	Malabar G	-
677873	Blue 57	18/03/2000	Chick	F	Picard	-
677874	Blue 58	19/03/2000	Juvenile	F	Picard	01/2002
677875	None	21/03/2000	Adult	M	Île aux Cèdres	-
677876	None	22/03/2000	Chick	F	Île aux Cèdres	-
677877	None	22/03/2000	Adult	F	Île aux Cèdres	-
677878	White 35	30/03/2000	Adult	-	Polymnie	-
677879	Blue A6	30/03/2000	Chick	-	Polymnie	-
677880	Blue A7	31/03/2000	Chick	M	Polymnie	-
677881	White 36	31/03/2000	Adult	F	Polymnie	04/2001
677882	White 37	31/03/2000	Adult	F	Polymnie	-
677883	White 38	31/03/2000	Adult	F	Polymnie	04/2001
677885	None	01/04/2000	Chick	-	Polymnie	-
677886	White 39	01/04/2000	Adult	-	Polymnie	-
677887	Blue 59	19/12/2000	1 year	M	Picard	01/2002
677888	Blue 60	21/12/2000	1 year	M	Picard	04/2001
677889	Blue 62	21/12/2000	1 year	F	Picard	01/2002
677890	Blue 63	24/12/2000	1 year	M	Picard	04/2001
677891	White 40	27/12/2000	Adult	-	Malabar G	10/2001
677892	White 41	27/12/2000	Adult	-	Malabar G	10/2001
677893	White 42	27/12/2000	Adult	-	Malabar G	05/2001
677894	White 43	27/12/2000	Adult	-	Malabar G	-
677895	Blue 64	20/01/2001	Chick	F	Picard	-
677896	Blue 65	20/01/2001	Chick	F	Picard	02/2001
677897	Blue 49	30/01/2001	1 year	F	Picard	03/2001
677898	Blue 67	03/02/2001	Chick	F	Picard	-
677899	Blue 70	03/02/2001	Chick	M	Picard	-
677900	Blue 71	09/02/2001	Chick	M	Picard	-
677901	Blue 72	09/02/2001	Chick	M	Picard	-
677902	Blue 73	09/02/2001	Chick	F	Picard	-
677903	Blue 74	26/02/2001	Chick	M	Picard	-
677904	Blue 75	26/02/2001	Chick	M	Picard	-
677905	Blue 76	27/02/2001	Chick	M	Picard	-
677906	Blue 77	28/02/2001	Chick	M	Picard	01/2002

Metal band	Plastic band	Banding date	Age at banding	Sex	Banding location	Retrap
677907	Blue 78	28/02/2001	Chick	F	Picard	01/2002
677908	Blue 79	19/03/2001	Chick	F	Picard	-
677909	Blue 80	19/03/2001	Chick	M	Picard	-
677910	Blue 81	19/03/2001	Chick	F	Picard	-
677911	White 44	28/03/2001	Adult	-	Malabar MC	10/2001
677912	White 45	28/03/2001	Adult	F	Malabar MC	10/2001
677913	Blue A9	28/03/2001	Chick	M	Malabar MC	-
677914	Blue 10	28/03/2001	Chick	M	Malabar MC	-
677915	White 46	28/03/2001	Adult	F	Malabar MC	-
677916	White 47	28/03/2001	Chick	F	Malabar MC	10/2001
677917	Blue 11	28/03/2001	Chick	M	Malabar MC	05/2001
677918	Blue 12	28/03/2001	Chick	F	Malabar MC	-

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