Thesis Collection

Conservation of the forest-living native birds of Mauritius

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for the degree of Doctor of Philosophy in Ecology

at the University of Kent at Canterbury

1994

Contents

Abstract

Maintaining the biodiversity of Mauritius is one of the world's highest conservation priorities. Eight of nine surviving forest-living native bird species are threatened, yet the population limiting factors had not been convincingly diagnosed for any species, and conservation has focused on the short-term needs of the three non-passerine species.

I propose an economical strategy to increase and sustain the population viability of all forest species. I studied the five threatened passerine species, especially the Mauritius Fody *Foudia rubra*.

These were largely associated with native forest, much of which was unoccupied by most native bird species. Although invasion of the native forest by exotic plants may reduce food availability, the previous claim that this limited the population of certain species was unsupported.

Nest predation by introduced mammals was severe. Over most of the range, recruitment could not sustain fody populations. Surplus birds from areas of higher productivity supplemented these populations. The fody distribution thus comprised source and sink areas. The richest source area was an exotic *Cryptomeria japonica* grove, to which nesting of the Pink Pigeon was also restricted. I argue that *Cryptomeria* allows concealment of nests in a habitat avoided by predatory mammals.

I propose that nest predation is the proximate factor limiting the distribution and population of the pigeon and fody and, together with habitat destruction, was the main cause of decline.

Long-term conservation requires habitat management. The existing rehabilitation strategy for mainland plant communities neglects the predator problem. To address this, habitat enhancement using selected native and exotic plants is proposed, including the creation of groves of *Cryptomeria*. Restoration of offshore islets, including predator eradication, would provide habitat to which threatened birds should be translocated. To maximize survival chances for all native biota, all three strategies should be pursued.

Acknowledgements

My work on Mauritius was carried out with the support and collaboration of the Government of the Republic of Mauritius. Special thanks are due to the Forestry Service and the Conservation Unit of the Ministry of Agriculture, Fisheries and Natural Resources, particularly Yousoof Mungroo, Ehsan Dulloo and Greg Middleton. Funding for the project came from an anonymous, private donor (via Wildlife Preservation Trust International), National Geographic Society, Bleitz Wildlife Foundation and British American Tobacco (Mauritius). At Wildlife Preservation Trust International, Jerry Eberhart helped to secure funding for my work; John Hartley did the same at the Jersey Wildlife Preservation Trust.

I was employed by the Mauritian Wildlife Appeal Fund (MWAF), and thank its council and especially the Secretary, Dominique Britter, for enabling me to concentrate on fieldwork. As director of the bird work, Carl Jones initiated the project and supported it through thick and thin. More than any other person, Carl made this study possible. Wendy Strahm provided much botanical information. MWAF fieldworkers, too numerous to mention them all, provided endless help and companionship in the field. Colin Taylor and Tim Liddiard enlivened hundreds of soaking hours in Pigeon Wood, and John Beaumont provided information on Mauritius Cuckoo-shrikes, but overall Kevin Duffy was the most dedicated passerine-watcher.

Many Mauritian naturalists know the island better than any visiting biologist and joined me either in the field or in fruitful discussions. Rivalz Chevreau de Montléhu, France Staub and Jean-Michel Vinson freely imparted their unique knowledge of Mauritian birds; Thierry d'Unienville and King How also provided many useful observations. Gabriel d'Argent, Danielle Florens and Joseph Guého identified plants and discussed botanical matters.

Many people around the world have provided help, advice and ideas in response to my approaches. I especially thank Dick Veitch and Dan Simberloff for encouragement at crucial times; they probably do not realize how much they contributed. Les Underhill advised on data analysis. Elsewhere, I thank Colin Bibby, Terry Greene, Reese Lind, Richard Major, Don Merton, Phil Moors and Robert Prŷs-Jones.

Every biologist working on the Mascarenes owes a debt to Anthony Cheke for his meticulous research on the ecological history of the islands. My debt is greater, as he provided much of the basis for my studies and dug out his raw data, as well as many obscure references, for my benefit. His was a hard act to follow.

At the Durrell Institute of Conservation and Ecology at the University of Kent, Mike Walkey made sure that I negotiated the various hurdles on the way to registration. Ian Swingland provided helpful suggestions.

My parents have always supported my exploits in distant countries and welcomed me home. During the writing up period, Frank Hawkins drew attention to numerous references. The maps for this thesis were produced with the very patient help of Nick Safford. Will Duckworth commented on drafts of various chapters and finally tackled the entire manuscript. It was he who in 1988 persuaded me that Mauritius would be a better place to go than Mauretania. Finally, Lesley Smart provided limitless support and encouragement in the later stages of the fieldwork and throughout the writing up, including commenting on every draft of every chapter. Thanks to her, I am one of few biologists to have returned to a British winter after a long stint on a tropical island, and enjoyed writing it all up.

Conventions followed

Nomenclature

Bird taxonomy and scientific and English nomenclature follow Dowsett & Forbes-Watson (1993). For Indian Ocean species, this differs from Diamond (1987) in a few of the English names and in the inflection of *Zosterops chloronothus* (not *chloronothos*). *Zosterops b. borbonicus* is referred to as the Réunion Grey White-eye, although it is not a full species. Unless otherwise stated, "the fody" refers to the Mauritius Fody *Foudia rubra*. The Aldabran subspecies of Red Forest Fody *F. eminentissima aldabrana* is referred to as the Aldabran fody. Mammal and reptile nomenclature follow Corbet & Hill (1991) and Tonge (1989) respectively.

For plants, the new, but incomplete *Flore des Mascareignes* (Bosser *et al.* 1976-continuing) is followed where possible; this work, usually cited according to the author for each family, is simply referred to by its title. Species not covered by *Flore des Mascareignes* follow Mabberley (1987).

Maps and place names

The following maps were used: United Kingdom Directorate of Overseas Survey (D.O.S.) 1:25,000 (series Y881 [DOS 329] edition 6-OS 1991, 14 sheets), D.O.S. 1:100,000 (series Y 682 [DOS 529] 'Mauritius and Rodrigues' edition 4-DOS 1983) and French Institut Géographique National (I.G.N.) 1:100,000 Carte Générale 'Ile Maurice' (1990). Where place names and spelling differ, priority is given to the D.O.S. maps, with the following exceptions.

1. Mixing of languages is avoided (for example, Rivière du Poste is used in place of River du Poste).
2. Piton de la Petite Rivière Noire is referred to as Black River Peak (as it is commonly called, and signposted).
3. Land owned by the state (formerly called Crownland, but now State Land) is divided into parcels, which are delineated and named on unpublished Forestry Service maps. Many of the State Land names appear on the D.O.S. maps, but are misplaced. The Forestry Service boundaries are in current use on Mauritius, and are followed here.
4. Certain features are not named on any of these maps. Common usage on Mauritius is followed, and these localities are marked on my maps (Figs 2.5, 2.6 and 2.10).
5. For two localities important to the birds, I could trace no established, unique name, and I therefore use new names. "Pigeon Wood" has been widely used among visiting biologists for at least ten years to refer to the breeding site of the wild Pink Pigeons. "Piton Paul" is used to describe a low mountain in the extreme south-east of Les Mares, because this area is known as Plaine Paul. Confusingly, one local informant called this hill Piton Poule, which is used by D.O.S. and I.G.N. for a different mountain only 2.5 km to the south-east.

Units

The metric system is used. Measurements from literature given in archaic units are quoted unchanged, but with the metric equivalent.

Abbreviations and definitions

The following abbreviations are used without further explanation in the following chapters.

BOU	British Ornithologists' Union
ICBP	International Council for Bird Preservation (now BirdLife International)
IUCN	International Union for the Conservation of Nature and Natural Resources (now The World Conservation Union)
UMZC	University Museum of Zoology, Cambridge
C/3	A complete clutch of three eggs
MK	Mauritius Kestrel
PP	Pink Pigeon
EP	Echo Parakeet
CS	Mauritius Cuckoo-shrike
BB	Mauritius Black Bulbul
PF	Mascarene Paradise Flycatcher
GW	Grey White-eye
OW	Mauritius Olive White-eye
MF	Mauritius Fody

The term *fruit* is used in its broadest sense, as the ripe seeds and structure surrounding them, including associated parts such as the fleshy receptacle.

Other special terms are defined in the text where they are used.

Chapter 1. Introduction

1.1 The island and its native biota

Mauritius is one of the Mascarene islands, a volcanic archipelago which includes two other high islands (Réunion and Rodrigues) and various small satellites in the south-west Indian Ocean. Mauritius covers 1865 km^2 and lies 840 km east of Madagascar (Figs 1.1, 1.2). The Mascarenes have never been united or connected to another landmass. The huge shield volcano which first brought the island into existence collapsed, to be overlaid by younger lava flows, most now variably eroded into soils. The relief is now mostly mild, with low plains in the north and east rising to a central plateau reaching around 700 m in the south-west. The terrain is broken by small (no higher than 824 m) but spectacular mountains, and by the Black River Gorge system in the south-west.

Although already known to Arab sailors, its isolation caused Mauritius to remain unknown to Europeans until the early sixteenth century, and it was not colonized until 1638. The history of its human colonization since then is reviewed by Toussaint (1972) and Addison & Hazareesingh (1984). By the 1980s, the human population was around one million, making the island one of the world's most densely populated states (Anon. 1991).

The ecological history of all three Mascarene islands is reviewed by Cheke (1987a). The islands once supported one of the richest and most extraordinary vertebrate faunas of any oceanic archipelago, including several endemic genera and two endemic families: the dodos and solitaires (Raphidae, all now extinct) and the boa-like snakes Bolyeriidae, one of which (*Casarea dussumieri*) survives (some authors consider these as subfamilies of the pigeons Columbidae and boas Boidae respectively). For the last three centuries, however, the native fauna and flora of the islands have been subjected to the negative influences of exotic plants and animals, habitat destruction and hunting. As a result, the native Mascarene biota is one of the world's most famously devastated. The majority of the native vertebrates is extinct and most of the native vegetation destroyed, especially on Mauritius and Rodrigues; Réunion retains a considerable area of native forest, although even this is endangered by invasion of exotic plants (Macdonald *et al.* 1991) and forestry practices damaging to native ecosystems (Moutou 1984, Cheke 1987b).

Excluding non-breeding visitors (mostly shorebirds), the surviving native avifauna of Mauritius consists of eleven land-birds, two resident waterbirds and eight regularly nesting

Fig. 1.1. The islands of the western Indian Ocean

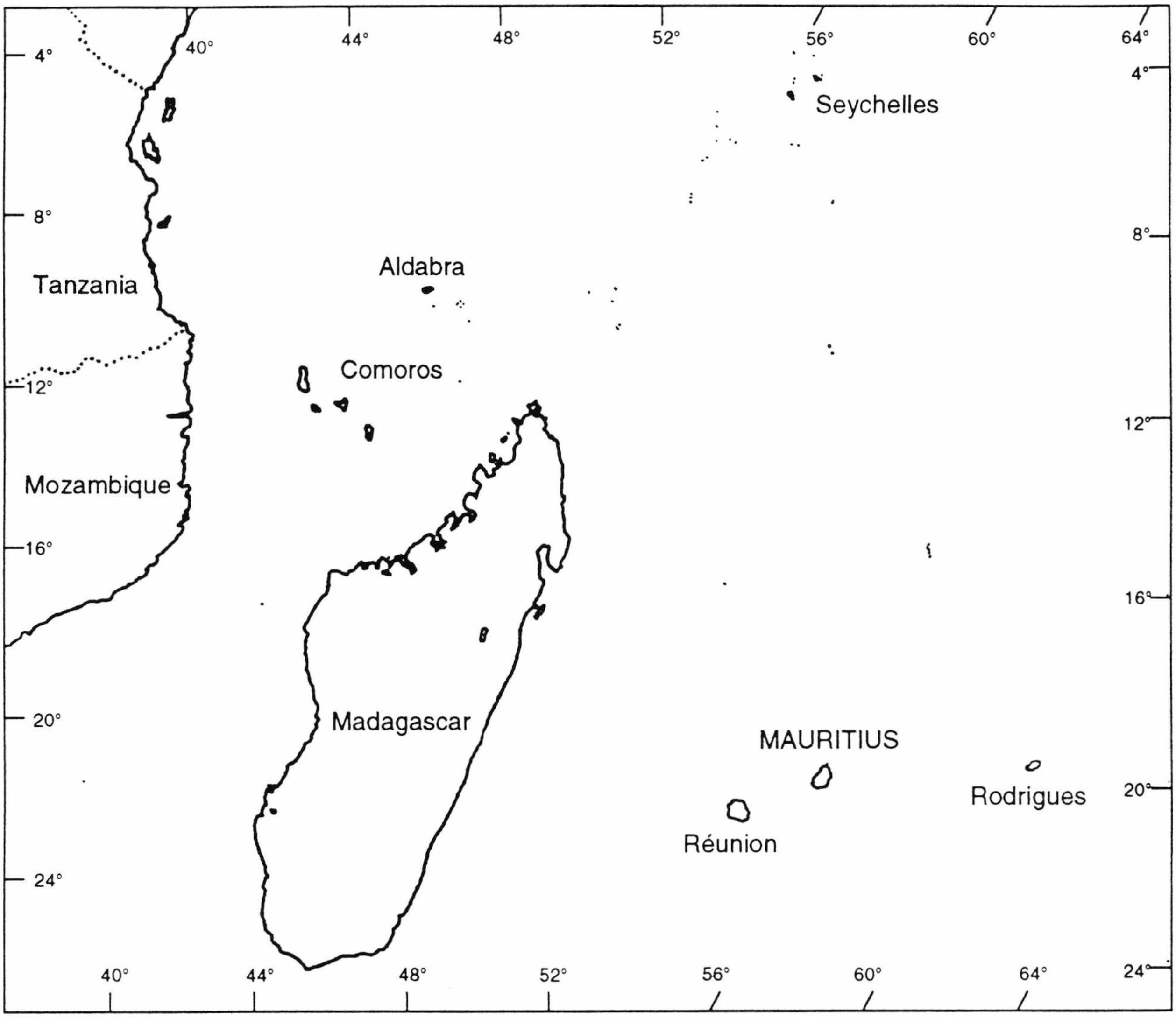
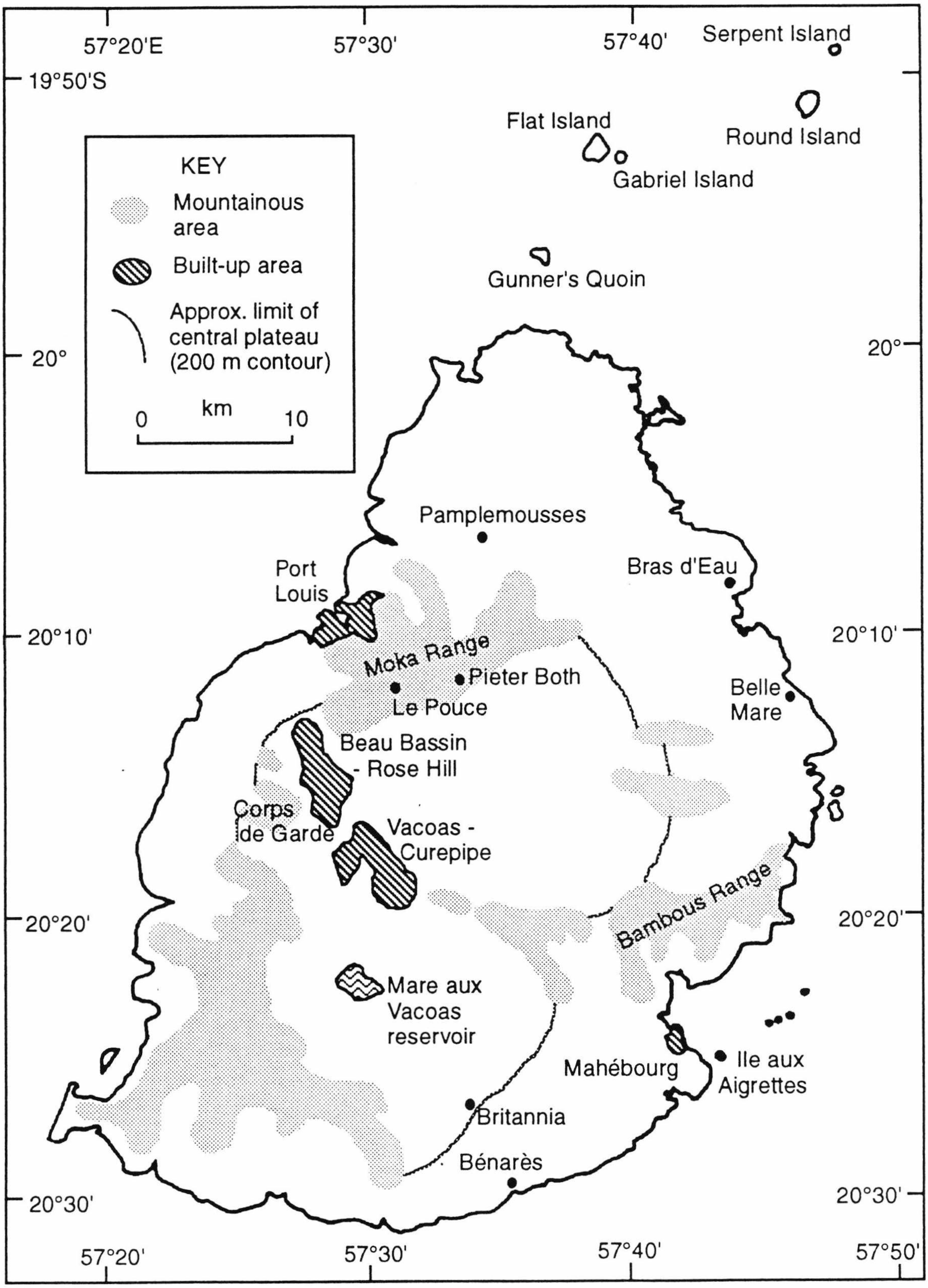


Fig. 1.2. Mauritius, showing localities mentioned in the text outside the south-west and central-east



seabirds. The two waterbirds, Moorhen *Gallinula chloropus pyrrhorrhoa* and Green-backed Heron *Butorides striatus javanicus*, are non-endemic subspecies, are not associated with forests and have wide global distributions. Of the true seabirds, only the White-tailed Tropicbird *Phaethon l. lepturus* nests on the Mauritian mainland, but this subspecies has a wide global distribution. This leaves eleven true land-birds (Table 1.1). Neither the Mauritius Swiftlet nor the Mascarene Martin is a forest bird, although both are often seen over the forest (Cheke 1987c); neither is endemic to Mauritius or globally threatened. This study was restricted to the forest-living native birds and therefore only the remaining nine species will be considered further. Anticipating the frequent references that will be made to the Réunion counterparts of Mauritian birds, Table 1.1 includes all extant land-birds native to Réunion.

At least nine endemic bird species have become extinct in historical times on Mauritius. Among the survivors, the Mauritius Kestrel, Pink Pigeon and Echo Parakeet have been heavily publicized as three of the world's rarest and most endangered birds (Jones 1987). Of the other six forest-living native birds, the most recent Red Data Book (Collar & Stuart 1985) lists four species (the cuckoo-shrike, black bulbul, olive white-eye and fody) as threatened. The flycatcher is rare on Mauritius, but not threatened at species level because of the existence of a safe population (of the other subspecies) on Réunion. Only the Grey White-eye is abundant and apparently safe on Mauritius.

At least 17 mammal, 27 bird and seven herptile species have been naturalized at some time since Mauritius was 'discovered' by Europeans (Cheke 1987a). Of these exotics, 12 mammal, 18 bird and all seven herptile species still survived in 1993 (Table 1.2).

Table 1.1. Extant native land-birds of Mauritius and Réunion. Species on each line are believed to be closely related. Former existence (probable or certain) of a closely related but extinct taxon on the other island is indicated by +. Levels of endemism for extant species ignore former existence of same species elsewhere (for example, the Echo Parakeet is considered endemic to Mauritius although the extinct Réunion Parakeet may have been conspecific).

** = single-island endemic species,
* = species endemic to Mauritius and Réunion,
*# = species endemic to Mauritius and Réunion, with separate race on each,
= subspecies endemic to Mauritius and Réunion.
= subspecies endemic to Réunion

Family	Mauritius	Réunion
Hawks/Eagles Accipitridae	+	Réunion Harrier ## *Circus m. maillardi*
Falcons Falconidae	Mauritius Kestrel ** *Falco punctatus*	+
Pigeons Columbidae	Pink Pigeon ** *Nesoenas mayeri*	+
Parrots Psittacidae	Echo Parakeet ** *Psittacula echo*	+
Swifts Apodidae	Mauritius Swiftlet * *Collocalia francica*	Mauritius Swiftlet * *Collocalia francica*
Swallows Hirundinidae	Mascarene Martin # *Phedina b. borbonica*	Mascarene Martin # *Phedina b. borbonica*
Cuckoo-shrikes Campephagidae	Mauritius Cuckoo-shrike ** *Coracina typica*	Réunion Cuckoo-shrike ** *Coracina newtoni*
Bulbuls Pycnonotidae	Mauritius Black Bulbul ** *Hypsipetes olivaceus*	Réunion Black Bulbul ** *Hypsipetes borbonicus*
Chats/Thrushes Turdidae	(no Mauritian counterpart)	Réunion Stonechat ** *Saxicola tectes*
Monarchs Monarchidae	Mascarene Paradise Flycatcher *# *Terpsiphone bourbonnensis desolata*	Mascarene Paradise Flycatcher *# *Terpsiphone b. bourbonnensis*
White-eyes Zosteropidae	Grey White-eye *# *Zosterops borbonicus mauritianus*	Grey White-eye *# *Zosterops b. borbonicus*
White-eyes Zosteropidae	Mauritius Olive White-eye ** *Zosterops chloronothus*	Réunion Olive White-eye ** *Zosterops olivaceus*
Weavers Ploceidae	Mauritius Fody ** *Foudia rubra*	+

Table 1.2. Vertebrate species introduced to Mauritius which survived in 1993 and occurred in forested habitats. Gamebirds (two species), ducks (two species), Indian House Crows *Corvus splendens*, European Rabbits (*Oryctolagus cuniculus*, possibly extinct) and goats are omitted, as they did not occur in forest. Dates of introductions are given as the time of the first definite record (Cheke 1987a), then rounded to the nearest 50 years. Status in forest is given as common (c), rare (r) or unknown (?), from Cheke (1987a) and personal observation. For mammals, English names in common use are given in square brackets.

English name	Scientific name	Date introduced	Status in forest
Mammals			
Tail-less Tenrec	*Tenrec ecaudatus*	1800	c
House Shrew	*Suncus murinus*	1800	c
Crab-eating Macaque	*Macaca fascicularis*	1600	c
Indian Hare	*Lepus nigricollis*	1750	r
Roof [Ship] Rat	*Rattus rattus*	1600[1]	c
Brown Rat	*Rattus norvegicus*	1750	r
House Mouse	*Mus musculus*	1700	r
Small Indian Mongoose	*Herpestes auropunctatus*[2]	1900	c
Feral Cat	*Felis catus*	1700	c
Wild Boar	*Sus scrofa*	1600	c
Timor [Rusa] Deer	*Cervus timorensis*	1650	c
Birds			
Feral Rock Dove	*Columba livia*	1850	r
Malagasy Turtle Dove	*Streptopelia picturata*	1800	c
Spotted Dove	*Streptopelia chinensis*	1850	c
Barred Ground Dove	*Geopelia striata*	1750	c
Rose-ringed Parakeet	*Psittacula krameri*	1900	c
Red-whiskered Bulbul	*Pycnonotus jocosus*	1900	c
Common Myna	*Acridotheres tristis*	1750	c
House Sparrow	*Passer domesticus*	1850	r
Village Weaver	*Ploceus cucullatus*	1900	r
Madagascar Red Fody	*Foudia madagascariensis*	1850	c
Common Waxbill	*Estrilda astrild*	1850	c
Spice Finch	*Lonchura punctulata*	1850	r
Yellow-fronted Canary	*Serinus mozambicus*	1750	r
Reptiles			
House geckoes[3]	Gekkonidae	1750	r
Agamid lizard	*Calotes versicolor*	1900	r
Blind snake	*Typhlina bramina*	1850	?
Wolf Snake	*Lycodon aulicum*	1900	r
Amphibians			
Frog	*Ptychadena mascareniensis*	1800	c
Toad	*Bufo regularis*	1900	c

Notes

[1] Roof Rats may have colonized from shipwrecks before 1600.

[2] The mongoose has usually been considered to be *H. edwardsi*, but recently measured specimens are all *H. auropunctatus* (C. G. Jones and D. Simberloff verbally); *H. edwardsi* probably never occurred.

[3] Four species of house geckoes have been introduced since 1850; a fifth, *Hemidactylus frenatus*, may be native.

1.2 The importance of the biodiversity of Mauritius, and the threats it faces

Because of its biological importance and the high degree of threat to its wildlife, Mauritius is widely regarded as one of the world's highest priorities for the conservation of threatened species. Collar & Stuart (1988) reviewed the importance to threatened species of forest areas in Africa and related islands, ranking each according to the number of threatened species they contained. The forests of south-west Mauritius gained the highest score. ICBP (1992) analysed the distributions of all the world's bird species with restricted ranges. Taking into account the degree of threat to the entire ecosystem and its importance to other animal groups and also plants, they identified Mauritius as a critical area (the highest priority rank) for the conservation of biological diversity.

Fragments totalling less than 100 km^2 of native forest survive, and the native birds are largely associated with these. Even in reserves, the native forests are progressively degrading, and this therefore presents a chronic problem for the native birds. The degradation takes the form of a gradual shift in floristic composition towards exotic species, but the mechanisms responsible are not understood (Lorence & Sussman 1986, 1988). Several exotic animals have been shown to be capable of affecting the native flora, for example by destroying native plants, seedlings, fruit or seed, or by spreading exotic plants; birds, deer, pigs, monkeys, rats and giant snails *Achatina* spp. are thought to be the main culprits (Cheke 1987a,c,d, Strahm 1988).

The factors causing declines in all forest-dependent birds in Mauritius have been described as deeply interrelated and largely irreversible (Collar & Stuart 1985). Threats suggested include habitat destruction, habitat degradation, resource and interference competition from exotics, nest predation, hunting, diseases, cyclones, genetic problems and organochlorine pesticide use (Rountree 1951, Vinson 1956, Staub 1976, Collar & Stuart 1985, Cheke 1987a,c, Jones 1987).

1.3 Conservation on Mauritius up to 1989

1.3.1 *Early efforts*

Conservation on Mauritius until 1987 was reviewed by Cheke (1987d); the following is a brief summary. Modern conservation efforts began in earnest in 1951, with the establishment of the first nature reserves, which were chosen on purely botanical grounds (Vaughan 1968) and omitted much of the most important bird habitat (Cheke 1987c). From September 1973 to February 1975, a BOU expedition was on the Mascarenes, spending most time on Mauritius (Diamond 1987). The expedition carried out detailed surveys and general autecological studies on the native birds, with special emphasis on the threatened species (Cheke 1983, 1987c), and additional studies on avian blood parasites (Peirce *et al.* 1977). These studies included all the native passerines. Of the latter, the Mauritius Fody was recognized as the most endangered. An introduction of this species to Réunion was attempted in 1975, but was unsuccessful (Cheke 1987c).

International conservation organizations have been closely and continuously involved since 1973, when a captive breeding programme began, supervised by expatriate biologists. Bird conservation work until the early 1980s was dominated by efforts to preserve the kestrel and pigeon. During the 1980s, the programme was expanded to include the Echo Parakeet, with monitoring of the wild population and attempts to maintain the species in captivity. Plant conservation work also intensified during the 1980s, with an internationally funded plant conservation programme. Small areas (up to a few hectares) of the least degraded forest were fenced to exclude deer and pigs, and weeded of exotic plants. Rare plant species propagated in nurseries were planted in these exclosures. Ecological restoration of two offshore islets (Ile aux Aigrettes and Round Island) began, aiming to rehabilitate the native habitat of coastal areas.

1.3.2 *The situation in 1989: the start of the present study*

In order to appreciate the importance of, and the rôle to be played by, work on the passerines, it is necessary to consider the bird conservation measures being implemented on Mauritius in 1988-89, immediately before this study started. In particular, I examine whether all native bird species were benefitting, or were likely to do so; I ask whether the factors limiting bird populations had been firmly identified; and I question the long-term applicability of the measures being implemented.

The Mauritius Kestrel population declined to less than ten individuals in the mid 1970s (Collar & Stuart 1985, Temple 1986, Jones 1987). Cheke (1987a) suggested that organochlorine pesticide use was the main cause of the kestrel's decline in the 1950s and 1960s. These pesticides have caused declines in other raptor populations (Ratcliffe 1980), and were used in Mauritius mainly between 1949 and 1970 (Ricaud 1975, Mamet 1979).

According to Cheke's hypothesis, pesticide residue levels in the environment decreased gradually after 1970 until the habitat again became suitable, without any need for long term habitat repair.

The recovery programme for the Mauritius Kestrel therefore relied mainly on the release of captive-bred or captive-reared birds into unoccupied habitat. The principal management techniques were supplemental feeding, provision of nestboxes, modification of natural cavities and predator control (Jones *et al.* 1991a). By early 1989 the free-living kestrel population had reached 60 (Jones *et al.* 1991a). The recovery programme for this species was showing signs of success, and the conservation of the Pink Pigeon and Echo Parakeet had clearly emerged as the greatest challenge to bird conservation efforts on Mauritius.

No work, apart from occasional monitoring, was being carried out on the less than 20 wild Pink Pigeons, but the species was breeding well in captivity. Management techniques had been tested during a trial release programme at Pamplemousses (Todd 1984), and releases had started in 1987 in the native forest of Brise Fer, an area where the species had become extinct ten years earlier (Jones *et al.* 1988, 1992). Seventeen birds had been released at Brise Fer by mid 1989, and one juvenile had fledged from the released population (Jones *et al.* 1992). Impoverished food supply, especially in late winter, was considered to be the main factor limiting the population of the pigeons in the wild (Jones 1987, Jones & Owadally 1988), although no data had been presented to support the hypothesis. The shortage was said to be caused by a combination of native forest degradation and resource competition from exotics. Therefore the main management procedure for captive-bred pigeons reintroduced into the wild was the provision of supplemental food (Jones *et al.* 1988). Introduced mongooses were also controlled around the release site, as they were thought likely to be predators of adult pigeons feeding on the ground.

For the Echo Parakeet, the wild population (around 15 birds, including three pairs) was being monitored closely. As for the pigeon (but also with no supporting data), food shortages were thought to be a major limiting factor, and so attempts were being made to habituate the wild birds to accept supplemental food (Mauritius Wildlife Appeal Fund 1988). Nestboxes were maintained in the native forest, in case nest sites were limiting the population; none was used. Two young had been harvested as founders of a new captive breeding project in late 1987, but these died before reaching maturity.

The measures being implemented in 1989 were strongly biased towards 'hands-on' management, in particular supplementary feeding and release of captive-bred or captive-reared birds. Three points of concern arise. Firstly, the conservation measures being implemented were species-specific and offered no increased security to the passerines. Secondly, although reduced food availability had been claimed to be the cause of the rarity of the pigeon and parakeet, supporting evidence was inadequate to indicate a causal relationship. Neither this, nor other potential limiting factors, had been studied quantitatively, and so the possibility existed that other causes of decline might be more important. If this were so, the continued implementation of the established conservation measures could fail to avert the extinction of these species. Thirdly, even if the cause of decline had been correctly identified, the measures being used in an attempt to combat it were not sustainable indefinitely. Supplemental feeding and reintroduction from captivity are both expensive measures, requiring continuous human effort. They are appropriate to the rescue of a species close to extinction, but the long-term security of the species can only be ensured if rescue efforts are coupled with efforts to address ultimate problems that are the result of environmental change (Temple 1978a, Cade & Temple in prep.). If food shortages were confirmed as a threat, long-term measures would be needed to enrich the natural food availability of the habitat.

1.3.3 *The special case of the Mauritius Kestrel*

The kestrel programme was destined for success: by 1994 the free-living population appeared to be self-sustaining and intensive management ceased (Jones *et al.* in prep.). The project succeeded, apparently because the factor (pesticide use) which caused the kestrel's most recent and severe range reductions, and so nearly led to its extinction in the 1970s, had ceased to operate.

The conservation biology of the Mauritius Kestrel therefore differed fundamentally from that of the Pink Pigeon and Echo Parakeet. Organochlorine pesticides or their metabolites are stored in animal fats and so are passed from prey to predator, accumulating in predators at the top of the food chain. Vegetarian birds, such as the Pink Pigeon and Echo Parakeet, may be less likely to accumulate residues, although all birds are susceptible. These species were considered to have declined for other reasons, which are likely still to be operating. Therefore, reintroduction for these species cannot be expected to be successful in the long term, unless the limiting factors are identified and the habitat improved in order to reduce the effect of these factors.

1.4 The aim of this study

The main goal for conservation action on Mauritius is the maintenance or restoration of self-sustaining populations of all species in native ecosystems. The aim of this study was to propose a strategy to increase the viability of the populations of all forest-living native birds on Mauritius. The strategy needs to meet three main criteria. Firstly, the increased viability must be sustainable in the long term without requiring continuous, intensive human management. This permits the continuation of some management, but this should be minimized. Sustainability is most likely to be achieved by addressing the ultimate problems likely to result from inevitable environmental change. Secondly, the strategy must be economical, so that it could be implemented with the resources likely to be available. Thirdly, the strategy should not compromize the survival chances of other life forms (such as plants, reptiles and invertebrates).

To pursue this objective, I concentrated my studies on the native passerines, with special attention to the Mauritius Fody. The work took place between August 1989 and September 1993.

1.5 The value of studies on the passerines of Mauritius

In this section, I justify studies on the native passerines on two main grounds. Firstly, the passerine bird community, comprising two thirds (6/9) of the surviving forest-living native avifauna, includes highly threatened yet neglected species in need of new conservation measures. Secondly, it may be easiest to understand some of the causes of decline of all forest-living native birds, using data collected for the passerines.

1.5.1 *Conserving the passerine species*

As indicated above, during the 1970s and 1980s, the limited resources available for bird conservation were directed at the three critically endangered non-passerine species. Although all the native passerines except the Grey White-eye were found to have populations on Mauritius of 350 pairs or less in 1975 (Cheke 1987c), none was monitored between 1975 and 1989. The second Red Data Book (King 1978-79) gave a reminder of the threatened status of the cuckoo-shrike, flycatcher (Mauritian race), olive white-eye and fody. King's omission of the black bulbul was the result of preliminary but overoptimistic interpretation of the BOU expedition data (Cheke 1987c); Collar & Stuart (1985) rightly included the species in the third edition, and also called for a new survey of the cuckoo-shrike. The same authors (and also Cheke 1987d) urged for a re-census of the Mauritius Fody; their text on the fody ended with the following lament: "It is a sad reflection on the impact of Red Data Books to read that, in May 1970, a year or so before clearance began at Les Mares [which eliminated more than half the fody's population], an entry on this species was published by Vincent (1966-1971) "in a 'last ditch' attempt to emphasize the need for immediate action" to save it. This attempt has yet to begin.".

Censuses and autecological studies of the native passerines are fundamental requirements for their preservation (Temple 1978a, Simberloff 1988, Green & Hirons 1991). In 1989, surveys of the native passerines were amply justified on the grounds of the threatened status of these species.

1.5.2 *Understanding the conservation needs of the whole bird community*

The threats faced by forest birds on Mauritius apply in varying degrees to all species. I suggest that the populations of the passerines are following a similar trajectory to those already taken by the Pink Pigeon and Echo Parakeet.

Although certainly not doomed, the Pink Pigeon and Echo Parakeet are nearly extinct in the wild. When a species approaches extinction, the autecology of the last wild survivors may be a poor guide to the ideal conditions for the species. The last wild Hawaiian Geese *Branta sandvicensis* survived in volcanic montane shrubland (Berger 1978). However the most successful reintroduction effort derived from an accidental "release" into lowland pasture grazed by cattle and devoid of mongooses *Herpestes auropunctatus* (Black *et al.* 1993, Pratt 1994). Similarly in New Zealand, the last wild Takahe *Porphyrio mantelli* population lives in alpine tussock grassland (Mills *et al.* 1984), but translocated birds have fared better on predator-free offshore islets (Craig & Veitch 1990). In both cases, certain limiting factors (such as predation) had left the populations restricted to refuges which were in many other ways sub-optimal.

As already indicated, the factors limiting the populations of the Echo Parakeet and Pink Pigeon had, in 1989, been only tentatively identified. This was partly a result of these species' tiny populations. For example, the Echo Parakeets numbered three pairs, and only one or two breeding attempts were monitored per year in the late 1980s (Jones &

Duffy 1993); very little could be said about the breeding success of this species. Since about 1977, the entire wild Pink Pigeon population had nested in one grove of the introduced conifer *Cryptomeria japonica* surrounded by native forest (Jones 1987), for reasons completely unexplained; the absence of any nesting activity outside the grove as a control hampered the search for the explanation.

The relatively wide distributions and large populations of the threatened passerines may make it easier to understand their conservation needs, than those of the pigeon and parakeets. These needs may apply equally to the pigeon and parakeet; if so, I suggest that studies on the passerines are likely to be a powerful way to discover the causes of decline of all forest-living native bird species.

1.6 Design of this study

1.6.1 *Setting the scene*

The first necessity in this study was to carry out a habitat survey, with special attention to the extent of native vegetation, in order to highlight areas likely to support native bird populations. The results are summarized and mapped in Chapter 2.

The distributions and populations of all the passerine species then had to be surveyed in relation to the vegetation. This gives an immediate impression of the viability of populations. Patterns of distribution can be identified, which are likely to be determined by the factors limiting the whole population. The results of the census and distribution studies are given in Chapter 3.

1.6.2 *Diagnosis of the limiting factors*

The aspects of the birds' ecology which were studied in most depth were selected using a combination of the available literature (in particular Collar & Stuart [1985], Cheke [1987c] and Jones [1987]), and preliminary data which I gathered during survey work in the 1989-90 breeding season. Of the threats previously identified, nest predation by exotic mammals and impoverishment of food supply seemed potentially the most serious in the long term.

The possibility that food shortages were limiting the population of any passerine species was not supported by any published evidence, nor by any signs that I saw in the distribution of any species. However, in view of the deterioration of the native forest, selected aspects of the feeding ecology most relevant to conservation were studied, and are described in Chapter 5.

The few published data available on breeding success for the passerines indicated very heavy nest predation rates, and Cheke (1987c) had suggested that the low densities of Mauritius Fodies that he found in 1973-75 were attributable to this. One of the most striking results of the preliminary survey work was the discovery that the densest concentration of breeding Mauritius Fodies occurred in the same *Cryptomeria* grove where all wild breeding by Pink Pigeons took place. During the 1989-90 season, the fates of the eight fody nests found led to the suspicion that breeding success for fodies might be consistently higher there than elsewhere. It seemed possible that the presence of higher than average densities of fodies in this grove was related to lower than average predation rates, implying that nest predation was influencing bird distribution.

The top priority for further field research was therefore an investigation of the patterns of breeding success and their causes and effects. Locating and monitoring nests was both difficult and time-consuming, and occupied most of the fieldwork time available. The patterns of breeding success and their suggested causes are set out in Chapter 6. Many of the features of the birds' distributions, identified in Chapter 3, could be explained by the observation that breeding success was extremely variable geographically. The effects of geographical variation in breeding success on bird populations are discussed in Chapter 7.

The monitoring of nests allowed the collection of many data concerning the breeding biology and annual cycles of the birds. These were supplemented by observations outside the breeding season in order to complete the picture of the annual cycles. The results are in Chapter 4.

1.6.3 *Proposal of conservation strategies*

The understanding of the limiting factors and threats leads to a rationale for conservation measures. Provision of food and safe nest sites are key factors. To complete the work, I discuss existing strategies for bird conservation, and suggest certain modifications. I also propose a new, economical habitat management strategy for mainland areas, using plant species selected specifically to increase the survival probability of the birds.

Chapter 2. Climate and vegetation of the study area

2.1 Climate

The climate of Mauritius is described in detail by Padya (1989). Cheke (1987c) reproduced relevant data from earlier editions of the same text (Padya 1972, 1984). A summary is given here, along with some new, unpublished data provided by the Mauritius Meteorological Service (MMS).

Of the climatic features which may affect bird ecology, data are available for rainfall, humidity, temperature and cyclones. Mean rainfall and temperature data are given for Pamplemousses (a hot, dry, lowland locality) and Curepipe (a cool, wet upland locality). To show the association with rainfall, humidity data are given for Vacoas, a locality with intermediate climate. Existing data on the annual cycles of the birds (Cheke 1987c) suggested a main breeding and moulting season from September to May; mean data are therefore plotted from June to May in order to keep the subsistence period and the breeding and moulting season intact.

Most of the studies were carried out where the native birds were concentrated, in the very wet areas of the south-west of the central plateau. Monthly rainfall data for the whole study period were obtained for Pétrin, a locality within the main study area. These are compared to the long-term averages from Arnaud, a locality with closely similar rainfall, 4 km away to the north-east. Table 2.1 gives summary statistics for these localities.

Table 2.1. Summary statistics for localities from which climate data are given. All data are from Padya (1989) except the rainfall at Pétrin, which is deduced from the map of 1961-90 averages (MMS unpubl.). nd = no data available.

Locality	Altitude/m	Mean annual rainfall/mm	Mean temperature/°C	Mean % humidity
Pamplemousses	79	1527	23.6	77
Curepipe	564	3177	19.6	nd
Pétrin	660	c. 3500	nd	nd
Arnaud	576	3730	nd	nd
Vacoas	424	2188	21.1	82

Seasons

The annual variation follows the same pattern all over the island (Figs 2.1, 2.2). The wettest, hottest months are December to April (summer), with frequent tropical depressions, which cause heavy rain; temperatures in the lowlands may reach 35°C. September to November are the driest months. In the coastal lowlands, the winter is relatively dry, with monthly mean rainfall below 100 mm from June to November. On the plateau there is only a reduction in rainfall at this time; here, in the coldest months of June to August, days of continuous low cloud and drizzle are frequent and night temperatures may drop to 5°C.

Mean humidity and rainfall

Humidity appears to be associated with rainfall (Fig. 2.1). The 3500 mm isohyet approximately encloses an area where the relative humidity never drops below 95% (Padya 1989).

The central plateau is extremely wet and humid, most of it receiving an average of over 3000 mm of precipitation (Fig. 2.3) and probably close to 5000 mm in the wettest places (Montagnes Cocotte and Lagrave). Annual rainfall over 3000 mm is regarded as a high figure in continental rain forests (Mabberley 1992). The heaviest rainfall is brought by cyclones or tropical depressions; a series of depressions brought almost continuous rain to the area of Les Mares and the Savanne Mountains for four weeks in February and March 1992 (Fig. 2.4).

Rainfall during the study

Fig. 2.4 indicates that monthly rainfall often differs greatly from the mean, depending mainly on the number of tropical depressions affecting the area. At Pétrin during 1989-93, the two most striking deviations from the averages were the following: rainfall in December 1990 to February 1991 was less than half that expected (in effect, the wet season did not begin until March), and rainfall in February 1992 was three times the February average.

Compared to the 1931-60 averages mapped by Padya (1972 and in Cheke 1987c), there seems to have been a slight overall reduction in rainfall, with no longer a 4800 mm isohyet.

Fig. 2.1. Annual rainfall and humidity patterns on Mauritius. Rainfall (hundred-year averages) is shown for one wet and one dry locality, humidity for an intermediate locality. All data from Padya 1989. Humidity is strongly associated with rainfall.

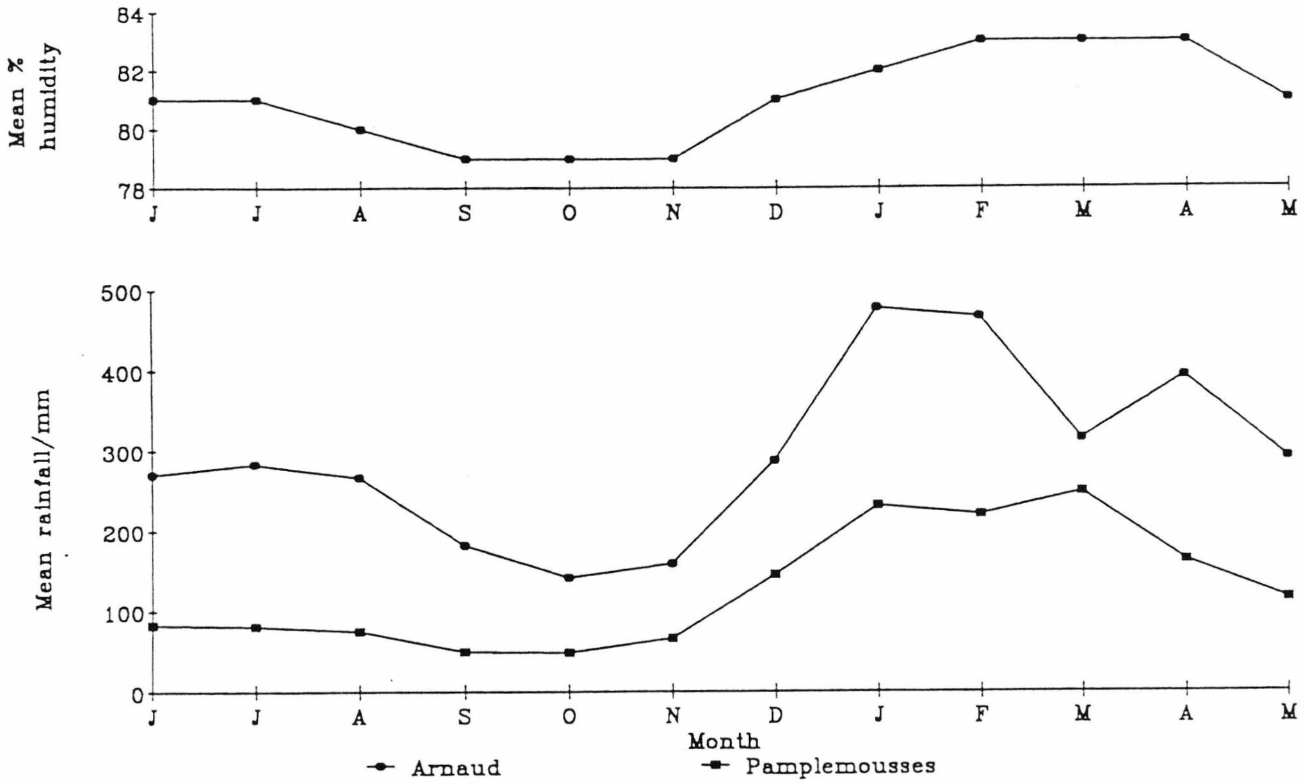


Fig. 2.2. Annual temperature patterns on Mauritius, for hot and cool localities: Curepipe is the closest locality to the main study area for which data exist (Padya 1989).

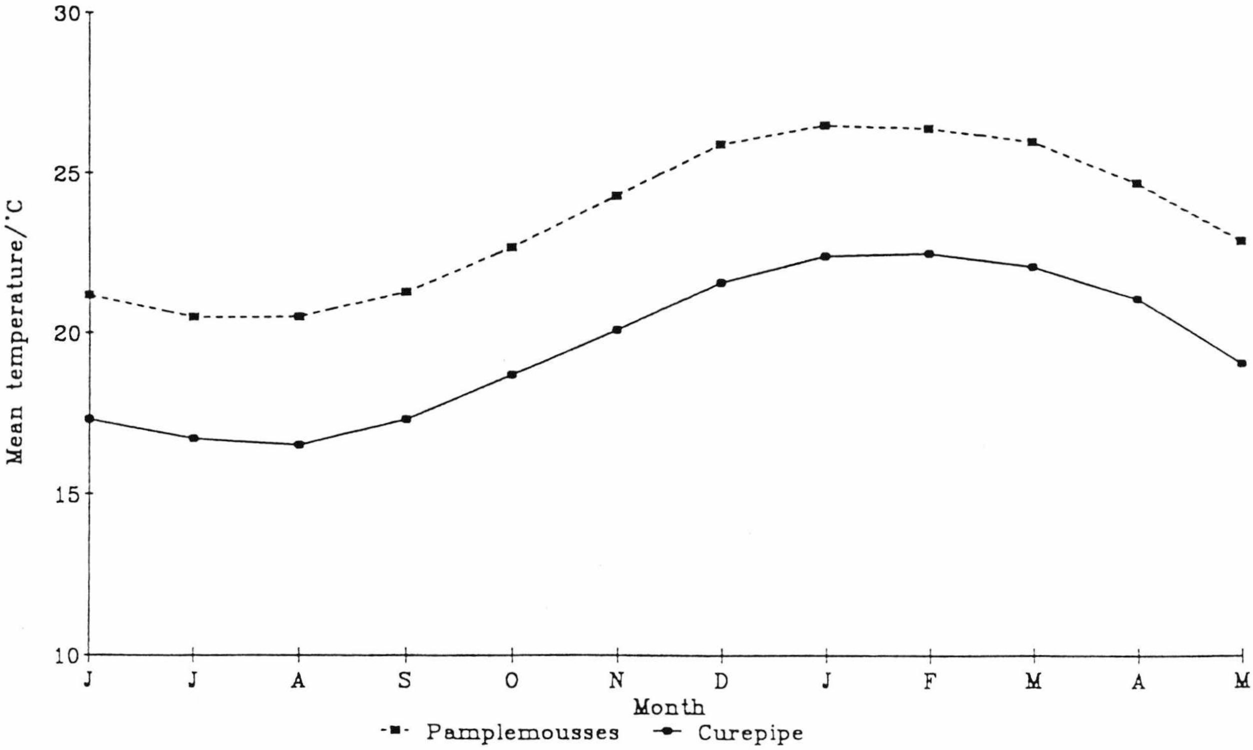


Fig. 2.3. Mauritius, showing rainfall in mm (1961-90 averages: black lines) and topography (shading). Rainfall data provided by Mauritius Meteorological Service (unpublished). Contours at 200 m, 500 m and 670 m.

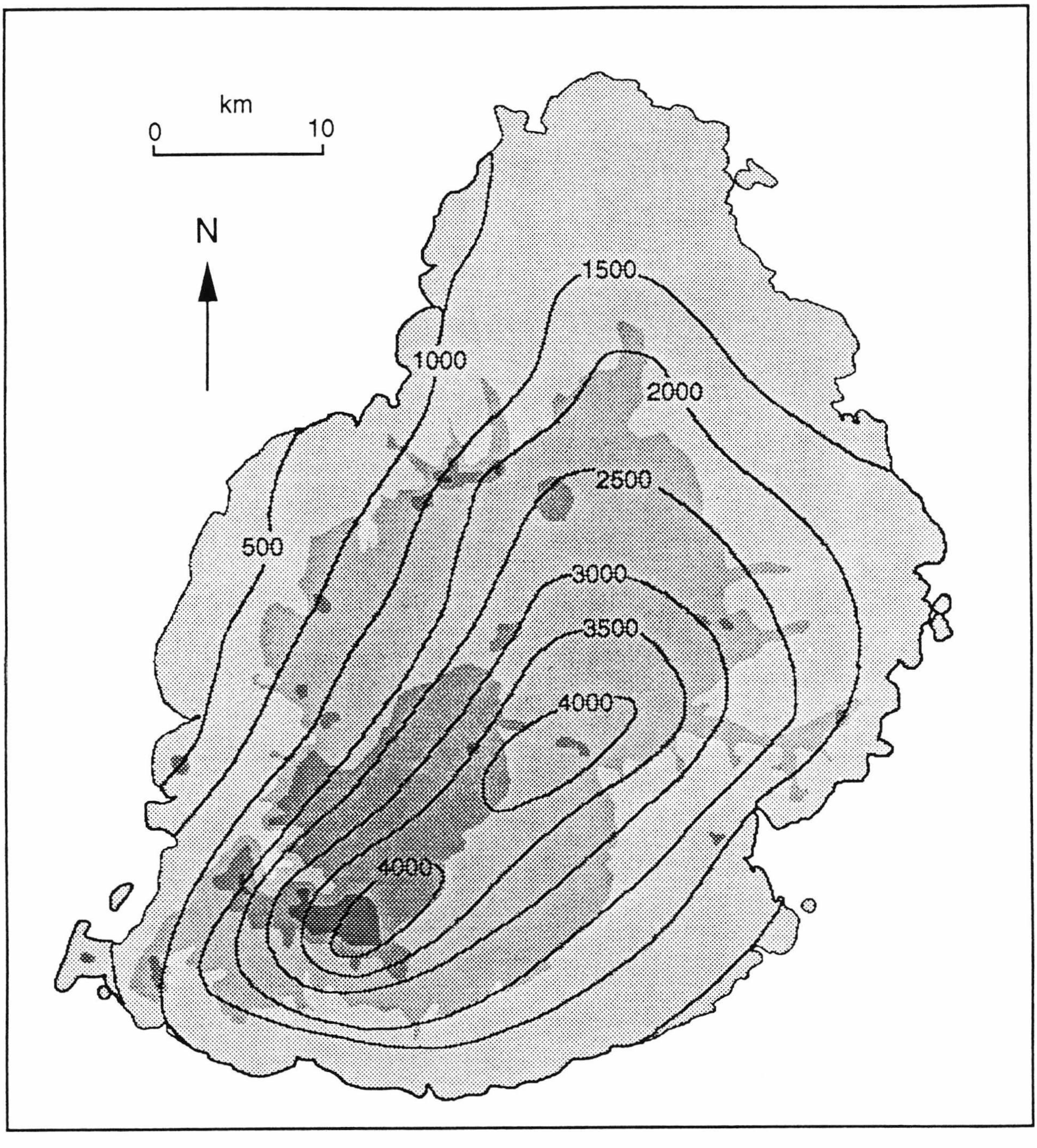
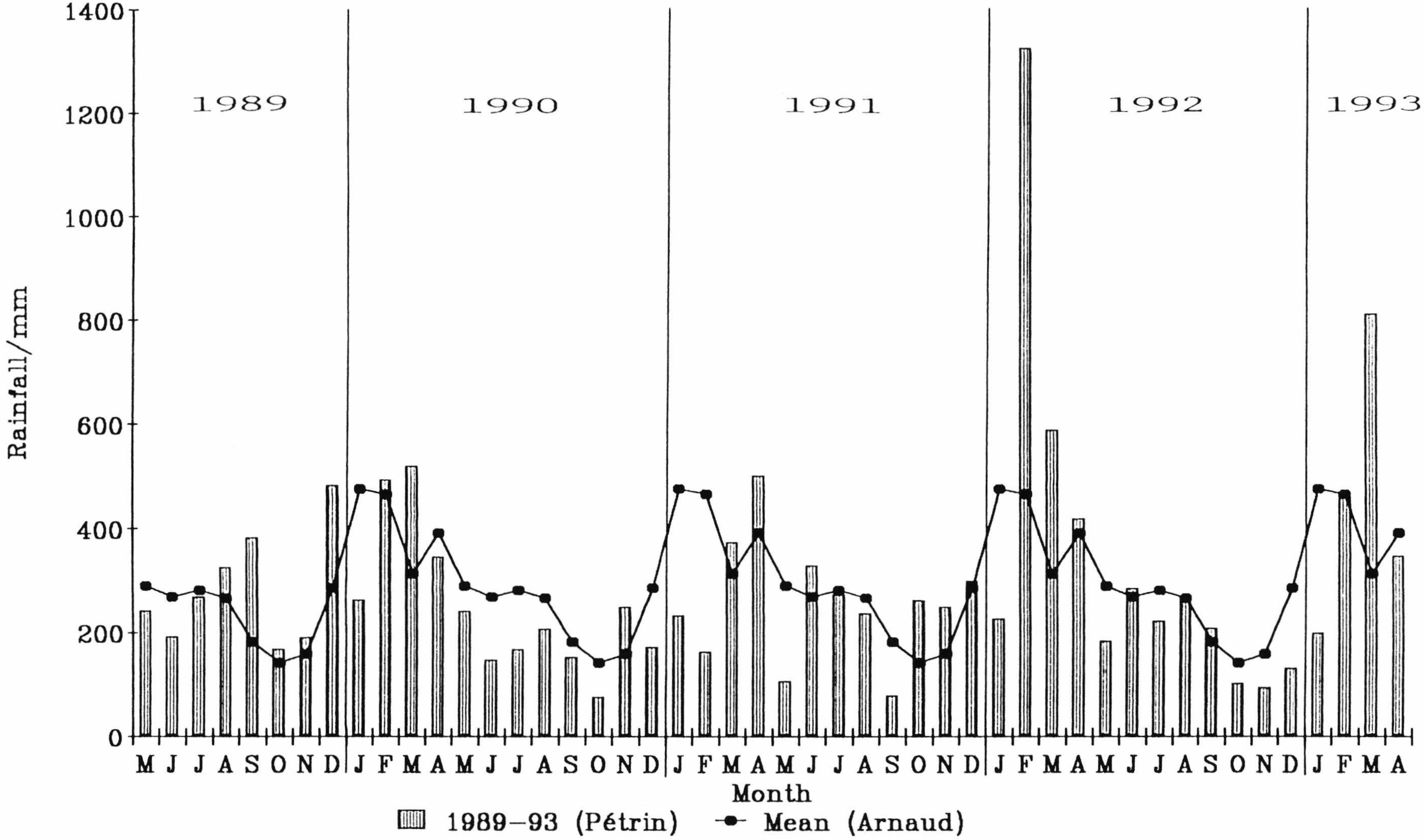


Fig. 2.4. Comparison of monthly rainfall measured in the study area (Pétrin) with the mean for 1887-1980 at a nearby station (Arnaud). Pétrin data from Mauritius Meteorological Service (unpubl.), Arnaud data from Padya (1989).

Note (1) that the heavy rains started 2-3 months late in March 1991, and (2) the high rainfall in February 1992. Both events occurred during the main bird breeding season.



Cyclones

Tropical depressions regularly develop in summer between 5°S and 30°S in the Indian Ocean (Padya 1976). Some intensify to become cyclones, which may strike Mauritius. Intense cyclones (*sensu* Padya 1972: sustained wind speeds for one hour over 70 miles per hour [110 km/hr]) occur on Mauritius on average less than once per decade, but 21 separate depressions produced gusts over 100 km/hr on Mauritius between 1970 and 1989 (MMS unpubl.). During the period of this study, no depressions reached even the latter intensity. The last intense cyclones to produce gusts over 200 km/hr on Mauritius occurred in 1975 (see Cheke 1975a, 1987c), 1979, 1980 and 1983. Therefore, the study was carried out during an unusually prolonged cyclone-free period. This run ended with Cyclone Hollanda in early 1994.

2.2 History of the vegetation

The native plant communities, and especially the upland climax forest, were described in detail by Vaughan & Wiehé (1937 [with map], 1941), but since then much has been cleared and the rest degraded (Lorence & Sussman 1986, 1988). Originally, higher areas supported a lower moist montane tropical evergreen forest (with patches of cloud forest), scrub (including ericoid) and marsh vegetation depending on edaphic (soil) conditions (Vaughan & Wiehé 1937, Lorence 1978). In the rain shadow a drier, semi-deciduous forest dominated, with palm savanna in coastal areas of the north and west. The classification of vegetation types proposed by Vaughan & Wiehé (1937) is followed here, but using the more modern terminology of Lorence (1978).

Destruction of the native vegetation began as soon as people colonized Mauritius (Brouard 1963, Cheke 1987a and references therein). Today only a small fraction of the native forest area of Mauritius has avoided total clearance. All palm savanna was quickly lost, except on Round Island (Brouard 1963, North & Bullock 1986), but areas of the evergreen and semi-deciduous forests survive, mostly on mountain slopes in the south-west and centre-east. However, poor regeneration by native plant species, combined with invasion by exotics, has left all of the native forest in a variably degraded state. The commonest invasive exotics, which will be referred to in the text, are listed in Table 2.2, along with the main plantation species.

Table 2.2. The commonest naturalized exotics, plantation trees and ornamentals, which will be referred to in the text. Vernacular names in inverted commas (") are local names; other English names are those which are in common, international use. Scientific names are used in the text. Species marked with an asterisk (*) are the only member of their genus on Mauritius and will be referred to only by their genus. Sources: Brouard (1963), Owadally (1973, 1980), Lorence & Sussman (1986, 1988).

Naturalized exotics	Plantation trees (P) or ornamentals (O)
Rubus alceifolius (Rosaceae) "Piquant loulou" (bramble)	*Pinus* spp.[1] (Pinaceae) Pine (P)
Psidium cattleianum (Myrtaceae) Strawberry Guava ("Chinese Guava")	*Cryptomeria japonica* (Cupressaceae)* Japanese Red Cedar (P)
Syzygium jambos (Myrtaceae) Rose-apple	*Callistemon citrinus* (Myrtaceae)* Bottlebrush (O)
Ligustrum robustum var. *walkeri* (Oleaceae)* Privet	*Eucalyptus robusta*[2] (Myrtaceae) Swamp mahogany (P)
Ravenala madagascariensis (Musaceae)* Travellers' Tree	

Notes

[1] The main plantation species is *P. elliotti* (?=*P. caribaea*); also present are *P. taeda* and *P. tabuliformis* (?=*P. sinensis*).

[2] *E. kirtoniana* is also present in the uplands, but most upland eucalypts were believed to be *E. robusta*. In dry areas, *E. tereticornis* and some *E. citriodora* are grown.

After Brouard's (1963) general account of forestry practices, Cheke (1987a) reviewed the history of forest clearance on Mauritius until the notorious destruction of the native forests of Les Mares, Kanaka and Grand Bassin in the early 1970s. Cheke (1987c) provided a descriptive summary of the vegetation as it was in 1975, including an approximate map showing the native forest areas of the south-west. No more detailed map has been published, although slightly modified versions of Cheke's map were used by Jones (1987) and Safford (1991).

A unique (and, as will be shown, crucial) characteristic of the forest from Montagne Cocotte to Combo and north to Grand Bassin is the patchwork of relict native patches, plantations and small groves of various exotics (mostly *Eucalyptus robusta*, but also *Cryptomeria*, *Pinus*, *Araucaria*, *Juniperus* and *Cinnamomum camphora*). Other native forest areas lack such groves of exotics. They are too small for their creation to have been individually documented, but they must date from P. Koenig's directorship of the Forest Department (1903-1929). After much previous debate, in these areas Koenig implemented a policy of "improvement fellings" by systematic exploitation of dead and dying trees, and planted up gaps in exploited (but not necessarily completely cleared) areas (Koenig 1912-

28, 1926, Edgerley 1963, Brouard 1963, G. A. d'Argent verbally 1992). *Eucalyptus* was preferred in marshy areas, the other species in better drained sites, although *Cryptomeria* proved versatile (Brouard 1963). This haphazard practice was stopped by G. N. Sale, the next Director (by then referred to as Conservator), who preferred larger blocks (Sale 1931, Brouard 1963).

2.3 Extent of native forest in 1989-1993

2.3.1 *Introduction*

Since one of the first requirements of this study was to assess the distributions and populations of all the native land-birds, it was clearly important to visit all native forest areas. Since the latter are not authoritatively identified on any map, and the very existence of certain patches is widely ignored, it seems worthwhile to provide a summary of the extent of native forest and the condition of adjacent areas, which are largely or entirely covered in exotic vegetation.

2.3.2 *Methods*

Only the mainland of Mauritius was considered. The map and survey results of Cheke (1987c) were used as the starting point, and all areas indicated as native forest were visited. Once the identification features of the dominant native and exotic plant species had been learnt, a brief, overall assessment was made of the vegetation at each site visited. Viewpoints (summits, ridges and hillside clearings) were used to view wider areas, since native forest, and also the commoner exotic species, could readily be located by the habit and colour of the canopy. Finally, in January 1993, copies were obtained (from the Ministry of Housing, Lands and Town and Country Planning) of aerial photographs of the south-western forests (the whole island was covered), taken in 1991 at approximately 1:20,000 scale. Many vegetational features were easily identified but most required ground-truthing: for example, in the photographs, young *Eucalyptus* in a mixed exotic thicket was indistiguishable from low, degraded native forest.

Degradation by exotics is a gradual process, creating a continuum between unaltered native forest and totally exotic vegetation. Cheke (1987c) did not define his boundary between native and exotic vegetation. The easiest visual check is a qualitative assessment of the proportion of native canopy remaining; application of a rigorous, quantitative definition would require time-consuming field work and the results would be of dubious value, since the ambiguous areas would *a priori* be of minimal importance.

Since some native bird species use the exotic vegetation abutting native forest, exotic habitats were also mapped around the native forest areas. The following categories of habitat were adopted.

1. Native forest and scrub. This category includes all areas with a sufficient proportion of native trees in the canopy (even if the undergrowth was a thicket largely or entirely composed of exotics, with no regeneration of native species), such that removal of all exotics would still leave most of the ground covered. The different native forest types were not distinguished.

2. Exotic forest and scrub. As well as true forest of exotics (for example, the floor of the Black River Gorge: Jones 1987), included in this category are areas which were probably never deliberately cleared of native vegetation but have degraded to the point of being exotic thickets with just occasional native plants (for example, the natural amphitheatre at the head of Grandes Gorges: Jones 1987).

3. Plantations. Anticipating the importance to nesting birds of plantations of exotics bordering or surrounded by native forest, these were described. Only the strip 100 m or so closest to the native forest was identified to species level since areas any remoter from native forest were generally irrelevant to native birds.

4. Other vegetation. This includes all habitats considered to be completely useless to forest birds. Most is sugar cane, tea and foodcrop plantation, along with some open country not presently in use.

All relevant information from the above sources was transferred to the Directorate of Overseas Survey 1:25,000 maps.

2.3.3 *Results*

The results are shown on Figs 2.5 and 2.6, and Table 2.3. The total area classified here as native forest is 92.8 km^2, or 5.0 % of the land area of Mauritius. Of this, 58.9 km^2 (65 %) is in the south-west (Fig. 2.5), 33.2 km^2 is in the centre-east (Fig. 2.6), and a tiny patch (Le Pouce, 0.7 km^2) survives in the north (Fig. 1.2). On the mainland, native forest occurs from 100 m altitude up to 828 m, the highest point on the island (Fig. 2.7). It must be remembered that none of this is in a pristine state.

Fig. 2.5 differs from Cheke's (1987c) map of the south-western forests as follows.

1. Cheke indicated the large areas which had been cleared during and immediately before his 1973-75 surveys, since surviving birds displaced from those areas were thought to be affecting his findings (for example, by increasing bird densities found in surviving native forest areas adjacent to the clearances). Twenty years on, the situation is assumed to have stabilized and the recent plantations are not distinguished from the older ones.
2. Cheke's map implies that upper Combo was cleared in the early 1970s; low, degraded native forest in fact persists over most of the area.
3. The mixed native and exotic forest, rich in native birds, of State Lands Kanaka to Mangin and Pradier (together called the Kanaka block) was said to have been destroyed in the late 1970s (C. G. Jones in Cheke 1987c). A small amount in fact survived until at least 1985 (A. S. Cheke verbally 1994), but had finally gone by 1989, except perhaps along riverbanks (pers. obs.). The Kanaka crater forest is highly degraded, as is that along the Rivière du Poste, except for a well-preserved patch to the north of the river, in State Lands Robin, Buvery and Denis, which was omitted from Cheke's map and surveys.

For analysis of bird distributions, the native forests of Mauritius are divided into seven main regions: the six shown in Fig. 2.8, plus the Moka Range. Each region is divided into areas, as shown in Fig. 2.9.

Macchabé Area, Southern Slopes and Fouge Range

The two large blocks of native forest in the south-west (the Macchabé Area and the Southern Slopes) could be considered contiguous. They are separated by the deep Grandes Gorges valley, which contains patchy native forest especially in the valley bottom and in sheltered pockets on the slopes, but is 400 m deep and 1.5 km across from rim to rim. A similar situation exists on the slopes of Tamarin Gorge, which separates the Trois Mamelles - Mondrain forests from those of Brise Fer - Tamarin Falls. Good forest is found in sheltered valleys on the west side of the Black River Gorges (below Black River peak), between completely degraded spurs.

A band of *Syzygium jambos*, about 500 m thick, forms the lower border of the native forest of the Southern Slopes, from east of Piton du Fouge to Combo, excepting Bel Ombre (although even here it dominates in places).

Several of the small *Eucalyptus* groves, and also the *Cryptomeria* grove (Pigeon Wood), surrounded by native forest around and above Bassin Blanc (Southern Slopes) contain some native vegetation, unlike the larger blocks of plantation. Most of these groves are too small to appear on Fig. 2.5 and so are included with the native forest; Fig. 2.10 distinguishes these groves. Pigeon Wood is detailed on Fig. 2.11.

Plateau Relicts

Relict patches of native vegetation, up to 2.1 km^2 in area, are scattered over a wide area of the southern part of the central plateau. Although some are very close to the main forest blocks (Bois Sec is only 0.5 km distant), their isolation and the sedentary behaviour of some birds justifies separate treatment for these patches. In addition, some rivers in this area have native vegetation (not mapped) along their banks.

The condition of the vegetation of these relict patches varies greatly. Thanks to long-term management, Perrier supports the finest remnant *Sideroxylon* formation (Guého 1988) but is far too small (1.5 ha) to support forest bird populations. Bois Sec (5.9 ha), Gouly Père (10.9 ha) and Les Mares (5.1 ha) nature reserves are also floristically rich. In State Lands Gouly Père and Declerc, tiny areas of native forest also survive outside the two latter reserves. The unprotected, previously overlooked patch north of the Rivière du Poste opposite Kanaka crater contains varied forest, rich in *Calophyllum*, *Sideroxylon* and *Gaertnera*, similar to the taller parts of State Land Raoul (pers. obs.). In the Midlands area, Montagne Lagrave supports a rich cloud forest (rainfall over 4000 mm) with the highest Pteridophyte diversity in Mauritius, and neighbouring Montagne Laselle has rare native heath vegetation (Lorence 1978). The remaining patches (Monvert, Jouanis, Piton du Milieu and Montagne d'Hauvillard) appeared much poorer (pers. obs.); indeed, Jouanis was being slowly cleared when I visited (December 1992).

Bambous Range

The Montagnes Bambous include some of the best preserved of Mauritian forests (Cheke 1987c), especially the *Sideroxylon* formation (wet forest) above Ferney (Lorence 1978). Dry forest (rainfall 2000 mm) occurs on Montagne Chat (W. A. Strahm verbally 1990). The area between Montagne Laselle and Montagne Table à Perrot is very poor, heavily dominated by *Ravenala*; parts of this area could be considered as native forest, but it is classified as exotic in Fig. 2.6, in order to emphasize the much better condition of Lagrave and the Bambous. Most of the Bambous Range is managed for deer, with a belt (about 500 m thick) of pastures interspersed with patches of native forest and much introduced mango *Mangifera indica* forming the lower border of the native forest area. The precise border of the native forest was not ground-truthed throughout the Montagnes Bambous; in doubtful cases, it was usually taken to be approximately 0.5 km above the limit of the cultivated land.

Central-east Relicts

Much of Montagne Blanche is dominated by *Ravenala* although in places, especially the eastern end, this is interspersed with native forest. Areas without *Ravenala* are instead full of *Ligustrum*, *Hiptage*, *Syzygium jambos* and *Psidium cattleianum*. Montagne Fayence has, by contrast, very little *Ravenala* and many native trees forming a continuous canopy in places.

Moka Range

In the Moka mountains of the north, the only native area is the botanically rich, cloud forest (Lorence 1978) nature reserve on Le Pouce (69 ha); elsewhere in these mountains (for example, Pieter Both) only occasional native plants survive amid exotic thickets.

Outlying areas

Innumerable rivers and streams drain south and east from the central plateau, and many are bordered by a strip of partly native forest, with much *Ravenala* and *Syzygium jambos*, protected as River Reserves (Vaughan & Wiehé 1937). Some of these were visited, but are not mapped. A few exotic forest areas are relevant, most obviously the mixed plantations at Bras d'Eau, on the young lavas of Plaine des Roches; other plantations and *Syzygium jambos* thickets, such as those between Nicolière and Midlands, were not surveyed.

Finally, native vegetation survives on a few offshore islets. Excluding littoral plant communities (such as mangroves), Ile aux Aigrettes (25 ha) has dry forest (Parnell *et al.* 1989) and Round Island (169 ha) has the last remnant palm savanna (Vaughan & Wiehé 1937, Vinson 1964). Ecological restoration of these and other islands has a key role to play in the future of conservation of flora and fauna in Mauritius (Chapter 9); however, no native landbirds are yet present.

Table 2.3 (overleaf). Native forest areas of Mauritius in 1993. Forest types follow the map in Vaughan & Wiehé (1937) and lists of localities in Lorence (1978), using the latter's terminology. CF=Cloud Forest, HS=Heath and Scrub, RF=Rain Forest, WF=Lower Montane Wet Forest (*Sideroxylon* Formation and High Forest), DF=Dry Evergreen Forest. Forest types in brackets are present over only a small part of the area.

Table 2.3. See previous page for legend.

Forest patch	Area/km^2	Altitude range/m	Native forest types
Fouge Range			
Piton du Fouge - Piton Canot	4.5	100-598	WF, (DF)
TOTAL	4.5	100-598	
Southern Slopes			
Black River Peak	7.9	200-828	WF, (DF)
Bel Ombre (upper)	5.9	400-700	WF
Bel Ombre (lower)	7.6	200-400	WF
Alexandra Falls	2.8	400-700	RF, WF
Plaine Champagne	4.5	650-714	HS, WF
Cocotte - Savanne	4.5	450-772	CF, RF
Combo	5.4	150-704	WF
Le Bouton/Grandes Gorges	1.4	250-650	WF
TOTAL	40.0	150-828	
Macchabé Area			
Pétrin - Raoul	1.1	640-670	HS, WF
Macchabé - Brise Fer	8.9	300-650	WF, (HS)
Tamarin Falls - Trois Mamelles	2.6	180-600	WF, DF
TOTAL	12.6	180-670	
Plateau Relicts			
Bois Sec - Rivière du Poste	0.7	500-700	WF, RF?
Monvert	0.6	600-620	WF
Jouanis	0.5	460-540	WF
Perrier	0.01	550	WF
Midlands (Mt Lagrave area)	4.0	350-638	CF, WF, (HS)
TOTAL	5.8	350-700	
Bambous Range			
Montagnes Bambous	26.0	100-626	WF, (DF)
TOTAL	26.0	100-626	
Central-east Relicts			
Montagne Blanche	2.0	250-532	WF
Montagne Fayence	1.2	250-433	WF
TOTAL	3.2	250-532	
Moka Range			
Le Pouce	0.7	700-812	CF
TOTAL	0.7	700-812	
TOTALS	92.8	100-828	-

Fig. 2.5. South-west Mauritius, showing vegetation and principal man-made features

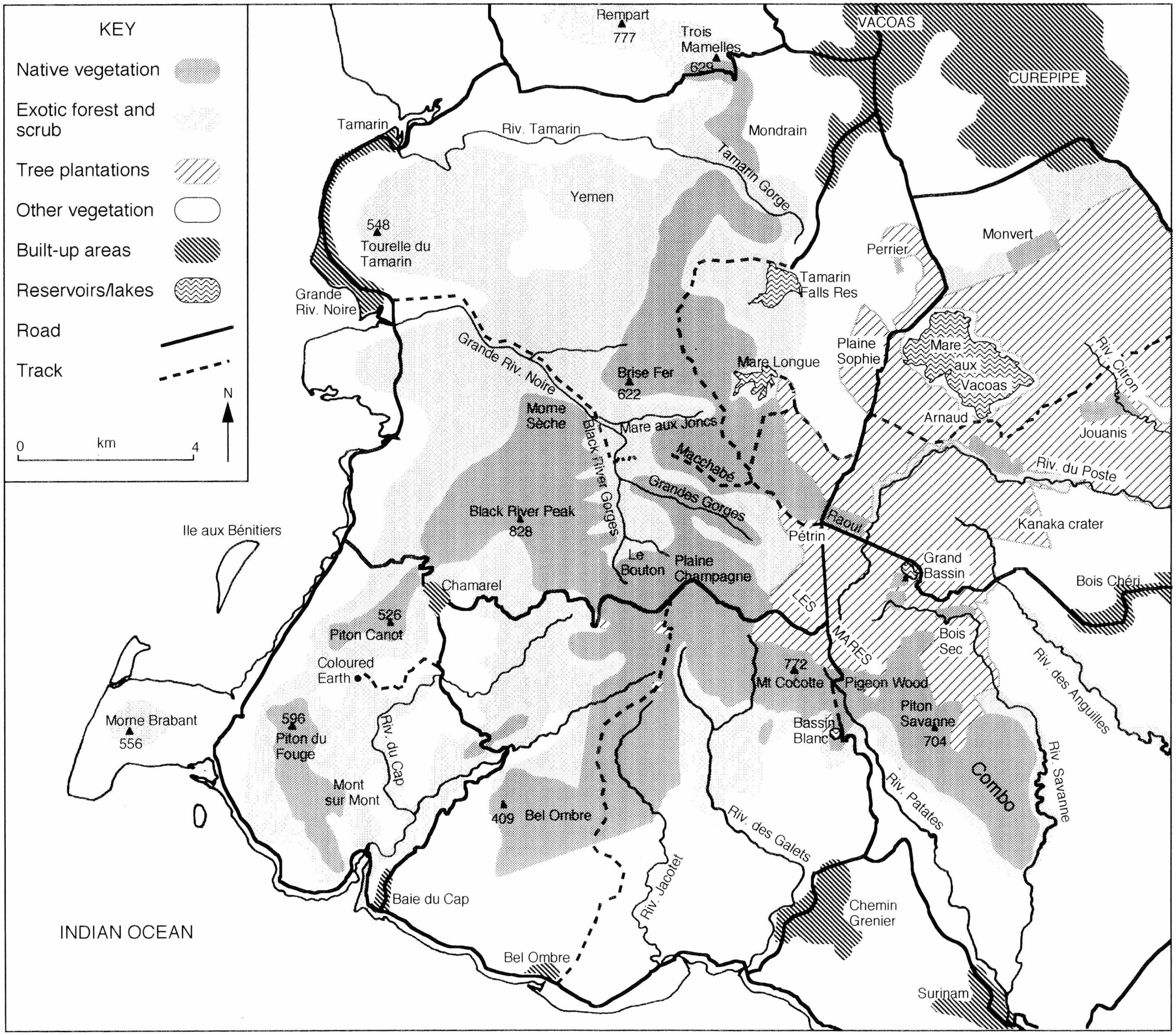


Fig. 2.6. Central-east Mauritius, showing vegetation and general features. Tree plantations not shown as none abuts native forest.

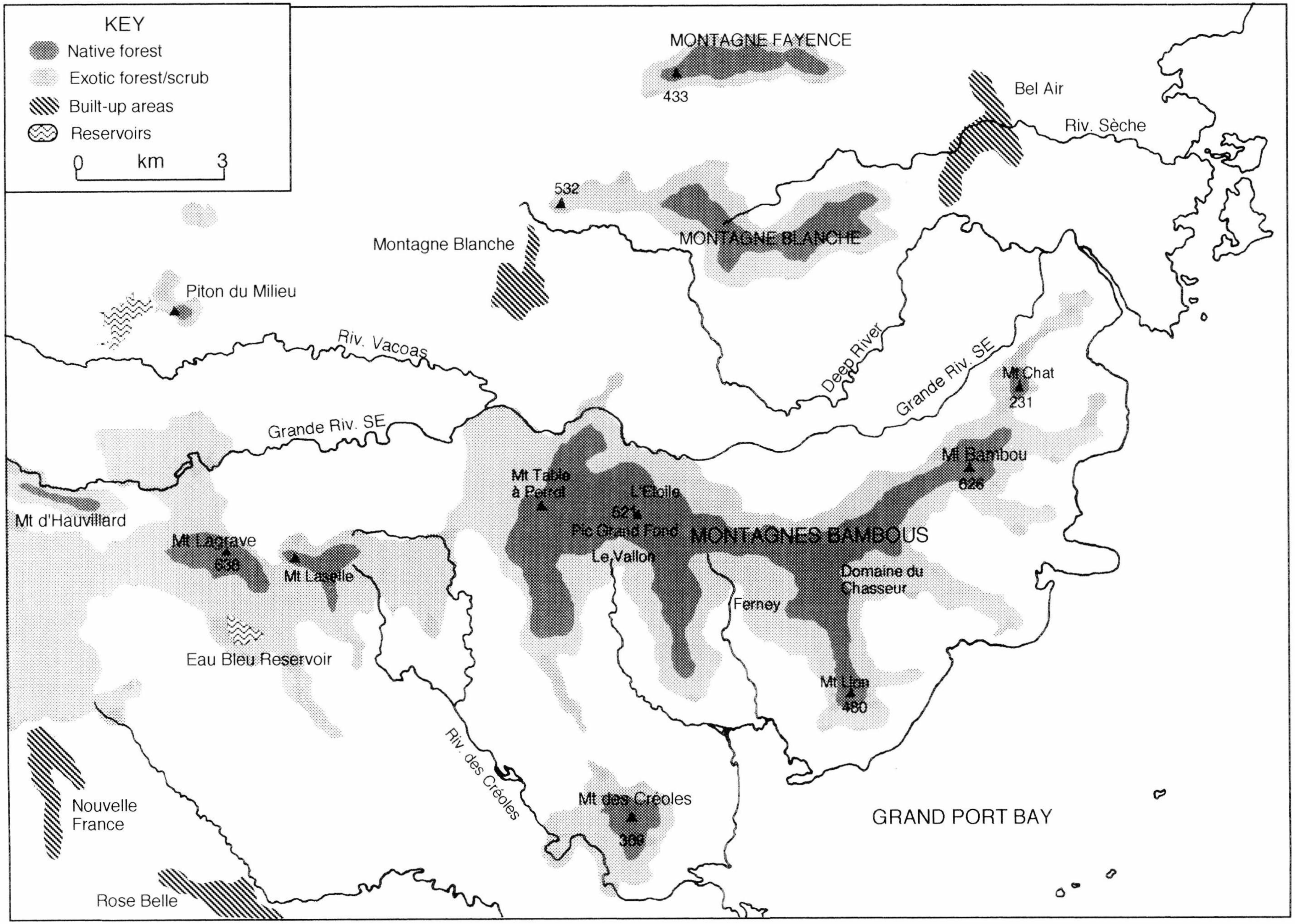


Fig. 2.7. South-west Mauritius, showing native forest, rivers and contours.

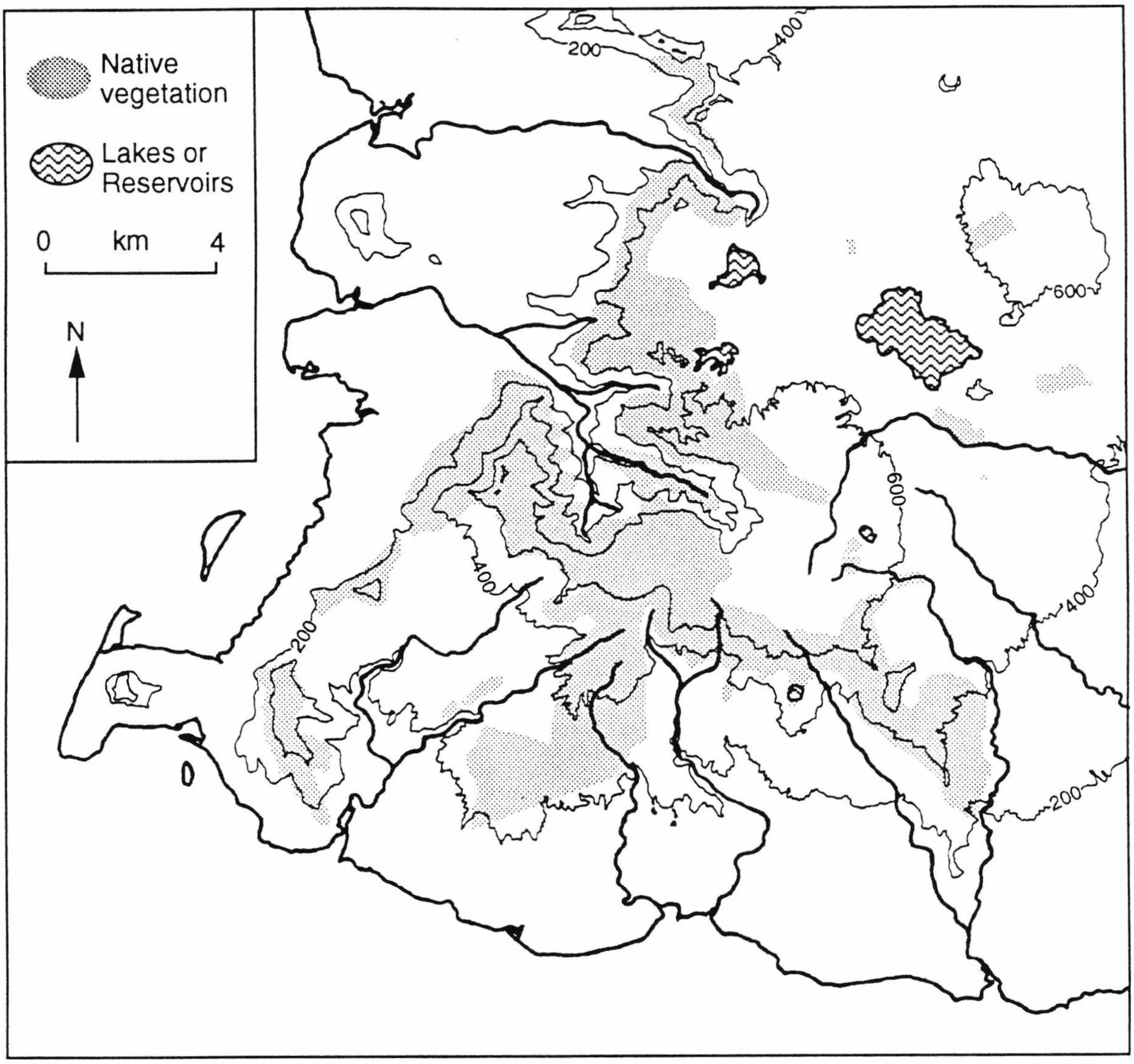


Fig. 2.8. Southern Mauritius, showing native forest areas (shaded) and names and boundaries of the regions referred to in the text.

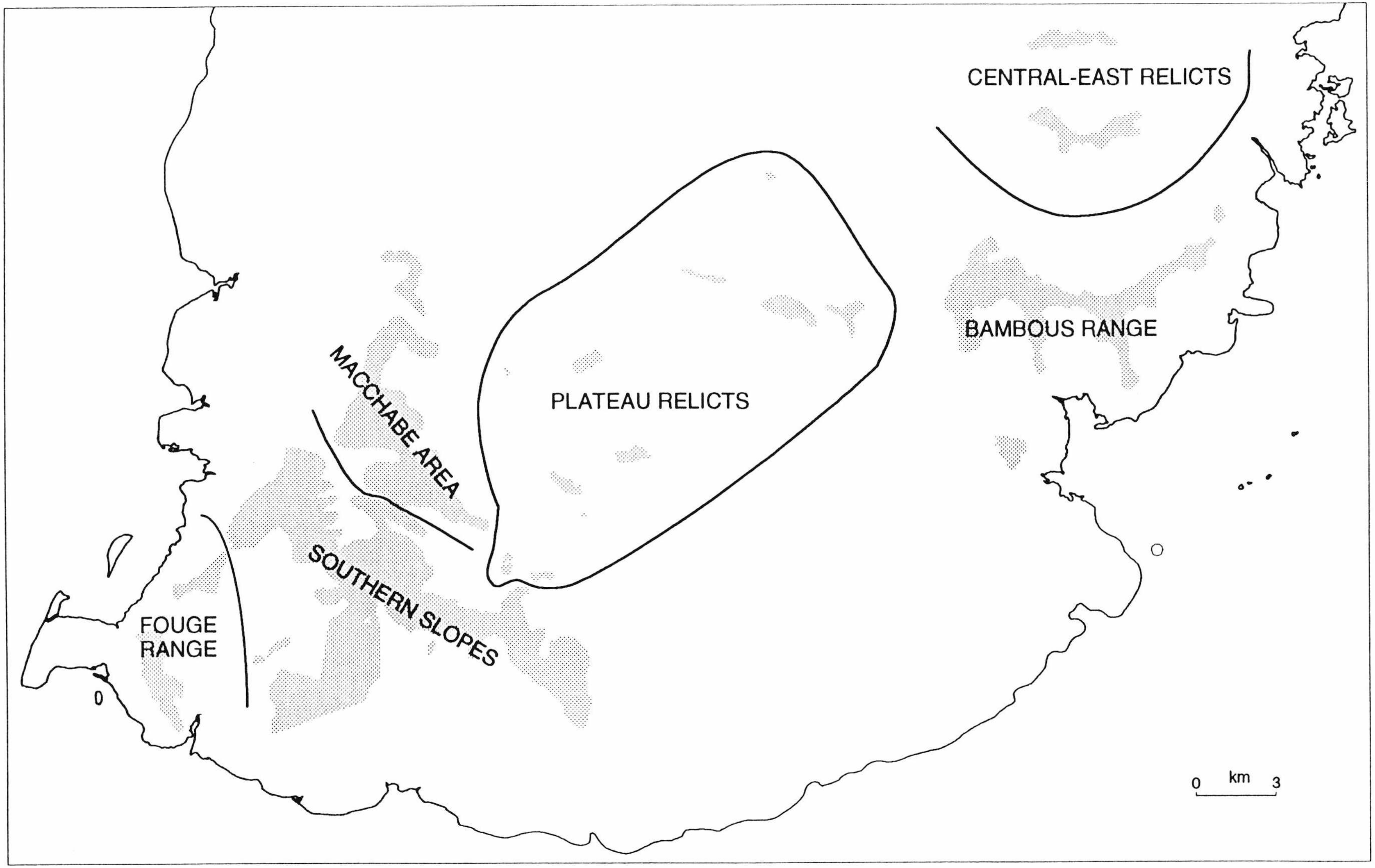


Fig. 2.9. South-west Mauritius, showing names and boundaries of the native forest areas referred to in the text

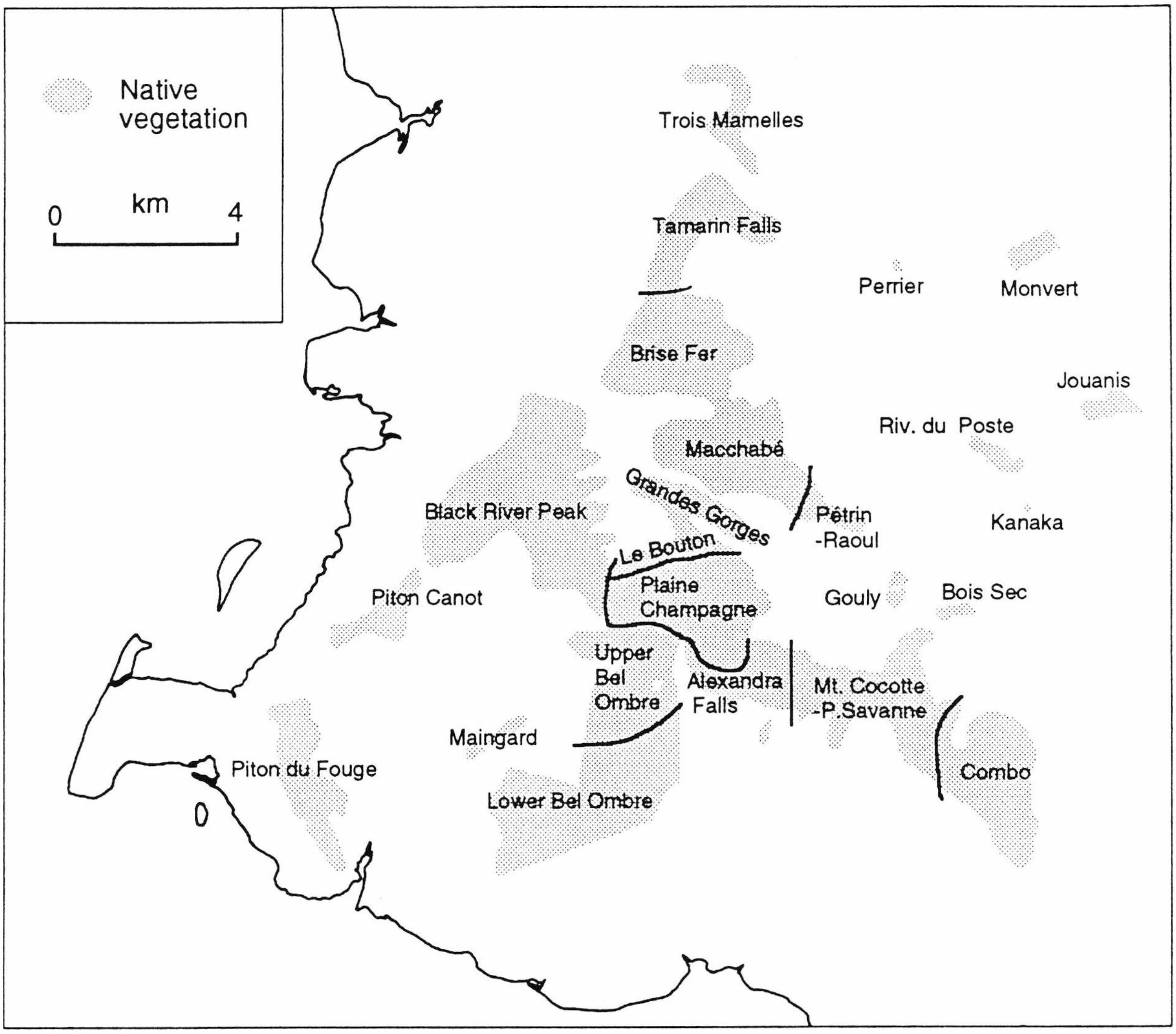


Fig. 2.10. The Montagne Cocotte - Bassin Blanc - Piton Savanne area of the Southern Slopes of Mauritius

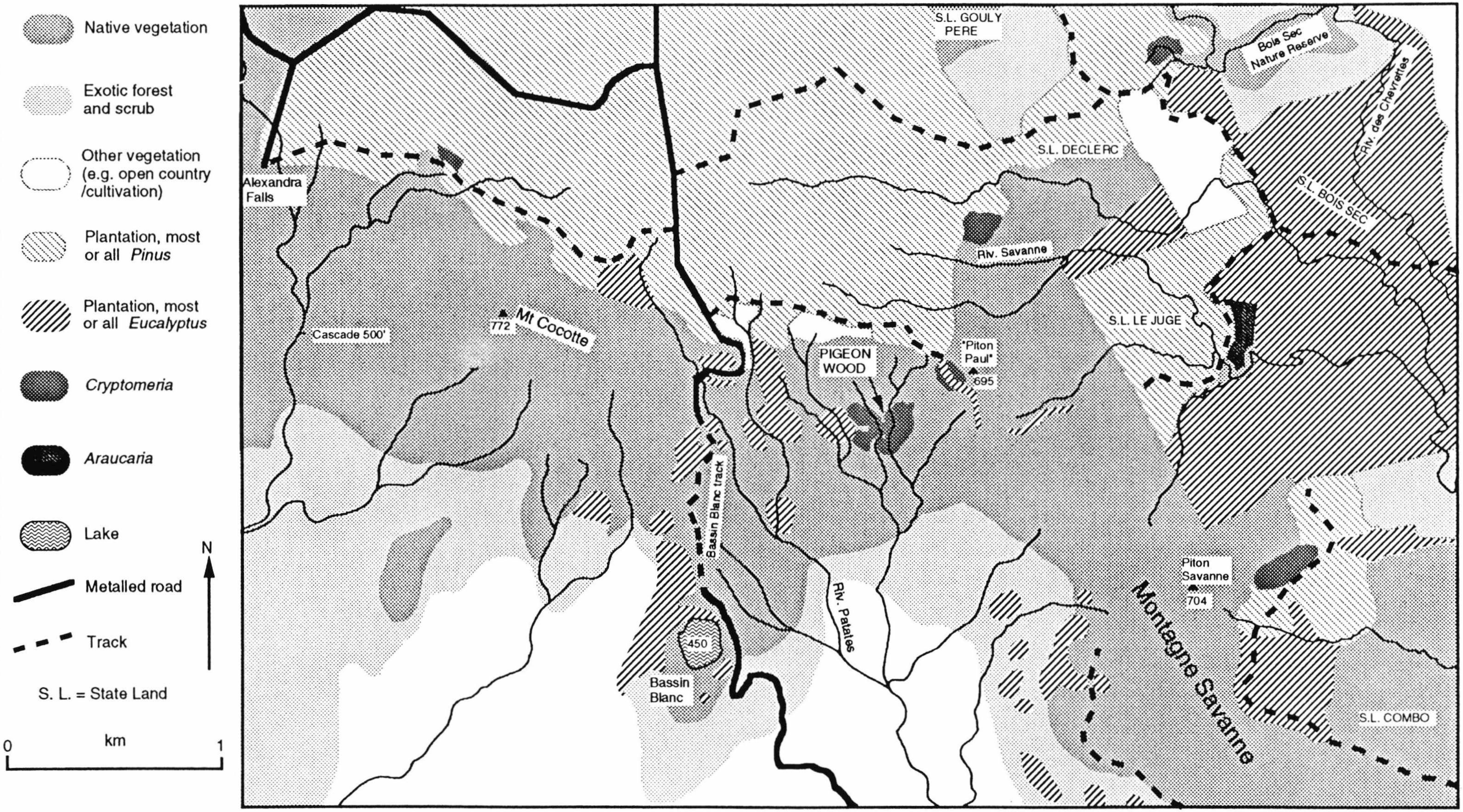
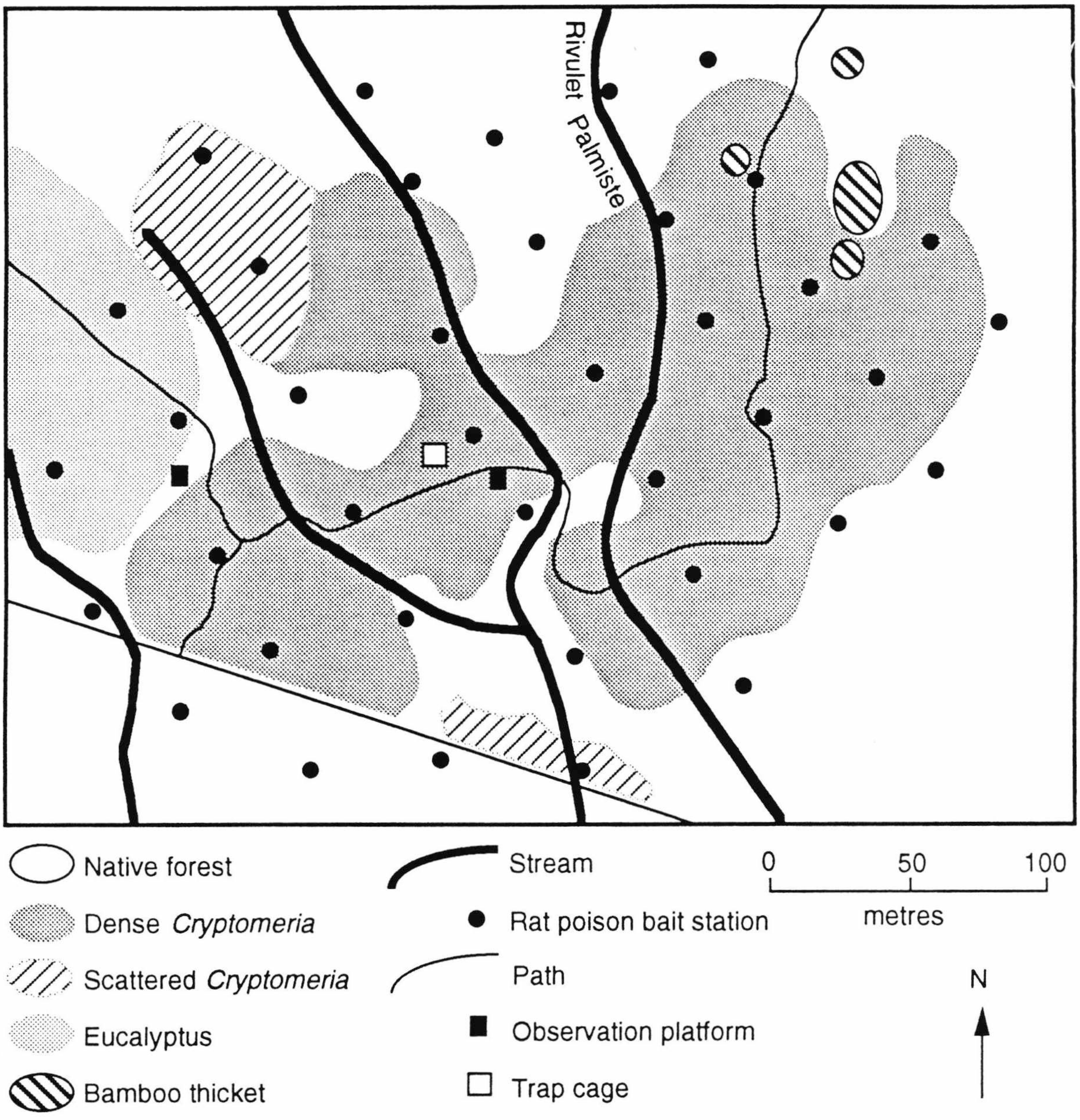


Fig. 2.11. Pigeon Wood, showing vegetation and general features



Chapter 3. Censuses and distribution studies of native land-birds

3.1 Introduction

Reliable knowledge of population size and distribution is a fundamental requirement for the conservation of rare species (Green & Hirons 1991). Distribution studies may reveal key factors of a species' ecology and conservation needs (Bibby *et al.* 1992). The distribution and habitat requirements of the forest-living native birds of Mauritius are often difficult to understand, because the populations are small and their environment has been much modified. The discovery of even a few individuals of a native species at a new site can substantially increase understanding of its status and requirements. When habitat or land use changes are occurring, or protected areas are being created (as on Mauritius at present), it is important to know what proportion of populations will be affected or protected, in order to assess their viability. Finally, a population estimate is the single detail most frequently requested by those interested in endangered species; these include government planners and decision-makers assessing extinction risk, and the media, who usually seek no more than a few fundamental facts. The figure given must be accurate and consistent with other studies if extinction likelihoods are to be predicted correctly and confidence in biologists is to be maintained.

The only previous census of the Mauritian native passerines was carried out by the BOU expedition in 1973-75 (Cheke 1983, 1987c). Observations made during brief return visits by Cheke in 1978 (Cheke 1979) and 1985 (Cheke 1985) suggested that important changes in distribution and population had occurred, but these were not documented in detail.

Therefore, every area in Mauritius thought possibly to hold populations of forest-living native birds was visited. The precise aim was to define the population size and distribution of each species on a very fine scale, in relation to their use of habitat features. Much-needed conservation measures can only be proposed if the habitat requirements are fully understood. Although population monitoring alone would not help the species, the study was also expected to provide baseline data that would enable future observers to detect changes in population size and distribution.

In this chapter, I present the results of the censuses and distribution studies for each forest-living native passerine species, excepting the abundant Grey White-eye. The survey results are linked to the birds' use of habitat features, in particular for nesting and foraging, in subsequent chapters.

Two terms to be used require definition, following Species Survival Commission (1992). *Geographic extent* is the area encompassing the known, inferred or projected sites of occurrence of a taxon, excluding cases of vagrancy. *Range area* is the total area occupied by the taxon within its geographic extent, excluding cases of vagrancy.

3.2 Methods

3.2.1 *Census techniques*

To census bird populations in forest, three main techniques are available: line transects, point counts and territory mapping (Bibby *et al.* 1992). The four main factors affecting the choice of census method were: firstly, the need to relate distribution to habitat use; secondly, the extreme variation in bird density over short distances (Cheke 1987c, Safford 1991); thirdly, the usually impenetrable and extremely heterogeneous vegetation, due especially to variable levels of degradation by exotic plants, and to the presence of tree plantations of different species, as well as to varied native plant communities (Chapter 2); and finally, the small areas of native bird habitat (totalling less than $100km^2$).

Line transect methods are poorly suited to sampling the bird populations of small areas or dense vegetation and are likely to overlook the effects of very local habitat features (Bibby *et al.* 1992). I attempted to carry out several transects along tracks in Macchabé forest. For every cuckoo-shrike or black bulbul (the only study species present) seen or heard, I recorded the time and estimated location. The varying density of vegetation and convoluted terrain made estimating distances of calling birds (necessary if densities are to be calculated) unreliable. The most precise way of analysing the data from these transects was to plot the records to create a territory map. However, the resulting encounter rates for cuckoo-shrikes are given under that species.

Point count methods could have allowed small scale habitat variations to be related to the occurrence of individual birds. In addition, if methods and counting sites were standardised, future workers could detect fluctuations, with no need for a complete population census (as by Stevens *et al.* 1992 on the Comoro islands). In spite of these advantages, densities and population sizes derived from point count data are prone to large errors arising from inaccurate distance estimation or from violation of assumptions about moving birds, because the area surveyed is proportional to the square of the distance from the observer (Bibby *et al.* 1992). With transects the area surveyed is only linearly proportional to the distance from the route, the other dimension being distance along the transect, which can be measured precisely (Bibby *et al.* 1992). Both methods, being formalized, are fairly easy to replicate.

However, territory mapping was selected as the census technique, because examination of distribution at such a fine scale was needed to explain the birds' status. In order to establish the habitat features influencing the siting of territories, it was necessary to map territories, and relate these with the birds' feeding (Chapter 5) and breeding ecologies (Chapters 6 & 7). The different aspects of the overall studies were thus integrated; this was not only an efficient use of time, but also provided suggestions as to possible links between the status and its causal factors. My methods are given below in detail, because methods used to arrive at population estimates for other threatened species have often been inadequately documented (Green & Hirons 1991).

Each area of forest (native or exotic) was visited at least once, to assess the habitat and to search for birds. Then, from existing knowledge of the habitat requirements of all the species, and of the vegetation of Mauritius, promising areas were checked repeatedly to find as many birds as possible. All routes walked and bird records were plotted on maps. When the results of several visits to one area were plotted, clusters of records were sometimes identified. In low-density areas with apparently vacant habitat between territories, one cluster could often be equated to a single territory. In high-density areas with contiguous, exclusive territories within which the occupants roam freely, clustering is not guaranteed. In such cases, simultaneous records of more than one bird (especially territorial disputes) were helpful in delineating territories, as was a knowledge of typical territory size from known territories nearby. Discovery of nests allowed repeated observations of individual birds, heading towards or arriving from the extremities of their territories. Pairs nesting in adjacent territories were especially informative, as the birds did not have to be recorded simultaneously (so long as both nests were known to be active). The dense cluster of Mauritius Fodies in Pigeon Wood was not finally elucidated until a nest of every pair was found. Closely observed birds were often individually recognisable by unique markings, such as red markings away from the head and rump of male Mauritius Fodies, or, more temporarily, unusual feather abrasion.

The primary data therefore consisted largely of territory maps, the most important of which are shown in Appendix 1. In this chapter, the numbers of territories found in each area are given in a population table or map for each species. Cheke (1983: his Table 1) very usefully did this for the Mauritius Fody in 1973-75.

Where all territories of a species were thought to have been found, the population was estimated by counting territories. Densities were estimated using territory maps.

In less well surveyed areas, field data were plotted to produce territory maps which were complete over small portions of the area. Encounter rates were sometimes also calculated. Densities in these portions were derived by comparison of the territory maps or encounter rates with those from well surveyed areas. The suitability of the habitat for the species being surveyed was assessed (by comparison with well-surveyed areas) over the whole area, from extra visits to cover more ground (without detailed surveying) or by inspection of the vegetation from a raised viewpoint. If the habitat appeared similar throughout the area, the density found in the portion surveyed was assumed to apply throughout. If the habitat was not similar throughout, the different areas were visited to estimate densities. It seems that this was also Cheke's (1987c) method, although he did not say so explicitly.

If important populations are overlooked during the early searches, serious errors may arise when this census method is used. Subsequent census work based on these searches is liable to a deep-rooted bias, which may reinforce false initial impressions. Such bias was avoided by ensuring that all forest areas were covered in sufficient depth to be sure that such populations had not been overlooked. Coverage is discussed below.

Colour-ringing birds for individual recognition in the field would have helped to distinguish territories and given innumerable other benefits. Very little of this was attempted, because my mistnetting experience was too limited to work safely. Usually no one was present with any greater experience. The lack of colour ringing was one of the major shortcomings of my field methods, but I make no apology for this: see Butler & Merton (1992: 79) for the potential disasters caused by untrained handlers ringing endangered species.

3.2.2 *Assumptions*

Populations are given as a range of numbers of adult pairs. All the study species are monogamous and territorial, at least in the breeding season (Chapter 4). Some black bulbuls, olive white-eyes and (to a lesser extent) Mauritius Fodies foraged outside their exclusive territories. For the latter, only adult pairs or adult males acting territorially were taken to indicate a pair. For the former two, wanderers were sometimes recognizable as such and excluded from census data, for example olive white-eyes at isolated nectar sources amid *Pinus* plantations. However, such birds in suitable breeding habitat often could not be distinguished from birds which were on territories but not actively defending them. While breeding, birds presumably spent most time in their territories, and so the errors caused by wandering birds are probably minor.

Non-breeding birds (unpaired adults and pre-breeding immatures) were excluded when recognizable. Immature male cuckoo-shrikes and Mauritius Fodies were often distinctive (Chapter 4); the rarity of these suggested that pre-breeding immatures of all species were rare. Similarly, only three unpaired, fully red, territory-holding male fodies were confirmed during the four years. Those non-breeders wrongly included in census data are assumed not to affect substantially the overall results.

3.2.3 *Coverage*

Some species are easier to census than others, and so a given amount of coverage will produce more complete and precise survey data for some species than for others. In areas visited so frequently that all territories were known (such as Pigeon Wood and Bassin Blanc), the efficiency of detecting territories for any one visit or series of visits could be judged. The intensity of coverage for my census is defined in terms of two variables: the comprehensiveness of the network of routes used and the total effort in each area.

Figs 3.1 and 3.2 show the main routes followed in native forest and nearby exotic areas during my fieldwork between 1989 and 1993. The total effort in each native forest area is shown in Table 3.1, along with an overall assessment of coverage, which is defined as follows. "Good" coverage requires that no locality was more than 1 km from a route walked, *and* that the total effort exceeded 8 hr/km^2. For "fair" coverage, the limits for these figures are a maximum of 3 km and minimum of 2 hr/km^2, respectively. Table 3.2 explains what census data for each species can be expected from a given level of coverage. It must be stressed that these figures are approximate. For example, in one three-hour visit to State Land Raoul, all threatened native bird territories were found and mapped; the results were subsequently verified. This amounts to only 6 hr/km^2, which rates as "fair" coverage, yet this sufficed for a complete census.

Combining all four breeding seasons (1989-93), all areas of native forest on the island were given at least "fair" coverage, as defined above, except for Montagne Fayence (see below). In fact, almost all areas indicated were covered in the single 1992-93 breeding

Fig. 3.1. Vegetation of south-west Mauritius, showing main routes covered during survey work by me in 1989-93. Not all paths walked by me are shown.

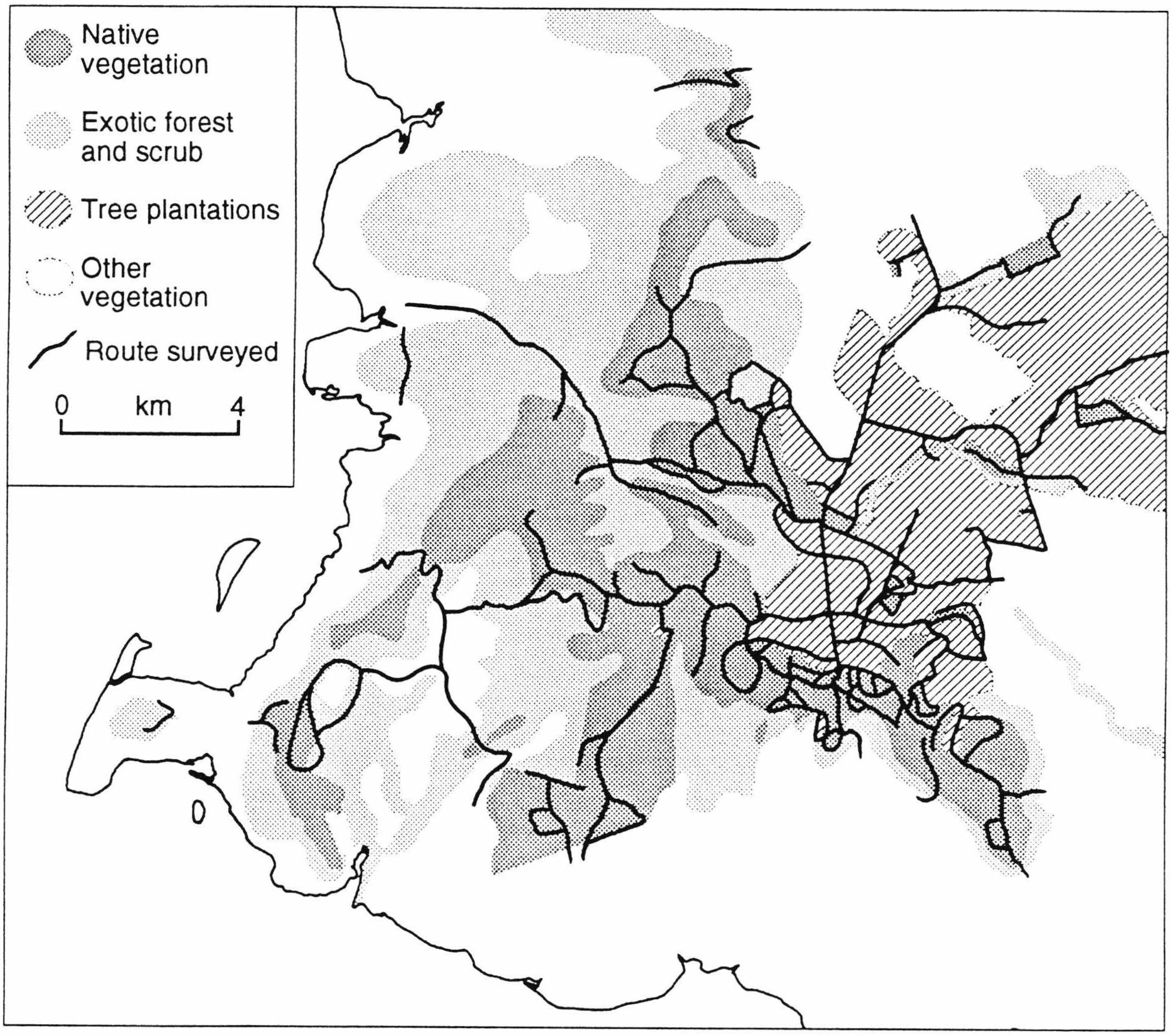
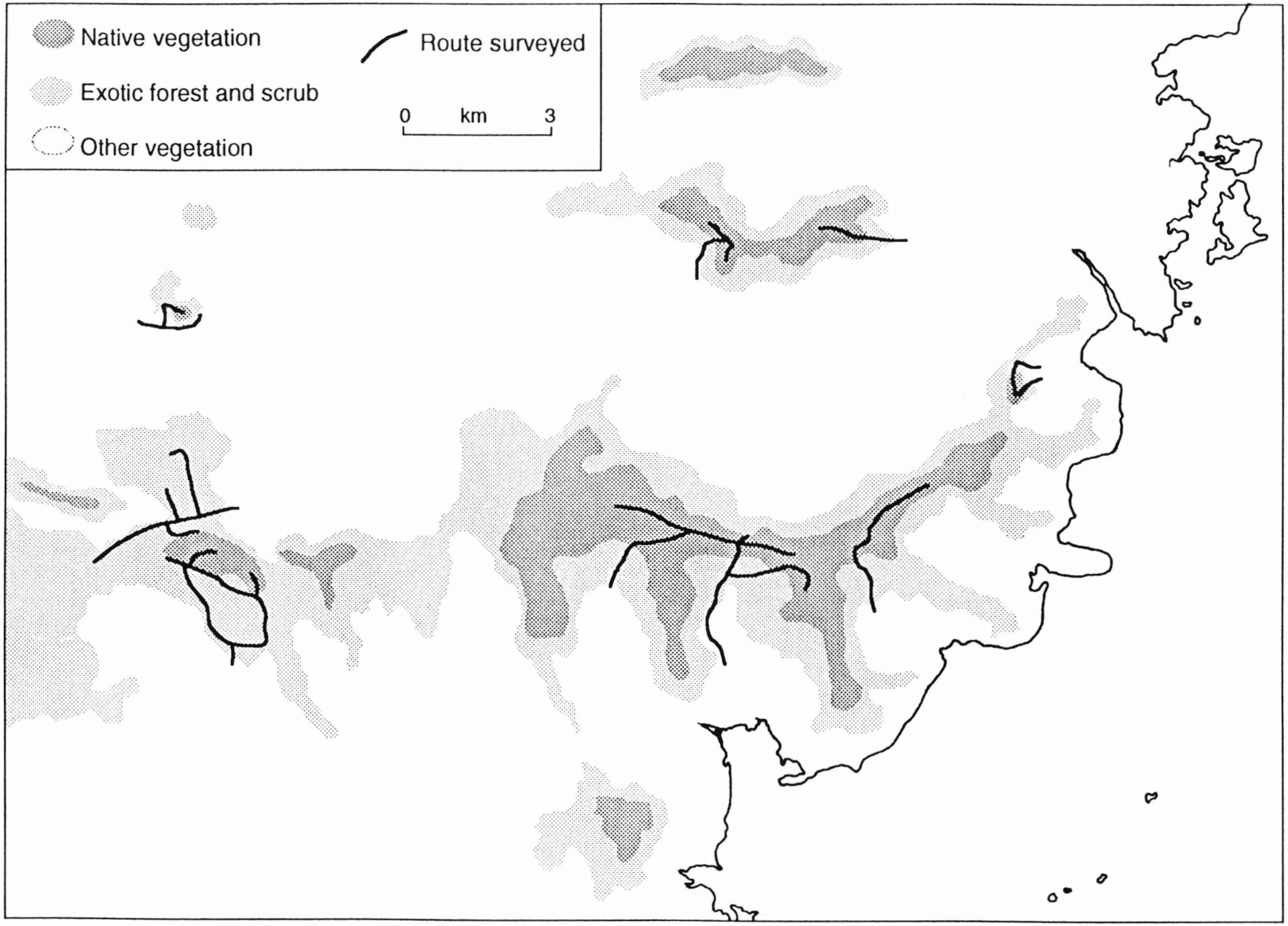


Fig. 3.2. Vegetation of central-east Mauritius, showing main routes covered during survey work by me in 1989-93. Not all paths walked are shown.



season. Failure to record a species was assumed to imply that no resident population was present in the area, except in the case of the flycatcher (which could occur in isolated pairs almost anywhere, and had a very short detection distance); wandering (presumably non-breeding) black bulbuls and olive white-eyes could appear almost anywhere. This assumption was justified because "good" coverage never once produced records of species which had not been found in the same area during "fair" coverage (again, excepting the flycatcher). Tree plantations and naturalized exotic vegetation were also checked, but in less detail since there was no doubt that very few native birds occurred in them (Staub 1976, 1993, Cheke 1987c, J.-M. Vinson *et al.* verbally).

Table 3.1. Survey effort and overall coverage in each native forest area, 1989-93.

Forest patch	Area (km^2)	Effort (hr/km^2)	Coverage
Fouge Range			
Piton du Fouge - Piton Canot	4.5	3	fair
Southern Slopes			
Black River Peak	7.9	6	fair
Upper Bel Ombre	5.9	8	good
Lower Bel Ombre	7.6	2	fair
Alexandra Falls	2.8	15	good
Plaine Champagne	4.5	8	good
Cocotte - Savanne	4.5	>50	good
Combo	5.4	4	fair
Le Bouton/Grandes Gorges	1.4	8	good
Macchabé Area			
Pétrin - Raoul	1.1	25	good
Macchabé - Brise Fer	8.9	50	good
Tamarin Falls - Trois Mamelles	2.6	9	fair
Plateau Relicts			
Bois Sec - Rivière du Poste	0.7	35	good
Monvert	0.6	5	fair
Jouanis	0.5	8	good
Perrier	0.01	>50	good
Midlands	4.0	3	fair
Bambous Range			
Montagnes Bambous	26.0	2	fair
Central-east Relicts			
Montagne Blanche	2.0	4	fair
Montagne Fayence	1.2	0	none[1]
Moka Range			
Le Pouce	0.7	8	good

Note

[1] Reliable information about the birds of Montagne Fayence was received from M. d'Unienville (verbally 1993).

In the 1989-90 breeding season (August to March) I concentrated on the olive white-eye and Mauritius Fody. The fody data were revised in 1990-91, when cuckoo-shrikes were also studied. Throughout the studies, black bulbuls and flycatchers were always noted, and preliminary results appeared for all species after the latter season (Safford 1991, 1992). Little surveying was done in 1991-92, except in the austral winters of those years. In 1992-93, very wide coverage was achieved; the fody was almost completely re-surveyed and the distributions of all species were finalized.

All data are my own, unless otherwise indicated. Many Mauritians, as well as recent visiting fieldworkers working with other wildlife, know the species well. In particular, R. Chevreau de Montléhu, F. Staub and J.-M. Vinson know the island better than any visitor and have paid attention to the passerines for decades (without conducting a census); their verbal reports and field notes were indispensible in confirming past and present distributions. For two small areas not visited by me, Montagne des Créoles (an outlier of the Montagnes Bambous) and Montagne Fayence, completely reliable reports were provided by C. G. Jones and M. d'Unienville respectively.

Table 3.2. Implications of different levels of coverage for census data on each study species, at any site where all species are present.

Species	Detection distance for song or commonest call[1]	Completeness of survey[2]	
		Good coverage	Fair coverage[3]
Cuckoo-shrike	100-500 m	Most territories found	Presence confirmed; approximate density
Black bulbul	100-500 m	Approximate density	Presence confirmed
Flycatcher	30-70 m	All territories crossed by route found	Presence only along route confirmed; possibly overlooked
Olive white-eye	30-100 m	Approximate density	Presence confirmed; possibly overlooked
Fody	50-150 m	Most territories found	Presence confirmed

Notes:

[1] Detection distances are a very rough guideline; lower figures are for an observer walking through closed canopy forest, higher figures for an exposed vantage point, both assuming bird does not approach or flee from the observer.

[2] "Good" and "fair" coverage are defined in the text.

[3] "Presence confirmed" also means that lack of records implies absence.

Table 3.3. Estimated distribution area and population of forest-living native passerines of Mauritius in 1975 and 1993. All data from 1975 are taken or deduced from Cheke (1983, 1987c). Geographical extent has not changed greatly for any species since 1975.

Species	Status in 1975		Status in 1993			Comments
	Range area (km^2)	Population (pairs)	Range area (km^2)	Geographical extent (km^2)	Population (pairs)	
Cuckoo-shrike	27	210-220 [180-190][1]	36	130	200-340	Expansion into lowlands?
Black bulbul	78?	200	78	500	225-340	No major change
Flycatcher	dispersed	<250 [<320][2]	dispersed	1000	125-230	Severe decline except Bras d'Eau
Olive white-eye	40	350 [275][1]	32	250	140-260	Severe decline in density
Fody	>33.7	247-260 [145][1]	14.7	68	104-120	55% decrease in range area and population

Notes

[1] Population sizes expected by Cheke (1987c), following habitat loss in 1970s.

[2] Corrected estimate, as population estimated at Bras d'Eau in 1975 is a known underestimate (see text).

3.3 Results

The results are summarized in Table 3.3. The following accounts detail the distribution, population size and changes since 1975 for each species in turn.

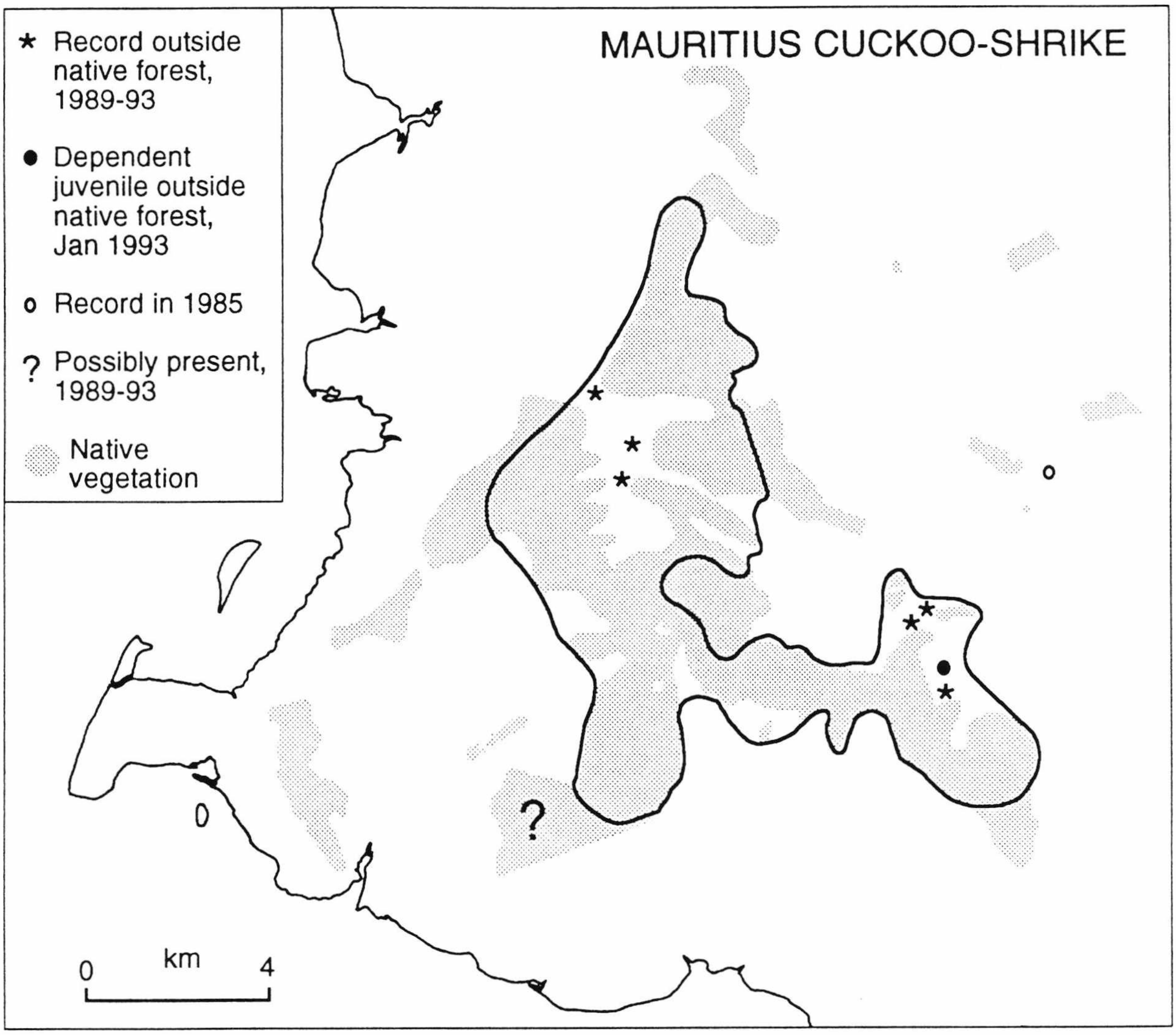
3.3.1 *Mauritius Cuckoo-shrike*

Distribution

The cuckoo-shrike occurred in 1989-93 largely in the native upland forest of Macchabé - Brise Fer, Black River Peak and the southern scarp from Bel Ombre to Combo (Fig. 3.3). As in 1975, there was no sign of cuckoo-shrikes anywhere around Piton du Fouge nor on the Lagrave and Bambous Ranges. J.-M. Vinson told Cheke (1987c) that he may have heard one in the Montagnes Bambous in 1973, but by 1992 (verbally, to me) Vinson had dismissed this record. In addition to my own searches, several fieldworkers, familiar with the cuckoo-shrike and its song, have spent many months studying kestrels in the Bambous without finding cuckoo-shrikes (C. G. Jones, R. E. Lewis, M. A. C. Nicoll *et al.*, verbally). Those surviving in the Gouly - Bois Sec area included a territory in totally exotic vegetation in State Land Le Juge (dependent juvenile seen). A few occur on the Yemen escarpment (between Tamarin Gorge and Brise Fer) but there are no recent records from Tamarin Gorge (C. G. Jones, verbally) and there are certainly none in Mondrain nature reserve or below Trois Mamelles (Strahm 1988, pers. obs.). In the west, there are no records from the oft-visited lowland forests of Morne Seche and north-west of Chamarel but the mixed native and exotic forest between Black River Peak and Chamarel was unchecked.

On 28 November 1991, N. M. C. Garbutt (verbally 1991) saw a silent, medium-sized passerine with a thick bill, grey upperparts and white underparts in Le Pouce nature reserve, in the Moka mountains. It jumped from perch to perch, with occasional flights hugging the canopy. Of passerines known on Mauritius, this description fits only a male cuckoo-shrike. The nearest known cuckoo-shrikes occur 20 km from Le Pouce, a site much visited by naturalists (I checked the area twice), many of whom know cuckoo-shrikes well; there are no historical records anywhere in the Moka Mountains. All evidence suggests that they are highly sedentary. This report deserves to be placed on record but is so unlikely that more observations are needed before the presence of cuckoo-shrikes on Le Pouce can be accepted.

Fig. 3.3. Distribution of the Mauritius Cuckoo-shrike in 1993. Solid line encloses distribution.



Population

In the best areas for cuckoo-shrikes, encounter rates during walking periods over two hours varied from no birds at all, up to one every 8 min. In known territories, the occupants were detected on average only one or two times in four by an observer walking steadily, but spending 30-60 min at one point would often reveal all territories within detection distance (see Table 3.2). Therefore, about four visits to an area, including stops of up to an hour, were usually sufficient to find nearly all territories.

The birds appeared to hold exclusive territories. Juveniles and sub-adult males were rare, but readily identified and discounted from survey data, and no certain unpaired adults were seen. Therefore all sightings of adults were assumed to indicate a territory containing one pair. In Macchabé - Brise Fer, well-watched territories in which nests were found covered 4-6 ha (Cheke [1987c] found 4.5-6 ha). From mapped sightings in this area in 1990-91, territories were distinguished mainly by seeing or hearing birds simultaneously in adjacent territories; a few nests were also found. The data were consistent with contiguous territories in the 4-6 ha range. Although precise territory boundaries could be drawn in many ways, the resulting maximum density estimate of 25 pairs/km^2 hardly varied. The south-facing escarpment from upper Bel Ombre to Piton Savanne held up to around 12-15 pairs/km^2, Black River Peak and Gorge, lower Bel Ombre and Combo somewhat less.

The total population estimated in 1991 is rounded to 200-340 pairs, of which about one third were in Macchabé - Brise Fer (Table 3.4); there is no reason to think this had changed by 1993. Much of the error range comes from Bel Ombre, a large area, most or all inhabited by cuckoo-shrikes; within Bel Ombre, local densities seemed to vary greatly but time did not allow the detailed work needed to census this area well.

Changes since 1975

Cuckoo-shrikes have disappeared from State Land Raoul, the Kanaka area and Jouanis since 1973-75, presumably because the surviving native forest relicts are small in area, and too remote from other suitable habitat for immigration to compensate for mortality. The last record near Kanaka was one by the Rivière du Poste opposite the crater in 1985 (A. S. Cheke verbally 1994). Densities at Alexandra Falls (28 pairs/km^2 in 1975) have approximately halved.

There may have been an expansion into lowland areas since 1975. In the Black River Gorges in 1989-93, cuckoo-shrikes occurred almost wherever there was native forest (especially Grandes and Petites Gorges, Mare aux Joncs and all the western valleys from Feeder Jules Edouard to Rivulet Escalier) and sometimes even in exotic forest (such as that around the ford below Plateau Remousse). These areas were hardly surveyed in 1973-75 (A. S. Cheke verbally 1994), but C. G. Jones believes that some were unoccupied during his own early fieldwork, which began in 1979. Birds are now present in areas of both lower Bel Ombre (down to around 250 m) and Combo (to 340 m) where Cheke (1987c) searched and found none: Cheke found none below 400 m in Bel Ombre and none at all in Combo.

Cheke (1987c) estimated a population of 210-220 pairs in 1973-75, but expected the then recent native forest clearances to reduce this by about 30 pairs. My estimate appears to indicate an increase; this may be explained by expansion into lowland areas, discussed above, rather than an increase in density in traditional areas, because there is no evidence that densities have changed since 1975 in upper Bel Ombre, Black River Peak and Macchabé - Brise Fer.

Table 3.4. Distribution and population of the Mauritius Cuckoo-shrike in 1990-91. Cuckoo-shrikes did not always occupy the whole of the area of the forest patch; for example, the north and western part of Black River Peak was unoccupied, and part of lower Bel Ombre may have been unoccupied. Densities varied greatly within some forest patches. For example, Black River Peak held 10 pairs/km^2 in some areas but isolated pairs (given here as 1 pair/km^2) in others. The mean density on Black River Peak lay within the range 4-6 pairs/km^2; this range was multiplied by the area occupied to calculate maximum and mimimum populations. na=not applicable.

Forest patch	Area occupied (km^2)	Density: mean [range] (pairs/km^2)	Pairs found	Pairs estimated
Black River Peak	4.0	4-6 [1-10]	9	16-24
Black River Gorges	3.0	3-5 [1-5]	8	9-15
Upper Bel Ombre	5.9	6-10 [5-15]	12	35-59
Lower Bel Ombre	4.1-7.6	3-8 [1-15]	3	12-61
Alexandra Falls - Piton Savanne	7.3	6-8 [5-15]	31	44-58
Combo	3.0	3-5 [1-10]	3	9-15
Gouly - Bois Sec[1]	0.3	na[1]	4	4
Macchabé - Brise Fer	6.9	10-15 [1-25]	51	70-105
TOTAL	34.5-38.0	-	121	199-341

Note

[1] In the Gouly - Bois Sec area, pairs were scattered in a matrix of native forest patches and exotic tree plantations, much of which was unsuitable habitat; single density figures would be misleading.

3.3.2 *Mauritius Black Bulbul*

Distribution

This was by far the most widespread native forest species, apart from the Grey White-eye. Black bulbuls were found in nearly all the native forest (other than dwarf forest) areas visited, and also on Montagne des Créoles (C. G. Jones verbally 1990, not visited by me) (Fig. 3.4). Exceptions were: in the south-west, Mondrain reserve and Trois Mamelles (suggesting absence north of Tamarin Gorge, as noted by Cheke 1987c); in the east, Montagne Blanche (two visits to different areas, yielding no records) and Montagne Fayence (not visited but M. d'Unienville (verbally 1993) has never seen them); Cheke had no information on these two mountains. None occur in the Moka mountains (Staub 1976, Cheke 1987c, F. Staub and J.-M. Vinson verbally, pers. obs.).

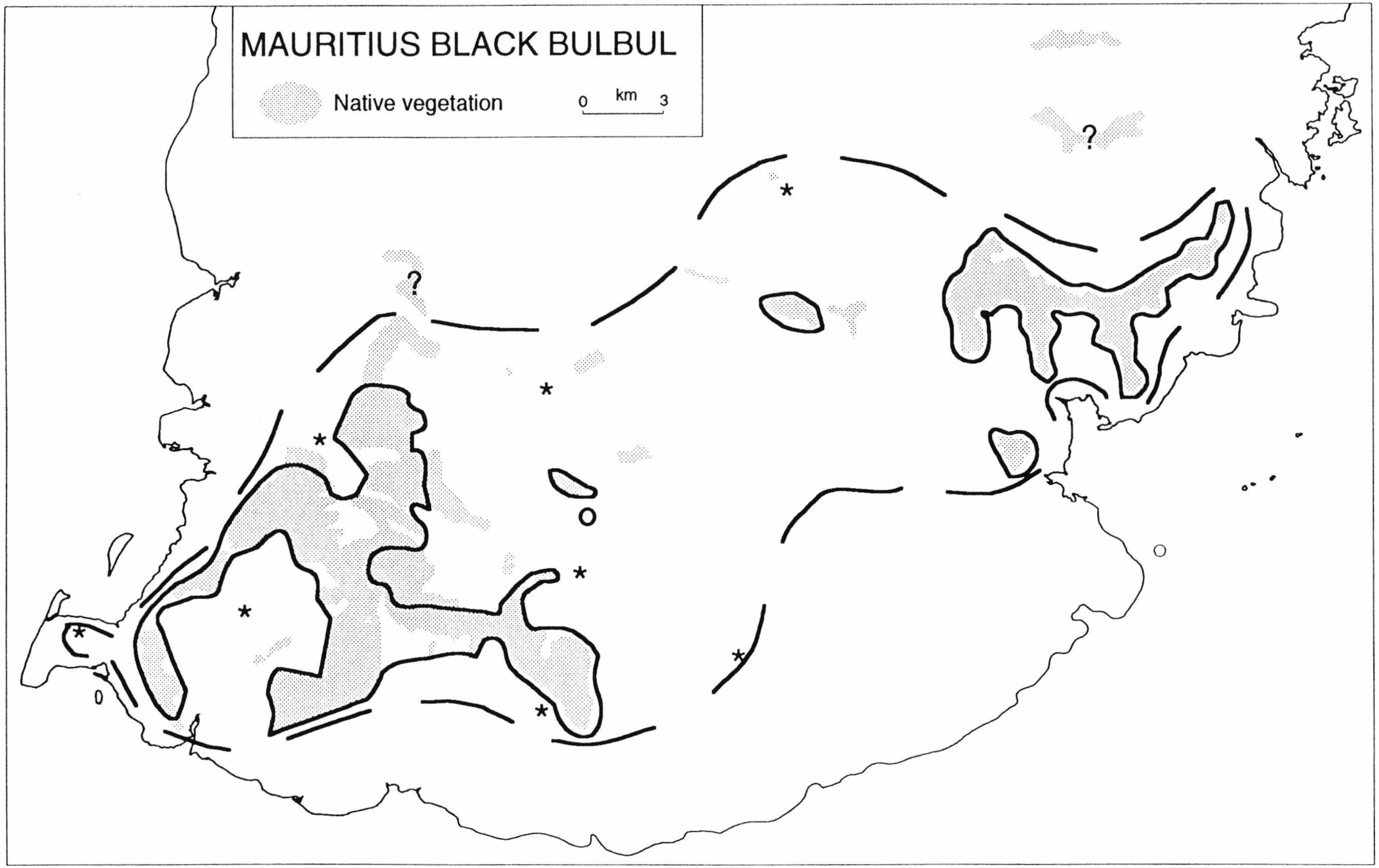
Away from native forest, records came from Morne Brabant, the Chamarel area including Chamarel Falls and wholly exotic parts of the Black River Gorges. Very small numbers were scattered over central and southern parts of the plateau, with records from north of Mare aux Vacoas (but no records from Perrier reserve) and various valleys: Rivière du Poste, Ruisseau Marron, Rivière Dragon and around Piton du Milieu (pers. obs.; W. A. Strahm, T. d'Unienville and J.-M. Vinson verbally).

Population

Records plotted on maps showed little clustering, probably because of the large home ranges, so that it was often impossible to relate sightings in one area on different days. Immatures not holding territories (sometimes associating with breeding pairs) confuse the picture further. However, this species seemed to be fairly evenly (but sparsely) distributed within its range, so the method of calculating densities from field data in well-surveyed areas and using them to estimate populations elsewhere was satisfactory.

Approximately 80 territories were found in the south-west in the four seasons combined; the BOU expedition found 72 (Cheke 1987c) and estimated 140 there. In Macchabé, encounter rates of black bulbuls averaged about one tenth of those for cuckoo-shrikes. In native upland forest heavily invaded by *Psidium cattleianum* and *Ligustrum* (such as Black River Peak and Montagne Lagrave), the density of black bulbuls was 2.5-4 pairs/km^2, whereas more varied habitat, such as that found between Montagne Cocotte and parts of Combo, held up to 10 pairs/km^2. From territory mapping, and taking into account scrubby areas unsuitable for black bulbuls, 45-50 pairs were estimated between Montagne Cocotte

Fig. 3.4. Distribution of the Mauritius Black Bulbul in 1993. Solid line encloses main distribution, where birds were regularly encountered. Dashed line encloses area used by wandering birds, based on isolated records in 1989-93, marked with asterisks (*). Question marks (?) indicate where wandering birds may occur but have not been recorded.



and lower Combo. The remaining 68 km^2 of native forest contained 170-270 pairs. Scattered birds outside main native forest blocks (see *Distribution*) probably add 10-20 pairs. The population is thus estimated at 225-340 pairs (Table 3.5).

Changes since 1975

Cheke (1987c) estimated 200 pairs, with only 50 (25%) on Montagne Lagrave and the Bambous Range; the BOU expedition hardly covered the latter area, but I found black bulbuls relatively common throughout it (as have all kestrel fieldworkers who have worked there recently) and estimate that it held about 35 % of the total. I doubt that this indicates a great increase since 1975; my greater coverage allowed confirmation of a wider distribution than Cheke expected, with good numbers in little-visited spots.

There is thus no evidence of any major change in either distribution or population since 1975, apart from a small reduction in range area caused by native forest destruction.

Table 3.5. Distribution and population of the Mauritius Black Bulbul in 1989-93. Mean and ranges of densities are given as for the cuckoo-shrike (Table 3.4). na=not applicable.

Forest patch	Area occupied (km^2)	Density: mean [range] (pairs/km^2)	Pairs found	Pairs estimated
Mt Cocotte - Combo	10	4.5-5 [1-15]	28	45-50
Other SW native forest	38	2.5-4 [1-10]	45	95-152
Central-east native forest	30	2.5-4 [1-10]	15	75-120
Scattered (valleys etc)[1]	na	na	4	10-20
TOTAL	78		92	225-342

Notes

[1] See *Distribution*: these pairs were scattered in tiny patches of suitable habitat, largely surrounded by cultivation, so that densities and range areas are not meaningful.

3.3.3 *Mascarene Paradise Flycatcher*

Distribution

In recent decades, flycatchers have been recorded from localities scattered all over Mauritius. The distribution appeared to be relictual, with very few pairs scattered over a wide area. In the south-western forests none was found north of Macchabé; the most likely site between Tamarin Gorge and Trois Mamelles (a region included in the distribution given by King [1978-79], presumably via S. A. Temple) is Mondrain reserve, where there are certainly none (Strahm 1988; see also doubts in Cheke 1987c). Outside the south-west I only saw flycatchers in State Land Bras d'Eau in the north-east, and three pairs in a small valley near Bénarès (known locally as Ruisseau Baptiste; on the 1:25,000 map it is the unnamed stream between the Feeder Baptiste and River St Amand).

Of the four other localities outside the south-west confirmed by Cheke (1987c), I found none around Piton du Milieu or Montagne Lagrave (but am not at all sure that they were absent), and did not visit Belle Mare Ponds or the Pouce valley. The only habitat visited in the north was Pamplemousses Botanic Gardens; no flycatchers were found. M. Maurel (from Bénarès, *per* T. d'Unienville, verbally 1992) knew of other south coast valleys holding birds, including the River St Amand; there are certainly none in the River Gros Ruisseau, east of Senneville (O. Griffiths verbally, pers. obs). M. d'Unienville (verbally 1993) has never seen them in many years of visiting Montagne Fayence.

Population

Most observations were of pairs; the very few single grey-headed birds were not assumed to indicate a pair since immatures may resemble females. This species has small, exclusive territories (1-2 ha) and a quiet song and rarely emerges from the shade of the shrub layer. It was possible to spend hours in the canopy of Pigeon Wood (which held at least four pairs) with no sign of flycatchers, so prominent viewpoints were of little use in surveying them. Walking through suitable habitat and 'spishing' (see Smith 1975) often attracted the birds; unless close to a nest, they usually soon lost interest in the observer, and so birds responding further along a trail were likely to be different. Noisy territorial disputes were common. Cheke (1987c) reckoned to find known pairs on 30-40% of visits, with which I agree, but this applies only to territories crossed (or nearly so) by the route walked. Territories (or small clusters of them) were often isolated in expanses of apparently homogeneous habitat. There was thus no way of predicting whether flycatchers would be present, and their absence from an area could only be confirmed if every hectare was combed.

In the south-west during 1989-93 birds were found at 42 precise localities, including seven completely reliable reports from other observers. However, the three records from Macchabé - Brise Fer in 1989-93 were all isolated, not repeated, sightings (the last in February 1991), despite my intensive surveys of cuckoo-shrikes there, and the almost daily presence in the area of an observer familiar with flycatchers and their calls (K. Duffy verbally 1990-93). Only 31 territories were observed in the 1992-93 breeding season in the south-west, barely a third of the total for any other native passerine. Density varied

Fig. 3.5. Locations of all sightings of Mascarene Paradise Flycatchers in south-west Mauritius in 1989-93. All points are believed to refer to separate territories.

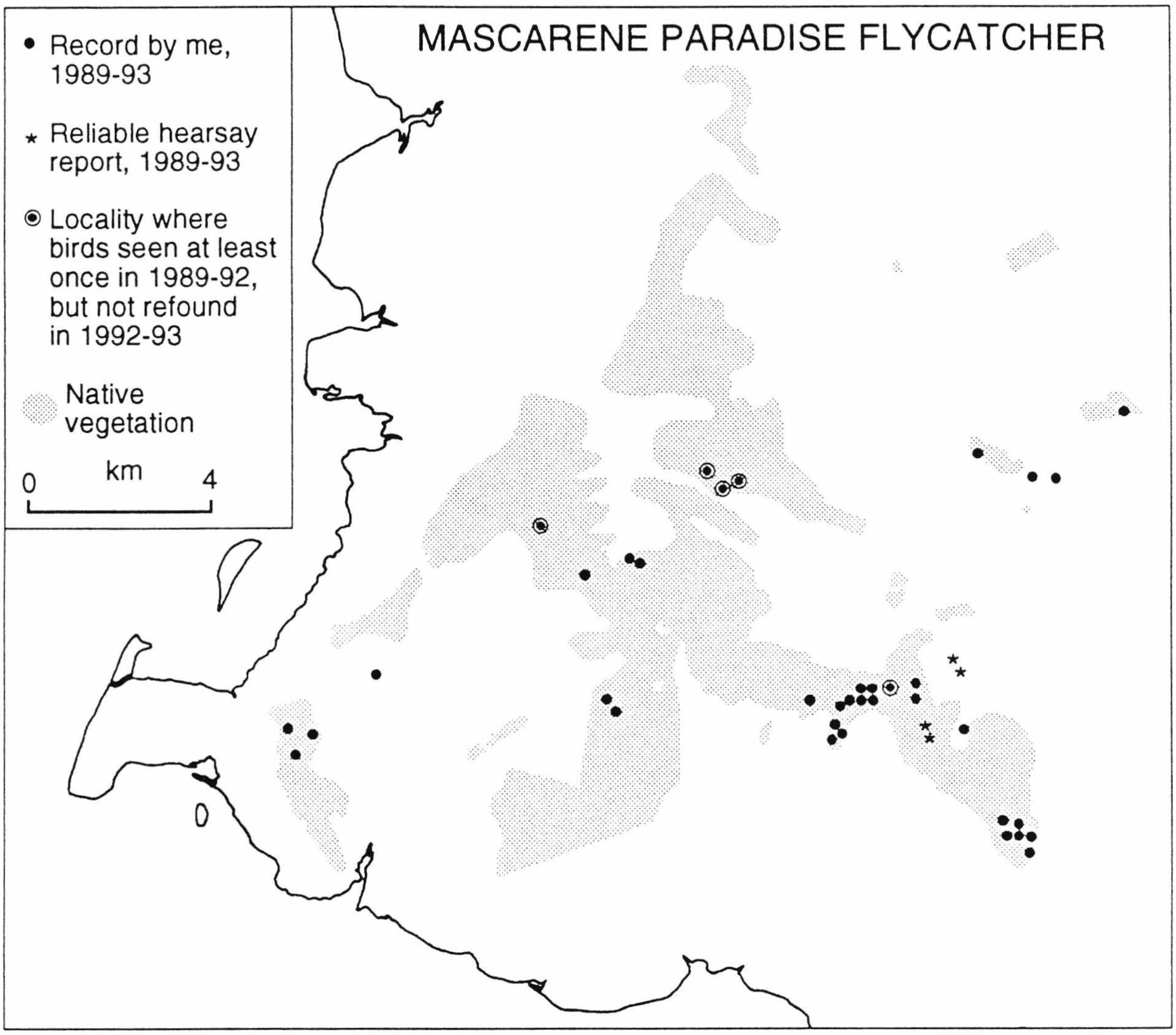
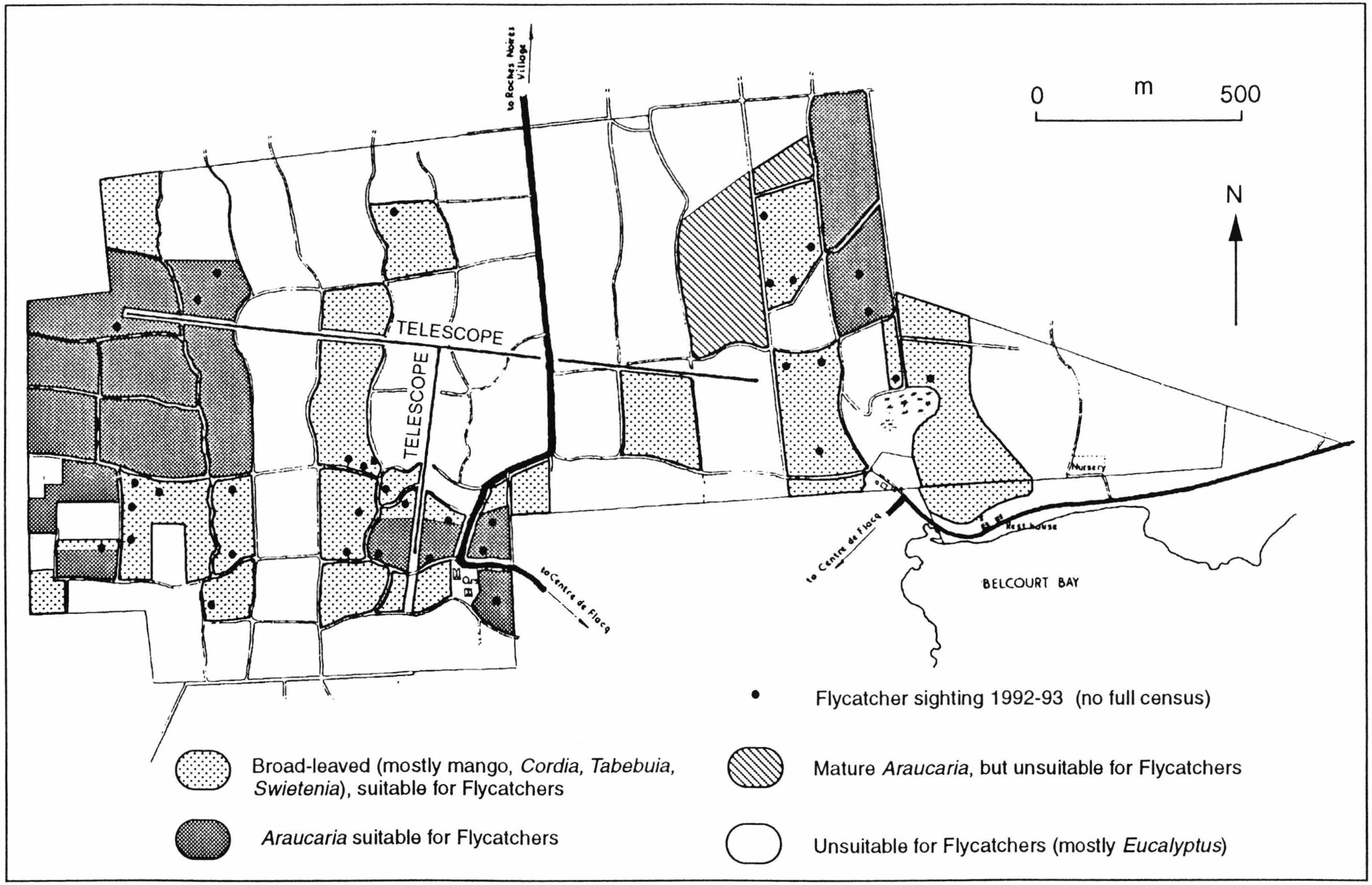


Fig. 3.6. State Land Bras d'Eau, showing habitat suitable for Mascarene Paradise Flycatchers in 1993. All vegetation is exotic. The radio telescope is a large fence-like structure which leaves an open swathe about 10 m across through the habitat.



from about 65 pairs/km^2 in Pigeon Wood (four pairs in 6 ha: 1.5 ha per pair), down to apparently completely isolated pairs (one pair/km^2, if this can be called a density) on Black River Peak. The Pigeon Wood density is the same as at Bras d'Eau (Cheke 1987c, see below). The native forest areas (including Piton du Fouge, Montagne Lagrave and the Montagnes Bambous) are estimated to contain 60-90 pairs, between two and three times the number of territories observed in 1992-93. Fig. 3.5 shows the locations of all sightings in 1989-93; the population may be monitored in future by searching for a selection of these.

The population in State Land Bras d'Eau was much easier to assess. Detailed mapping was carried out in two different breeding seasons and once in winter, in the same area where Cheke (1987c: his maps 10-12) had worked, all with very similar results. In 1993, all suitable-looking blocks were found to be occupied; about 32 territories were found in an incomplete census. Fig. 3.6 shows the habitats, indicating suitable areas (1.63 km^2) and sightings; some mature *Araucaria* was unsuitable (checked carefully without finding birds) probably because an unusually open canopy caused a reduction in shade, understorey and apparently also in flying insects. Allowing 1.5 ha per pair gives a density of 65 pairs/km^2. Prime habitat covering 1.63 km^2 could contain 109 pairs, but at least some *Araucaria* and orchard areas held about half this density. I suggest that a model assuming that 30-70 % of the suitable habitat contained only 30 pairs/km^2 is acceptable. The Bras d'Eau population is thus estimated at 66-89 pairs.

Further, undiscovered populations are likely to exist in other exotic areas, but few (and none as large as that at Bras d'Eau) could have escaped the notice of Cheke's and my surveys and the knowledge of our local informants. I suggest 50 pairs as the maximum number that that such areas (apart from the south-west, centre-east and Bras d'Eau) could contain. This gives a population of 125-230 pairs.

Changes since 1975

This species is known by many Mauritians. All agree that it has declined very seriously and has disappeared from many areas recently inhabited (R. Chevreau de Montléhu, F. Staub, J.-M. Vinson *et al.* verbally). Some told me of one or two pairs that they knew of, but the decline has been so severe that if the birds reported were last seen several years ago, they may relate to now extinct populations. In addition to the information gathered by Cheke (1987c), F. Boucher (verbally 1993) recalled having seen them all around l'Etoile and Deep River, on the northern slope of the Montagnes Bambous and in adjacent valleys, but said that now only one or two might survive in l'Etoile. Flycatchers used to (early 1970s?), but no longer, occur in Mahébourg museum grounds (S. Paupiah, verbally 1993).

Quantitative assessment of the changes since 1975 requires comparison of my data with the raw data of the BOU expedition (Cheke unpubl.), considering the south-west and Bras d'Eau separately.

The BOU expedition found 41 territories in the south-west (Cheke unpubl.), a similar total to mine, but this does not indicate similar populations in 1975 and 1993, because coverage differed. Ten territories marked on Cheke's (unpubl.) territory maps (around Macchabé, Raoul, Alexandra Falls and Bois Sec) were not found when I carefully checked these precise locations, suggesting a marked decline within surviving habitat. Additional flycatcher habitat has been lost at Kanaka and Parc-aux-Cerfs, where Cheke saw 12 of his 41 territories (see Cheke's [1987c] Map 8; also Cheke unpubl.). Flycatchers appeared to be sedentary, so that areas occupied in 1973-75 but not in 1989-93 are more likely to indicate a decline than merely emigration. Therefore up to half of the birds which Cheke saw in the south-west in 1973-75 may have been lost by 1993. Assuming this sample is typical, a decline of around 50 % is indicated. I observed similar numbers to Cheke because I checked more habitat although fewer birds were present.

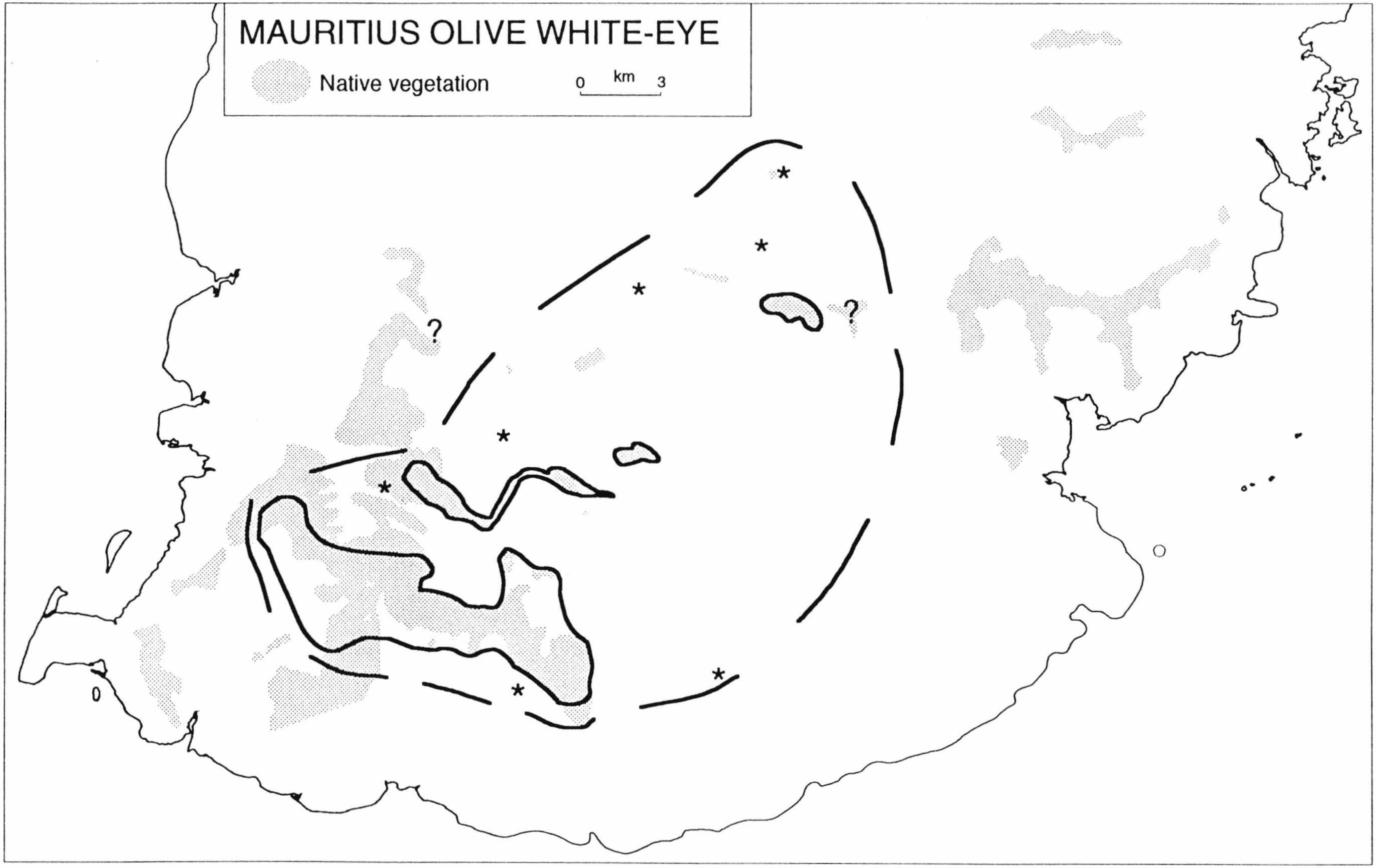
Cheke did not check throughout at Bras d'Eau and estimated only 20 pairs there (Cheke unpubl.). Cheke (1987c) estimated a maximum for the whole island of 250 pairs ("probably somewhat less"). Assuming no change at Bras d'Eau, Cheke's (1987c) population estimate for 1975 can be revised to a maximum of 320 pairs, compared to a maximum of 230 pairs in 1993. The apparently inexorable decline towards extinction in the south-west highlights the importance of the Bras d'Eau population.

3.3.4 *Mauritius Olive White-eye*

Distribution

Olive white-eyes were widespread in the upland native forest, but absent from the whole Macchabé Area and Fouge Range, excepting a few pairs in the dwarf forests of State Lands Florin to Raoul (Fig. 3.7). Staub (1988) included Piton du Fouge (and Mont-sur-Mont) and probably Morne Brabant; I found none, and received no reports of olive white-eyes, in these areas, but did not check the southern part of the Fouge Range. Cheke (1987c and verbally 1994) recorded a few birds in 1973-75 at Tamarin Falls, where I

Fig. 3.7. Distribution of the Mauritius Olive White-eye in 1993. Solid line encloses main distribution, where birds were regularly encountered. Dashed line encloses area used by wandering birds, based on isolated records in 1989-93, marked with asterisks (*). Question marks (?) indicate where species may regularly be present, but this has not been confirmed.



found none. The precise eastern limit of the range (between Montagne Lagrave and Pic Grand Fond in the Montagnes Bambous) is unknown.

The usual lower altitudinal limit in Combo and Bel Ombre was 350-400 m in 1993, but birds wandered below this, for example one on 17 March 1993 by the Rivière Patates at Mont Blanc (220 m). They can exploit small, isolated areas of habitat, occurring over a wide area of the central plateau, including all the native relicts around Grand Bassin and Bois Sec, Rivière du Poste and Jouanis, east to Montagne Lagrave and Eau Bleu Reservoir. Additional recent records, most in winter and referring to birds visiting exceptional nectar sources, have come from Britannia Sugar Estate (richly vegetated valleys through sugar cane and gardens containing Bottlebrush), Macchabé (one record only), Plaine Sophie and even gardens in Curepipe (T. d'Unienville, J.-M. Vinson & K. Duffy verbally; pers. obs.).

Population

The elusive habits and large, overlapping home ranges of this species make surveying it difficult. In 1989-90, I found 63 pairs and estimated 130-181 pairs (Safford 1991). Most areas were revisited in 1992-93 (and previously unvisited areas checked) and the results agreed closely with my earlier survey. However, even this large error range was too small, exaggerating the precision. Birds kept the same territories year after year, and so some data from 1989-90 have been included in the updated survey.

Coverage was good over most of the distribution. Territory mapping in the best-surveyed areas yielded highest densities of 15-20 pairs/km^2 (mainly between Montagne Cocotte and Piton Savanne, with good numbers also in the native relicts of the Bois Sec - Grand Bassin - Rivière du Poste area) and elsewhere around 6 pairs/km^2. However these densities were derived from clusters of territories within the stated areas; there seemed to be large 'gaps' where birds were only ever seen passing through, rather than being seen regularly on territory. If this impression is correct, the lower of the estimates in Table 3.6 would apply. If birds were in fact present throughout at these densities, a higher population estimate results, giving a rounded estimate of 140-260 pairs, between one-and-a-half and three times the number found.

Table 3.6. Population and distribution of the Mauritius Olive White-eye, 1973-75 and 1992-93. Figures for 1973-75 are from Cheke's (unpubl.) raw data.

Forest patch	Pairs estimated in 1973-75	Pairs found in 1989-93	Pairs estimated in 1993
Black River Peak - Chamarel	16	7	30-100
Plaine Champagne	79	7	
Upper Bel Ombre	58	4	
Alexandra Falls - Piton Savanne	93	41	51-68
Bois Sec/Le Juge - Rivière du Poste	11	18	20-25
Florin - Pétrin - Raoul	22	5	6-12
Combo	25	3	20-35
Lagrave	15	2	
Southern/central plateau (scattered)	4	3	10-20
Other areas (cleared since 1975)	23	0	0
Total	346	90	137-260

Changes since 1975

It will always be difficult to compare different censuses of this species. Comparison of encounter rates could be dangerous because of the species' erratic movements; for example, most birds seen from platforms in the canopy of Pigeon Wood were making for the large *Syzygium jambos* thickets (for nectar) below. The rates would depend on the state of the nectar supply, which varies unpredictably, as much as they would on the number of territories around Pigeon Wood. In general it is likely that a territorial bird with a small range area which defeats precise census attempts using territory mapping will be no easier to census in any other way.

The distribution mapped by Cheke (1987c) appears not to have changed greatly. In 1973-75, the BOU expedition found 120 pairs and Cheke (1987c) estimated a population of 350 pairs. Cheke (1987c) originally expected the population to drop by about 20% (to about 275 pairs) following the native forest clearances of the 1970s. Returning in 1985, he suspected (verbally 1994) that an even more serious decline had occurred. This was confirmed by my census in 1989-90 (Safford 1991), which was consistent with the lower number of pairs I actually observed and the much increased ratio of Grey to olive white-eyes at Alexandra Falls (4:1 in 1973-75, 15-20:1 in 1989-90). The difference between the maximum totals is accounted for by losses at Alexandra Falls, Plaine Champagne, Pétrin - Raoul and Bel Ombre.

3.3.4 *Mauritius Fody*

Distribution

Mauritius Fodies occurred in 1989-93 mainly on the southern escarpment between upper Combo and Montagne Cocotte. They were almost absent from Alexandra Falls and Plaine

Fig. 3.8. Distribution of the Mauritius Fody in 1993. Solid line encloses distribution.

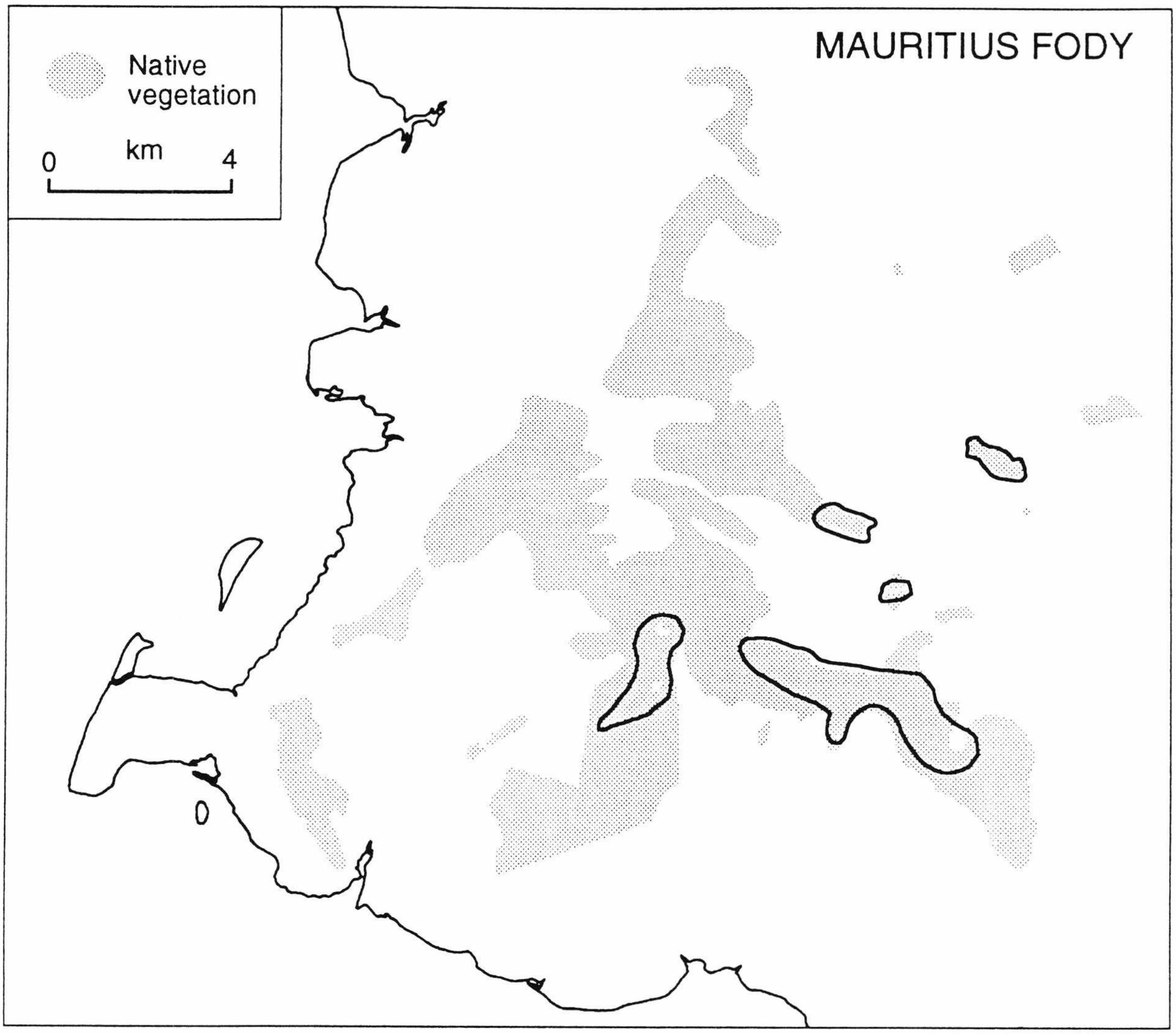


Fig. 3.9. Mauritius Fody territories (see Chapter 3) and nest site choice (see Chapters 6 & 7) in 1989-93 in the Montagne Cocotte - Piton Savanne area. In each mapped territory, the confirmed or expected choice of nest tree (native or exotic) of the resident pair in that territory is indicated. n=nest(s) found only in native trees, x=nest(s) found only in exotic (plantation) trees. For territories in which no nests were found, the predicted choice of nest tree (see Section 6.3.3) is given in brackets.

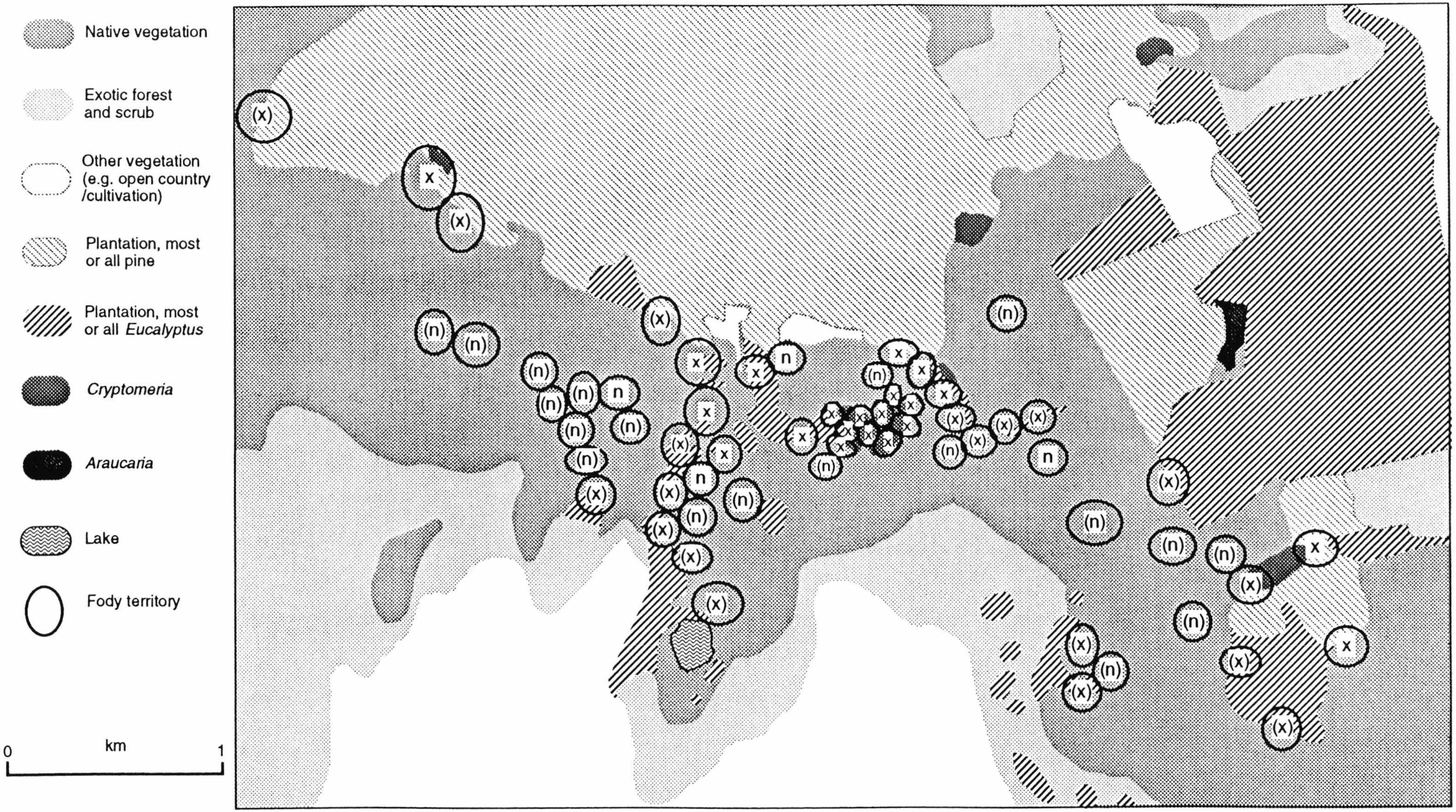
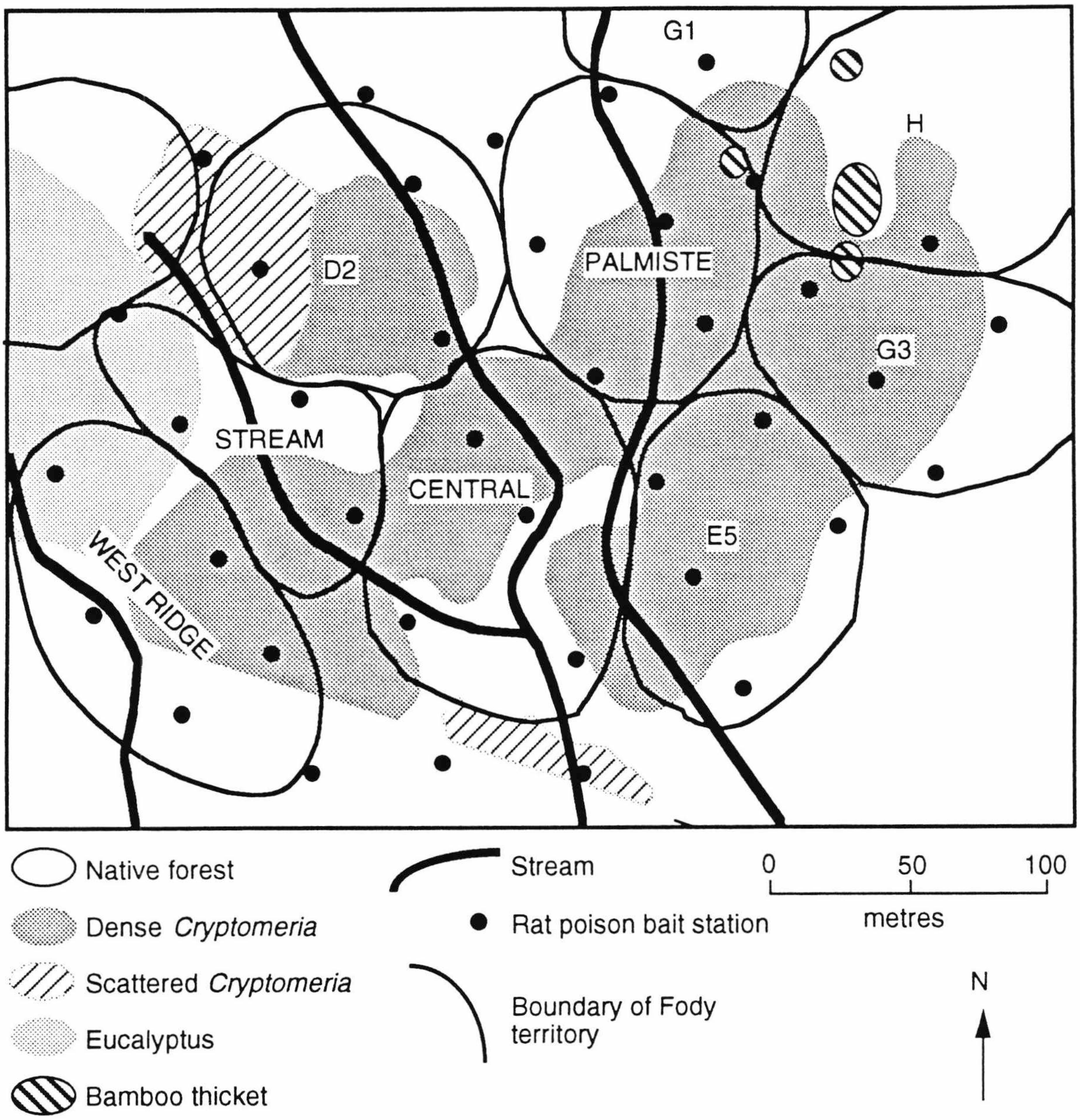


Fig. 3.10. Pigeon Wood, showing names and approximate boundaries of Mauritius Fody territories referred to in the text. All nine pairs whose territories extended into the dense *Cryptomeria* of Pigeon Wood habitually nested in *Cryptomeria*.



Champagne, but reappeared in Bel Ombre, from the top of the scarp down to 430 m. Outlying populations survived on State Land Raoul, around Grand Bassin and Gouly Père, and north of the Rivière du Poste opposite Kanaka (Fig. 3.8).

Confusion with part-moulted Madagascar Red Fodies causes unlikely claims (Cheke 1987c, Safford 1991); any reports outside the above area need close scrutiny.

Population

During preliminary survey work in 1989-90, I found 57 pairs and estimated a total population of 81-102 pairs (Safford 1991). Little was added until the 1992-93 season, when all but four known territories were rechecked and the whole range was thoroughly surveyed, including visits to all the 'possible' areas I had previously missed. Nearly all of the range area was thoroughly checked and nests were found in 30 territories, increasing the precision of the estimates.

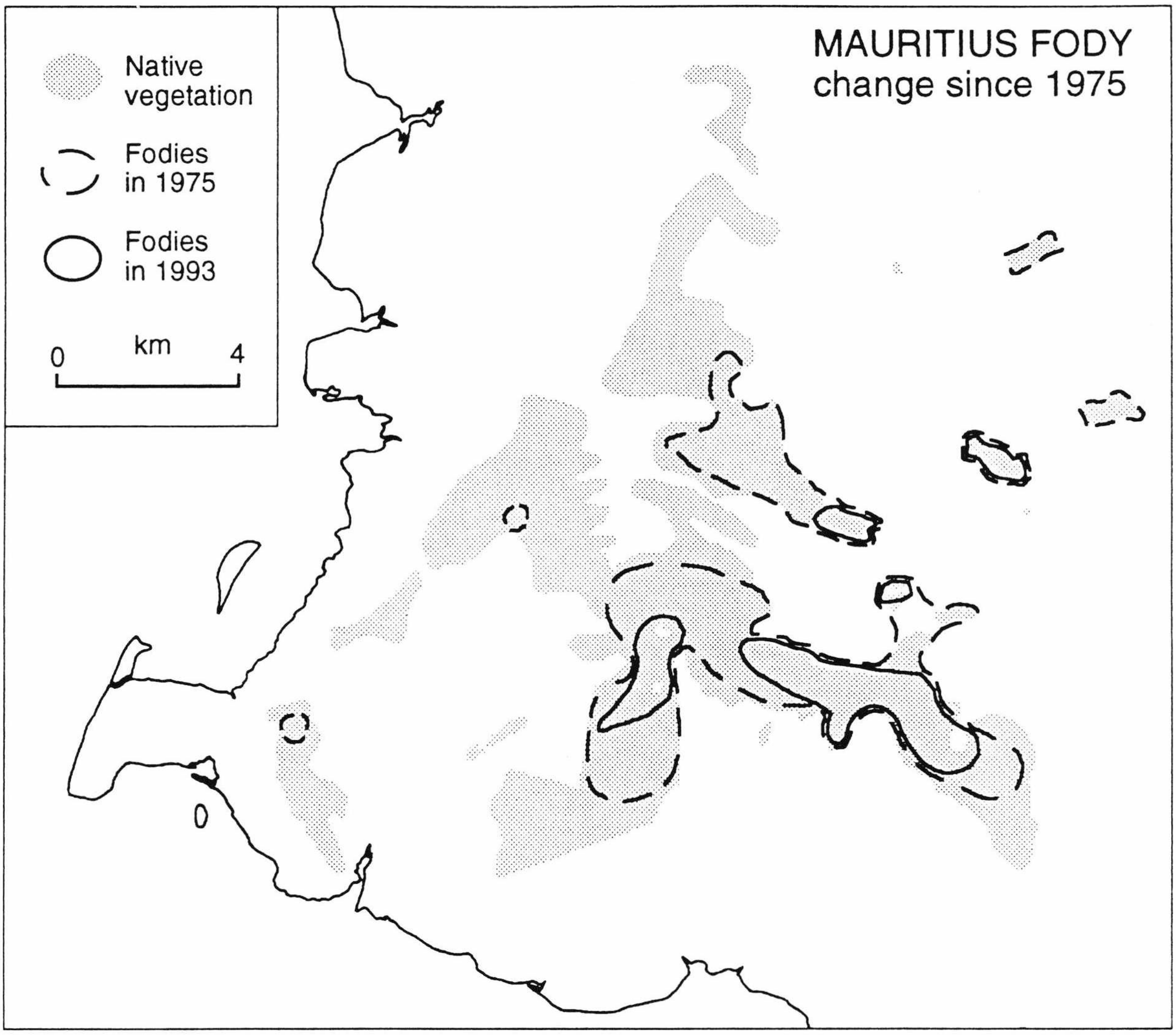
Table 3.7 summarizes the results in 1992-93. The population in 1993 was estimated at 104-120 pairs. About 80 % of territories were mapped. The discrepancy between the results of my 1989-90 survey (Safford 1991) and the present one stems from a consistent underestimation of numbers on the southern escarpment, and certainly not an increase in the fody population. Territories were far less evenly distributed within the occupied distribution than previous studies (Cheke 1987c, Safford 1991) had found: some small areas achieved very high densities (Fig. 3.9), leaving other areas almost empty. The unique cluster in and around Pigeon Wood (Fig. 3.10) held around one pair per ha (100 pairs/km^2), and other areas between Piton Savanne and Montagne Cocotte held up to 30 pairs/km^2, but elsewhere territories were so unevenly distributed that density figures would not mean much.

Changes since 1975

R. Chevreau de Montléhu (verbally 1992) believes that numbers have declined by about 60 % since the early 1970s. Comparison of my data with the BOU expedition results (Cheke 1987c) for 1973-75 confirms this. The Mauritius Fody has totally disappeared since 1975 from Piton du Fouge, Black River Peak, Macchabé - Brise Fer and the Parc-aux-Cerfs and Kanaka blocks (all suitable habitat has been destroyed at Kanaka), and nearly so from Alexandra Falls and Plaine Champagne. The range has also contracted in Combo and Bel Ombre (Fig. 3.11).

The population and range area of this species have both declined by 55 % since 1975

Fig. 3.11. Distribution of the Mauritius Fody in 1975 and 1993. 1975 distribution excludes areas of habitat cleared since then (such as the Kanaka area), and assumes that the Rivière du Poste patch was occupied in 1975.



(Table 3.7). Jones (1980, cited by Collar & Stuart 1985) guessed that the population had declined to 20-40 pairs by 1979, but later regarded this as an underestimate. It is most unlikely that the population collapsed so disastrously and then recovered to its 1993 level. Instead, I suggest that the population dropped rapidly in the late 1970s after the 1971-75 forest clearances, with further (but less serious) declines caused by the subsequent destruction of native forest in the Kanaka area and Gouly (Chapter 2). In addition to these setbacks, the population may have been declining continuously for many years, even without the effects of clear-felling, so that the population in 1993 was likely to be at its lowest ever level.

Table 3.7. Distribution and population of the Mauritius Fody in 1975 and 1992-93. Data for 1975 are from Table 1 in Cheke (1983).

Forest patch	Pairs estimated in 1975[1]	Pairs found in 1992-93	Pairs estimated in 1992-93
Pétrin - Raoul	6	5	5
Rivière du Poste	no data[1]	4	4-5
Grand Bassin/Gouly Père	10	2	2
Bel Ombre	43	15	20-25
Alexandra Falls	100	1(-4)[2]	2-4
Montagne Cocotte - Piton Savanne		55(-56)[2]	65-72
Combo	7	4	6-7
Other areas	81-94	0	0
TOTAL	247-260	86(-90)[2]	104-120

Notes

[1] The forest patch by the Rivière du Poste which held fodies in 1992-93 was overlooked by Cheke.

[2] Additional territories found in previous seasons, not checked in 1992-93.

3.4 Discussion

In this section, the census method is discussed and the general patterns of the distributions and populations are described. These features cannot be explained without detailed consideration of limiting factors (such as habitat quality and predation); these were investigated as part of the overall study, and are discussed in the following chapters. Table 3.8 examines the importance of each area of forest for birds.

3.4.1 *Evaluation of the census methods*

For Mauritian birds, any census method depending on estimating densities in selected areas, and using these to calculate populations in larger areas, will meet with a major problem: the extreme variation in density over very small distances. This was most severe for the flycatcher and fody. In 1989-93, the former reached 65 pairs/km^2 in Pigeon Wood, but only isolated pairs occurred in the forest around Pigeon Wood, with no birds at all found in the similar forest around the top of the Bassin Blanc track. The fody also reached high density (100 pairs/km^2) in Pigeon Wood and about 30 pairs/km^2 immediately outside Pigeon Wood. If the areas holding widely differing densities were discrete, then densities could be estimated separately for each; however, this was not so. Territory mapping was successful in determining the extent of the high-density clusters. A precise census using this technique required very intensive field work, which was feasible over the tiny range area of the fody (less than 15 km^2, with most in fact in only 5 km^2), but not the flycatcher (except at Bras d'Eau), whose population estimate therefore had a larger error range (60-140 pairs excluding Bras d'Eau).

The cuckoo-shrike and black bulbul occurred over larger areas at less variable densities and so were more straightforward to census. The olive white-eye showed a more clumped distribution than the latter two species, and its mobility introduced additional difficulties. Overall, no species proved impossible to count; error ranges were 15 % (16/104) of the minimum total population estimate for the fody and 50-86 % for the other species, the biggest error margins being for the flycatcher and olive white-eye.

Territory mapping provided acceptably precise population estimates, but also was particularly fruitful in providing the "close view" needed to relate the distribution, especially of the fody, to vegetational features. These results are related to the studies on diet and especially nest predation (Chapters 5 and 6), and provide the basis for the understanding of the species' status and conservation. Formal methods, most likely point counts, could have been easier and quicker to replicate, allowing future surveyors to detect changes in densities without a complete census. However, changes to populations are often more evident from changes in distribution limits (as Fig. 3.11 shows for the Mauritius Fody) than in density. Perhaps ideally, point counts could have been carried out as well as territory mapping, but time did not allow this.

3.4.2 *Distribution*

In 1989-93, the native forest birds of Mauritius were very unevenly distributed in the surviving native forest areas. The most obvious general feature of the distributions was the poverty of the eastern native forests (Montagnes Bambous, Blanche and Fayence).

These areas constituted a third of all native forest, and all the passerine species occurred at least until the 1930s (F. R. G. Rountree in Cheke 1987c). By the 1970s, only black bulbuls were known to occur there; kestrels have been successfully reintroduced to the Bambous since 1987 (Jones *et al.* 1991a). The isolated Fouge Range was nearly as poor, although flycatchers also survived. The Plateau Relicts supported more native birds than might have been expected from their small areas. Black bulbuls and olive white-eyes remained common in some of these fragments. A few Mauritius Fodies and cuckoo-shrikes survived in the Grand Bassin - Rivière du Poste area.

The main south-western forest block, associated with the Black River Gorges and the escarpment falling away south from the plateau, supported the majority of native birds of all species. The two main areas of forest (the Southern Slopes and the Macchabé Area) could be said to meet in Grandes Gorges Valley, which contains very patchy native forest but is around 400 m deep and 1.5 km across (from rim to rim).

Even within these areas, the birds were very unevenly distributed. All lowland areas were very poor (Cheke 1987c), although a few cuckoo-shrikes and black bulbuls occurred. Overall, the Macchabé Area was much poorer in most native bird species than the Southern Slopes, but was very important for Echo Parakeets (pers. obs.) and cuckoo-shrikes. Areas of high forest on the Southern Slopes (such as on the path to Black River Peak and lower Bel Ombre) had a similar bird community to that of Macchabé, but few or no Echo Parakeets (pers. obs.). Dwarf forest (as at Plaine Champagne and Florin - Pétrin - Raoul) was unsuitable for black bulbuls and cuckoo-shrikes (Cheke 1987c), and rarely supported Mauritius Fodies (Safford 1991). However, the 4.5 km^2 of native forest, interspersed with groves of exotics on the Southern Slopes, between Montagne Cocotte and Piton Savanne (including Pigeon Wood), supported the most important concentration of threatened birds in Mauritius, and was of overwhelming importance for the Pink Pigeon, olive white-eye and Mauritius Fody (Safford 1991).

3.4.3 *Population trends and changes since 1975*

The five threatened passerines have had varying fortunes since the BOU expedition census in 1975 (Cheke 1987c): each has followed a clearly different trend. The cuckoo-shrike and black bulbul appear to have at least maintained numbers. The former may have increased in direct proportion to the increase in range area; this suggested increase is due to expansion into existing but vacant habitat, rather than newly created habitat. The reasons for the vacancy of cuckoo-shrike habitat in 1973-75 require investigation. The flycatcher, olive white-eye and fody have all declined seriously. The former was still widely scattered, but even more fragmented in range than it was in 1975. The olive white-eye population declined more than would be expected from the 20 % decrease in its range area; this represents a decrease in density in areas where the birds survived. The population and range area of the fody both declined by around 55 %.

Considering now changes in the relative importance of the various forest areas, most of the isolated patches lost species. Fodies disappeared from Piton du Fouge, Bois Sec, Jouanis and Monvert; cuckoo-shrikes from Raoul, Jouanis and Rivière du Poste. Plaine Champagne and Alexandra Falls were still important, but far less so than in 1975, when the latter held high densities of all native passerine species and was rated the best single locality for seeing native birds (A. S. Cheke verbally 1991). By 1989-93, anywhere between Montagne Cocotte and upper Combo was richer than Alexandra Falls (pers. obs.), and it is only since 1975 that the exceptional importance of the former area has become clear.

3.4.4 *The effect of the clearance of Les Mares*

The unique, marshy forest of Les Mares was cleared in 1971-75 (Cheke 1987c). This area had previously been very rich in native birds (Cheke 1987c, Jones 1987, L. R. Chevreau de Montléhu, F. Staub and J.-M. Vinson verbally). The BOU expedition surveys were conducted as the main clearances were being completed. No censuses of the passerines were carried out before the clearance started or immediately after it finished. My censuses took place fourteen years after the main clearance finished, although some further destruction took place in the Grand Bassin and Kanaka areas into the 1980s (Chapter 2). Therefore the immediate effects of the clearance cannot easily be judged. However, this habitat loss was by far the greatest change to which the native biota of Mauritius was subjected in the 1970s and 1980s, and must have caused many of the differences between the results of the BOU's and my surveys.

It is likely that, as Cheke (1979, 1983, 1987c) hypothesized, the birds seen by the BOU expedition in 1973-75 included surviving birds displaced from areas already cleared. The displaced birds had presumably settled in the nearest available native forest, so that densities were higher than they had been before the clearances. Cheke (1987c) predicted that the bird species affected would decline to the carrying capacity of the restricted habitat area.

The Pink Pigeon and Echo Parakeet suffered very severe declines during the 1970s, probably because of this habitat destruction (Jones 1987). The cuckoo-shrike, black bulbul and flycatcher were probably not very seriously affected, as the low, open forest of Les Mares (Vaughan & Wiehé 1937) may have been sub-optimal habitat, although other areas destroyed during the same period, such as Kanaka and Parc-aux-Cerfs, were more important (Cheke 1987c).

Of the passerines, the fody and olive white-eye have declined the most since 1975. This is likely to have been caused mainly by the destruction of Les Mares, which apparently held large numbers of these species (Cheke 1987c). My surveys of these species reveal that the declines were more severe around Alexandra Falls and Plaine Champagne than around Piton Savanne (including the Pigeon Wood area), and that the total declines in their populations were even more severe than Cheke (1987c) expected. The explanations for these two observations are probably to be found among the complex effects of geographical variation in breeding success; this subject is discussed in Chapter 7.

Table 3.8 (overleaf). Native forest areas of Mauritius and their importance for forest birds. Boundaries between forest patches are shown on Figs 2.8 and 2.9.

In the column for each species, the numbers indicate the percentage of the total Mauritian population using in the area (not only for breeding); if less than 10 %, a + is shown, indicating presence only. Species confirmed as occurring in an area, but rarely or in very small numbers, are given (+). Bird species marked with a question mark (?) were not recorded from the area indicated between 1989 and 1993, but may occur rarely or in small numbers.

For each bird species, an assessment of overall distribution is given in each of the seven forest regions: a=absent, r=rare, w=widespread. The Grey White-eye is not included.

Notes on Table 3.8

[1] Population data for the Mauritius Kestrel refer to the 1993-94 season, from Jones *et al.* (in prep.). Several pairs occurred outside native forest areas. Pairs are included in named forest area if their territories were likely to extend into that area.

[2] A reintroduced population of Pink Pigeons in Macchabé - Brise Fer is presently dependent on close management, and is not self-sustaining.

Forest patch	Area /km^2	Native birds present, with % of population if >10 %							
		MK[1]	PP	EP	CS	BB	PF	OW	MF
Fouge Range									
Piton du Fouge - Piton Canot	4.5	+				+	+		
TOTAL	4.5	w	a	a	a	w	w	a	a
Southern Slopes									
Black River Peak	7.9	10	(+)	(+)	+	+	(+)	+	
Bel Ombre (upper)	5.9		(?)	10	20	+	(+)	+	18
Bel Ombre (lower)	7.6	(+)		(+)	10	+	(?)		
Alexandra Falls	2.8		(+)	(+)	+	+	(?)	+	(+)
Plaine Champagne	4.5		(?)	(+)	+			+	(+)
Cocotte - Savanne	4.5		100	(+)	15	10	10	30	60
Combo	5.4				+	+	+	+	+
Le Bouton/Grandes Gorges	1.4	+		+	+	+	+	(?+)	
TOTAL	40.0	r 16	r 100	r 10	w 60	w 50	w 20	w 70	w 90
Macchabé Area									
Pétrin - Raoul	1.1			+				+	+
Macchabé - Brise Fer	8.9	+		90	35	10	(+)	(+)	
Tamarin Falls - Trois Mamelles	2.6	+			(+)	(+)	(?)		
TOTAL	12.6	w 10	a[2]	w 90	w 35	w 15	r	r	r
Plateau Relicts									
Bois Sec - Riv. du Poste	0.7			(+)	(+)	+	+	+	+
Monvert	0.6							(?)	
Jouanis	0.5					(?)	+	+	
Perrier	0.01					(?)			
Midlands	4.0					+	(?)	+	
TOTAL	5.8	a	a	r	r	w	w	w	r
Bambous Range									
Montagnes Bambous	26.0	37				35	(?)		
TOTAL	26.0	w 37	a	a	a	w	a/?r	a	a
Central-east Relicts									
Montagne Blanche	2.0						(?)		
Montagne Fayence	1.2								
TOTAL	3.2	a	a	a	a	a	a/?r	a	a
Moka Range									
Le Pouce	0.7	+							
TOTAL	0.7	r	a	a	a	a	a	a	a
TOTALS	92.8								

Chapter 4. Annual cycles and breeding biology of the forest-living native birds

4.1 Introduction

All the forest-living native land-birds of Mauritius are threatened, the Mauritius Fody critically so (Safford 1991, Collar & Stuart 1985, Chapter 3). A clear picture of their annual cycles and breeding biology is required for the design of conservation programmes or future studies.

In addition to the practical conservation value, the differing adaptations to island life shown by Mauritian bird taxa are valuable to the study of island biology. Fody taxa are widespread in, but endemic to, the western Indian Ocean islands and the genus is the most promising in the region for the study of general traits of island birds. Detailed studies exist for the Seychelles Fody *Foudia sechellarum* (Crook 1961, Brooke 1985) and Madagascar Red Fody *F. madagascariensis* on Seychelles (Crook 1961); the Aldabran fody *F. eminentissima aldabrana* (Frith 1976); and the Rodrigues Fody *F. flavicans* (field data: Cheke 1987e; in captivity: Darby *et al.* 1984). The other five races of Red Forest Fody *F. eminentissima* (one in Madagascar's humid forests and four on the Comoros) have not been studied. Data for the Mauritius Fody fill a gap in this suite of knowledge.

The breeding success and productivity of all species were the subjects of more detailed investigation (Chapter 6). In this chapter, I present data that provide an impression of each species' breeding biology, demographic parameters, population dynamics and seasonal movements (with special attention to the Mauritius Fody). I then discuss the practical conservation value of the information, and make comparisons with other bird species and communities, particularly those on western Indian Ocean islands.

The non-threatened Grey White-eye is included in this chapter because its annual cycles are presumably determined by the same factors as those of the other species.

4.2 Methods

Most data were collected during the census work (at all seasons) and the studies on breeding success. The paucity of ringing prevented collection of data on mortality or longevity.

4.2.1 *Mauritius Fody*

In general, the endangered status of the species, its evident dependence on a small number of productive pairs and the paramount importance of collecting unbiased data on breeding success constrained certain aspects of the study. In order to ensure that data on breeding success were reliable, it was necessary to monitor frequently the progress of breeding attempts.

Nests were found throughout the fody's distribution, but observations were concentrated in Pigeon Wood, an area found to have an exceptional concentration of breeding fodies (nine pairs nesting in 6 ha), and the only place where nesting attempts regularly succeeded. For reasons explained in Chapter 3, ringing was confined to one brood of three pulli (colour-ringed), and two adults (a male colour-ringed and a female metal-ringed, in different territories). Three of the nine territories were monitored intensively as they could be seen from platforms in the canopy (Figs 2.11 and 3.10): every breeding attempt, and also many of the nests which were started but then deserted in-between attempts, were followed in the 1991-92 and 1992-93 seasons. Four birds in these three territories were recognisable: in the 'central' territory, the male was colour-ringed; in the 'stream' territory, the male had a very unusual, disyllabic 'plick' call ('p-plick') and the female always uttered a stream of 'plick' calls as she approached a nest (unlike all the other 28 nesting females I watched); in the 'west ridge' territory, the female was metal-ringed. Elsewhere, closely observed males were frequently recognisable by unique red markings away from the usual red areas on the head and rump, although the unusual red areas changed between seasons.

A major problem was the impossibility of checking the contents of nests; nearly all nests were totally inaccessible, high in trees and at the ends of long, flexible branches (Fig. 4.1). Nine of the ten fody nests reached (out of 102 found) were only just accessible in dry weather. Only one was easily checked, but was destroyed by predators before eggs were laid. The domed shape and entrance tube meant that the contents could only be checked by touch using the fingertips; doing this 10 m or more up a tree, hanging on with the other hand, was difficult, extracting the contents even more so. Furthermore, efforts to reach nests may have guided predators (especially the intelligent monkeys) to nests (see Chapter 6; also Major 1990). Pulleys, as used by Crook (1961), were out of the question for the same reason.

Therefore, nests were never checked directly without a special reason for doing so. In practice, this meant that the adults' behaviour was usually the only clue to the status of an intact nest, and long watches to quantify behaviour were carried out. After failure or fledging, nests were sometimes collected by more drastic measures, which usually damaged them.

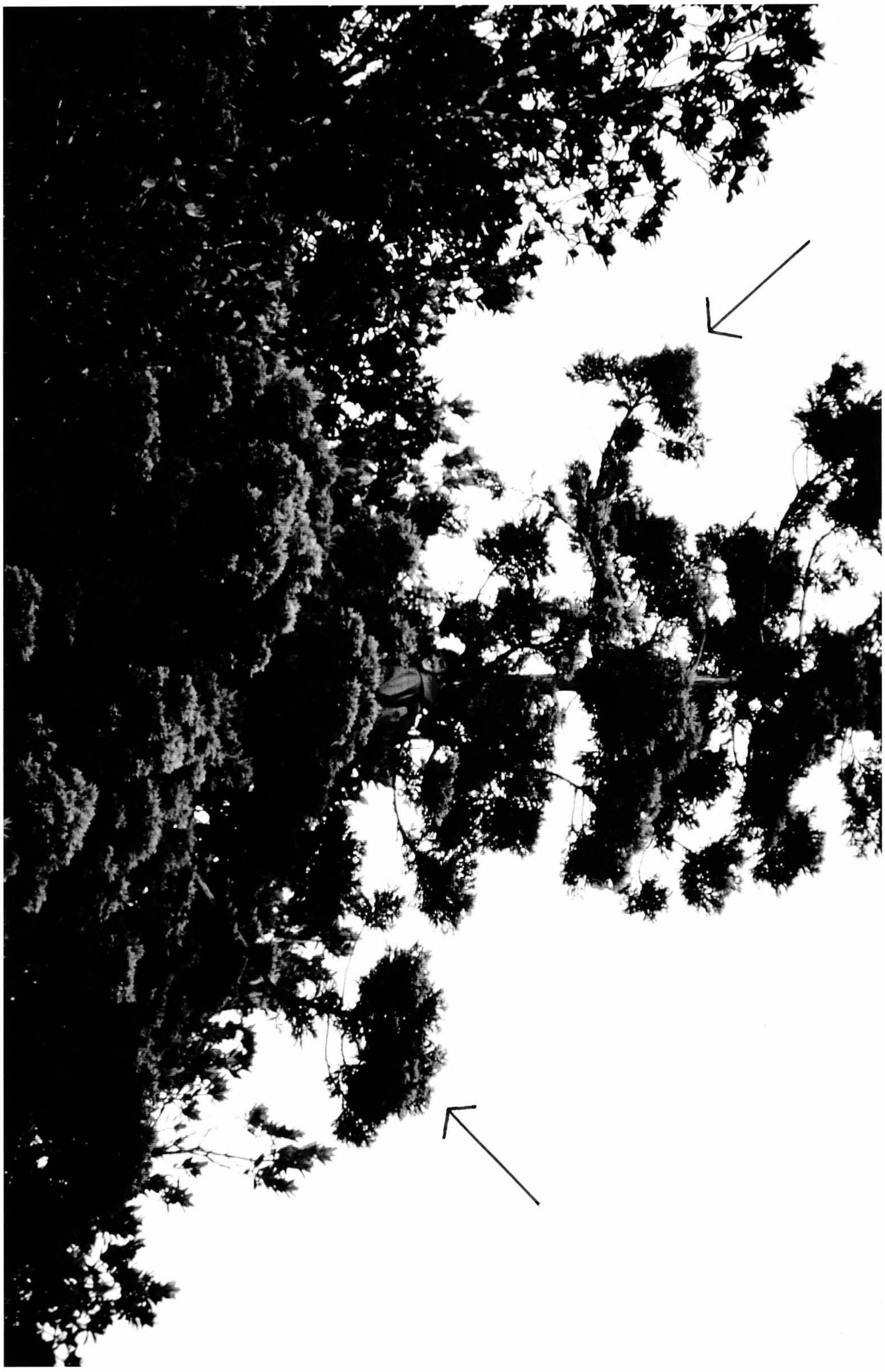
Additional data regarding juvenile development were collected from two captive birds. I found these on 12 October 1992, less than two days old, on the ground in Pigeon Wood, directly below a nest which had just been torn open by a predator (which, astonishingly, had missed them). They were hand-reared to fledging in the Black River aviaries and survived until April and May 1993.

4.2.2 *Other species*

General methods were the same as for the fody, but long watches to quantify behaviour were rarely carried out. The only birds ringed were four flycatcher broods (three of which fledged) and one adult (netted fortuitously when attempting to catch fodies). The open nests of all species made the contents or nesting activities easier to check than for fodies, although nests were equally rarely visited, again because of the risk of guiding predators. The main data collected regarded breeding season, clutch and brood size, length of breeding episode, number of broods, breeding success (and hence overall productivity per season), moult periods and seasonal movements.

Fig. 4.1 (overleaf). Part of a mature *Cryptomeria japonica* tree on the edge of Pigeon Wood. Arrows indicate two Mauritius Fody nest sites used in 1991-93. On the left is a mature native *Calophyllum eputamen* var. *grandis*, with habit and leaf type typical of native trees.

Note (1) the difference in habit and foliage density between the native trees and the exotic conifer, and (2) the inaccessibility of the nest sites. Unlike this example, most *Cryptomeria* in Pigeon Wood forms a continuous canopy, so that nest sites are shielded by the foliage of surrounding trees.



4.3 Results

The results for each of the passerine species are summarized in Table 4.1.

Table 4.1. Annual cycles and known demographic parameters of native passerines of Mauritius.

Body weights are taken from Cheke & Jones (1987). Months are coded (i=January, xii=December). Incubation, fledging and juvenile dependency periods are given in days; the length of the breeding episode is the number of days from the laying of the first egg to the independence of the young (Rowley & Russell 1991). Clutch sizes are given as the known range and (in brackets) mode. Figures in square brackets are tentative, where the parameter was never measured directly; see text. Moults: C=complete (including primaries and tail), P=partial (not including primaries and tail), V=variable (that is, including a variable number of primaries).

	CS	BB	PF	GW	OW	MF
Body mass/g	44[1]	73[1]	11	8	8	18
Laying months	ix-ii	x-ii	ix-i	ix-ii	ix-i	ix-ii
Clutch size	2-3	2-3	2-3	2	2	2-4 (3)
Incubation period	24	14-16	15-16	13	13	13-14
Fledging period	24	21	13-14	10	[10]	18-19
Juvenile dependency	90	>30?	40	[14]	<14	14
Breeding episode	140	>70?	72	[40]	<40	45-50
Max. no. of broods	1	1	2	[3]	[3]	3
Post-breeding moult	C	C	C	C	C	C
Post-juvenile moult	P	V	P	?	?	V

Notes

[1] includes the following weights from D. Merton *per* C. G. Jones (*in litt.*): cuckoo-shrike ♂♂ 43, 39; ♀♀ 44, 49; black bulbul ♂ 69, unsexed 70.

4.3.1 *Mauritius Cuckoo-shrike*

Territoriality and movements

All evidence suggests that Mauritius Cuckoo-shrikes are monogamous, which is typical of the family (Lack 1968, Keith *et al.* 1992). Territories were defended by singing year-round, and also by aerial displays when intruded upon (see below). Although no birds were marked, all but one piece of evidence indicates cuckoo-shrikes to be highly sedentary: the single report from Le Pouce (Chapter 3), whilst not fully acceptable, may indicate that exceptional feats of dispersal can be achieved. Apart from this, none was ever recorded more than 500 m from known territories. The winter distribution was exactly the same as that in summer.

Breeding season

Regarding pair bonding, Cheke (1987c: 172) noted that pairs "start feeding together in very close association" and also saw interactions with birds from neighbouring territories more frequently from August onwards (presumably compared to the winter period of April to July). I cannot confirm such a change of behaviour. I saw pairs feeding close together, as well as territorial singing by males and intraspecific aggression, in all months. The most spectacular examples of the latter were aerial duels, involving up to four birds. I saw duels six times between September and February, too rarely to state that they did not occur at other times. The pair bond appears to be strong year-round.

The earliest report of breeding activity is an attempted copulation on 20 August; earliest and latest recorded dates of incubation were 28 September (clutch completed) and 4 March (J.-M. Vinson, S. A. Temple and J. Horne in Cheke 1987c); allowing 45-50 days from egg-laying to fledging (see below), the brood Temple (in Cheke 1987c) saw on 13 November 1973 also came from a clutch laid in late September. Allowing 20-25 days for incubation, for the six nests I followed in 1989-93 where eggs were laid, clutches were laid in October (two, earliest on 10 October), November (one) and December (three); the seventh nest was built on 6 February but was immediately destroyed by cyclonic winds. Including these nests, in this study 16 fledged broods in juvenile plumage (therefore less than two months old; see below) were seen between December and March, with most records in January and February (pers. obs, K. Duffy & J. Beaumont verbally). This information suggests an egg-laying season from late September to late February, with a peak in November to January, and no breeding activity (apart from parental care) from April to early August.

Breeding Biology

The two recorded clutches prior to this study were both of two eggs (Newton in Pollen 1866, illustration in Carié 1921). The only definitely complete clutch I saw was C/2. In one nest, three chicks were present for about 12 days after hatching, but two days later only two were present; these were later taken by a predator. Confirmed fledged brood sizes were one, two and three (once each). I conclude that up to three eggs are laid, not all of which are always reared. For one clutch, the two eggs were laid on successive days (pers. obs.).

Few data exist on incubation and fledging periods. One clutch I recorded was destroyed by a predator 18 days after completion; J. Horne (in Cheke 1987c) gave an incubation period of about 3½ weeks. For two nests found containing very young chicks, fledging periods were at least 22 and 24 days. Such protracted development of the young (around 50 days) is typical of the Campephagidae (Marchant 1979, Smythies 1985, Keith *et al.* 1992). Both sexes participate full-time at all stages of breeding (pers. obs.).

Cuckoo-shrikes' ability to lay repeat clutches was confirmed. A pair failed by predation on Brise Fer on 18 November 1991; the first egg of the new clutch was laid 14 days later, in a new nest 10 m from the previous one (in the same tree species: *Diospyros tesselaria*).

A brood which fledged on 31 December 1991 was still in the territory and being attended by the parents on 8 April (and the family was seen on many dates in-between), indicating a dependency period of over three months. The prolonged juvenile dependency precludes a second brood in the same season.

Moult of adults

Adults undergo a complete post-breeding moult. I saw adults in wing or tail moult between 16 March and 14 June (five obs.). It is not clear whether they moult while fledged offspring are still dependent (as often occurs in tropical passerines: Fogden 1972), or wait until the young are independent; if the latter is the case, late breeding birds might not begin moulting until June, which could explain the male specimen in the Rijkmuseum van Natuurlijke Histoire, Leiden, one-third moulted on the late date of 20 July (Mees in Cheke 1987c).

Juvenile and subsequent plumages

Whilst juvenile (*sensu stricto*) and adult plumages are documented (for example, Staub 1976), immature Mauritius Cuckoo-shrikes show very variable plumages, whose sequences were totally unknown before this study. Understanding these plumages is essential to interpreting sightings of immatures, and therefore to understanding the species' demography.

The very distinctive juvenile plumage (brown with buff 'scales' above, pinkish white with dark streaks below) is well illustrated in Pollen (1866) - as are the adults - and described by Benson (1971) from a specimen in the UMZC. One brood of three was observed regularly on Brise Fer for three months after fledging, and another single juvenile was seen in Pigeon Wood in nearly every month from fledging (7 December 1990) until 28 March 1992, when its plumage was close to that of an adult male. Although these birds were not ringed, their regular presence and the obvious progression of their plumages denies any suggestion that other birds were involved.

Three weeks after fledging, the members of the Brise Fer brood were largely in juvenile plumage, but with clear rufous patches on the underparts, similar in colour to an adult female's underparts. Three weeks later, all three had gained a female-like plumage (brown above, rufous below), with some remaining buff-tipped feathers above and pinkish patches below. The latter remnants of juvenile plumage had nearly all been lost two months after fledging, but the juvenile wing and tail feathers may have been retained; this female-like plumage was retained until the last sightings, three months from fledging.

The Pigeon Wood bird was still in juvenile plumage with a few rufous patches six weeks after fledging. At over three months (late March) it was, however, very striking. The mantle, rump, tail and some wing coverts were like those of an adult female; only the outer three or so greater coverts were tipped creamy. The crown was greyer than the mantle, but not as grey as on an adult male. The underparts were whitish (not the grey of an adult male), with an irregularly-shaped orange gorget on the upper breast and orange also on the flanks, contiguous with the rufous rump colour. The strongly creamy- or buff-fringed remiges (including tertials) were probably retained juvenile feathers. A dark eyestripe and whitish supercilium were more prominent than on any adult. This plumage was retained until at least August (although faded), but in late September, clear grey was emerging above and below on the body. By late November it was noted singing for the first time, and was largely in adult male plumage, but with brown patches remaining on the nape and rump and orange on the flanks; the remiges and tail seemed still unchanged since juvenile plumage (brownish with pale fringing partly worn off). One grey tertial (as on an adult male) contrasted obviously with the older, brown ones. This plumage was retained until 28 March, when the whole of the wings and tail had finally moulted into adult male plumage (some rectrices still regrowing), and a few brownish body feathers persisted.

A later juvenile (Pigeon Wood, January - March 1993), also seen frequently, quickly moulted from juvenile plumage into female-like plumage, but with paler orange underparts. Another female-plumaged bird begged successfully from a presumed adult pair (Brise Fer, 31 March 1992).

All the other birds I saw in full juvenile plumage were during the breeding season and attended by adults (see above). Additional birds with a mixture of adult male and female characters (but clear white on the underparts, like the first Pigeon Wood bird) were seen in February, April and December; they appeared to be independent of adults. Of three *C.*

typica skins in the Muséum d'Histoire Naturelle, Réunion (only one is listed by Cheke & Jones 1987), one is labelled as male (collected by Bewsher in 1872) in plumage closely resembling an adult female, but with white tips to the outer greater coverts, alula and tertials (pers. obs.). Benson (1971) noted that some male museum specimens showed rufous patches, possibly a sign of immaturity.

These observations are consistent with the following sequence of moults and plumages. Juvenile plumage is lost within about two months of fledging, by a body moult into an adult female-like plumage, in which males show a variable amount of white mixed in below; some males may lack this white. A further body moult takes place at the start of the following breeding season (around September), when more adult characters appear, but at least some males do not gain full breeding plumage until the complete moult at the end of the season (around March). Therefore females do not change much in appearance once they have lost juvenile plumage, but males take over a year to reach adult plumage, and probably do not breed until nearly two years old.

Acquisition at first moult of a plumage similar to the adult female is typical of the cuckoo-shrike family Campephagidae (Keith *et al.* 1992). The extreme sexual dimorphism shown by the two Mascarene cuckoo-shrike species (male *C. newtoni* of Réunion is similar to the Mauritian species, but the female is brown above and barred brown on white below: see Barré & Barau 1982) is not shown by any African cuckoo-shrike (Benson 1971). However, three Australasian species, *Coracina tenuirostris, C. schisticeps* and *C. melaena*, show similar dimorphism: males grey (black in *C. melaena*), females rufous (barred below like *C. newtoni* in some races of *C. tenuirostris* and *C. schisticeps*). Examination of skins in The Natural History Museum (formerly British Museum [Natural History]), and also Coates (1990), shows that these species have a very similar sequence of immature plumages to the Mauritius Cuckoo-shrike: a pale-fringed juvenile plumage is rapidly replaced by an adult female-like sub-adult plumage. Males acquiring adult plumage show a patchwork of grey or black (adult male) and rufous (adult female-like) feathers. In the sequence of immature plumages, the Mauritius Cuckoo-shrike apparently differs from the Australasian species only in the presence of white on the underparts of some sub-adult males; this general similarity further supports Benson's (1971) suggestion of an Asian origin for the Mascarene cuckoo-shrikes.

4.3.2 *Mauritius Black Bulbul*

Territoriality and movements

There is no evidence for polygamy. Black bulbuls vigorously defended a territory covering about 1 ha around active nests, but wandered outside this area in a home range of up to 0.5 km^2 (Cheke 1987c, pers. obs.). In west Pigeon Wood, the same *Cryptomeria* tree was used for the first nest found in the 1992-93 season as in 1991-92, and so it is likely that the same pair was involved in the two seasons. However in the intervening non-breeding season, often no black bulbuls were present in Pigeon Wood, and there were very few precise localities where birds could always be found throughout the year. As shown in Chapter 3, in 1989-93 black bulbuls appeared occasionally over a wide area of southern Mauritius, but the distances travelled by these birds is unknown.

Therefore, many birds probably wander outside the breeding season but reclaim traditional breeding territories. I agree with Cheke (1987c) that the small groups of black bulbuls seen at any time are likely to be family parties, as is the case for the Seychelles Black Bulbul *H. crassirostris* (Greig-Smith 1979). The rare larger groups (I once saw eight) may merely result from coincidental meeting of more than one group.

Group breeding is a possibility: at one nest (Pigeon Wood, February 1991), what appeared to be a third, duller bird fed the young at least once; the failure of the nest soon after prevented further observations.

Breeding season

Summarizing all evidence including museum specimens with enlarged testes, Cheke (1987c) found breeding indications from October to February. The earliest sign I saw was a nest being built on 16 November; the latest was a clutch completed on 27 February. When the latter nest failed on about 4 March, the parents quickly began moulting (13 March) and no further breeding attempts ensued (although the species is capable of repeat nesting: see below).

It is therefore possible that the onset of breeding is later than for the cuckoo-shrike, but the season seems to end at about the same time, with the latest broods not fledging until April.

Breeding biology

The clutch is reported to be "rarely more than two" (Guérin 1940-53); groups of two, three and five eggs are in the UMZC, but these are not proven to be clutches (Cheke 1987c). I saw two complete clutches, both C/3, and a brood of two nestlings less than a week old. One C/3 was completed in four days, the first and second eggs being laid two days apart. Although three-egg clutches appear to be frequent, a brood size greater than two has not been documented. Cheke (1987c) only saw undoubted juveniles twice in 1973-75: a single and a family party (number uncertain). Of six records of fledged juveniles in 1989-93 (three seen by me; also K. Duffy, K. Hodder and C. Taylor verbally), four were single, and twice two were seen.

In 1991, I watched two successive nests of a pair (both birds were recognizable by feather wear and bill staining, for 11 hours of incubation and six hours of post-hatching care. Both birds defended the nest and fed the young, but only one (presumably the female) was seen to build the nest, incubate or brood the young. The presumed male often guarded from a watchpoint 5 m from the nest, driving off intruders as big as Pink Pigeons. Guérin (1940-53) reported that the male incubated only in the middle of the day; my data, including several hours around midday, contest this.

Because all nests were depredated, I have no data on incubation or fledging periods; Guérin (1940-53) gave these as 14-16 days and three weeks respectively. No data exist on the duration of juvenile dependency; family parties may remain together after the young have begun to feed independently.

The one replacement clutch seen was started only 8-9 days after the previous nest failed (the adults were individually recognizable). There was no evidence for multiple broods, as no successful nest has ever been documented.

Moults and plumages

Juveniles are very dingy greyish-brown, with dark, dull bare parts, lacking the bright chestnut remiges shown by *H. crassirostris* of Seychelles (which make Seychelles birds with retained juvenile remiges very obvious: Cheke 1987c, pers. obs.). Of my three juvenile sightings on Mauritius (17 January to 15 March), all were in body moult. Two presumed siblings had both replaced some secondaries with adult-like feathers. Juveniles clearly moult soon after fledging. Cheke (1987c) thought that the post-juvenile moult was a complete one, but had very few data; it remains possible that some juvenile feathers are retained, as I saw occasional adult-like birds with browner-looking wings or individual remiges.

For adults, the clearest indication of an immediate post-breeding complete moult came from the breeding pair which failed in early March and immediately entered complete moult (see above). Other records of certain adults in complete moult were in February to April, and birds often looked "immaculate" in April and May. However, Cheke (1987c) found a specimen in Muséum National d'Histoire Naturelle, Paris, in wing moult, dated 24 August.

The age at first breeding is unknown.

4.3.3 *Mascarene Paradise Flycatcher*

Territoriality and movements

Cheke's (1987c) ringing studies indicate that flycatchers are typically monogamous. At all regularly visited sites (especially Pigeon Wood and Bras d'Eau), adults remained on territory and sang all year. However, none of the eight fledged birds which I colour-ringed in three nests in Pigeon Wood was seen after independence. Cheke (1987c) made similar observations at Bras d'Eau, attributing them to juvenile dispersal.

Between January and April 1993, flycatchers were easily found in their normal haunts (Combo, Bassin Blanc, Bras d'Eau), as in other years, but totally disappeared from Pigeon Wood, where at least four pairs had been present since at least 1987 (H. G. Young verbally, pers. obs.). I searched unsuccessfully for them during 28 visits to Pigeon Wood between 21 January and 1 April 1993; T. Liddiard (verbally) also found none during the same period. They were conspicuous in Pigeon Wood in the same months of other years. In mid April 1993, flycatchers were back in Pigeon Wood (T. Liddiard verbally); it is not known whether the same birds had returned, since only one had been ringed. A possible explanation of this unexpected disappearance is the use of the potent "1080" (Sodium monofluoroacetate) poison in day-old chickens scattered round Pigeon Wood from November 1992 to January 1993, in an attempt to control cats and mongooses that were killing Pink Pigeons. Chicks were left out for several days, and dead flies were often seen on them. Flycatchers feed by gleaning or sally-gleaning from the understorey (Cheke 1987c, pers. obs.) and would be very likely to exploit such a food source, or to take living but contaminated flies, ingesting poison in the process. The reappearance of flycatchers would then have occurred by recolonization, as Cheke (1987c) suggests is possible. Alternatively, the resident population could have temporarily departed; if true, this is inexplicable, but these events show that future observers need to pay close attention to the flycatcher's status. "1080" use was discontinued as soon as the disappearance of flycatchers was noticed.

Breeding season

From 13 clutches at Bras d'Eau, Cheke (1987c) recorded egg-laying between September and January; my observations did not extend the known duration of the breeding period there. Upland clutches laid before November have not been recorded before (Cheke 1987c); in the six nests that I found in native upland forest, allowing 29 days (see below) from laying to fledging, clutches would have been laid between 25 September and late December, with three clutches in October. The known breeding seasons at Bras d'Eau and in the uplands are therefore similar.

Breeding biology

The usual clutch size at Bras d'Eau is three (Cheke 1987c), like the two clutches I observed in the uplands; C/2 appears also to be regular in the uplands (Newton in Hartlaub 1877). Claims of up to C/5 (Clark 1859, cited by Cheke 1987c; also Guérin 1940-53) need substantiation.

Four broods I recorded (in nests but close to fledging) were of two (once) and three (thrice); one of the latter was from C/3. Four out of five successful nests monitored by Cheke (1987c) at Bras d'Eau resulted in three young fledging from C/3.

Both sexes nest-build, incubate and feed the young (pers. obs.). The incubation and fledging periods are 15-16 days and 13-14 days respectively (Staub 1973, 1976, Cheke 1987c, pers. obs. of one nest, which took 29 days from completion of the clutch to the brood fledging). In Pigeon Wood, I saw one youngster (colour-ringed), near the end of post-juvenile moult, still dependent 33 days after fledging. The only attempted second brood seen began with a clutch laid 6-7 weeks after the first brood fledged. This is consistent with dependency lasting through this moult but not long after, as Cheke (1987c) found at Bras d'Eau. There appears to be insufficient time for a third brood. Following nest predation, construction of a new nest began within two days and the first egg of the repeat clutch was laid ten days after predation (data from a colour-ringed female).

Moults and plumages

The yellow mouth and frequent wing-shivering of adults sometimes lead to their misidentification as dependent juveniles, which are in fact distinctively plumaged, with whitish underparts and all-rufous upperparts (Benson 1971, pers. obs.), until they moult, when they come to resemble adult females. With reliable data, Cheke (1987c) reported that the post-juvenile moult is of body feathers, some wing coverts and alula only, starts two weeks after fledging and takes three weeks. He also confirmed that the complete moult of adults follows the breeding season. The usual age of first breeding is unknown, but some birds may attempt to breed at one year old, before full adult plumage is gained (Cheke 1987c).

4.3.4 *Grey White-eye*

Territoriality and movements

Cheke (1987c) recorded group breeding and flocks are seen at all times of year, but the territoriality, pair bonding and relationship between flocking and breeding are not understood. Evidence for philopatry (fidelity to a home area) is provided by the difference in size between upland and lowland birds and the sighting of a bird at exactly the same place on Macchabé as it had been ringed five years before (Cheke 1987c). In addition, Grey White-eyes are absent from many offshore islets (such as the northern islets, and even Ile aux Aigrettes, only 600 m offshore, although they are present on Ile aux Bénitiers, 1.5 km offshore: pers. obs.).

Breeding season

Because of its abundance, more data on the breeding season were available from this study for this species than for any other except the intensively studied Mauritius Fody. Table 4.2 summarizes these data (which are for the uplands only), indicating that almost all breeding occurs between September and March, with a peak from October to February. The June nest (Pigeon Wood, 6 June 1991) was found on the ground, but was in good condition and certainly not months old. As Horne (1987) has shown, *Z.b. mauritianus* has a prolonged song containing "soft and elaborate warbled phrases". I only heard this song between September and March (like the olive white-eye), at all times of day. The dawn chorus was, however, dominated by chirping calls of this species, rather than song. My data confirm the breeding period suggested by Cheke's (1987c) very limited data; he also suggested that lowland birds may on average start and finish nesting earlier, but I cannot confirm this.

Table 4.2. Timing of breeding indications of the Grey White-eye in upland Mauritius, 1989-93.

Month	Abandoned or intact depredated nests[1]	Adults carrying nest material	Nests with eggs	Adults carrying food[2]
September	1	0	0	0
October	1	3	0	2
November	6	4	2	3
December	8	0	0	4
January	9	3	0	4
February	14	0	0	0
March	3	0	0	0
June	1	0	0	0
Total	43	10	2	13

Notes

[1] Only nests in fresh condition (retaining their usual shape) are included. Disused nests are expected to disintegrate within a month, especially in rainy conditions. Therefore these nests were assumed to have been active within a month before being found.

[2] Includes fledged juveniles and chicks still in the nest.

Breeding biology and moult

The usual clutch size is two, rarely three (Cheke 1987c; I saw two C/2). The incubation period is unknown, but likely to be similar to that of the olive white-eye (about 12-13 days). Rountree (in Cheke 1987c; one nest) gave a fledging period of about ten days. Breeding episodes in the family Zosteropidae are typically short, with incubation and fledging periods of 10-12 days each (Moreau & Kikkawa 1985). The brood size and dependency period are unknown, as juveniles are very difficult to distinguish from adults. Adults enter a complete post-breeding moult, the timing of which depends on when breeding stops (Cheke 1987c; I saw moulting birds in March to May).

4.3.5 *Mauritius Olive White-eye*

Territoriality and movements

The species is pair-living (Gill 1971, Cheke 1987c, Safford 1991), implying that pairing is usually monogamous. Like the black bulbul, olive white-eyes of unknown provenance appeared occasionally over a wide area of the southern central plateau. However, some, such as an isolated pair on State Land Raoul throughout the studies (1989-93), remained on territory all year. At all seasons, territories were defended by calling and chasing off intruders, but many birds foraged outside these limits (Cheke 1987c). Safford (1991) noted song only between September and March. Further observation did not extend this, although the brief, inconspicuous song (Horne 1987, Safford 1991) could have been overlooked if given much less often in winter than in summer.

Breeding season

Like other observers, I very rarely saw clear signs of breeding activity. It is not clear that mutual preening is a breeding indication (as Cheke 1987c thought), since I once saw this on 6 April (Safford 1991), which is well outside the main courtship period for the other native species. Carié (1904) reported a laying season from September to November. The BOU expedition and I saw breeding indications suggesting laying between October and January (Cheke 1987c, Safford 1991).

Breeding biology

The only two nests found recently both contained C/2 (Safford 1991, Chevreau in Staub 1993), which is typical although C/3 has occurred rarely (Newton in Hartlaub 1877, Carié 1904). For the 1990 nest, the incubation period was certainly less than 15 days (Safford 1991), actually probably 12-13 days, like other white-eyes (see Grey White-eye, above). No successful nests nor certain juveniles (which may lack eye-rings, as do certain other *Zosterops* species: Maclean 1985) were seen by me or the BOU expedition, leaving the incubation and fledging periods unknown. Carié (1904) noted that the groups of four or five seen after fledging soon separated. These observations suggest that two or three juveniles may fledge, but very soon moult and become independent. The presumed short dependency period should allow multiple broods. Repeated sightings of the Raoul pair carrying nest material in November, December and January (Safford 1991) suggest that repeat clutches are laid, as by all other native land birds.

My only definite record of an olive white-eye presumably in moult was a tailless bird on 10 May, consistent with the expected complete post-breeding moult. No other source gives any data.

4.3.6 *Mauritius Fody*

Territoriality and movements

Monitoring recognisable individuals showed that territories were in general occupied exclusively and permanently by one monogamous pair.

There is almost no previous information on the behaviour of the Mauritius Fody in winter. Newton (1959) thought it "not gregarious but tends to remain in pairs throughout the year". Cheke (1987c) and I noted feeding associations with Grey White-eye flocks more often in winter than in summer. Cheke's report (in Safford 1991) of a bird outside breeding territories at Macchabé was in fact less than 200 m from a territory (A. S. Cheke verbally 1994).

I found that territorial behaviour in winter was precisely the same as during the breeding season, but less time was spent actively defending territory, especially during the middle of the day. This made the birds less conspicuous in winter, when they could be entirely overlooked. However, winter visits to breeding territories at dawn or especially dusk invariably revealed the males (in eclipse plumage but sexed by their voice and blackish bills) perching prominently in tree-tops, singing strongly, 'plick' calling (see Horne 1987) from their usual perches, and chasing conspecifics which responded with 'buzz-squeak' calls and were therefore females (because this call was only given by females: pers. obs.). This was confirmed throughout the range: Pigeon Wood (where the two ringed birds - male and female in different territories - were always recognisable), Savanne Mountains, Bassin Blanc track, Montagne Cocotte and Bel Ombre. In short, Mauritius Fodies do not "become vocal and territorial" in August (*contra* Cheke 1987c: 203, and also *contra* C. G. Jones in Cheke 1987c, who reported no territorial behaviour from March to July during 1979-83); they are in fact both vocal and territorial all winter.

No flocking was seen, the largest group being eight on 4 February 1991, which appeared to comprise two family parties. No such parties were recorded in winter, possibly because juveniles seemed to be ousted from their natal territories once independent. There were no records of Mauritius Fodies during 1989-93 outside the breeding distribution.

Given the apparent reduction in territory defence, birds in winter are probably relatively free to trespass in neighbouring territories, and this (along with wandering juveniles) may explain the odd sightings of single birds flying high overhead; this also occurs in the breeding season. However, there is no evidence that territory-holding birds abandon their territories for more than a few days and then claim them back. The poor breeding success leaves few immatures in the population, and few, if any, adults lack a territory.

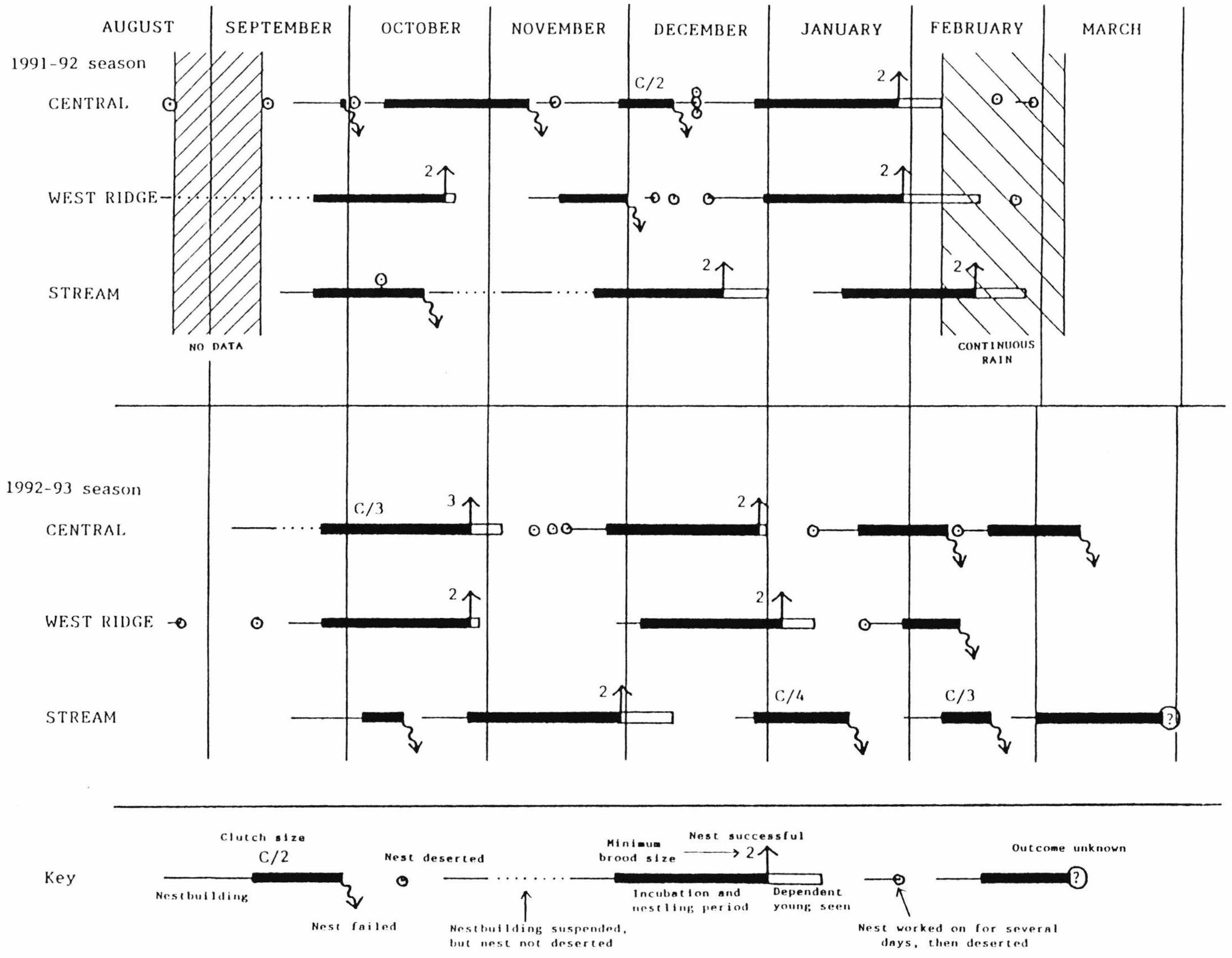
Most extraordinary is the report of a roosting movement of 60 Mauritius Fodies flying singly, in pairs or loose groups from the Plaine Champagne area to the south-west slopes of Montagne Cocotte in the last half-hour before sunset on 16 May 1984 (C. G. Jones in Collar & Stuart 1985, also quoted by Cheke 1987c and Safford 1991). There were probably more fodies in 1984 than now (but not many, since the main declines caused by the 1970s forest destruction must by then have ceased), so this would have been about a fifth of the population.

My many observations appear to leave no possibility of such numbers occurring at one place. Even in the unlikely event of all immatures associating together, there could hardly be so many, so Jones's report implies that adults had abandoned their territories to roost elsewhere. With this in mind, in addition to fieldwork throughout the range at all times of day, evening watches were carried out in 1991-92 between March and July at Montagne Cocotte (six dates), Alexandra Falls (two dates), Bel Ombre scarp top, and Grand Bassin. At all sites, only the usual territory-holding Mauritius Fodies were seen. Small numbers of Madagascar Red Fodies sometimes flew over, especially at Alexandra Falls; although not as many as 60 were seen on these watches, such numbers are common in these areas (for example, 50 at Alexandra Falls in June 1991). Unlike the Mauritius Fody, they are known to roost communally (pers. obs., Greig-Smith 1982). The roosting movement in 1984 was most likely to have involved only Madagascar Red Fodies, which, despite their longer tail, are often difficult to distinguish from Mauritius Fodies in fast flight.

Breeding season

All breeding activity in the three closely monitored territories in the 1991-92 and 1992-93 seasons is summarized in Fig. 4.2. The breeding season was highly synchronized throughout the population. Males (only excepting 'half red', presumably immature birds) acquired breeding plumage in mid August to early September, and lost it in late March to April (see *Moults*). The earliest nests were found being built on 20 and 22 August 1991 and 25 August 1992 (two nests), by pairs with males not yet in full breeding plumage, but these nests were all deserted or activity was suspended until September. The earliest

Fig. 4.2. Summary of all breeding activity by three Mauritius Fody pairs in Pigeon Wood, studied during two successive breeding seasons



fledged young were seen on 22 October 1991 and 27 October 1992 (two broods), implying first egg-laying on about 19 and 24 September respectively (the latter date was confirmed for one nest). The latest clutches were completed on 28 February 1991 and around the same date (not precisely known) in 1993; young would have fledged around 1 April. Breeding activity therefore occurs from late August to early April. Table 4.3 and Fig. 4.2 show that once the season is underway, there is no peak of breeding activity; effort is continuous (weather permitting; see below) from September to February.

The very late wet season in 1991 (Chapter 2) did not seem to affect the fodies' annual cycles. In 1992, continuous rain from 7 February to 6 March (Chapter 2) apparently terminated the breeding season for the birds studied: breeding attempts that were already in progress were completed, but all four nests started during this period were abandoned and no eggs were laid (Fig. 4.2). Cyclones can have the same effect, depending on their severity and timing; cyclone Gervaise on 6 February 1975 certainly did so (Cheke 1987c).

Table 4.3. Number of Mauritius Fody nests found and clutches laid in each calendar month for the 1991/92 and 1992/93 seasons combined. Previous seasons' data are excluded to avoid bias due to evolving nest-finding skill. The number of clutches completed per month does not relate directly to the number of nests started; eggs were often laid in the calendar month after the nest was started.

Month	Aug[1]	Sep[1]	Oct	Nov	Dec	Jan	Feb	Mar
Nests started	4	9	14	15	15	15	11	0
Clutches completed	0	7	8	6	6	7	5	0

Note

[1] I was away from Mauritius from 23 August - 15 September 1991 and therefore presumably missed some nests being started and deserted in this period.

Incubation and parental care

For three clutches with data on laying intervals, eggs were laid at daily intervals. I recorded one C/2, five C/3 and one C/4. Clutch sizes other than three have not been confirmed before. The eggs are pale blue-green, like those of Madagascar Red Fodies. Three clutches which I measured in the field are detailed in Table 4.4.

Table 4.4. Measurements (in mm) of three Mauritius Fody clutches. All were confirmed complete clutches.

Locality Territory Date	Pigeon Wood Central Feb 1991	Pigeon Wood Central Dec 1991	Pigeon Wood Stream Feb 1993
Dimensions	19.0 x 14.1	18.2 x 14.2	18.0 x 13.6
	18.1 x 14.3	18.3 x 13.9	18.4 x 13.8
	19.5 x 14.1		18.2 x 13.6

The ability to distinguish between eggs of Mauritius and Madagascar Red Fodies would be useful, particularly when eggs (or broken shells) are found on the ground. Both species lay pale blue or blue-green eggs (Newton 1959), with no difference in intensity of colour (pers. obs.). Table 4.5 shows measurements of Mauritius Fody eggs in 1865 and 1991-93, and of Madagascar Red Fody eggs in 1991-93. Clearly, eggs of the two species are not reliably distinguishable using these measurements, nor by colour.

Clutch size and egg colour in the Mauritius Fody are typical of the genus. The Seychelles Fody is the exception, laying only one to two white eggs (Crook 1961).

Table 4.5. Egg measurements (mm) of fodies on Mauritius. Ranges, means and standard deviations.

	Mauritius Fody		Madagascar Red Fody
Source; no of clutches (no of eggs)	This study; 3 (8)	Cheke and Jones[1]; 4 (10)	This study[2] 4 (11)
Dimensions; range	18.0-19.5 x 13.6-14.2	18.4-19.9 x 13.0-14.6	17.3-19.4 x 12.9-14.0
mean±SD	18.5±0.6 x 14.0±0.3	19.2±0.5 x 13.9±0.5	18.2±0.7 x 13.5±0.3

Note

[1] Ten eggs, presumed to be four clutches, in UMZC, collected in 1865; Cheke & Jones (1987) gave standard errors; I have converted these to sample standard deviations.

[2] I found one C/2 and three C/3; C/4 has also been recorded (Carié 1916, Newton 1959).

The exact dates of both egg-laying and hatching were only known for one nest (C/3, Pigeon Wood, 1991): one egg was laid daily 26-28 February, the first hatched by 12 March, second and third by 13 March (nest checked around midday). This gives an incubation period (from completion of the clutch to hatching of the last egg) of 13 days. In another nest, incubation lasted 13-14 days (hatching date not known exactly).

Both hatching and fledging dates were not known exactly for any nest. In one case, eggs hatched on 9 or 10 October, the first juvenile fledged on 27 October, followed by two more on 28 October, giving a fledging period (from the last chick hatching to the last juvenile fledging) of 18-19 days. In this nest, the first egg was laid on 24 September, so from the laying of the first egg to the last chick fledging took 34 days. In another nest, this period was 31 days.

The large volume of data I collected regarding parental rôles (Safford in prep.) may be summarized as follows. Both sexes built the nest, although only the female added the lining. All incubation and brooding was carried out by the female. The male joined the female in feeding the young around 4-6 days after hatching; thereafter, both sexes fed the brood equally often.

Juvenile dependency, dispersal and development

Post-fledging dependency was difficult to assess without ringing, due to the mobility of the young. From a brood fledging to the building of the next nest took 12-32 days (mean 21 days, n=11, 5 pairs); by this time any lingering juveniles were being repulsed by their parents, and no juvenile was seen being fed more than 11 days after fledging. For the only brood colour-ringed as pulli, there was no sign of the young in their natal territory ten days after fledging. One was seen 100 m off ('two territories away') 23 days after fledging, where it had joined up with a 1-2 day old brood and was begging (unsuccessfully) from the younger brood's parents. These data indicate a short post-fledging dependency, probably about two weeks.

Firm data on behaviour after dependency are even scarcer. One of the colour-ringed brood was seen 82 days after fledging, about 100 m from its natal territory ('two territories away'), and the same bird again seven days later together with an unringed bird, a similar distance in the opposite direction, but both times in a different territory to the previous observation. On each occasion it abruptly flew off high, showing no respect for territory boundaries. It is likely that independent juveniles wandered (how far is not clear) around the vicinity of their natal territory, but certainly did not remain in that territory, as this would have been detected in the territories which were watched intensively. Some of the many observations of brown birds flying high and far over occupied territories presumably referred to wandering juveniles.

'Half-red' (presumably immature: see *Moults*) males appear to be capable of breeding (Cheke 1987c) but are often unpaired (pers. obs.). It is therefore most likely that some birds attempt to breed for the first time when about one year old, others at two years.

Repeat nesting, number of broods and potential productivity

Following the failure of a nest, the usual courtship and nest-building behaviours ensued; nest predation is dealt with in Chapter 6. Construction of the next nest began as little as two days later. In eight cases where dates were approximately known, replacement clutches were started 14, 15, 18, 19, 19, 19, 32 and 37 days (mean 22 days) after the failure.

Brood sizes of both two and three were regular; how often birds fail to rear all their chicks is not known. The Seychelles Fody typically only fledges one young from a usual clutch of two (Brooke 1985). If all attempts were successful, the first brood could fledge in late October, the second in late December and a third in late February, a potential productivity of up to three broods per pair per year (Fig. 4.2). Nest predators prevented any pair that I studied achieving this. Each female laid three to five clutches per season, and those with higher failure rate may produce more. The 'Stream' female's third and fourth clutches in 1992-93 were C/4 and C/3, so there was no sign of reduction below the mode (C/3) as the season progressed.

Multiple broods are also confirmed for the Aldabran and Rodrigues Fodies, new clutches being started by the former as little as ten days after the previous brood fledged (Frith 1976, Cheke 1987e). The Seychelles Fody is singly brooded.

Moults and plumages

As Cheke (1987c) has shown, the pre-breeding moult involves only the body feathers, whereas a complete moult takes place after breeding. The male therefore enters eclipse plumage after breeding. A female was already moulting primaries while incubating on 23 February 1991, but a male on 19 February 1992 was replacing lost red cheek feathers with identical ones, and did not begin the moult into eclipse until a month later. Most observations of wing and tail moult took place in March and April. No moulting birds were seen in June, so the moult seems usually to be complete by the end of May.

The only data on post-juvenile moult come from the two captive birds (fledged 26 October 1992): one had regrown two missing tertials with identical feathers by 28 November, but both were in complete moult from 10 January to at least mid February 1993, replacing body feathers, some tertials, wing coverts, inner primaries and perhaps outer secondaries, but apparently not the tail. Neither bird was moulting when they died on 30 April and 13 May 1993. This indicates a variable post-juvenile moult one to four months after fledging.

'Half-red' or brown males in the breeding season are probably young from the previous or current season, their rarity consistent with low breeding success. If they acquired any red in the post-juvenile moult (the captive birds certainly did not), they would presumably retain it through the winter, but this was never seen. Cheke (1987c) reported birds moulting into red plumage at any time during the breeding season, although it is not clear whether these birds were truly moulting, or had merely acquired partial breeding plumage with their previous moult.

Juveniles have yellowish horn bills, soon darkening to greyish horn or sepia with paler cutting edges, like females (Safford 1991). The only black-billed, brown-plumaged birds I saw were adult males in eclipse plumage.

4.4 Discussion

4.4.1 *Relevance to conservation*

It is difficult to predict which biological details will be of greatest importance to a species's conservation; two examples follow in which basic background information was essential. The disappearance of flycatchers from Pigeon Wood in early 1993 could have been dismissed as merely due to temporary emigration, had previous studies not indicated that the species is highly sedentary. This led to the realization that the use of "1080" poison for predator control may have caused the death of the flycatchers due to consumption of affected insects; as a result, "1080" poison use was quickly halted. The population census method (Chapter 3) depended fairly heavily on the assumptions that the passerines are territorial and monogamous. The studies on the breeding biology justified these assumptions.

However, three aspects of the annual cycles of particularly obvious importance to conservation planning are discussed below.

Mobility

In Mauritius, suitable habitat has been (and continues to be) degraded and fragmented (Chapter 2), new habitat is occasionally created (such as the plantations at Bras d'Eau;

Cheke 1987c) and the populations of several bird species are small (Chapter 3). Migration of birds from the existing range area into distant, unoccupied areas may lead to colonization of newly created habitat, or recolonization of areas made vacant by local extinctions. This allows exploitation of all suitable habitat. Replenishment from elsewhere of dwindling populations reduces the risk of local extinction (the "rescue effect": Brown & Kodric-Brown 1977). Occasional migration between small subpopulations helps to maintain genetic variability, the loss of which is a threat to any small population (Lacy 1987). The movement of individuals between sub-populations reduces the risk of inbreeding depression (Simberloff 1988). Mobility can, however, expose populations to risks not faced by sedentary individuals: for example, a wandering bird returning to its usual range could bring a contagious disease back with it. The mobility of a species can therefore affect its extinction probability, and consequently also action plans for its recovery.

For example, the poor dispersal ability of the Mauritius Kestrel resulted in its failure to recolonize outlying areas (such as the Montagnes Bambous) where reintroduced populations now live at very much higher densities than the original wild birds did (and still do) in the Black River Gorges (Jones *et al.* 1991a, Cade & Jones 1992).

The cuckoo-shrike, flycatcher and Mauritius Fody appear to be highly sedentary, remaining on territory all year, and so, like the kestrel, seem unlikely to recolonize isolated, vacant habitat patches. The fody and flycatcher in the south-west are anyway unlikely to expand their ranges while their populations are small and declining.

Black bulbuls and olive white-eyes are more mobile than the other rare passerines, although some pairs are sedentary and some wandering birds may return to nest in the same territories year after year. Their movements are, however, largely limited to the areas indicated in Chapter 3. That these species remain in most of the Plateau Relicts, unlike the fody and cuckoo-shrike, may well be due to their greater mobility, but they are unlikely to reach very remote habitat patches, such as restored offshore islets.

The rôle of juvenile dispersal is poorly understood on Mauritius. Juvenile (natal) dispersal in birds is almost invariably more widespread than adult (breeding) dispersal (Greenwood 1985); there is evidence for this for the flycatcher on Mauritius (Cheke 1987c). This could allow occasional colonization of isolated sites, but while recruitment is very low and much suitable but vacant habitat exists close to existing populations, as on Mauritius for nearly all species at present, long-distance juvenile dispersal seems unlikely.

These observations suggest that, as for the kestrel, translocation may be appropriate to:

(1) allow the cuckoo-shrike to exploit suitable habitat now isolated from its current range, most obviously the Montagnes Bambous (see Section 8.2.4), and (2) allow all species to extend their ranges into newly created or restored habitat, if these become available. Translocations are discussed further in Chapter 9.

Vulnerability to nest predation

Predation away from nests is likely to be rare, as no specialist predators of arboreal birds occur on Mauritius. Pink Pigeons feeding on the ground are very vulnerable to cats and mongooses (Section 8.2.1), but for the remaining species nest predation is presumably far more important.

Certain traits (especially distraction behaviour and choice of safe nest sites) enable the birds to reduce the frequency of predation on their nests. Predation rates and their causal factors are investigated and discussed in Chapter 6. The effect that nest predation has on bird populations also depends on the birds' ability to compensate for predation by rapid recruitment, persistent breeding attempts or high survival rates (Moors 1983); these are governed by the demographic parameters, and are discussed here. The combination of these traits and parameters may render certain species especially vulnerable to increased predation of nests or of adults, and affect the ability of populations to recover following relaxation of these (or other) pressures.

Whatever the breeding success, the recruitment of which a species is theoretically capable depends on the clutch size and ability to lay repeat clutches and rear multiple broods. All the species (passerines and non-passerines) are capable of rapid repeat nesting and can lay clutches of two or more eggs, as on Aldabra (Prŷs-Jones & Diamond 1984; see Section 4.4.2 below). The Pink Pigeon (pers. obs.), Mauritius Fody, flycatcher and very probably also the two white-eyes are multiply brooded. The kestrel, parakeet, cuckoo-shrike and probably also black bulbul are restricted to a single brood per year by the protracted development of their young.

Survival and longevity are among the most important parameters determining birds' ability to survive heavy nest predation. I have no data on these aspects for Mauritian birds. Mortality figures given in Bruford *et al.* (1991) for the Pink Pigeon were 25 % juvenile mortality and 10-15 % adult mortality; these are plausible estimates but cannot have been based on field data since at that time only five adult pigeons had been ringed (pers. obs.). The annual adult survival of the black bulbul and fody on Aldabra were estimated at around 85 % (Prŷs-Jones & Diamond 1984), a rate not unusual in tropical passerines (Fry 1980). The closely-related Mauritian species may achieve a comparable figure, since mortality factors are probably similar.

The arrival of exotic nest predators is likely indirectly to have affected adult and juvenile survival as well as directly reducing breeding success, as Prŷs-Jones & Diamond (1984) suggested on Aldabra. In pristine Mauritius (or Aldabra), breeding success must have been very much higher than it is now, but intra-specific competition would therefore also have been more intense at the end of the breeding season when numbers were highest, presumably resulting in higher mortality (especially of juveniles).

Each species appears to have strengths and weaknesses in relation to surviving predation. It is impossible to predict how these features will combine to affect resilience to nest predation. Cuckoo-shrike populations might seem especially vulnerable to any increase in the severity of nest predation, but are apparently holding their own (Chapter 3), a fact all the more surprising given the cuckoo-shrike's habit of nesting in fairly exposed positions in predator-rich habitat (Chapter 6).

Effect of cyclones

Cyclones strike the Mascarene islands, especially Rodrigues, every few years (Padya 1989, Chapter 2), but are rare on the Comoros (Louette 1988) and very rare on Aldabra (Walsh 1984). The Seychelles lie outside the cyclone belt (Padya 1989). Cyclones may cause direct mortality during the storm and strip fruit and flowers from trees, resulting in temporary food shortages, but the high rainfall may later lead to a temporary resource superabundance or 'flush' (Jones 1987). The destructive effects of cyclones might be expected to lead to mechanisms for increasing productivity, in order to make up losses. There is no evidence that this is the case on Mauritius, but on Rodrigues (the most oft-afflicted island), losses may be recouped by rapid, opportunistic breeding at any season (Cheke 1987e, C. G. Jones verbally, pers. obs. of much breeding by Rodrigues Fodies in April 1991, following Cyclone Bella), permitted by the resource 'flush'.

4.4.2 *Island biology*

General features of the annual cycles and breeding biology are now discussed, and compared to other island avifaunas when relevant.

Mixed species flocking

Mixed species flocking in winter is typical of tropical forest passerines, including those in Madagascar (Eguchi *et al.* 1993). In Mauritius, the abundant Grey White-eye forms single-species flocks (Gill 1971, Cheke 1987c, pers. obs.), which the other (much rarer) species sometimes join, but I never recorded more than two individuals of these attendant species in one flock. Cuckoo-shrikes and Mauritius Fodies regularly join Grey White-eye flocks; flycatchers, black bulbuls and olive white-eyes do so more rarely. There is no evidence that the typically sedentary cuckoo-shrikes, flycatchers or fodies ever follow flocks beyond the edges of their territories; this is consistent with the maximum of two (a pair) of each species seen per flock.

Flocking is likely to facilitate foraging; predator avoidance, the other commonly suggested advantage (Morse 1970: 165), is probably not a major reason for mixed species flocking on Mauritius, since predation on adult birds must be rare (see Section 4.4.1). Overall, mixed species flocking is not prominent on Mauritius, perhaps mainly because of the rarity of the attendant species. The phenomenon is much more obvious on Réunion (pers. obs.), where the Grey White-eye is again the nuclear species (*sensu* Moynihan 1962) but the attendant species are much commoner than their Mauritian counterparts.

Timing of the annual cycle

The annual cycle of all Mauritian forest-living native passerines consists of three main phases. The breeding season and complete moult take place largely from September to May. The moult immediately follows the breeding season, but may occur later than May in the cuckoo-shrike and black bulbul, which have a long juvenile dependency period. This normally leaves a mid-winter subsistence period from June to August.

The annual cycles of the kestrel and parakeet follow a similar pattern, except that the moults are more protracted and, for the parakeet, partly coincident with breeding (Jones 1987). The Pink Pigeon's cycle is quite different, with breeding in any month, but least often in October and November; its moult is also variable, but tends not to occur in August and September (Jones 1987).

Growth of body tissues requires protein. For birds, this is needed most when feeding young and moulting (O'Connor 1984). All the Mauritian passerines, and also the kestrel, presumably gain most of their protein from animal prey. Their annual cycles are likely to follow a complex of vegetational, climatic and prey (invertebrates, and geckoes for kestrels, cuckoo-shrikes and black bulbuls) abundance cycles, themselves interrelated, as

Snow & Snow (1964) suspected in Trinidad.

On Mauritius, data are only available for the climatic cycles (Chapter 2). The passerines breed in the early summer dry season (September to December) and the hotter, rainy season (January to April), therefore including both the wettest and the driest months of the year. Moult, following this, also includes both wet (April) and dry (May) months. Therefore the breeding and moulting season encompasses the entire wet season, and also a few months on either side. Rainfall does not appear to affect the timing of the birds' annual cycle directly, apart from the obvious effect of cyclones or continuous heavy rain (Fig. 4.2). Some tropical forest birds avoid breeding in seasons of very heavy rains and continuous mist (Serle 1981); in the Mauritian wet season, rain and mist are rarely so continuous as to have such an effect. The subsistence period coincides with the coldest winter temperatures.

On Aldabra, flying insect abundance peaks during the summer rains (Frith 1975); the same seems likely to be true on Mauritius. If so, and if applicable to overall insect biomass, this would be sufficient to explain the overall timing of their breeding and moulting period; the main wet season is too short to contain the whole breeding and moulting period, so that some dry months must be included. There is evidence that nest predation rates are lower during the drier months of September to December (Chapter 6); this could offset the deleterious effect of the (possibly) lower food availability at this time.

The seasonality of nectariferous flowers (especially *Hypericum lanceolatum*) is very important to the altitudinal movements of the Réunion Olive White-eye (Cheke 1987b). The Mauritius Olive White-eye is less tied to single food-plant species, but nectar seemed scarcest in winter and most abundant from September to December which is the main flowering season for native plants (Vaughan & Wiehé 1941) and also for the introduced bottlebrush *Callistemon citrinus* (Section 5.3.3). For both olive white-eye species, the importance of nectar supply to breeding is unclear.

For the vegetarian Pink Pigeon and Echo Parakeet, many native fruits appear in the wet season but some fruit and flowers are present all year. With unlimited supplemental food and control of Roof Rats, Pink Pigeons bred all year in 1992-93, but before this management began, the non-breeding period probably corresponded to the time of least fruit and flower abundance. Parakeets feed young mainly in the wet season.

The complete post-breeding moult found in Mauritian passerine species is typical of cyclically breeding tropical passerines (Stresemann & Stresemann 1966); its timing varies according to the end of breeding. Unlike the Mauritian and other fodies, the Seychelles

Fody has a complete pre-breeding moult, which Brooke (1985) tentatively linked to the variability of the timing and severity of the lean period that follows moult. This demonstrates the evolution of strongly differing characteristics within a genus of seemingly closely related and ecologically similar species.

Clutch size

Clutch size is the only population parameter reliably known for most Indian Ocean birds. Table 4.6 shows the clutch sizes of the native land-birds of Mauritius, compared to those of their closest congeners on other Indian Ocean islands, including Madagascar, which is regarded as a 'continental' landmass (and may be the source region for most of the island species: Benson 1961, Diamond 1984, Cheke 1987c, Louette 1988). Particularly instructive are the genera *Falco*, *Hypsipetes*, *Terpsiphone*, *Zosterops* and *Foudia*, with native taxa present on four or more islands or archipelagoes. The general pattern is very obvious: birds on the Comoros, Aldabra or Mauritius have a clutch size similar to the continental average (Madagascar), whereas Seychelles birds have a smaller clutch size.

Clutch sizes on Aldabra and Seychelles have already been compared by Prŷs-Jones & Diamond (1984). The biotic and climatic cycles on Seychelles are less marked and more irregular than on Aldabra (Walsh 1984), leading to greater environmental stability and minimal resource 'flushes'. Madagascar, the Comoros and Mauritius show, like Aldabra, strong and fairly regular climatic seasonality, even though between them they include a wide variety of overall climates (see Donque 1972, Ergo 1984, Chapter 2). The similarity of clutch sizes on the more seasonal islands strongly suggests that the smaller clutch size on Seychelles is related to the greater environmental constancy, but the determining factor is unclear. Ricklefs (1980) argued that small clutches could result when environmental stability minimizes resource 'flushes' and supports bird populations close to the food limit all year. In such conditions, parent birds cannot find enough food to rear large broods, and small clutches are the result.

Island birds can probably change clutch size in response to selective pressures, as Van Noordwijk *et al.* (1980) showed to be possible for the Great Tit *Parus major* over a few generations. However, there is no evidence that clutch sizes have changed historically for any of the species in Table 4.6. This is consistent with the limiting factor being related to climate, which has apparently not changed historically, unlike most other ecological features of the Indian Ocean islands.

Table 4.6. Clutch sizes (usual ranges, with modes in brackets where one clutch size dominates) of native land-birds of Mauritius and their closest congeners on other Indian Ocean islands. Taxa involved in Seychelles, Aldabra, Comoros and Madagascar are as follows (indicated with S, A, C or M respectively): *Falco araea* (S), *newtoni* (A, M); *Columba polleni* (C); *Psittacula wardi* (S-extinct); *Collocalia elaphra* (S); *Coracina cinerea* (C, M); *Hypsipetes crassirostris* (S), *madagascariensis* (A, C, M); *Terpsiphone corvina* (S), *mutata* (C, M); *Zosterops modestus* (S), *maderaspatanus* (A, C, M); *Foudia sechellarum* (S), *eminentissima* (A, C, M). Data for Mauritius: Cheke 1987c, Jones & Owadally 1988, this study; Seychelles and Aldabra: Prŷs-Jones & Diamond (1984); Comoros: Benson (1960); Madagascar: Langrand (1990). A question mark indicates that no data are available; a dash indicates that the genus is absent.

	Mauritius	Seychelles	Aldabra	Comoros	Madagascar
Kestrel *Falco*	2-4 (3)	2-3	3-4	-	4
Pigeon *Nesoenas (Columba)*[1]	1-2 (2)	-	-	1	-
Parakeet *Psittacula*	2-3	?	-	-	-
Swiftlet *Collocalia*	1-2 (2)	1	-	-	-
Swallow *Phedina*	2	-	-	-	2-4[4]
Cuckoo-shrike *Coracina*	2-3	-	-	?	1[5]
Black bulbul *Hypsipetes*[2]	2-3	1-2	2-3	2-3	3
Paradise flycatcher *Terpsiphone*	2-3	1	-	2-3	3
generalist white-eye *Zosterops*	2	2	2-3 (3)	2	2-3
Olive white-eye *Z. chloronothus*[3]	2	-	-	-	-
native forest fody *Foudia*	2-4 (3)	1-2 (2)	2-4 (3)	3	?

Notes

[1] Although the Pink Pigeon is often placed in *Columba*, *C. polleni* is not closely related.

[2] On the Comoros, the forest-adapted *H. parvirostris* is ecologically closer than *H. madagascariensis* to the Mauritius Black Bulbul (Louette & Herremans 1985, pers. obs.), but its clutch size is not documented.

[3] The Comoros and Seychelles both have or had a second *Zosterops* (*mouroniensis* and the extinct *semiflavus*, respectively), but neither is ecologically close to the Mascarene olive white-eyes (pers. obs. of specimens and live birds).

[4] Langrand (1990) gave 3-4; Turner & Rose (1989) gave 2, without a reference.

[5] A clutch size of one would make this species unique among Malagasy passerines, and needs confirmation.

Whatever the proximate factors controlling clutch sizes may be, in this respect Seychelles, not Mauritius, holds the exception among Indian Ocean avifaunas; no further discussion is warranted here.

Other demographic parameters

Only the fodies are sufficiently known to allow comparisons between Mauritian species and those elsewhere in the region. As already pointed out, the Mauritius, Rodrigues and Aldabran Fodies are multiply brooded, unlike the Seychelles Fody. This is consistent with an overall slower rate of breeding of Seychelles birds, compared with Mascarene and Aldabran birds, and correlates with the proven difference in clutch sizes.

Chapter 5. The feeding ecology of the native passerines

5.1 Introduction

Island endemic birds often have broader ecological niches than do their mainland counterparts (Lack 1976). In some cases, the niche expansion includes dietary changes (Diamond 1970). Many bird families which have colonized many islands are generalized feeders (for example, white-eyes Zosteropidae: Moreau & Kikkawa 1985). Catholic feeding habits are therefore common in island birds. Intraspecific variation in diets is likely to be temporal, individual and geographical; foraging studies must address this (Morse 1990). Geographical variation is often particularly wide for generalized feeders: Prŷs-Jones & Diamond (1984) estimated that the diet of Seychelles Fodies on Cousin island was 30 % nectar (from the proportion of all feeding observations), but Komdeur (1990) pointed out that on Frégate island they appear to do without nectar entirely.

The diets of the forest-living native land-birds of Mauritius are composed largely of animal matter (mainly arthropods and geckoes), nectar, fruit and flowers (Staub 1976, Cheke 1987c, Jones 1987, Safford 1991). Feeding ecology has only been studied for the Mauritius Kestrel, Pink Pigeon and Echo Parakeet (Jones 1987). For the passerines, Cheke (1987c) gave much anecdotal information on all aspects of feeding ecology. The two most threatened passerines (the olive white-eye and fody) feed mainly on arthropods and nectar. Both take very readily to the nectar of introduced plant species (Safford 1991), whereas none of the exotic bird species is a nectar specialist; this gives great potential for enrichment planting to benefit specifically the native birds. The birds were very flexible in the amounts of each food class taken and quick to exploit temporarily abundant food sources (pers. obs.). However, preliminary observations (Cheke 1987c, pers. obs. 1989-90) had suggested that the cuckoo-shrike preferred large arthropods and geckoes, so that its diet and foraging techniques were likely to be more restricted than those of the other species.

The priorities for this study were set according to the importance of the data for future habitat management. The main aims of the present studies on feeding ecology were therefore to document the Mauritius Cuckoo-shrike's diet of animal matter and to discover which native and exotic food-plants were, or could be, most useful to the native nectar-feeding birds.

As well as investigating these issues, in this chapter I review the literature and present new data regarding the diet of the Mauritius Black Bulbul, and fruit-feeding by native passerines. All of these data are relevant to conservation planning.

Impoverished food supply, particularly in late winter (August to November), has been claimed or implied to be one of the main factors limiting the populations of the Pink Pigeon and Echo Parakeet (Jones 1987, Jones & Owadally 1988, Bruford *et al.* 1991). This belief has been one of the factors determining conservation measures implemented for these species (Jones *et al.* 1988, 1992, Bruford *et al.* 1991, Jones & Duffy 1993). At the end of this chapter, I review the evidence for the suggestion. No such claim has been made for the passerines.

5.2 Animal feeding

5.2.1 *Mauritius Cuckoo-shrike*

Prey items

As animal food items for Mauritius Cuckoo-shrikes, the BOU expedition recorded only a *Phelsuma* gecko, four 2-3 cm caterpillars (Lepidoptera), a 6-8 cm stick insect (Phasmida) and a 1 cm "green insect", but most items were too small to identify (Cheke 1987c). Previously, beetles, mantides, moths and weevils had been mentioned (Desjardins in Oustalet 1897, d'Emmerez in Manders 1911).

During this study, the diet was studied by direct observation of food items. Away from nests, observations were made entirely opportunistically, rather than to any rigid schedule (time did not allow the latter). At three nests containing young, watches of 1-5 hr were carried out, noting the sex of the visiting parent, time of each feed, size or identity (see below) of each food item and any other circumstances of interest. Most data were collected from a few birds and were therefore not independent, preventing confident extrapolation to the whole population.

The method of direct observation biased the data to an unknown extent towards large, conspicuous or distinctive prey items. This bias arose because it was often impossible to tell whether an attempt to catch a small item was successful, especially if the item was eaten quickly, or if the bird flew directly away with it. Observations were used for analysis only where a captured prey item was seen. Less biased methods, such as use of emetics or stomach pumping (Rosenberg & Cooper 1990) were impractical due to the difficulty of trapping birds and the risk of mortality; analysis of stomach contents was also discounted as the data so gathered would not justify specimen-taking for this rare species.

The size of items could be judged by comparison with the bird's bill, which measures about 23 mm exposed culmen (Cheke & Jones 1987). No item appeared to exceed 10 cm. Items of a length comparable to the bill length were classified as 2-4 cm. Small prey items (less than 2 cm long) were rarely identifiable, but on items larger than this, some detail could usually be seen, such as colour, general shape, presence of wings, legs or long antennae. Geckoes (sometimes tailless) were readily distinguished from arthropods, although the occasional gecko's tail (the animal presumably having escaped by shedding it) was more difficult to identify. Since adult cuckoo-shrikes have been known to eat fruit and might take other classes of food, food items were not assumed to be either arthropods or geckoes unless confirmatory details were seen; this results in the "unidentified" category in Table 5.1. This classification is robust as it makes no assumptions other than that the observer is accurate in distinguishing geckoes from arthropods and in comparing the size of the latter to the bird's bill. Items were never seen to be broken up (other than removal of limbs) and no food passing was seen between adults, so it is assumed that the size of the item eaten or fed to the young was the same as the size of the prey item caught and that the bird feeding the young (or, away from nests, eating the prey item) had itself caught that item.

Table 5.1. Food items of the Mauritius Cuckoo-shrike. Numbers of geckoes (all sizes combined) and arthropods (by size class).

	Items fed to young in nests							Items eaten by adults			Totals
Site	Pigeon Wood		Brise Fer 1		Brise Fer 2		Other	All sites			
Sex[1]	♂	♀	♂	♀	♂	♀	♂♀	♂	♀	o	
Arthropods <2 cm	7	4	27	9	5	6	1♂	3	0	4	66
Arthropods 2-4 cm	9	8	51	28	24	10	3♀	11	7	3	154
Arthropods >4 cm	1	3	32	10	6	3	1♀	11	7	2	76
Geckoes	0	1	0	12	9	6	0	3	3	1	35
Unident.	0	1	1	14	8	9	0	0	0	0	33
Totals	17	17	111	73	52	34	5	28	17	10	364

Notes

[1] sex of the bird which caught the prey item (for nests, not the sex of the chick to which the item was fed; this could not be determined).

A total of 309 food items was brought to young in three nests by their parents and a further 55 were caught and eaten by fully-grown birds (adults and fledged young) away from nests. Therefore, 85 % of the 364 food items noted were fed to nestlings. The following comments on the identity of the prey items are made with much caution. It has not been possible to provide a confident breakdown of arthropods taken according to taxonomic order, because of the difficulty of identification.

Of 296 arthropod items seen, 82 (28 %) were 1-4 cm long, stout, green insects, sometimes with legs visible; they appeared to be bush crickets (Orthoptera: Tettigoniidae). A further 74 (25 %) were insects with long abdomens and total body length 3-10 cm; both mantides (Dictyoptera: Mantodea) and stick insects (Phasmida: Phasmatidae) were identified, but the great majority were certainly stick insects, and the largest arthropod prey items seen were the fat-bodied females of large green stick insects. From the largest items (including the latter), the legs were removed before eating or feeding to young (see *Foraging techniques*, below). The remaining 140 arthropod items comprised the following: 18 adult butterflies or moths (Lepidoptera; 1-2 cm body); nine caterpillars (Lepidoptera; up to 3 cm); 15 reddish-brown bush-crickets (1-3 cm body); 11 clear-winged, stout, black-bodied insects, probably cicadas (Homoptera: Cicadidae), but perhaps also Hymenoptera or Diptera (up to 3 cm body); 11 spiders (Arachnida; up to 3 cm body); two dragonflies (Odonata); and 74 indeterminate (but definitely arthropods) due to small size or lack of any visible distinguishing features (several were probably beetles Coleoptera).

All of the geckoes seen presumably belonged to the only two diurnal species common in the upland forest, *Phelsuma guimbeaui* and *P. cepediana* (both were identified); in lowland areas, *P. ornata* also occurs (Vinson 1976). Many of the 33 'unidentified' items were simply dark blobs and so could have been almost any arthropod with appendages removed, or some other type of food.

Comparison of diets of adults and nestlings

The diets of nestling and fully-grown cuckoo-shrikes can be compared. At nests, each feed was easily watched and all items brought to the nest were recorded, whether identified or not. However, food items caught by adults away from nests were only recorded when identified. Therefore, for the purposes of this comparison the unidentified items have to be ignored.

When all identified food items were included, the diets of nestlings and fully-grown birds (adults and fledged young) differed significantly (Table 5.2a: $\chi^2_3=8.2$, $P<0.05$). For the first few days after hatching, the chicks cannot cope with prey items such as geckoes and large stick insects; such items did not regularly appear until the chicks were about a week old. This could account for the greater number of large arthropods taken by adults, and hence the overall difference in diets. When the 38 identified items seen to be fed to the young during the first week after hatching are excluded, no significant difference is found between the diets of the nestlings and the fully-grown birds I watched (Table 5.2b: $\chi^2_3=4.7$, $P>0.05$), when arthropods are classified by size only and unidentified items ignored.

These results are consistent with the hypothesis that the diets of adult and nestling Mauritius Cuckoo-shrikes do not differ, except that nestlings under a week old are not given the largest items.

Individual variation

Individual birds differ in the prey selected for feeding to their nestlings. The three nesting adults for which more than 50 food items were seen ('Brise Fer 1', both parents; 'Brise Fer 2', male only) brought significantly different sets of prey items (Table 5.2c: $\chi^2_8=50$, $P<0.001$). These two nests were only 600 m apart in Lower Montane Wet Forest, and a similar range of prey items must have been available. The 'Brise Fer 1' male and female differed most obviously from each other, as the male brought a total of 54 1-4 cm green bush-crickets (49 % of all items he brought) and no geckoes, whilst the female brought five green bush-crickets and 12 geckoes. It is impossible to state whether this difference is consistently sex-related, because such a high proportion of the data were collected from only three pairs.

Summary of prey items

Overall, 81-90 % of 364 observed food items for Mauritius Cuckoo-shrikes were arthropods, the remainder being 10 % geckoes and 0-9 % unidentified items (the latter possibly in fact arthropods). Because of their greater mass (3-9 g when adult: Jones 1987), geckoes presumably formed more than 10 % of the total mass eaten. No evidence was found for differences between the diet of the nestlings and that of fully grown birds (adults and fledged young), except that large items were not provided until the young were about a week old. Arboreal insects, especially bush-crickets and stick insects, were eaten more than other arthropod groups such as spiders, lepidoptera (adults and caterpillars), dragonflies and cicadas.

Individual birds differed in the items selected, both in the ratio of geckoes to arthropods, and in the proportions of each type of arthropod. It was not clear whether the latter difference was sex-related. This individual variation confirms the dangers of extrapolating dietary conclusions from a few individuals to the whole population. However, it is certain that the species' diet consists largely of large, arboreal arthropods and geckoes.

Foraging methods

Birds jumped or flew from perch to perch, scanning the vegetation about them, searching trunks, branches, twigs or foliage, but never the ground (none of six items seen dropped to the ground was retrieved). When prey was spotted up to a few metres away, it was generally captured by gleaning from a perch, or jumped at and caught as the bird landed ("leap-snatching": Cheke 1987c). Aerial captures were also frequent, either by hovering briefly next to vegetation masses, or occasionally in direct flight. As noted by Cheke (1987c), larger items were held in the bill and immediately beaten against branches before being eaten or brought to young. This certainly served to remove the legs of large insects; lepidoptera wings were never seen to be removed, but beating them produced a shower of wing scales. Good visibility within the vegetation would seem important for such a foraging method, and this may help explain the absence of cuckoo-shrikes from dense, low dwarf forest (as at Pétrin and Plaine Champagne), their preference for better-preserved native forest not too invaded with a dense understorey of *Psidium cattleianum* and *Ligustrum* (such as Macchabé - Brise Fer), and their willingness to forage in exotics such as *Callistemon*, *Cryptomeria* and even *Eucalyptus* (although the latter were rarely productive). Of course, other factors are also likely to influence their distribution.

When pairs were together, the male often foraged a few metres higher in the vegetation than the female, although no data were collected to substantiate this. Males usually sang from near the treetops, whereas females did not sing; the male's foraging level could be associated with his display level, as Morse (1968) suggested for certain Parulids.

Tables 5.2a-c. Contingency tables constructed for analysis of patterns of Mauritius Cuckoo-shrike diets, using χ^2 statistics.

Table 5.2a. Comparison between the diets of nestling and of fully-grown (adults and fledged young) Mauritius Cuckoo-shrikes. The number of each type of food item is compared to the number expected (in brackets) from the proportion of the totals, if no difference existed in the diets. $\chi^2_3=8.2$, $P<0.05$: significant difference.

	Nestlings	Fully-grown	Totals
Arthropods <2 cm	59 (55.03)	7 (10.97)	66
Arthropods 2-4 cm	133 (128.4)	21 (25.59)	154
Arthropods >4 cm	56 (63.37)	20 (12.63)	76
Geckoes	28 (29.18)	7 (5.82)	35
Totals	276[1]	55	331

Notes

[1] excludes 33 unidentified items (see text)

Table 5.2b. Comparison between the diets of fully-grown (adults and fledged young) Mauritius Cuckoo-shrikes and of nestlings over a week old. The number of each type of food item is compared to the number expected (in brackets) from the proportion of the totals, if no difference existed in the diets. $\chi^2_3=4.7$, $P>0.05$: no significant difference.

	Nestlings	Fully-grown	Totals
Arthropods <2 cm	38 (36.55)	7 (8.44)	45
Arthropods 2-4 cm	118 (112.91)	21 (26.09)	139
Arthropods >4 cm	55 (60.92)	20 (14.08)	75
Geckoes	27 (27.62)	7 (6.38)	34
Totals	238[1]	55	293

Note

[1] excludes 22 unidentified items (see text)

Table 5.2c. Comparison between the items fed to nestlings by three individual adult Mauritius Cuckoo-shrikes; birds included only from Brise Fer forest, and if more than 50 items were seen. The number of each type of food item is compared to the number expected (in brackets) from the proportion of the totals, if no difference in food brought existed between the three adults. $\chi^2_8=50$, $P<0.001$: significant difference.

Site	Brise Fer 1		Brise Fer 2	Totals
Sex	♂	♀	♂	
Arthropods <2 cm	27 (19.3)	9 (12.7)	5 (9.03)	41
Arthropods 2-4 cm	51 (48.4)	28 (31.9)	24 (22.7)	103
Arthropods >4 cm	32 (22.6)	10 (14.8)	6 (10.6)	48
Geckoes	0 (9.88)	12 (6.50)	9 (4.63)	21
Unidentified	1 (10.8)	14 (7.11)	8 (5.07)	23
Totals	111	73	52	236

5.2.2 *Mauritius Black Bulbul*

Prey items

Relatively few observations were made of black bulbuls feeding on animal matter. Of the six nests found none was easy to watch and anyway all failed long before young would have fledged. I saw 27 food items brought to nestlings and 13 partially identified items taken by adults; these small samples show no sign of differences and so are not separated in Table 5.3, which includes feeding records from the literature. The BOU expedition made 13 observations of black bulbuls feeding on animal matter, but prey were rarely identified (Cheke 1987c).

From these data, the animal prey of the black bulbul appears to consist mostly of insects, but geckoes are very important, especially considering their greater mass.

Table 5.3. Insect- and gecko-feeding by the Mauritius Black Bulbul.

Food item	Number taken (this study)	Additional sources
Phelsuma gecko	10	Cheke 1987c
Stick insect	2	
?Bush-cricket	4	
Clear-winged insect (?Cicada)	4	
Caterpillar	1	Newton 1960
Butterfly	0	Cheke 1987c
Dragonfly	2	
Indeterminate arthropod	10	"large black insects" from bark (Cheke 1987c)
Unidentified	7	
Total	40	

Foraging methods

Cheke's (1987c) categorization of foraging techniques accounted adequately for all those I observed (gleaning from leaf-bases, twigs and branches and clumsy "fly-catching"), except that birds also regularly crashed into foliage bundles and then sallied after small insects which they had flushed. Foraging techniques and prey selected both overlap with those of the Mauritius Cuckoo-shrike; black bulbuls may use the "leap-snatching" method less and make more frequent aerial sallies, but data are lacking. Of course, the black bulbul takes very much more fruit than the cuckoo-shrike (see Section 5.4).

5.2.3 *Insect-feeding by other threatened native passerines*

Previous observations on insect-feeding by the smaller native passerines (Cheke 1987c, Safford 1991) are summarized below, along with a few additional, personal observations.

The Mascarene Paradise Flycatcher is the only totally insectivorous species, feeding in or below the canopy by sallying, sally-gleaning and gleaning. Prey items are usually very small, probably including many mosquitoes and items of similar size, but also larger items such as butterflies and moths (Lepidoptera), spiders (Arachnida) and damselflies (Odonata) (pers. obs.). This feeding method appears to require "good visibility and still air under a closed canopy with ample, but not dense, undergrowth on which to perch and rest" (Cheke 1987c: 184).

The Mauritius Olive White-eye is an opportunistic gleaner, foraging at any level, from dense tangles of *Rubus alceifolius* near the ground, up to the foliage and large branches of canopy trees. Aerial insects are often caught in direct flight; prey is also sought in flowers and moss and *Usnea* lichen growing on trees, and cocoons and spiders' webs are robbed (Safford 1991). Most prey items are tiny invertebrates; from the few occasions when the prey was visible, I have nine observations of adult insects (up to 2 cm) and eight of larvae (including caterpillars up to 2 cm). Gill's (1971: 50) claim that the species "rarely forages for insects... but rather restricts its feeding activities to flowers" (for nectar) is quite incorrect. There seems to be no special vegetational structure requirement for olive white-eyes to forage, and they often do so in exotic plant species.

The Mauritius Fody forages mainly by chiselling or probing into dead wood and "searching the bark of living trunks, branches and epiphytes" (Cheke 1987c: 202). Birds also glean from leaves, leaf-bases and flowers; females may do this more (Cheke 1987c). Larvae, especially wood-boring species, appear to be typical prey items, but adult invertebrates are also taken at times, including grasshoppers and crickets, alate termites/ants, spider's webs and their contents, and several other unidentified insects (Cheke 1987c, pers. obs.: see below).

Despite the apparent specialization of its main foraging technique, the Mauritius Fody shows signs of the versatility that is well-known for the Seychelles Fody (Crook 1961, Bathe & Bathe 1982) and increasingly also for the Rodrigues Fody (Cheke 1987e, C. G. Jones verbally, pers. obs.). Three anecdotal observations demonstrate this. A 3 cm bush-cricket (an unusually large, chitinous food item) was not eaten whole, but instead held in the feet against a branch, where the soft abdomen contents were extracted and the rest was discarded. On both 16 November and 26 December 1991, two males in Pigeon Wood repeatedly sallied for flying insects (hovering to catch them, then returning to their perches) from the tops of *Cryptomeria* trees. On the latter date, Grey White-eyes and Red-whiskered Bulbuls (neither typically aerial feeders) were doing the same thing and many swiftlets were feeding low over the trees, suggesting that a major emergence of alates was taking place; in Africa, *Pycnonotus* bulbuls often exploit such emergences in this way (Brooke 1973, Keith *et al.* 1992). A male Mauritius Fody nectar-feeding on the abundant flowers of *Sideroxylon puberulum* (State Land Raoul, 18 November 1990) frequently grabbed bees (hundreds of which were also nectar-feeding in the same tree) with its bill and then dropped them; no bees were eaten.

5.3 Nectar feeding

5.3.1 *Introduction*

One Mauritian native bird species, the olive white-eye, is a specialist nectar feeder, with appropriate morphological adaptations, such as a very long bill (Gill 1971). This species has large, non-exclusive home ranges (20-30 ha or more: Cheke 1987c, Safford 1991) in which nectariferous plants are visited. Nectar feeding is one of the dominant features of the ecology of the Réunion Olive White-eye, which has intra-island migrations to exploit certain preferred foodplants, especially *Hypericum lanceolatum*, *Sophora denudata* and *Forgesia borbonica* (Cheke 1987b). None of these plants grows on Mauritius but Mauritius has more diverse native flora than Réunion (Cadet 1980, Strahm 1993 & in prep.), including bird-pollinated species such as *Trochetia blackburniana* and *Bakerella hoyifolia* (Staub 1988). The far more fragmented and degradated state of the Mauritian forest must have restricted the feeding ecology and seasonal movements of the Mauritius Olive White-eye. However, in general habits and attentiveness to flowers, the two olive white-eye species are similar (pers. obs.).

Two more species, the Mauritius Fody and Grey White-eye, frequently take nectar but are less morphologically specialized for doing so. There is no evidence of seasonal movements to exploit nectar sources for either, and fodies seem only to visit flowers within their exclusive territories. A fourth species, the black bulbul, has once been seen to take nectar.

Safford (1991) listed all the plant species on record as being used by the two white-eyes and the fody, based on observations from August 1989 to April 1991 (excepting May to July 1990) and also previous observers' reports. An amended list is presented here, based on my 270 observations (1989-93, all months), separating native (Table 5.3a) and exotic (Table 5.3b) plant species. The following discussion relates mainly to the Mauritius Olive White-eye and Fody, as these are the threatened species. Because of its wide distribution outside native forest, the Grey White-eye has many more plant species available to it. Wider observations on Grey White-eyes might reveal plant species of potentially great use to the threatened species.

My data were highly biased by the repeated use of the same routes, so my observations of nectarivory were not analysed quantitatively. Even if data had been collected in a manner allowing such analysis, it would have been difficult to rank in any meaningful way the plant species in order of their importance to each bird species. Many of the native species richest in nectar are extremely rare, for example *Bakerella hoyifolia*, *Trochetia* spp. and *Dombeya* spp. (*Flore des Mascareignes*, Staub 1988). The naturalized distribution of certain exotic plant species overlaps the ranges of the rare nectarivorous birds only narrowly (for example, *Eriobotrya japonica*) or not at all (for example, *Tabebuia pallida*). It is possible to predict the main plant species which would have been used on pristine Mauritius; at present, this is largely of academic interest, but it should be borne in mind when native habitats are restored. If areas outside the current bird distributions were to become suitable for nectarivores, plant species (exotic or native) which are hardly used at present might become very important; for example, if Mauritius Fodies had access to *Tabebuia pallida*, it would probably be used as much by them as it is by Rodrigues Fodies (Cheke 1987e, pers. obs.).

5.3.2 *Native plant species*

As nectar sources for the Mauritius Olive White-eye in pristine Mauritius, Staub (1988) considered the most important native plant genera to be *Bakerella* (Loranthaceae), *Syzygium*, *Eugenia* and *Monimiastrum* (Myrtaceae), *Dombeya* and *Trochetia* (Sterculiaceae) and *Gaertnera* (Rubiaceae). *Bakerella hoyifolia* is the only native member of a genus much used by nectarivorous birds in Madagascar (pers. obs.), but is now very rare on Mauritius (*Flore des Mascareignes*, Staub 1988). *Dombeya* spp., now also rare on Mauritius, are abundant and much used on Réunion (Cheke 1987b), Madagascar and the

Comoros (pers. obs.). The distribution of native *Eugenia* species (*Flore des Mascareignes*) barely overlaps the ranges of the olive white-eye and fody. Three *Monimiastrum* spp. are available to the birds in the south-west, but there are no records of birds taking nectar from them.

This leaves three genera mentioned by Staub (1988) which are still important to the birds. The systematics of *Syzygium* spp. are complex, but 14 native species are described in *Flore des Mascareignes*; several are very rare. Specific identification is difficult. This genus is still widely used by native nectarivores (fodies and both white-eyes), but is not now abundant enough to be particularly important to the birds. In some species (such as *S. mauritianum*), the flowers grow directly off the trunk, which is thought to favour pollination by reptiles (van der Pijl 1972), but this does not prevent birds from nectar feeding.

The four extant *Trochetia* spp. were discussed in detail by Staub (1988), who considered the olive white-eye to be the "faithful pollinator" of *T. blackburniana*, the most widespread species. The flowers are red or white, 2-4 cm deep, open bell shapes. Probably only olive white-eyes have bills long enough to allow a direct (frontal) approach on *Trochetia*, but nevertheless sometimes they (or perhaps only certain birds) 'cheat', by piercing the corolla at the base (the indirect, or lateral, approach) (Safford 1991). The Grey White-eye has only been seen to feed indirectly on *Trochetia*, the Mauritius Fody not at all.

Of the 13 native *Gaertnera* species (another complex genus), about five are well-known and occur in the range of the fody and olive white-eye. The white flowers have a very narrow, almost closed, corolla tube 1-2 cm long, and the nectar could not be reached directly by any native bird. Despite the abundance of *Gaertnera*, I made only one observation of an olive white-eye possibly nectar-feeding on it (probably *G. edentata*, 6 February 1990, State Land Raoul), and never saw a Grey White-eye use it. White-eyes may be unable to reach *Gaertnera* nectar; A. S. Cheke (verbally 1994, from field notes) did not see white-eyes definitely nectar-probing *Gaertnera*.

However, for the Mauritius Fody I recorded eight prolonged feeding incidences on *Gaertnera* (probably *G. psychotrioides*) at five different sites (30 November - 9 January). The birds plucked the flowers with the bill and then either delicately mandibulated the base (presumably squeezing out nectar) or held them against a branch with the feet and inserted the bill up the base of the corolla, before discarding them. Each flower was processed in about two seconds, on average more than ten flowers per minute. This method is similar to that used by Madagascar Red Fodies on *Lantana*, described by Melville (1979).

Variations on the method are typical of *Foudia* species on detachable flowers with corolla tubes: Madagascar Red Fodies on *Gaertnera* (pers. obs.), Seychelles Fodies on *Morinda citrifolia* (Prŷs-Jones & Diamond 1984), Rodrigues Fodies on *Tabebuia pallida* (Cheke 1987e; pers. obs.) and captive Rodrigues Fodies on *Lantana* (C. G. Jones verbally 1991). This destructive technique must preclude pollination, but allows fodies to use *Gaertnera* a great deal. The créole name for the fody, *oiseau banane* (Cheke 1982), seems as likely to refer to its fondness for 'Bois Banane' (*G. psychotrioides*) as for banana *Musa* spp. flowers. The latter have also been used in the past (L. R. Chevreau de Montléhu verbally 1992), but no longer occur in the fody's range.

Bertiera zaluzania, *Aphloia theiformis*, *Sideroxylon puberulum*, and *Labourdonnaisia calophylloides* and/or *Mimusops erythroxylon* (none mentioned by Staub 1988) are abundant species which produce many flowers. Although each flower is not very rich in nectar, they are important nectar sources for fodies and both white-eyes. *Chassalia* is very closely related to *Gaertnera* and may be used in a similar way; however the conspicuous and nectariferous *Chassalia coriacea* has not been seen to be used, although it is common in parts of the ranges of the olive white-eye and fody (as noted by Safford 1991). The other 12 native species in Table 5.3a appeared to be less important, most being used occasionally by olive white-eyes only, or yet to be confirmed.

Sophora denudata is seasonally important to the Réunion Olive White-eye (Gill 1971, Cheke 1987b); *S. tomentosa* occurs along the coast of Mauritius (*Flore des Mascareignes*) and might also prove suitable.

5.3.3 *Exotic plant species*

All the native nectarivorous birds take readily to exotic foodplants. The selection of plant species available is of course fortuitous, as none was purposely introduced as a nectar supply for birds. At present, by far the most important exotic nectariferous plants for Mauritius Fodies and olive white-eyes are *Syzygium jambos*, *Callistemon* and *Eucalyptus robusta* (Safford 1991; also Cheke 1987c, Staub 1988). These species provide so much nectar that, in places, they are used more than any native plant species. The only observation of a Mauritius Black Bulbul nectar feeding was on *S. jambos* (Bassin Blanc, 9 October 1991), and the Réunion Black Bulbul takes nectar from *Eucalyptus* spp. (Cheke 1987b).

S. jambos flowers all year and forms monotypic stands in many humid areas (Vaughan & Wiehé 1937), including the lower edge of the native forest along the south-facing scarp from Chamarel to Combo. In 1989-93, olive white-eyes occurred throughout this latter belt of *S. jambos*, and in Pigeon Wood they were often seen flying directly up or down the scarp between the native forest and the *S. jambos* belt. When found in *S. jambos*, they were almost always seen nectar feeding, and their presence was certainly attributable to the abundant nectar supply. Similar observations were made along the Rivière du Poste and at Eau Bleu Reservoir. Fodies fed on *S. jambos* more rarely, as their distribution barely overlapped with the main stands.

Callistemon and *E. robusta* provide abundant nectar, mainly in August to January and March to August respectively although *Callistemon* has some flowers all year. *Callistemon* is an ornamental, planted widely along roads and tracks on the plateau, and has not penetrated the native forest, whereas *E. robusta* is present in plantations and as small groves within native forest, especially between Combo and Montagne Cocotte. The largest concentration of olive white-eyes that I have seen was four pairs nectar feeding along a 100 m line of *Callistemon* in State Land Le Juge, 600 m from native forest (2 December 1991). The 'dry country' *Eucalyptus* species (on Mauritius, mostly *E. tereticornis* and some *E. citriodora*, but only outside the ranges of olive white-eyes and Mauritius Fodies) are also nectariferous, and *E. citriodora* is much used by nectar feeding birds in Madagascar (pers. obs.).

Other notable species on Table 5.3b are as follows. *Eriobotrya japonica* (loquat or bibasse), *Tabebuia pallida*, *Hibiscus* spp. *Erythrina variegata* and *Grevillea* spp. are rare or absent from the ranges of the Mauritius Fody and olive white-eye, but would presumably be used if available. *Rubus alceifolius* is abundant but poor in nectar. The two most abundant, invasive plant species, *Psidium cattleianum* and *Ligustrum*, seem too poor in nectar for birds to use them; I once saw an olive white-eye pluck a *Ligustrum* flower, but missed seeing the outcome. The one observation on *Psidium* in Table 5.3b was possibly of insect-feeding in a flower.

Table 5.3a (overleaf). Native plant species used for nectar-feeding by native Mauritian birds. Status is given as IUCN threat category and applies to populations on Mauritius only, following Strahm (1993 & in prep.); exotics have not been categorized. Nt=Not threatened, E=Endangered, V=Vulnerable, R=Rare (see IUCN 1980).

Some of the plant species listed have not been seen to be used for nectar by native Mauritian birds, but are used by the Réunion Olive and Réunion Grey White-eyes and the Rodrigues Fody on their respective islands; these are indicated with R. Some observations (indicated) may have been of birds taking insects rather than nectar from flowers. Observations requiring confirmation are given in brackets.

Sources: a, this study; b, Gill (1971); c, Horne (1987); d, Cheke (1987c); e, Cheke (1987b); f, Cheke (1987e); g, Staub (1988); h, D. Strasberg (*in litt.* 1992); i, C. G. Jones (verbally 1991); j, L. R. Chevreau de Montléhu (verbally 1992).

Table 5.3a. Native plant species used for nectar-feeding by native Mauritian birds.

Plant species	Status	Grey White-eye	Olive white-eye	Mauritius Fody
Flacourtiaceae				
Aphloia theiformis	Nt	a	a	a,d
Erythrospermum monticolum	Nt		d	
Pittosporaceae				
Pittosporum senacia	Nt	eR		
Sterculiaceae				
Trochetia uniflora	E	(g)	b,d	
Trochetia triflora	V	g		
Trochetia blackburniana	R	a	a,g	
Dombeya spp.		bR,eR	aR,bR,eR,(g)	
Meliaceae				
Turraea rigida	E		a	
Cunoniaceae				
Weinmannia tinctoria	E	eR	eR	
Myrtaceae				
Syzygium commersonii	R		a	
Syzygium contractum[1]	R		d	
Syzygium glomeratum	Nt			a
Syzygium latifolium[2]	R		d	
Syzygium mauritianum	R	d	a	a
Syzygium venosum[3]	R		(c)	
Syzygium spp.		a	a	a,d
Eugenia spp.			eR,(g)	
Monimiastrum spp.			(g)	
Rubiaceae				
Bertiera zaluzania	Nt	a,d	a,d	a
Chassalia petrinensis	V		a	
Gaertnera spp.		(d)	(d),(g)	a
Sapotaceae				
Mimusops maxima	V		a	
Mimusops erythroxylon[4]	V	(a)	(a)	(a)
Sideroxylon puberulum	Nt	a	a	a
Labourdonnaisia calophylloides	V	a	a	a
Ebenaceae				
Diospyros cf. *D. pterocalyx*	V		a	
Diospyros revaughanii	V		a	
Apocynaceae				
Tabernaemontana mauritiana	Nt			a insects?
Loganiaceae				
Geniostoma sp.	R	hR	bR	
Nuxia verticillata	V		hR	
Loranthaceae				
Bakerella hoyifolia	V		b	

Notes

[1] Cited by Cheke (1987c) as *Eugenia obovata*.

[2] Cited by Cheke (1987c) as *Eugenia scandens*.

[3] Cited by Horne (1987) as *Eugenia dupontii*, then by Cheke (1987c) as *E. obovata*.

[4] Identification of *M. erythroxylon* was not confirmed, due to similarity of *L. calophylloides*.

Table 5.3b. Exotic plant species used for nectar-feeding by native Mauritian birds. Details as for Table 5.3a, but status is not given as this has not been categorized.

Plant species	Grey White-eye	Olive white-eye	Mauritius Fody
Guttiferae			
Harungana madagascariensis	a	a	
Theaceae			
Camellia sinensis	d	d	a
Malvaceae[1]			
Hibiscus rosa-sinensis			fR
Malpighiaceae			
Hiptage benghalensis	d		
Meliaceae			
Melia azedarach		bR	
Leguminosae			
Erythrina variegata	b,d		iR
Rosaceae			
Rubus alceifolius	a	a	a
Rubus rosifolius	a		
Eriobotrya japonica		aR,eR	
Crassulaceae			
Kalanchoe bryophyllum	bR		
Combretaceae			
Terminalia belerica	d insects?		
Myrtaceae			
Syzygium jambos	g	a,d,g	a,d
Callistemon citrinus	a,d,g	a,d,g	a,d,g
Psidium sp.	d insects?		
Eucalyptus robusta	a	a	a,d
Caprifoliaceae			
Lonicera sp.		aR	
Oleaceae			
Ligustrum robustum		(a)	
Convolvulaceae			
Ipomoea congesta	d		
Solanaceae			
Solanum auriculatum		eR	
Bignoniaceae			
Tabebuia pallida			aR,fR
Verbenaceae			
Lantana camara	a,d		
Holmskioldia sanguinea	d		
Lauraceae			
Litsea monopetala		a	
Litsea sp.	d insects?	d	
Proteaceae			
Grevillea sp.	d insects?	eR	
Musaceae			
Musa sp.	d	bR	j
Agavaceae			
Agave sp.		eR	

Note

[1] Native *Hibiscus* species, and also hybrids, may also be suitable.

5.4 Fruit feeding

The best-known native frugivores are the Pink Pigeon and Echo Parakeet, for which see Jones (1987). The rarefaction of these species, and the extinction of other frugivores (parrots Psittacidae, other pigeons Columbidae, dodos Raphidae, skinks *Leiolopisma*, tortoises *Geochelone* and fruitbats *Pteropus*, excepting the surviving *P. niger* on Mauritius), must have had severe effects on the native vegetation, especially by restricting seed dispersal (Cheke 1987a).

Among native passerines, the Mauritius Black Bulbul is the main fruit-feeder, to the extent that E. Newton (1861, and in A. Newton 1876) wrongly believed it to be entirely frugivorous. All the other native bird species, excepting the flycatcher and olive white-eye (see below), have been seen to take fruit, albeit the cuckoo-shrike only once: *Elaeodendron* (=*Cassine*) *orientale* in Macchabé forest (Cheke 1987c), although Desjardins (in Oustalet 1897) also reported berries in the diet.

In 1989-93, I only recorded fruit-feeding by the black bulbul, Grey White-eye and fody. Due to its critical status, most attention was paid to the latter, so that rather few fruits were seen to be taken by black bulbuls, and many more certainly remain to be found. I saw at least two further native fruits taken by black bulbuls, but could not collect them for identification. Table 5.4 lists all native and naturalised exotic fruits which have been taken by native bird species.

On both Mauritius (Table 5.4) and Réunion (Cheke 1987b), the native fruit most frequently taken by all frugivorous birds may be the abundant *Aphloia theiformis*, but, as with nectariferous plants, the species that the birds would have used most on pristine Mauritius may now be rare. For example, all native palms are now very rare in native forest on Mauritius, but Cadet (1980) believed the black bulbul to be the main dispersal agent of *Acanthophoenix rubra* on Réunion, where this palm is commoner.

Certain other native plant species or genera are considered bird dispersed, and therefore could be expected to be taken by Mauritius Black Bulbuls. These are only included in Table 5.4 if they have been seen to be eaten; yet to be confirmed are *Monimia ovalifolia* and *Tambourissa* spp. (Lorence 1985), *Antirhea*, *Chassalia*, *Bertiera*, *Fernelia*, *Antidesma* and *Erythroxylum* (Cadet 1980; *Psychotria* was listed, but the species referred to are placed in *Chassalia* by *Flore des Mascareignes*).

The list of exotic fruits used is an eclectic one: 21 species from 17 families, varying in size and form, from mangoes *Mangifera indica* to the small, black berries of *Lantana* *camara*. None is known to be especially important to black bulbuls, but T. d'Unienville (verbally 1992) reported that they visited his garden at Britannia (well outside native forest) especially to feed on champak *Michelia champaca*; this tree is uncommon where I worked most, excepting Combo, where its use was confirmed (1 February 1993). There is still no record of Mauritius Black Bulbuls feeding on the super-abundant Strawberry Guava *Psidium cattleianum* fruit. Cheke (1987b) and I (in 1991) were often told that the Réunion species does so a great deal, and even that its altitudinal movements are associated with fruiting *P. cattleianum*; these claims need substantiation. In addition to the fruits of native and naturalized exotic trees, Mauritius Black Bulbuls take various sweet fruits when available, including grapes, apples, papaia, mulberries, raspberries and cherries (Guérin 1940-53, Jones 1980 cited by Cheke 1987c, Jones & Duffy 1993, pers. obs.).

The two Réunion white-eyes feed regularly on fruit (Cheke 1987b, T. Bègue verbally 1991, D. Strasberg *in litt.* 1992), apparently more so than the Mauritian forms now do; the Mauritius Olive White-eye is not yet proven to take fruit. This is likely to be mainly a result of what is available in the distribution of the olive white-eye, where most observations on both white-eye species have been carried out.

From November to February, Mauritius Fodies often fed on *Homalanthus populifolius* fruit (many more observations since the single noted by Safford 1991), whereas I very rarely saw them feed on *Ardisia crenata* and only once on *Ossaea marginata*.

5.5 Other feeding methods

Safford (1991) described but could not explain Mauritius Olive White-eyes apparently licking or scraping (using the bill) leaf surfaces; some or all of the leaves selected were damaged. The birds were probably in fact feeding on sweet secretions, analogous to lerp (coats of sap-sucking insects), manna (sugary granules from damaged *Eucalyptus* leaves) or honeydew (a sweet secretion produced when insects, such as aphids or scale insects, tap the phloem of plants but do not extract all the nutrients it carries). All of these are important in the diets of some Australian honeyeaters Meliphagidae (Pyke 1980). On Réunion, both white-eyes take sap from *Claoxylon glandulosum* (Gill 1971).

Mauritius Black Bulbuls have been seen to eat flowers of the exotic Morning Glory *Ipomoea congesta* (Cheke 1987c) and ("frequently") of the native *Nuxia verticillata* (C. G.

Jones in Cheke 1987c), but flower feeding is very much commoner in the Pink Pigeon and Echo Parakeet (Jones 1987).

Evidence for cuckoo-shrikes and black bulbuls taking eggs and nestlings is reviewed in Section 6.1.1; the frequency of such behaviour is unknown (and entirely unproven for the black bulbul).

Table 5.4 (overleaf). Plant species used for fruit-feeding by native Mauritian passerines.

Status is given as IUCN threat category and applies to populations on Mauritius only, following Strahm (1993 and in prep.); exotics have not been categorized. Nt=Not threatened, E=Endangered, V=Vulnerable, R=Rare (see IUCN 1980).

Some of the plant species listed have not been seen to be used for fruit-feeding by native Mauritian birds, but are used by the Réunion Black Bulbul, and Réunion Grey and Olive White-eyes; these are indicated with R. Records requiring confirmation are given in brackets.

Sources: a, this study; b, Cheke (1987c); c, Guérin (1940-53); d, 'Dr J. C.' (1861, cited by Cheke 1987b); e, D. Strasberg (*in litt.* 1992); f, Cheke (1987b); g, Cadet (1980); h, Newton (1960); i, C. G. Jones (verbally 1993); j, Dr Ragavoodoo (verbally 1993); k, Jones (1980) cited by Cheke (1987c); l, T. d'Unienville (verbally 1992); m, Lavergne (1978); n, Staub (1976); o, Gill (1971); p, Safford (1991).

Table 5.4. Plant species used for fruit-feeding by native Mauritian passerines.

Plant species	Status	BB	GW	OW	MF
Native species					
Flacourtiaceae: *Aphloia theiformis*	Nt	a,b,c	eR,fR,oR	eR	a
Guttiferae: *Calophyllum* cf. *C. eputamen*[1]	R	b			
Burseraceae: *Protium obtusifolium*	Nt	b			
Celastraceae: *Cassine orientale*[2,3]	Nt				
Sapindaceae: *Allophylus cobbe*[4]	R	dR			
Myrtaceae: *Syzygium glomeratum*	Nt	a,b			
Syzygium sp.		a			b
Eugenia sp.[5]		eR	oR		
Melastomataceae: *Warneckea trinervis*	Nt	a			
Araliaceae: ?*Gastonia* sp.		b			
Sapotaceae: *Sideroxylon* sp.[6]		fR			
Loranthaceae: unidentified mistletoe		fR			
Moraceae: *Ficus* sp.		fR			
Liliaceae: *Cordyline* sp.			oR		
Palmae: *Acanthophoenix rubra*	E	(gR)			
unidentified palm (?native)		(h)			
Exotic species					
Magnoliaceae: *Michelia champaca*		a			
Flacourtiaceae: *Flacourtia jangomas*		i			
Meliaceae: *Melia azedarach*[7]		j			
Icacinaceae: *Apodytes dimidiata*		a			
Anacardiaceae: *Mangifera indica*			i		
Schinus terebinthifolius			(i),fR,oR		
Rosaceae: *Rubus alceifolius*		k			
Myrtaceae: *Syzygium jambos*					(c)
Psidium cattleianum		(fR)	eR,oR		(c)
Psidium guajava		l			
Melastomataceae: *Ossaea marginata*		a			a,b
Myrsinaceae: *Ardisia crenata*					a,b
Oleaceae: *Ligustrum robustum*		b,k			
Solanaceae: *Solanum auriculatum*		mR	oR		
Verbanaceae: *Lantana camara*		n	(a),fR,oR		
Lauraceae: *Litsea monopetala*		b,i,j			
Euphorbiaceae: *Homalanthus populifolius*			a		a,p
Ulmaceae: *Trema orientalis*			eR	eR	
Moraceae: *Artocarpus heterophyllus*		h			
Morus alba		c			
Palmae: unidentified palm		(h)	eR		

Notes

[1] cited as *C. tacamahaca*, but following revision of the genus (*Flore des Mascareignes*), more likely this species.

[2] formerly *Elaeodendron orientale*.

[3] used by Mauritius Cuckoo-shrikes (single observation: Cheke 1987c).

[4] originally given as *Schmidelia integrifolia* by 'Dr J. C.'; *Schmidelia* is a synonym of *Allophylus*, considered by Mabberley (1987) to contain one polymorphic species.

[5] 'Petit Nèfle' fruit is eaten by black bulbuls and both white-eyes on Réunion (T. Bègue verbally 1991); this is probably a *Eugenia* sp..

[6] *S. borbonicum* (a Réunion endemic) identified, but similar Mauritian species exist.

[7] a tree known locally as "lilac", probably this species.

5.6 Feeding ecology of forest-living exotic passerines

The feeding ecology of the exotic forest birds is of conservation importance, since resource competition has been suspected between them and certain of the native species (Temple 1974, Cheke 1987c, Jones 1987). Most birds successfully introduced to the Mascarenes are allotopic with the natives (Simberloff 1992), but four exotic passerine species are common in the forest: Red-whiskered Bulbul, Common Myna, Madagascar Red Fody and Common Waxbill (Table 1.2). An indication of the relative abundance of these species in forest is provided by encounter rates during timed census work (mainly for surveying cuckoo-shrikes): Red-whiskered Bulbul 10-50 birds/hr, Madagascar Red Fody, waxbill and myna 2-10 birds/hr. The latter rate was similar to that of the cuckoo-shrike. Clearly, the exotic bulbul is very abundant, whilst the other species are rarer but still at densities comparable to those of the threatened native birds. Other exotics occur much more rarely. No exotic bird species has been studied in any detail on Mauritius, but existing knowledge on the diets of the exotic passerines commonest in forest is summarized below.

Red-whiskered Bulbuls on Mauritius are omnivorous, taking seeds, fruit, flowers, nectar, insects, sugar cane pulp, probably young geckoes and possibly birds' eggs (Carié 1916, Jones 1987, Staub 1993, pers. obs.). Mynas are omnivorous and were reported by Carié (1916) to take fruit, vegetables, insects, molluscs, lizards and birds' eggs and young. Madagascar Red Fodies on Mauritius are predominantly seed-eaters, but take some insects, nectar and berries (Carié 1916, Cheke 1987c, pers. obs.). Insects, taken especially when feeding young, are gleaned from branches, foliage or flowers, or occasionally by aerial sallying (Cheke 1987c, pers. obs.). Waxbills typically take seeds (especially grasses), but also fruit and insects (pers. obs., as in Africa: Maclean 1985).

Table 5.5 shows the plant species used by nectar-feeding exotic birds; all were also used by native birds. Judging from relative frequency of observations, nectar forms on average a smaller component of the diet of the exotic birds than of the native birds. Mauritius Fodies and olive white-eyes were always dominant over the exotics at nectar sources.

The overlap in fruit and arthropod species eaten by native and exotic birds is unknown, but probably considerable, since none of the exotics appears specialized. Fruit-feeding Mauritius Fodies shared *Ardisia* and *Homalanthus* with Red-whiskered Bulbuls. Native and exotic birds are among the dispersal agents for many of the commonest exotic plants (Vaughan & Wiehé 1937, 1941, Cadet 1980, Lavergne 1978, Cheke 1987a), including *Rubus alceifolius*, *Ligustrum*, *Psidium cattleianum*, *Syzygium jambos*, *Litsea* spp., *Lantana*, *Solanum auriculatum* and *Wikstroemia indica*.

Table 5.5. Plant species used for nectar-feeding by exotic birds. Exotic plant species are indicated with an asterisk (*). Sources: a, this study; bR, Cheke (1987e) - on Rodrigues; c, Cheke (1987c).

Plant species	Red-whiskered Bulbul	Madagascar Red Fody
Aphloia theiformis	a	
*Rubus alceifolius**		a
Syzygium glomeratum	a	
*Syzygium jambos**		bR
*Callistemon citrinus**	a	a
*Eucalyptus robusta**		a
Bertiera zaluzania	a	
Gaertnera sp.		a
Sideroxylon puberulum	a	a
*Tabebuia pallida**		bR
*Lantana camara**		a,c
Grevillea sp.*		c

5.7 Discussion

5.7.1 *Diet studies on the native passerines*

Studies on the diet of the Mauritius Cuckoo-shrike confirmed its preference for large arboreal arthropods and *Phelsuma* day-geckoes. Many of the former are phytophagous insects (especially Orthopterans and Phasmids), which are typically less abundant and less taxonomically diverse in exotic plants than in natives (Southwood *et al.* 1982). This may explain why the highest densities of cuckoo-shrikes are in the best-preserved native forests of Macchabé - Brise Fer. *Phelsuma* geckoes are, however, very common in certain exotics, such as palms, *Ravenala* and mango (pers. obs.). The extent to which geckoes or different insects could replace the currently dominant items in the diet is not known.

As preliminary observations had suggested, native nectarivores readily take nectar from exotic plants, and exotic birds are less nectarivorous than native birds. Whether or not the exotic and native birds compete for certain other resources (see below), there seems no doubt that planting nectariferous plants would preferentially help the native birds. Whilst the olive white-eye is more specialized than most white-eyes (Gill 1971), it is not tied to particular food-plants, nor is there evidence that any plant species depends on olive white-eyes for pollination. Its bill is similar in size and shape to sunbirds (Nectariniidae) of the genus *Anthreptes* (Safford 1991), which are regarded as generalized (Delacour 1944). Clearly, a bird with an *Anthreptes*-like bill can be called a generalist if it is a sunbird (a specialist family), but a specialist if a white-eye (a generalist family). My data show the Mauritius Olive White-eye to be a generalized nectar-feeder, regardless of taxonomy.

5.7.2 *Evidence for impoverished food supply limiting bird numbers*

Two main processes could reduce the amount of food available to the birds: habitat degradation and resource competition. If acting independently, the former would reduce primary food production, while the latter would reduce availability of food produced in the habitat. In practice, the two processes may occur simultaneously and be connected: a reduction in resource abundance caused by degradation may result in intensified competition.

Habitat degradation

All the native forests of Mauritius are degrading, for a variety of interrelated biotic causes which allow invasion by exotic plant species (Lorence & Sussman 1986, 1988). Several of the dominant exotics form dense thickets which are poorly suited to most of the foraging techniques of the native birds such as the cuckoo-shrike. In addition, a reduction in the percentage of native plant species would presumably reduce the availability of food associated with native plants, especially edible plant parts and phytophagous arthropods (see Section 5.7.1). Discussing the Echo Parakeet, Jones (1987) aptly described the effect of forest degradation as a dilution of the food supply. However, many exotic plant species are much used for foraging by native birds, and this food source is likely to compensate for the loss of native plants, but to an unknown extent.

Jones (1987) suggested that food for Pink Pigeons and Echo Parakeets would be in shortest supply in late winter, when few native plants produce flowers or fruit. Winter food shortages have been consistently considered an important limiting factor on populations of these two species (Jones 1987, Jones & Owadally 1988, Bruford *et al.* 1991). As evidence, Jones (1987) quoted the former existence of fat cycles (not demonstrated this century), in which the birds (and other frugivorous and herbivorous Mascarene vertebrates) laid down fat in summer and autumn, to be used in winter when food was scarce. Like the captive birds (Jones 1987), wild Pink Pigeons are capable of breeding in any month, but they only bred in late winter when given extra food (pers. obs. 1992-93).

These observations provide good evidence that less food is available in late winter than at other seasons, which is likely to explain the lack of breeding by unmanaged wild pigeons at this time. This is a completely normal situation for birds in seasonal environments. There is as yet no evidence to support the belief that *winter* food shortages limit the population.

Competition for food between native birds and exotic vertebrates

Most previous hypotheses of resource competition between native and introduced birds on the Mascarene islands were reviewed by Simberloff (1992). Published hypotheses of resource competition fall into two main categories. Firstly, established populations of native and exotic species living side by side might compete for the same resource. Secondly, exotic species might prevent expansion of natives into non-native habitat; it is implied that the natives would be capable of expanding into exotic habitat, but that the resources needed by the native birds are exhausted by the exotic birds (for example, Echo and Rose-ringed Parakeets: Jones 1987).

Although the resource being competed for is often not stated, published hypotheses (see Cheke 1987c, Jones 1987, Simberloff 1992) appear to be derived from perceived aspects of dietary overlap between sympatric native and exotic vertebrates. On this simple basis, many more competitive interactions for food could be hypothesized; exotics involved could include monkeys, rats, columbids, Rose-ringed Parakeets, Red-whiskered Bulbuls, mynas and Madagascar Red Fodies. All of the natives could be affected, but the Pink Pigeon, Echo Parakeet, cuckoo-shrike and black bulbul seem to show the most dietary overlap with these exotics. No exotic vertebrate is a small, arboreal insectivore, and so the flycatcher, olive white-eye and Mauritius Fody appear fairly safe from resource competition with exotics. However, for all hitherto postulated competitive interactions, the final effect on bird populations has not been determined. Indeed, the mechanism by which the exotics exclude the natives has rarely been specified, nor has it been demonstrated that the resource is in short supply or that competition occurs for it (Simberloff 1992).

The various exotics listed above hugely outnumber the threatened native species. It seems reasonable to suggest that competition for food is affecting the natives, but the most damaging of the exotic competitors cannot yet be identified.

The effects of interspecific competition on species distribution are notoriously difficult to demonstrate (Connell 1983). However, this does not mean that competition is any less likely to be an important structuring factor in communities (Morse 1990). In studies on competition on degraded islands, Mountainspring & Scott (1985) and Greig-Smith (1986) used methods which provided an instantaneous view of competitive displacement between pairs of bird species. The former authors (in the Hawaiian islands) grouped species pairs to suggest the existence of competition along a broad and diffuse ecological "front" between the native and exotic avifaunas. These methods did not consider competition between birds and mammals. They also could not be used to test the hypothesis that an exotic had already succeeded in excluding a native from exotic habitats, but Simberloff & Boecklen (1991) found little evidence that this had occurred in Hawaii.

Conclusion

Impoverished food supply may affect forest-living native bird populations in Mauritius, but supporting evidence is inadequate to indicate that this caused the decline of any species. Food supply may, however, be limiting the number of breeding attempts for Pink Pigeons. If nest predation operates in a probabilistic fashion (as is likely), increased frequency of breeding attempts (permitted by increasing the food supply) should result in more fledglings. This justifies the use of supplemental feeding as a management technique to increase productivity. The same may apply to Echo Parakeets, although even fewer data are available for this species. The importance of food shortages may have been hitherto overstated because the true impact of nest predation has been underestimated (for example, Jones 1987: 271; see Chapter 7).

All populations are ultimately limited by food supplies, although many ecological factors (such as predation) can reduce the proximate importance of food supply. Continuing forest degradation will, if unchecked, presumably result in further dilution of food supplies for all species (not only the Pink Pigeon and Echo Parakeet). Future conservation measures will need to find ways to provide adequate food in the long term. Combinations of selected exotics with natives may well provide acceptable conditions in a habitat less prone to degradation than the native forest (Cheke 1978). This strategy is explored in detail in Chapter 9. Collar & Stuart (1985) called for research to determine which tree species would be most appropriate for this strategy, as well as investigation of the effect of winter food shortages. I agree with this view. A review of the foraging data already collected opportunistically for the Pink Pigeon and Echo Parakeet would be a valuable start.

Chapter 6. Breeding success of the forest birds of Mauritius, with particular reference to nest predation by introduced animals

6.1 Introduction

The introduction of exotic predators to oceanic islands worldwide has adversely affected endemic faunas, which evolved in the absence of such predators (King 1980, 1985, Atkinson 1985, Johnson & Stattersfield 1990). This has long been thought to be the case on the Mascarene Islands. In 1691 Leguat (1708, cited by Hachisuka 1953, Cheke 1987a) noted that the now-extinct dove of Rodrigues nested on offshore islets "to avoid the persecution of the rats", and in 1741 Grant (1801, cited by Cheke 1987a) reported that monkeys had caused declines of Mauritian forest birds by eating their eggs.

Since then, much has been written on the supposed effects of introduced predators on the native Mascarene fauna (summarized in Diamond 1987). The nest predation rates on several endemic bird species, especially the Pink Pigeon, are very high, and breeding success therefore low (McKelvey 1976, 1977, Cheke 1987c, Jones 1987, Jones *et al.* 1989). However, there has hitherto been no detailed study of the effects of nest predation on populations of native bird species.

Detailed census work and distribution studies on the Mauritius Fody (Chapter 3), and the fates of the few fody nests found in the 1989-90 and 1990-91 breeding seasons (Safford 1991) suggested that nest predation had a profound influence on the bird's present status. The aim of this chapter is to describe and explain the patterns of breeding success of Mauritian forest birds, based on studies carried out largely in the following two seasons. The effects of these patterns of breeding success on bird populations are discussed in the next chapter.

6.1.1 *Potential nest predators*

Seven species of introduced mammal, six birds (three native) and one introduced reptile are potential predators of Mauritian forest birds and/or their eggs and young.

House Shrews, Small Indian Mongooses, Feral Cats and Brown Rats are largely terrestrial (Atkinson 1985, pers. obs.) and so would rarely be expected to reach birds' nests high in trees. The first three are common in the Mauritian upland forest (Cheke

1987a, Jones 1987, pers. obs.), but Brown Rats appear (from results of trapping: Section 9.5.2) to be rare. House Mice climb well and occur in the upland forests of Mauritius (Cheke 1987a); however, they may be scarce or localized, as I neither saw nor trapped one. Their capacity for nest predation is unclear, but Moors (1978) demonstrated their willingness to eat eggs and chicks of passerine birds. Crab-eating Macaques and Roof Rats are both abundant, arboreal and are proven to take bird eggs or chicks on Mauritius (F. Staub in Atkinson 1985, Safford 1991: 122). The latter two species are therefore likely to be the most important mammalian nest predators.

Among native bird species, Mauritius Kestrels catch birds (Jones 1987) but are not recorded as nest robbers. Horne (1987) suspected that Réunion Black Bulbuls had taken a brood of nestling Réunion Cuckoo-shrikes, although Cheke (1987b) thought rats more likely culprits. Nest-robbing of other species by Mauritius Black Bulbuls does seem conceivable, but I once saw one steal material from an unattended Mauritius Fody nest containing recently-hatched young, which were not molested. McKelvey (1976) twice watched female Mauritius Cuckoo-shrikes feed on Pink Pigeon eggs, by attacking the nest from below while the pigeon was incubating; once the male cuckoo-shrike seemed to 'distract' the pigeon at the same time. This occurred at two sites over a mile (1.6 km) apart and therefore presumably referred to different cuckoo-shrike pairs. These extraordinary observations have never been repeated, and perhaps were of a habit developed by few pairs. Temple (1978b) thought that cuckoo-shrikes "frequently eat eggs of smaller birds" but rarely those of Pink Pigeons; the basis of this sweeping statement is not documented. I saw no evidence of cuckoo-shrikes eating eggs, and no bird chicks were identified among the 364 cuckoo-shrike food items seen during my studies (Chapter 5). Nest predation by cuckoo-shrikes is unknown in Australia (R. E. Major *in litt.* 1994), where five *Coracina* spp. occur (Simpson & Day 1989).

Of the introduced bird species, Indian House Crows are potential predators (Feare & Mungroo 1990) but do not yet occur in the range area of the Mauritius Fody (pers. obs.). Carié (1916) claimed that the abundant Red-whiskered Bulbuls robbed nests of white-eyes on Mauritius, but did not publish his evidence, of which no subsequent author has found any. Nest predation by Red-whiskered Bulbuls is unknown in Australia (R. E. Major *in litt.* 1994). McKelvey (1976), Todd (1984), Cheke (1987c), Jones (1987) and Jones *et al.* (1989) suspected that Common Mynas rob nests, and McKelvey (1976) saw mynas rob and destroy a dummy nest containing a chicken's egg. However, they are still not proven to rob nests on Mauritius. In Australia, they are thought to displace native birds from nest cavities and this sometimes includes destruction of eggs, but are rarely nest predators *per se* (R. E. Major unpubl.).

Guérin (1940-53) also attributed nest predation to the introduced agamid lizard *Calotes versicolor* ("caméléon"), which is, however, almost absent from upland forest. On Serpent Island, native Bojer's Skinks *Scelotes bojerii* take many seabird eggs, possibly only if already pipped (Safford 1993), but *Scelotes (bojerii) fontenayi* of the upland forest of Mauritius is terrestrial and very small and so is an unlikely nest predator (indeed, *fontenayi* is probably a good species and not a race of *bojerii*: E. N. Arnold in Jones 1993).

6.1.2 *The present impact of nest predation*

Only nest predation by Crab-eating Macaques (henceforth referred to as monkeys), Roof Rats, mice and birds will be considered further. These three mammals were introduced over 300 years ago, mynas and Red-whiskered Bulbuls 200 and 100 years ago respectively (Cheke 1987a), and the other avian potential predators are native. The survival of the native birds may indicate that they are capable of sustained coexistence with the predators. At the opposite extreme, the critical status of certain species could now be seen as the final stages of an prolonged decline caused by interrelated factors, of which nest predation is critical: the decline to extinction of an initially healthy population may take longer than 300 years. Alternatively, nest predation may now pose the greatest threat to species which declined for other reasons: the ultimate and proximate causes of extinction may differ (Simberloff 1986). Only detailed study can determine the present rôle of nest predation, and whether it is an obstacle to be overcome if further extinctions are to be averted.

6.2 Methods

In this section, I give an explanation of the design of this study (especially, which species were selected for study), a brief description of my field methods, and accounts of how predator identification was attempted and of how the resulting data were analysed.

6.2.1 *Design of the study*

The aim was to discover the effects of nest predation on breeding success and viability of native bird populations. This could only be achieved by a study of nesting attempts by the birds. Studies restricted to the predators themselves could at best only prove their capability as such; those on the monkeys by Sussman & Tattersall (1980, 1986) did not do so.

While a detailed overview of all native species would be desirable, this was not feasible. The native non-passerines were too rare for a widespread sample of nests of many pairs to be found. For the passerines in the uplands, nests are difficult to find and there seemed no hope of finding large numbers of nests of all species. Although not only looking for nests, in two complete breeding seasons (1973-75) the BOU expedition only found nests of five or fewer cuckoo-shrikes, two black bulbuls, one flycatcher, three Grey White-eyes, no olive white-eyes and six Mauritius Fodies (Cheke 1987c). The native birds differ greatly from each other in nesting ecology, and most native birds were scattered over about 90 km^2 of fragmented native forest, heterogeneous in structure, composition and climate. Pooling data between species and between areas was expected to be more likely to obscure, rather than clarify, the patterns of predation. Therefore a single-species study, supplemented by as much data as possible for other species, was decided upon.

The Mauritius Fody was selected for intensive study because:

1. it was the most endangered of the passerines (Collar & Stuart 1985),
2. it showed a very patchy breeding distribution and unexpected nest site preference, possibly tied to breeding success (Safford 1991), and
3. with practice and perseverence, enough nests could be found to make the study worthwhile.

In addition, intensive monitoring of the wild Pink Pigeon population began in 1989, and many nests were found. This population averaged around 15-20 birds during 1989-93. All were nesting in the 6 ha *Cryptomeria* grove on the south-facing escarpment below Plaine Paul (the south-eastern part of the Les Mares plateau), known as Pigeon Wood. Nest data were extracted from field notes, progress reports and nest record cards (T. Liddiard, K. Swinnerton & C. Taylor, unpublished), supplemented by my own observations, and are also analysed here. A second pigeon population centred on Brise Fer is derived from birds released from captivity (Jones *et al.* 1992). Only one bird from the released population (thought to be the offspring of released birds) had become associated with the wild birds in Pigeon Wood by the time of this study; this bird's breeding activity is included in the following analysis. Apart from this individual, the released population did not regularly breed until late 1993 and their breeding attempts are excluded from this analysis. Their poor initial success was probably caused by problems associated with the release technique and the competence of the birds themselves, as much as to the environmental factors determining the breeding success of the wild birds.

Whilst Mauritius Kestrel breeding data deserve analysis, the results would probably not be comparable with those reported here because this species usually nests in cliff cavities in the lowlands (Jones 1987) or in nestboxes (Jones *et al.* 1991a). The kestrel will not be discussed further.

6.2.2 *Nest-finding and monitoring*

Most nests of all species were high, inaccessible and hidden from view, and so were found by following the birds, rather than searching through vegetation. The easiest time to find nests was during the building period.

For the Mauritius Fody, the intensive building period for each nest lasted three to six days (pers. obs.), when the male and female were often vocal and conspicuous. Thereafter, the adults visited the nest discreetly and nest-finding became very difficult. A few nests were found by hearing the calls of the chicks, which became audible well before fledging. Pigeon nests were found at any stage, by close monitoring of the whole population in Pigeon Wood.

For each nest, the following was recorded: precise locality, habitat features of the whole territory (such as overall degradation, groves of introduced trees), individual recognition characters of adults (for example, rings), phase of breeding cycle (if building, what stage), identity and height of plant species supporting nest, height above ground (often only estimated), position in tree (in relation to the trunk, branches and foliage) and likely accessibility to predators.

Once found, nests were normally checked every other day. For fodies, the contents were not visible because of the domed nest form, and nests of any species were very rarely actually visited, to avoid guiding predators to them (Chapter 4; see Major 1990). Since breeding attempts could fail without any visible damage to the nest, a visual check of the nest's intactness could not confirm that it was still active. Therefore, monitoring consisted of watches from ground level, waiting either for the arrival or departure (for fodies, usually silent and almost instantaneous) of an adult, or for a chick to call. From observation of average incubation visit periods and intervals between feeds, nest watches were set at one hour. After an hour with no activity at the nest, either the watch was extended, or the nest was viewed at closer range (by tree-climbing) to look for signs of predation, or the contents were checked (but only if this could be done without damaging the nest). Various pitfalls noted for fodies emphasized the need for caution in interpreting evidence: during the building period, some birds suspended activities for a few days (Fig. 4.2); eggs very occasionally did not seem to need incubation (possibly maintained by the sun at the correct temperature); chicks could go unfed for longer than one hour; and once a pair started to build a new nest while feeding young in another (Fig. 4.2). Each of these could have caused a nest to be classed wrongly as having failed or been deserted.

The outcome of a nesting record was classified in one of four ways: deserted, successful, failed or outcome unknown. A nest was deserted if activity ceased before eggs were laid, with no evidence of predation. Success was only confirmed when the fledged brood had been found. A nest was considered to have failed only if one of two cases applied: *either* it had been destroyed or emptied while still active, *or* all activity was abruptly transferred to a new nest site after the first egg was thought to have been laid. Therefore a nest which was destroyed when at an early stage of building was a failure, although there was no way of knowing whether it would later have been deserted. Predation was said to have occurred when a nest was attacked by any predatory species, regardless of its contents (even if empty). This left a few nests whose outcome was unknown, for example if a nest survived intact past the expected fledging date, but fledged juveniles could not be found due to bad weather.

For successful nests, the minimum number of fledged juveniles was recorded; counting the whole brood was often difficult (Section 4.3.6). For failures, the cause was noted where possible. All signs of damage were described; at this stage, no assumptions were made regarding the identity of the predators.

Early results suggested that Roof Rats were more important nest predators than had previously been thought, and that Pigeon Wood was a particularly important site for fodies as well as Pink Pigeons. Consequently, in December 1991 a continuous rat control programme in Pigeon Wood was initiated, using an anticoagulant poison (Brodifacoum). Baits were placed in tubes at 50 m intervals on a grid pattern (see Fig. 2.11), and renewed at one to two weekly intervals, following Innes & Williams (1990). The area of rat control increased until February 1992, when it extended slightly beyond the entire

Cryptomeria area of Pigeon Wood, therefore including the whole Pink Pigeon breeding area. Poisoning continued until the end of the project. For the study of Mauritius Fody breeding success, it might have been preferable to have delayed starting the control until the austral winter of 1992, to give single complete breeding seasons with and without rat control (since most nests were found in the breeding seasons before and after that winter). However, the status of the Pink Pigeon was considered too critical to allow any delay, since this species was also expected to benefit from the rat control. Rat control was not carried out in the Mauritius Fody's range away from Pigeon Wood because native bird densities (including fodies) were so low that impractically large poisoned areas would have been needed in order to take in several territories.

Supplemental feeding for the wild pigeons started in 1990 but was intermittent until February 1992, when unlimited food was made almost continuously available. This was much used by nearly all the pigeons, but not by any other native birds. Trapping of cats and mongooses began in Pigeon Wood in early 1993 (mongoose trapping having been very occasional before this); two cats and 19 mongooses were caught in the next six months. These management practices may have affected breeding success indirectly; for example, cat or mongoose control might have affected rat abundance.

Tables 6.1, 6.2 and 6.3 show the distribution and numbers of nests found, and indicate that Mauritius Fody nests were found almost throughout the bird's range area.

Table 6.1. The numbers of nests of all bird species found in upland Mauritius, 1989-93. Totals include nests from which eggs or young were taken for captive breeding (Pink Pigeon and Echo Parakeet), as well as those for which the outcome was unknown. Nest site data are available for all nests.

	Total nests found	Nests with known fate	Nest type
Native species			
Pink Pigeon[1]	69	59	open
Echo Parakeet[2,3]	10	7	tree cavity
Cuckoo-shrike	8	6[4]	open
Black bulbul	6	6	open
Flycatcher	9[5]	6	open
Grey White-eye[6]	9	1	open
Olive white-eye	1	1	open
Mauritius Fody	102	91	dome
Introduced species			
Red-whiskered Bulbul	25	5	open
Madagascar Fody	14	6	dome
Total	252	188	

Notes

[1] Eight clutches were taken for captive rearing; the outcomes of these nests are classified as unknown.

[2] 1987-88 and 1988-89 seasons included (one nest each season).

[3] Six clutches or broods were taken for captive rearing. Thrice, no second attempt was seen and the outcome of the nest is classified as unknown. When the birds recycled in the same nests (twice), the first clutch/brood is ignored here. Once, the single chick was rescued when close to death; the outcome of this attempt is treated as known (failure).

[4] Excludes one nest found as young were fledging.

[5] Includes three nests at Bras d'Eau (lowland; outcomes unknown).

[6] Included only if the nest was found *in situ*.

Table 6.2. Numbers of Mauritius Fody pairs whose nests were found, and total numbers of nests found, in each forest patch, 1989-93.

Forest area	Pairs estimated present	Pairs whose nest was found	Total nests found
Pétrin - Raoul	5	2	6
Rivière du Poste	4-5	0	0
Grand Bassin/Gouly Père	2	0	0
Bel Ombre	20-25	2	2
Alexandra Falls	2-4	1	1
Montagne Cocotte - Piton Savanne[1]	65-72	22	91
Combo	6-7	2	2
All	104-120	29	102

Note

[1] Pigeon Wood is within this area.

Table 6.3. Numbers of Pink Pigeon and Mauritius Fody nests found inside and outside Pigeon Wood, with and without rat control, in each breeding season 1989-93. Pink Pigeons were only known to breed in Pigeon Wood, and rat control was only carried out here. One season is defined here as August to July: fodies nest between August and April; pigeons may do so at any time.

Season	Nests found in Pigeon Wood				Nests found elsewhere	Total nests	
	No rat control		Rat control				
	Pigeon	Fody	Pigeon	Fody	Fody only	Pigeon	Fody
1989-90	11	2	-	-	8[1]	11	10
1990-91	12	6	-	-	3	12	9
1991-92	4	24	12	8	1	16	33
1992-93	-	-	30	30	20	30	50
All	27	32	42	38	32	69	102

Note

[1] Includes one nest found in 1988-89 season.

6.2.3 *Identification of the predators*

Unjustified speculation on the identity of the predators is rife in the literature, from McKelvey's (1977) assertion that monkeys destroyed 40 out of 48 pigeon nests in 1976, to the claim by Sussman, Jamieson & Tattersall (in Jones 1987: 268) that the Roof Rat was "the real culprit". No author has given direct evidence (such as witnessing the attack) for more than one or two predations. Signs seen have rarely been described and still less often compared with signs from known predators.

Since predation was never actually witnessed in the present study, identifying the predator depended on observation of signs. A review of previous work and anecdotal observations on signs left by known predators is first given.

Rodents

For open nests, the signs left by rodents are very variable. In a laboratory trial in New Zealand, Moors (1978) found that Roof Rats and House Mice attacked eggs *in situ*, making a large hole (often in the long axis of the egg, unlike a hatched egg), leaving small shell fragments embedded in the nest material, and rummaged in the lining to clean up spilt contents. Chicks were left variably mutilated and partly eaten, especially the brain, pectoral muscle and stomach contents.

On Mauritius, F. Staub (verbally 1991) watched a Roof Rat take a nestling cuckoo-shrike in daylight: the rat carried the chick down the trunk of the nest tree and away. Using several methods, Major (1991) proved that rats frequently carried eggs and chicks away from nests, leaving the nests undamaged.

On four dates in February and March 1990, I placed single Barbary Dove *Streptopelia 'risoria'* eggs in a used Grey White-eye nest (thin, tightly woven and open) one metre off the ground in bushes, all contained in the Pink Pigeon release aviary in Brise Fer forest. Of the potential predators, presumably only Roof Rats and mice could enter the cage and climb to the nests. All the eggs were taken within four days. One disappeared without trace. Two were removed leaving no trace in the nest, but large fragments (exactly as illustrated by Moors 1978) on the ground up to 3 m from the nest. One egg was also removed, again leaving a large fragment on the ground, but also small pieces in the nest. In no case was there any damage to the nest, nor droppings left in it. In 1992, adult Common Waxbills roosting in a similar aviary were mutilated (as Moors [1978] described for nestlings) and strewn around the cage.

Domed nests may require a different approach by the predator, resulting in different signs. The Aldabran fody *F. eminentissima aldabrana* builds a globular nest like that of the Mauritius Fody, but usually suspended between vertically hanging pinnae of coconut palm fronds, or from twigs (Mauritius Fody nests were never suspended in open airspace, but were always built in foliage). Frith (1976: 168) noted that Roof Rats almost always burst through the underside or the back of the chamber of the nest, and that "eggs were broken and eaten *in situ* or directly beneath the nest, droppings often being left at these points". Frith did not mention ever seeing rats attack as described, but the only other predator on Aldabra, the Pied Crow *Corvus albus*, left different signs.

Monkeys

That monkeys depredate nests on Mauritius is not disputed by any author, but few published observations indicate what signs are left when the monkeys do so. Jones (1987) plausibly claimed that complete dismantling of the nest structure was diagnostic of monkey predation on Pink Pigeons, but did not give the basis for this. F. Steele (in Jones 1987) once checked a known pigeon nest, to find it pulled apart and thrown out of the tree with no sign of any eggs; six to eight monkeys were in and around the nest tree. However, in a known monkey predation on pigeons in 1990 (confirmed by tooth marks in plastic eggs), the nest was left intact (Safford 1991).

In May 1991, wild-caught Mauritian monkeys, which had never before been fed eggs whilst captive, were presented with about ten Barbary Dove eggs, left on the ground rather than in nests. The monkeys unhesitatingly put the eggs whole into their mouths, and often carried them around before eating them. As they ate them, the monkeys dribbled out shell fragments a few millimetres across, followed eventually by strips of egg membrane with some flakes of shell attached. Chicken eggs, too big to fit in the mouth, were instead broken into and the contents sucked out, leaving large shell fragments.

Birds

A cuckoo-shrike predation on a Pink Pigeon nest, with a pigeon incubating, left a broken egg and a hole in the nest; a myna dismantled an unattended nest (McKelvey 1976). On Aldabra, Frith (1976) saw Pied Crows tear at fody nests, often bringing them to the ground, where the contents were eaten; Pied Crows are absent from Mauritius, but this may well typify attacks by larger passerines (such as mynas) on fody nests.

Conclusions

Certain criteria for identifying predators are common sense. It seems unlikely that a rodent would tear a nest to shreds and strew material over 3 m from the nest site (but a monkey or bird might), nor that a monkey would carefully reach inside a domed nest with an entrance tube to remove the contents without even ruffling the lining.

For any given predator, signs left at plundered nests may depend on many factors, including: nest shape (dome or open cup), type of attachment of the nest (a supported fody nest could be attacked by rodents through the entrance, but not if suspended with the entrance pointing into open airspace), strength of attachment (known to vary greatly for fodies, affecting the likelihood of the predator dislodging the nest), egg or chick size, looseness of nest construction and defense by the birds.

Confusion was increased by repeated attacks on the same nest after it had already been robbed. Safford (1991) recorded a three-day-old fody brood disappearing without any damage to the nest; the next day, the nest had been demolished, with material widely strewn. Successful nests had almost always been attacked when checked some time after fledging, and failed nests which had only been partially damaged usually suffered further damage later on. Therefore the damage observed cannot be assumed to have been caused by the original predator. The above evidence suggests that repeated attacks occurred too frequently for the phenomenon to be ignored, although frequent nest checks reduced the chances of such events ocurring undetected.

The only "predation" I witnessed occurred when one or more Grey White-eyes (not a recognized nest predator) stole material from a part-built (active but unguarded) flycatcher nest, pulling it apart in the process (Bassin Blanc, 9 October 1991). Had the event not been watched, but the nest later checked, it would have been recorded as a predation. Such incidents are likely to be rare enough to be negligible, as nests containing eggs or young were successfully defended by the parents when approached by other birds.

This review indicates that the sign left by a predator is not an unvarying characteristic of the predator species. However, certain signs appear to be diagnostic and, if repeated attacks can be discounted, the predator may thereby be identified.

Flack & Lloyd (1978) and Moors (1983) thought that Roof Rats were more serious nest predators than House Mice in their study areas in New Zealand where both rodents were present. Since there was also no direct evidence for nest predation by birds on Mauritius in this study, the assumption that all predations are due to Roof Rats or monkeys may approach the true situation. If so, predations are tentatively attributed to Roof Rats only in the following cases: contents are removed without damaging the nest (dome nests only); a hole is made in the nest and the contents removed (dome nests only); small egg shell fragments are embedded in the nest material or large pieces present near the nest site; chicks are mutilated as described above and left in or near the nest. Predations are attributed to monkeys only if the nest is torn up in the most violent fashion.

6.2.4 *Data analysis*

Breeding success is here defined as the proportion of all nests from which young fledge, excluding nests deserted by the birds before eggs were laid. The simplest estimator of breeding success is the percentage of all *observed* nests from which young fledged. The inclusion of nests found after eggs were laid may cause overestimation of breeding success (Mayfield 1961), due to bias against nests which failed earlier and so were not found. Ten Mauritius Fody and 20 Pink Pigeon nests with known fate were found after eggs had been laid. An estimator which avoids this bias is given by excluding all these nests, using the same calculation; however, this reduces sample sizes and requires discarding valuable data.

The Mayfield method is an alternative (Mayfield 1961, 1975), which takes account of the timespan of observation (defined as exposure). For a sample of nests, the exposure (nest-days) is summed, and divided into the number of nests destroyed during the observation period, to give the estimated daily mortality rate, and hence the daily survival rate (s). The probability of a nest surviving through t days is s^t. This is Mayfield's estimator of breeding success.

The sums of the incubation and nestling periods were taken as 38 days for the pigeon (the average observed during the study; nestling periods were very variable) and 32 days for the fody (Chapter 4); data collected before eggs were thought to have been laid were not used in the Mayfield analysis, because mortality rates during this period seemed to be variable (probably being influenced by the intensity of the adults' activities). The nest success calculated using the Mayfield method is therefore an estimate of the proportion of nests in which eggs were laid, from which young ultimately flew.

Johnson (1979) developed the Mayfield method and provided the variance of Mayfield's estimator as

$$\text{Variance} = (\text{exposure-losses})\text{x}\text{losses}/(\text{exposure})^3$$

The first two methods take into account only successful or failed nests; the Mayfield method allows inclusion of nests with unknown outcome, so long as data on exposure are available. Temporal variation existed in survival rates (for example, for pigeons they were highest during early incubation). Mayfield calculations taking this into account (Mayfield 1975, Johnson 1979) scarcely changed the estimated breeding success from those in which a single average mortality rate was used. Single mortality rates were therefore used over the incubation and nestling periods. Mayfield calculations excluded the nest-building period.

For multiply brooded species like the pigeon and fody, the mean number of fledglings per female per year (FFY) is the best measure of annual productivity (Rowley & Russell 1991). This is estimated from the breeding success, brood size and number of broods.

In order to understand the effects of predation, it was necessary to discover which of the variables recorded for each nest had the greatest effect on the likelihood of success. Because sample sizes in this study were fairly small, the variables whose effects were worth investigating in detail could be selected by inspection of the data.

Pink Pigeon

The only variable whose effect was investigated was the presence or absence of rat control. The mortality rates with and without rat control are therefore compared. Johnson (1979) compared mortality rates for two categories of nests by examining the distribution of the difference between the rates (means and standard errors). His method was stated to be applicable only to large samples, but he did not give an indication of minimum sample size, nor discuss comparison of small samples or the effect of unequal variances. Indeed, the sample sizes (and hence degrees of freedom) are undefined, as they are neither the number of nests, nor the number of losses. It is therefore not clear whether the use of Johnson's (1979) test is justified for the Pink Pigeon nest data, and I present the results of this test with caution.

Mauritius Fody

Variables whose effect was investigated were: (1) the breeding season in which the nest was found (that is, which of the four seasons of the study), (2) presence or absence of rat control, (3) nest tree species (*Cryptomeria* or other species), and (4) timing of the nesting attempt within the season (early, defined as eggs laid in September to December, or late, defined as eggs laid in January to March).

These explanatory factor variables were likely to be intercorrelated, and were therefore related to nest success using a generalized linear model with a binomial distribution and a logistic link function (McCullagh & Nelder 1989). The models were fitted using GENSTAT 5 (Genstat 5 Committee 1987). GENSTAT outputs the regression and residual deviance (whose sum is constant); the lower the residual deviance, the better the fit of the model. The principle was to discover which variables had to be included in the model (and which variables could be discarded) in order for the model to fit the data. Initially, models were used which fitted only one of the variables to the data. Attempts were made to improve the best one of these four models, by adding combinations of the other variables to the model. The importance of a variable can be judged by considering the difference in deviances between models including and excluding the variable; this difference has an approximately χ^2_v distribution, v being the number of degrees of freedom of the variable. The residual deviance for any model also has an approximately χ^2_d distribution, d being the residual degrees of freedom. The model which fitted the data ($P > 0.05$) using the fewest explanatory factors was used to suggest the most important factors in determining fody nest success. This analysis was carried out using all fody nests with known outcome, and repeated using only those found before eggs were laid.

6.3 Results

The outcomes of the nests are summarized in Table 6.4. The proportions of successful, failed and deserted nests should not yet be compared between species, as the Table 6.4 makes no allowance for factors which may cause variation in breeding success (such as rat control).

Table 6.4. The fates of all nests monitored with known fate in upland forests of Mauritius, September 1989-August 1993.

Species	Nests with known fate	Successful nests	Nests which failed due to			Deserted nests (no eggs laid)
			Predation	Other causes	Indeterminate	
Native species						
Echo Parakeet[1]	7	2	2	2	1	0
Pink Pigeon	59	16	15	9	5	14
Cuckoo-shrike	6	2	3	1	0	0
Black bulbul	6	0	5	0	1	0
Flycatcher	6	3	2	1	0	0
Grey White-eye	1	0	1	0	0	0
Olive white-eye	1	0	1	0	0	0
Mauritius Fody	91	20	34	2	5	30
Introduced species						
Red-whiskered Bulbul	5	0	5	0	0	0
Madagascar Red Fody	6	0	4	1	1	0
Totals	188	43	72	16	13	44

Notes

[1] 1988-89 season included (one nest found). See also notes on Table 6.1.

6.3.1 *Reasons for nesting failure*

Pink Pigeon

Most breeding failure was caused by predation (Table 6.4), which accounted for 8-10 out of 11 nesting failures before rat control was introduced. Other causes of failure were infertility of eggs, death of embryos, abandonment of nests for unknown reasons, squabs or eggs apparently falling out of the nest (twice during windy periods) and (once) a deformity in the squab.

Mauritius Fody

Of the 41 nesting failures, 34 were certainly due to predation. Two inaccessible nests containing eggs or young were either abandoned or depredated without visible damage, three disappeared during strong winds (but could have been depredated), one fell out of the tree in still conditions and one was abandoned; the latter two each contained an intact clutch. Therefore 83-95 % of all Mauritius Fody nesting failures were due to predation.

All species

Most nesting failures for the other species were caused by predation. Therefore, predation was by far the most common cause of nesting failure for all species. Cyclones have certainly destroyed active fody nests (Cheke 1987c: 205), and could at a stroke destroy almost all active nests, but there were no cyclones in the study period. There is no evidence that chilling of eggs, food shortage or other factors (including direct disturbance caused by this study) caused more than very occasional failure.

6.3.2 *Identity of the predators*

Pink Pigeon

The nature of the damage to the nest was not always noted by the observers, but evidence of Roof Rat predation was seen at 8 out of 20 nests where predation was certain or suspected; for a few of these the characteristic eaten-out shells were found, but more often only fragments on the ground below the nest or nearby. The nest was generally undisturbed. Two nests were completely destroyed; once, monkey faeces were found by the still-intact nest when a squab (almost fledging age) disappeared, leaving only feathers. Once, a well-grown squab and its father both disappeared at about the same time (possibly coincidence). Of course, when the only sign found is broken egg shell below a nest tree, the eggs could merely have been kicked out by the parents, which are notoriously clumsy (at least in captivity: Jones *et al.* 1989), and then eaten by any passing animal.

The evidence therefore implicates both Roof Rats and monkeys as predators of pigeon nests but sheds little light on their relative importance. The importance of birds as nest predators is unknown. The effectiveness of rat control at reducing predation rates (see Section 6.3.4) presumably indicates that Roof Rats had previously been very serious nest predators.

Mauritius Fody

The damage observed for the failed nests is given in Table 6.5, which indicates that the identity of the predator was inferred for only 11 out of 34 nests known to have been depredated: monkeys five times, rats six.

Table 6.5. Damage observed to 39 Mauritius Fody nests which possibly or certainly failed due to predation.

Damage to nest	Number of nests	Inference
Completely disappeared	1	No inference
Disappeared in strong winds	3	Predation not proven
Demolished, material widely strewn	5	Monkey
Torn open/apart	20	No inference
Nest *in situ* with hole in back[1]	6	Roof Rat
Intact, contents disappeared	2	No inference
Intact, fate of contents not known	2	Predation not proven
Total	39	

Note

[1] One of these nests also contained egg shell fragments.

Other species

The paucity of nests followed allows few inferences. Both predations on Echo Parakeets (with eggs) and all three on cuckoo-shrikes were attributed to Roof Rats, leaving typical egg shell fragments or dismembered chicks (for one of the cuckoo-shrike nests). The five black bulbul and two flycatcher nests which were depredated were found empty but hardly (if at all) damaged, although later were damaged further (shredded or torn free from their positions, recalling the repeated attacks on fody nests). Once a recently-hatched but dead black bulbul chick was found on the ground 10 m from the nest tree. The olive white-eye nest was torn free and discarded empty, like many Grey White-eye nests on Mauritius (Safford 1991). This appears most likely to be the result of monkey predation, since on Réunion two species of white-eye are common but their nests are not often found on the ground, and all the same arboreal predators except monkeys are present on Réunion (Safford 1991). I found or was shown 43 grounded nests in four years on Mauritius (Chapter 4).

The few nests of introduced birds suffered similar fates to those of the native birds. Madagascar Red Fody nests were shredded as if by monkeys, burrowed into by rodents or blown out by strong winds; Red-whiskered Bulbul nests were shredded or neatly emptied.

Conclusion

Whilst certain individual acts of predation could, using natural signs, be assigned to one species of predator, many could not. Furthermore, the ambiguity caused by repeated attacks could not be resolved. Where several possible predators are present, their identification using signs at failed nests is untrustworthy. Therefore the relative importance of each nest predator could not be judged, and manipulative methods (reviewed by Major 1991) are required to resolve this. In the following analysis, no attempt is made to separate the acts of different predators.

6.3.3 *Plant species chosen as nest sites*

Pink Pigeon

Of 69 nests, 66 were in *Cryptomeria*, one in a single, tall *Pinus taeda* on the edge of the *Cryptomeria* grove, one in the crown of a tree fern *Cyathea* sp. and one in a dense-canopied native tree (perhaps *Syzygium glomeratum*). The latter three were each used by a different pair who normally nested in *Cryptomeria*, demonstrating the occasional use of other tree species.

Mauritius Fody

At least one nest was found in the territory of each of 29 different territories (Table 6.6), ranging from 22 nests (only one active at any one time) in the 'central' territory of Pigeon Wood, to single nests in many other territories. All evidence indicates that fodies persist in the same territories year after year (Chapter 4), so these territories are assumed to have been occupied by 29 different pairs, amounting to about 26 % of the population. Table 6.6 shows that 23 of these 29 pairs were only seen to nest in the three main genera of plantation trees: *Pinus*, *Eucalyptus* and *Cryptomeria*. All nests were 1.5-17 m off the ground, in trees or shrubs taller than 2 m, as found by Safford (1991).

Most nests were found by following birds seen collecting nest material, which was usually collected in native forest, even for nests in a plantation (pers. obs.). In such cases, the data on choice of nest tree were unbiased, since the location and behaviour of the bird collecting material bore little relation to the location of the nest. However, nests were easier to find in territories which included good vantage points and penetrable vegetation. This biased nest-finding against pairs in Bel Ombre and on Montagne Cocotte (because of the terrain and vegetation), where few nests were found in proportion to the number of pairs present (Fig. 3.9, Table 6.2). I therefore suggest that the nest trees seen to be used by each pair were indeed typical of that pair, but that the proportion of the whole population which uses plantation trees differs from the proportion in my sample.

All territories were largely native forest, and so all 29 pairs had access to native trees to nest in. Of the five pairs seen to nest away from plantation trees, three had none of the latter in their territories whereas two did have a few available, but did not use them. Therefore 24 out of 26 pairs nested in plantation trees when available. From this information, the nest site choice (whether in a native or exotic tree) can be predicted from knowledge of the trees available in the territory.

Fig. 3.9 shows the confirmed or predicted nest site choice of each Mauritius Fody pair mapped from Combo to Alexandra Falls. From the nest tree data, plantation trees are assumed to have been used as nest sites by all pairs whose territory included a significant number of such trees in the form of small groves or plantation edges (rather than isolated trees). In Bel Ombre, the pairs associated with the small *Pinus* plantations were assumed to nest in them (confirmed for one pair; the other pair whose nest was found had no *Pinus* available and used native *Calophyllum*). All the pairs at Raoul, Grand Bassin/Gouly Père and Rivière du Poste were assumed to nest in the plantations (mostly *Pinus*) which surrounded these small native patches (confirmed for two pairs at Raoul).

It is thus predicted that 57 (63 %) of the 90 pairs whose territories were found nested in plantation trees. The estimated total Mauritius Fody population (104-120 pairs: Chapter 3) included 14-30 pairs which were not found, and whose nest tree choice cannot be judged. Therefore, I suggest that 57-87 pairs (50-70 % of the population) habitually nested in plantation trees.

In territories where both *Pinus* and *Eucalyptus* were available, no consistent preference was apparent. However, the 'stream' and 'west ridge' territories in Pigeon Wood both had abundant *Cryptomeria* and *Eucalyptus*, and one or two *Pinus*, for the birds to choose between (Fig. 3.10); each of 12 nests found in the former territory and eight of nine in the latter were in *Cryptomeria*, the exception being in a *Pinus*. Clearly, *Eucalyptus* was avoided by these pairs. A pair 1 km east of Alexandra Falls nested in the only patch of *Cryptomeria* (surrounded by *Pinus*, *Eucalyptus* and other species) in the vicinity.

Therefore, for pairs which had more than one of the three genera of plantation trees available, there may have been a tendency to nest in *Cryptomeria*.

Table 6.6. Tree species used as nesting sites by 29 pairs of Mauritius Fodies

Tree species	Number of pairs
Cryptomeria japonica only	10
Eucalyptus robusta only	4
Pinus spp. only[1]	5
Pinus or *Cryptomeria*	1
Pinus or *Eucalyptus*	1
Cryptomeria or *Eucalyptus*	2
Eucalyptus or other exotic[2]	1
native/other exotic[3]	5
All	29

Notes

[1] *P. elliotti* and at least one of *P. taeda* and *P. tabuliformis* were used.

[2] This pair built four nests in *Eucalyptus*; the fifth was in a dense *Lonicera* sp. (exotic) bundle in a single *Calophyllum eputamen* (native) left standing amid the *Eucalyptus* grove which held their previous nests.

[3] Species used were *Citrus aurantium* (a spiny exotic), and *Calophyllum eputamen*, *Homalium paniculatum*, *Nuxia verticillata* and *Labourdonnaisia calophylloides* (all native).

Other native bird species

Nest-finding was biased towards the areas where I searched for Mauritius Fody nests, and numbers of nests were small. The proportions of the populations associated with plantation trees cannot be estimated. Nest site choices did not differ from those described by Jones (1987) and Cheke (1987c) for native species, and Carié (1916) for the exotics, except for the following. The only cuckoo-shrike nests I found in or around Pigeon Wood were one in *Calophyllum eputamen* (native, growing amongst the *Cryptomeria*) and one in *Eucalyptus robusta*. The latter was the first recorded in an exotic tree; the rest were in native trees in Macchabé - Brise Fer. All six black bulbul nests (1-2 pairs in Pigeon Wood, one in Combo) found were 3-9 m up in *Cryptomeria*. The flycatchers in Pigeon Wood used saplings (four nests found in *Psidium cattleianum*, one in an unidentified native) growing under the *Cryptomeria*. The habit of nesting in *Pinus* plantations adjacent to native forest was noted by Safford (1991) for both white-eye species; three out of eight Grey White-eye nests found since then were similarly sited (*Pinus* was unavailable for the other five nests).

Selection of nest sites in or under plantation trees, when native trees are also available, is therefore confirmed for all the native passerine species. However, the cuckoo-shrike was unique in avoiding *Cryptomeria* when available (in Pigeon Wood), and about 70 % of its population was distributed in areas almost devoid of plantation trees (Montagne Cocotte to lower Bel Ombre, Black River Peak and Macchabé - Brise Fer: Chapter 3). The distributions of the black bulbul, flycatcher and olive white-eye were consistent with a high proportion of their populations nesting in or under plantation trees.

Introduced bird species

Red-whiskered Bulbuls and Madagascar Red Fodies both placed their nests anywhere from 30 cm up in grassy tangles in exotic thickets (unlike the Mauritius Fody), to dense terminal fronds high up in conifers: Carié (1916) did not find nests of either species so high. With so few observations on such abundant species, no conclusions can be drawn.

Did birds select exotic trees, or general areas dominated by exotics?

Two hypotheses are consistent with the data collected. First, the birds selected nesting areas dominated by exotic trees; the identity of the nest tree was less important. Second, they selected individual exotic trees, regardless of that tree species' abundance. To test these, data would be needed on nest tree choice in territories with scattered exotics in a native-dominated area (or vice versa). However, such areas were very rare: groves of exotics usually contained very few native trees, and the exotics were largely confined to these groves. Anecdotal evidence supports both of these hypotheses. Two examples are consistent with the first hypothesis: flycatchers nested in Pigeon Wood, but did not use the *Cryptomeria* trees; and a fody pair once nested in the single native *Calophyllum* in a *Eucalyptus* grove (Table 6.6: note 2). A black bulbul nest in Combo was in an isolated *Cryptomeria* in native forest; this is consistent with the second hypothesis.

6.3.4 *Breeding success and productivity, and their causal factors*

Tables 6.7 and 6.8 show the nesting data for the Pink Pigeon and Mauritius Fody. For the pigeon, analysis is relatively simple and estimated breeding success is included in the table. For the fody, the explanatory variables are first analysed to identify which variables were unimportant and could be pooled; then breeding success is estimated.

Table 6.7. Breeding success of the Pink Pigeon, August 1989 - July 1993. Only breeding attempts with known fate, where eggs were laid, are included. Breeding attempts where the whole clutch was taken into captivity are excluded. If nests found after incubation started are excluded, the figures in square brackets result. Data on exposure were collected for four additional nests with unknown outcome; these are not in the table but are included in calculations to estimate the breeding success using the Mayfield method. Success calculated using the Mayfield method includes 95 % confidence limits (in brackets).

	Number of nests		
Outcome of breeding attempt[1]	No rat control	Rat control	Totals
Success (one or more young fledged)	3 [1]	13 [5]	16 [6]
Failed: predation confirmed[2]	8 [6]	8 [4]	17 [10]
Failed: predation possible	2	3 [1]	4 [3]
Failed: not predation	1	7 [5]	8 [6]
Total nests	14 [10]	31 [15]	45 [25]
% of nests successful	21 [10]	42 [33]	36 [24]
% nesting success (Mayfield method)	9 (2-38)	35 (21-57)	27 (16-43)

Notes

[1] Of the eight whole clutches taken for captive rearing (all before rat control started), seven were replaced with dummy eggs. On five occasions the dummies were apparently attacked by predators, and twice they were incubated full term but might in fact have been attacked and not ejected from the nest. These eight nests are excluded from analysis.

[2] Includes two nests in which the juvenile was killed around fledging time, on or near the nest: if the bird was in fact killed after fledging, the nesting attempt would, strictly speaking, be considered as a success.

Pink Pigeon

The daily mortality rates with and without rat control were 0.027149 and 0.060109 respectively, and variances 0.000040 and 0.000309. The observed mortality rate without rat control was 2.2 times that with control.

Following Johnson's (1979) method for comparison of mortality rates, the difference of the means is 0.03296, the sum of variances 0.000349. The ratio of the difference to its standard error (the square root of the variance) is 1.76. If mortality rates did not differ, this ratio would be distributed as a normal variate with zero mean and unit standard error. The resulting value is not extreme enough ($P>0.05$) to reject the hypothesis that the mortality rates are equal with or without rat control. As pointed out in Section 6.2.4, the validity of this test is uncertain for this data-set. Whether or not the test is valid, rat control is not shown significantly to have affected the breeding success of the Pink Pigeon at the 5 % level, using the data collected during 1989-93. The observed daily mortality rates with and without rat control differed, but the sample size without rat control was small, so that the variance in this mortality rate was large (in other words, it was impossible to be sure that the high observed mortality rate was typical). With such a small sample, the difference in mortality rate would have to be very large to be statistically significant, whatever its biological significance.

Data collected in earlier studies confirm that the mortality rate without rat control observed in 1989-93 was typical, assuming that the causal factors had not changed. Studies on the wild birds in the 1970s and 1980s involved over 100 nests (compared to the 14 monitored during 1989-93), almost all in Pigeon Wood, and none with rat control. These data have not been pooled with 1989-93 data for quantitative analysis, because the exposure and number of successful nests were not stated. However, less than 10 % of eggs laid in these studies survived to produce fledged young (data summarized by Jones *et al.* [1989], from McKelvey [1976, 1977], Temple [1978b] and Jones [1987]). These data presumably included nests found after egg-laying, and were therefore likely to be optimistic. The breeding success in the 1970s and 1980s was thus not over 10 % (success was estimated as 9 % using the Mayfield method on recent data). Therefore a larger sample size would be most unlikely to show a mortality rate greatly different to that found in 1989-93. Even if sample size (without rat control) was only doubled, the difference between the mortality rates with and without rat control would become significant ($P<0.02$, same procedure as above; the larger samples may also make the Johnson test more robust).

I conclude that rat control was not shown to have affected the breeding success of the Pink Pigeon, using data from 1989-93, but that re-analysis of data collected previously would undoubtedly show that rat control did significantly improve the breeding success.

FFY for the pigeon cannot be calculated as the number of clutches per female per year before management started is unknown. Jones (1987) found an average brood size of 1.1 without management. Bruford *et al.* (1991) assumed that one clutch was laid per pair per year, but this was not based on studies of marked birds; if correct, this would give an estimated FFY of 0.1 (or 0.09x1x1.1) for unmanaged Pink Pigeons in Pigeon Wood. When supplemental feeding and predator control were introduced, nesting success, brood size and number of clutches per pair per year all increased, leading to dramatic increases in productivity. For example, from June 1992 to May 1993, one pair (both birds ringed) laid four clutches, fledging five young in the year. Further monitoring is needed to show whether such productivity can be sustained.

Table 6.8. Breeding success of the Mauritius Fody, 1989-93. If nests found after incubation started are excluded, the figures in square brackets result.

Nest tree species	*Pinus*/*Euc*/other		*Cryptomeria*				Total
Rat control	No rat control		No rat control		Rat control		
Time in nesting season	early	late	early	late	early	late	
Number of nests/outcome							
Success	0	0	8 [5]	1	9 [5]	2	20 [13]
Predation confirmed	12	6	4 [2]	3	2 [1]	7	34 [31]
Predation possible	2	1	1	1	0	0	5
Failed: no predation	0	1	1	0	0	0	2
Total nests	14	8	14 [9]	5	11 [6]	9	61 [51]

Mauritius Fody

Of the four explanatory variables, the model fitting the selection of *Cryptomeria* as the nest tree left the smallest residual deviance (Table 6.9). Adding time of breeding (early or late in the season) to the model containing only *Cryptomeria* improved the fit of the model (change in deviance = 8.2, $P<0.01$); breeding early in the season was more successful than late breeding. No significant improvement in the fit of the model was obtained by adding the remaining variables into the model containing *Cryptomeria* only. No other combinations of explanatory variables significantly improved the fit over the model containing *Cryptomeria* and time of breeding as explanatory variables. This model provided a satisfactory fit to the data ($P>0.1$). The analysis was repeated, excluding the ten nests which were found after egg-laying; this made no difference to the result.

I conclude that the Mauritius Fody nest data were satisfactorily described by a model having two explanatory variables. The use of *Cryptomeria* and breeding early in the season were the two factors identified as improving nest success. However, this result needs to be seen as provisional, because sample sizes were small and there were no observations in which rats were controlled outside *Cryptomeria*.

In order to estimate the fody's breeding success, I therefore pool data with and without rat control over all years. The resulting figures are shown in Table 6.10. In addition, breeding success is calculated with early and late nests pooled, because an average figure is needed for the breeding success in each habitat.

Table 6.9. Attempts to describe Mauritius Fody nest data using a model with various combinations of explanatory variables. The lower the residual deviance, the better the fit of the model. An asterisk (*) indicates a satisfactory fit ($P > 0.05$). DF=degrees of freedom.

Explanatory variables included in model	Residual DF	Residual deviance
Cryptomeria	14	26.3
Year	12	48.7
Rat control	14	43.0
Time of breeding	14	43.2
Cryptomeria + Rat control	13	26.1
Rat control + Time of breeding	13	33.3
Cryptomeria + Time of breeding	13	18.2*
Cryptomeria + Time of breeding + Rat control	12	16.8*
All	9	7.6*

Table 6.10. Percentage breeding success of the Mauritius Fody, 1989-93, according to nest tree choice and timing of breeding. Success calculated using the Mayfield method includes 95 % confidence limits (in brackets).

Nest tree	*Pinus*/*Euc*/Other			*Cryptomeria*		
Time in breeding season	early	late	all	early	late	all
All nests	0	0	0	68	21	51
Nests found before laying	0	0	0	67	21	45
Mayfield method	9 (2-48)	3 (0-60)	6 (1-28)	63 (44-89)	23 (9-58)	46 (32-67)

FFY can be estimated for birds inside and outside Pigeon Wood. The mean brood size for Mauritius Fodies is around 2.5 (Chapter 4). Three pairs in Pigeon Wood laid 22 clutches in two years, an average of 3.7 clutches per female per year (Chapter 4); females whose nesting attempts usually fail may lay more repeat clutches. For the three fody pairs in Pigeon Wood whose every breeding attempt was followed in 1991-93 (six pair years), ten broods each of 2-3 fledged, suggesting a mean FFY of around 4 (or 2.5x10/6) for these birds. Elsewhere, with 6 % nest success (estimated using the Mayfield method) and five clutches per season (the maximum number of clutches recorded for one pair), FFY is estimated at 0.75 (or 0.06x5x2.5).

6.4 Discussion

6.4.1 *Between-species variation in breeding success: behavioural aspects*

Two common strategies of nest predator avoidance occur on Mauritius: distraction behaviour (including direct aggression) and choice of a nest site invisible, inaccessible or unattractive to predators.

Kestrels, cuckoo-shrikes, black bulbuls and flycatchers show strong nest distraction behaviour: the adults scold, call at, fly at or strike intruders (Jones 1987, pers. obs.). Pink Pigeons (McKelvey 1976, Jones 1987, pers. obs.), black bulbuls and olive white-eyes (Guérin 1940-53) reportedly have injury-feigning distraction displays. However, for these two passerines I did not see this in six and one nest visits respectively; indeed, for the olive white-eye and fody, I saw no form of distraction behaviour.

Kestrels and parakeets nest in cavities (Jones 1987); hole nesters typically suffer fewer nest losses than open nesters (Lack 1954, Nilsson 1986). Cuckoo-shrike nests, eggs and young are very well camouflaged (pers. obs.). Fodies, black bulbuls and pigeons build large nests, which, like those of the cuckoo-shrike, are sometimes poorly hidden and readily accessible to arboreal mammals (Cheke 1987c, pers. obs.). Fodies and pigeons seem behaviourally very naïve to nest predation (D. V. Merton verbally 1992), often calling on approach to the nest and behaving conspicuously at the nest; male fodies are especially ebullient in these respects.

Considering behavioural characteristics only, fodies and pigeons therefore appear the most prone to nest predation of the native species.

6.4.2 *The effect of rat control, including a possible secondary effect*

The effect of poisoning on rat populations was unknown, although bait take was consistently high and rats were by far the most likely consumers of the poison. Using the same method in New Zealand, Innes & Williams (1990) found a 91 % reduction in Roof Rat activity. It is therefore likely that rat populations in Pigeon Wood were substantially reduced by poisoning.

The probably significant increase in breeding success shown by the Pink Pigeon in response to rat control is therefore not surprising, considering the evidence implicating rats as major nest predators. Clearly, rat control is a valuable short-term measure for increasing the productivity of this species, especially if combined with supplemental feeding. Supplemental feeding for pigeons intensified at the same time as rat control began and so it is impossible to separate the effects of these two management practices. It seems likely that rat control had a greater direct effect on breeding success (as distinct from productivity) than did supplemental feeding.

Since rat control appeared to increase pigeon breeding success, why was it not shown to affect fody breeding success? This is at present inexplicable, since evidence for severe rat predation was as strong for fody nests as for pigeon nests. It cannot be assumed that rat control does not in fact result in increased breeding success for fodies, because sample sizes in this study were small.

Predator control may have the secondary effect of increasing the number of nest losses caused by factors other than predation. For the Pink Pigeon, with rat control, 39 % (7/18) of failures did not occur by predation, compared to 9 % (1/11) without rat control. The sample is small, but the difference is consistent with the hypothesis that very heavy predation pressure masks other factors which affect breeding success, such as infertility or death of eggs, and death of squabs. Dead or infertile eggs could only be recognized as such by the parents (causing desertion) if incubated to full term; this and the death of squabs could rarely happen without rat control, because few clutches then lasted more than a few days.

6.4.3 *Reasons for the dependence of breeding success on nest-site choice*

The most important factors affecting siting of nests of Mauritian birds are likely to be predation and climate (for the latter, especially wind and rain). The Mauritius Fody nest data show that siting is very variable and is related to breeding success. Nests in dense *Cryptomeria* appear well protected against rain and wind, but *Pinus* and *Eucalyptus* do not give much if any greater protection than do the native tree species; indeed, native trees generally withstand cyclones better than do exotics (King 1945). There is no evidence that breeding failure caused by weather is more severe in native trees than in exotics. Instead, the breeding success of the fody has been shown to be dictated mainly by the predation rates in the various species of nest tree. Mauritius Fody nests in *Cryptomeria* had a significantly higher success rate than did those in all other tree species. Since nearly all Pink Pigeon nests were in *Cryptomeria*, no data exist on success in different tree species.

The dependence of breeding success on nest tree species may be explained in terms of two main factors: the structure of the trees, and the behaviour of the (presumed) main nest predators (Roof Rats and monkeys). The native trees are broad-leaved, with habit typical of lower montane tropical moist forest (Vaughan & Wiehé 1941, pers. obs.). By contrast, *Cryptomeria* has extremely dense foliage, and even a nest as large as a Mauritius Fody's can be hidden in a large terminal frond so as to be almost invisible from any angle; see Fig. 4.1. Nests on the inner branches (for example, those of Pink Pigeons and black bulbuls) are also well shielded from view by foliage. However, nests in *Pinus* and *Eucalyptus* are little or no better concealed than those in native trees.

Neither Roof Rats nor monkeys have been studied in Mauritian upland forest, nor do data exist on their densities in plantations and native forest. However, from anecdotal observations and the animals' behaviour elsewhere, inferences can be made on their habitat use.

Monkeys in the Mauritian lowlands, studied by Sussman & Tattersall (1980), fed largely on fruit (70 %), other plant parts (23 %) and invertebrates (5 %); snails, lizards and birds' eggs were also considered likely prey for forest-living populations. Forest-living Roof Rats in Malaysia (Harrison 1954), New Zealand (Best 1969, Daniel 1973, Innes 1979) and Galapagos (Clark 1981) were also omnivorous, with seasonal shifts between animal and plant food, according to availability. Most animal food was invertebrate; birds and their eggs were rare in stomach contents. For either species, foraging time is likely to be devoted mainly to searching out staple items. Therefore it is very unlikely that they would spend much time searching for nests, even though Cheke (1987c) reported monkeys "bird-watching" (the monkeys were presumed to be watching bird behaviour with a view to finding nests). I suggest that most nests that rats or monkeys take are found incidentally.

The floristically diverse Mauritian native forest supports a wide variety of edible plant matter (supplemented by the many naturalized exotics), and presumably also invertebrates, and this should result in high food availability to monkeys and rats. Plantations are, however, likely to be much poorer. Exotic plant species typically harbour fewer insects native to their adopted country than do native trees; this effect is strongest for taxonomically isolated plant taxa (such as conifers in Mauritius: no native species exist) and species with unusual phytochemistries, such as *Eucalyptus* (Strong *et al.* 1984). The three plantation tree genera support few epiphytes or other plant species growing underneath or alongside them. Although the uniformity of the plantations must result in poor food diversity, the plantation species do themselves produce seasonal food. Monkeys forage commonly in *Pinus* plantations, at least seasonally (pers. obs.), eating the bark, cambium and phloem of *Pinus* tops and branches; the more resinous *P. elliotti* is attacked less than *P. taeda* (Owadally 1980). Rats also eat *Pinus* cones (Owadally 1980). I saw many freshly chewed cones on the ground, along with a failed Mauritius Fody nest (with typical rat damage) in a *Pinus* plantation by State Land Raoul in December 1992. In one study in Madagascar, Brown Lemurs *Eulemur fulvus* entered *Pinus* and *Eucalyptus* plantations when flowers were available for feeding, but not at other seasons (Ganzhorn 1985). *Cryptomeria* seems to have least to attract rats or monkeys, with extremely sticky and persistent resin; I saw no sign of any animal eating its cones or shoots, and monkeys were rarely seen in Pigeon Wood.

Considering only the upland habitats used also by native birds, I suggest that the predators' usual foraging behaviour will cause them to make greatest use of the native forest, to use *Pinus* and *Eucalyptus* either less intensively or only seasonally, and to avoid *Cryptomeria*. This would reduce contact with the birds nesting in the latter habitats, thereby reducing the predation rate and ultimately increasing the breeding success. By the same token, the plantations are usually poor foraging habitat for birds, and native birds taking advantage of the nesting cover therefore also require better foraging habitat (usually native forest) in their territories. This is clearly seen in the distribution of fody territories (Fig. 3.9).

In short, I suggest that nests in groves or plantations of *Pinus* and *Eucalyptus* will, like those in *Cryptomeria*, experience a lower predation rate, and hence a higher success rate, than nests in native forest. This effect will not be as marked as it is in *Cryptomeria*, but will apply for all bird species. I therefore suggest that the nesting success estimated outside Pigeon Wood (6 %) is higher than the true average, because nearly all nests found outside Pigeon Wood were in *Eucalyptus* and *Pinus*; nests in native trees (believed to be the least successful category) were under-represented in my sample.

6.4.4 *The value of* Cryptomeria *as a nest tree*

In addition to the known selection of *Cryptomeria* for nesting by the entire wild Pink Pigeon population, this study has documented high productivity for Mauritius Fodies nesting in *Cryptomeria*. All 20 successful fody breeding attempts (and also 19 failures) occurred in *Cryptomeria*; the 22 in other tree species all failed. The successful nests were all in Pigeon Wood, with the exception of one in the small plantation of young

Cryptomeria near Alexandra Falls. The latter was the only nest monitored in a *Cryptomeria* grove away from Pigeon Wood, and the only successful nest out of 23 outside Pigeon Wood.

The higher productivity in Pigeon Wood compared to elsewhere is apparent also from my observations of dependent juveniles, which are easily found by their call and may be assumed to be in or near their their natal territory (Chapter 4). In the four breeding seasons combined, I saw dependent juveniles at least 50 times in and around Pigeon Wood (including many broods whose nest I had not found), but only three times at distances more than 200 m from Pigeon Wood: once each near Piton Savanne, Montagne Cocotte (both almost certainly nested in *Eucalyptus*) and Pétrin (in a *Pinus* plantation bordering native forest).

6.4.5 *Seasonal variation in breeding success*

For the Pink Pigeon, Jones (1987) found lower breeding success in January to May than in June to December. Too few pigeon nests were found during the 1989-93 studies to investigate this, but I found a similar pattern for Mauritius Fodies (although no breeding occurred between April and August). This is very likely to be related to the annual cycles of the predators. Roof Rats studied elsewhere show seasonal dietary shifts (see references in Section 6.4.3) and population fluctuations (for examples, Gomez 1960, Tamarin & Malecha 1971). Both factors could affect nest predation rates, but data are lacking on Mauritius, for both Roof Rats and monkeys.

6.4.6 *Evolution of the use of plantation trees for nesting: timescale and possible mechanisms*

Pinus spp., *Eucalyptus* spp. and *Cryptomeria japonica* all appear to have been first introduced to Mauritius in the early nineteenth century, but only began to be planted widely between 1880 and 1900 (Sale 1935, Brouard 1963, Edgerley 1963), when 20,000 acres (81 km^2) of plantations of these species (plus *Juniperus* sp. and camphor *Cinnamomum camphora*) were created on the central plateau, including Piton du Milieu and Grand Bassin (Brouard 1963); much further planting followed, including Koenig's (1926) policy of planting up gaps in native forest to produce the groves which still exist in the Bassin Blanc - Piton Savanne area (Chapter 2). The use of these trees as nest sites must therefore have arisen within the last 100 years.

For the Pink Pigeon, *Cryptomeria* has been used for nesting since at least the 1940s or 1950s (L. Edgerley in Jones 1987). Newton (1960) found a nest in a "Pencil Cedar" on Piton Capote in 1954; this was interpreted by Jones (1987) as *Cryptomeria*, but the name usually refers to *Juniperus* spp. (Mabberley 1987); whatever its identity, it is a conifer, so the use of exotic conifers in the 1950s is confirmed. By the 1970s, *Cryptomeria* accounted for nearly all nest trees, native trees being used only occasionally (Jones 1987), and extremely rarely by 1989-93 (this study).

For the Mauritius Fody, the habit of nesting in conifers (*Pinus* spp. and *Cryptomeria*) was well-established by the early 1970s (Cheke 1987c). In 1954-57, Newton (1959) noted an association with *Cryptomeria* and *Eucalyptus*, but did not state in what tree species he found nests. In 1967, J.-M. Vinson (verbally 1993, from field notes) found that the best area for native birds was south of Mare aux Vacoas, in and around State Lands Dayot and Arnaud. The vegetation here was a mixture of native forest, conifers, *Eucalyptus* and many exotics; black bulbuls, flycatchers and Mauritius Fodies were particularly common and Pink Pigeons were always present. No nests were found. At the same time, Vinson found the Macchabé - Brise Fer forests to be much poorer, with Mauritius Fodies almost absent, as in 1973-75 (Cheke 1987c). These observations strongly suggest that the fody was, like the pigeon, nesting in exotics by the 1950s.

How did the use of exotics as nest trees arise? The mechanisms determining future nest site choice in young birds are not well understood. Young birds develop habitat preferences by imprinting on to a certain environment (Hilden 1965). Imprinted attachments may be to the site of hatching (Klopfer & Ganzhorn 1985). Temple (1978c) cited examples consistent with the hypothesis that young birds imprint on the nest site from which they fledge. If the hypothesis proves true, the situation on Mauritius is easily explained.

The occasional use of atypical nest-trees has been demonstrated for both the Pink Pigeon and the Mauritius Fody (see Section 6.3.3). The use of plantation trees may have first occurred in this way, and the greater success rate in such trees would then have resulted in proportionally more juveniles fledging from these nests. The new nest site choice would persist if the choice of nest tree were passed down from parents to fledglings. This could be achieved if young birds imprint on the nest site in which they are reared, and so are likely to nest in similar sites when they mature. If this were true, the higher breeding success in plantation trees, especially *Cryptomeria*, compared to native forest could have led rapidly to the establishment of the new nesting tradition.

Alternatively, birds may instinctively prefer the plantation trees. I suggest that this hypothesis is unlikely because there is no obvious reason why the birds would know that these would be safer sites; in order for the tradition to persist, every generation would have to make the same choice independently.

6.4.7 *Breeding success of introduced birds*

In Kowhai Bush, New Zealand, Moors (1983) found predation rates in native and introduced birds to be similar, at around 64-70 %; in his study, 75-81 % of all nests failed. The few available data suggest that introduced birds in Mauritian forests also suffer levels of nest predation as severe as the natives. However, Madagascar Red Fodies on Mauritius suspend their nests more often than does the endemic fody; this could improve defence against predators, as Crook (1961) thought on Seychelles, thereby increasing breeding success.

To explain the survival of exotics, it is necessary to examine their ability to survive high levels of nest predation. This is done in the next chapter, along with the discussion of the effects of nest predation on native birds.

Chapter 7. The effects of nest predation on populations of Mauritian forest birds

7.1 Introduction

As pointed out in Chapter 6, information available before this study was carried out was insufficient to identify the past, present and future effects of nest predation on native Mauritian bird populations. However, unjustified speculation has still appeared. Discussing predation on native birds by monkeys, rats and mongooses, Sussman & Tattersall (1986) claimed that "it is unlikely that such predation... is the major agent of the endangerment of these species, for if it were, one would expect them to have disappeared long ago". They believed that habitat destruction was the main threat, and did not appear to entertain the possibility that extinction due to predation (or a combination of factors, of which predation was crucial) could take longer than 300 years.

The patterns of breeding success of the forest-living native birds of Mauritius were described, with special attention to the Pink Pigeon and Mauritius Fody, in Chapter 6. The results may be summarized as follows. Breeding success was exceedingly poor for most species in most areas. The dominant cause of nesting failure was found to be predation of eggs or chicks. All evidence pointed to both Roof Rats and Crab-eating Macaques being serious predators, but the precise proportions of all losses caused by each of these introduced mammals could not be determined. The Pink Pigeon, whose entire wild population bred in one 6 ha *Cryptomeria* grove, fledged young from only 9 % of nesting attempts without conservation management, increasing to 35 % with rat control and supplemental feeding. Between 50 % and 70 % of the Mauritius Fody population was believed habitually to select exotic plantation trees (*Cryptomeria*, *Eucalyptus* and *Pinus*) as nest sites. The breeding success of Mauritius Fodies nesting outside *Cryptomeria* was estimated at around 6 %. Most of these fody nests were in *Eucalyptus* or *Pinus*; it is likely that fodies nesting in native trees had a success rate lower still. Breeding success for fodies nesting in *Cryptomeria* was, however, around 46 %, with or without rat control. Of the fody nests found in *Cryptomeria*, nearly all were in the same grove (Pigeon Wood) as was used by the pigeons.

In this chapter, I examine the effects of nest predation, first on the autecology of the birds and then on the present status of bird populations. I then use both heuristic arguments and computer simulations to investigate whether nest predation is likely to have played a critical part in the mechanism by which the birds' present status has been reached. Species elsewhere in the western Indian Ocean region, which appear to be showing analogous patterns of distribution in response to predators, are identified. Armed with the fullest possible understanding of existing data, I propose a rationale for long-term conservation measures to take appropriate account of the predation problem. These measures are discussed in practical terms in Chapter 9.

7.2 Heuristic arguments

7.2.1 *Probable effects of predation on autecology*

In Chapter 6, it was demonstrated that Mauritius Fody nests in groves or plantations of *Cryptomeria* experience a lower predation rate, and hence a higher success rate, than nests in other tree species. It was suggested that *Pinus* and *Eucalyptus* were selected as nest trees because nests in these trees suffer a lower predation rate than do those in native trees. These effects were expected to apply to all bird species nesting in these trees.

The reduced predation rate in *Cryptomeria*, *Eucalyptus* and *Pinus* is consistent with the selection of these trees as nest sites by an estimated 50-70 % of the Mauritius Fody population (Section 6.3.3) and by the entire wild Pink Pigeon population. This nest site choice must be explained by the better breeding success. Safford (1991) had already suggested this for the fody, but had few supporting data. The breeding success of the Pink Pigeon in other trees cannot be studied and compared with that in *Cryptomeria*, because the whole population breeds in one *Cryptomeria* grove (Pigeon Wood). However, the pigeons' selection of *Cryptomeria* can be explained in the same way as can the fodies'.

The groves of plantation trees presumably provide blocks of habitat which the predators will avoid, so that species nesting in the groves will benefit even if their nest is not placed in the plantation species. This explains why flycatchers are concentrated in Pigeon Wood, although they do not nest in the *Cryptomeria* trees. The birds nesting on saplings of other tree species growing under the *Cryptomeria* would be expected to benefit from the scarcity of predators that the *Cryptomeria* provides.

All the other native passerine species use plantation trees as nest sites to unknown (but probably varying) extents, and this is likely to be for the same reason. The cuckoo-shrike appears to make the least use of plantation trees: its preference for building on horizontal branches at an open fork (Cheke 1987c, pers. obs.) may restrict its use of conifers, which have never been recorded as nest trees. Two out of five cuckoo-shrike nests I followed at Brise Fer (all in native tress) succeeded. If this sample is typical, the success rate is much higher than that of the Mauritius Fody outside *Cryptomeria*. As already pointed out (Section 6.4.1), cuckoo-shrike nests and chicks are remarkably well camouflaged and the adults are aggressive, which may aid survival where predators are common, but I have too small a sample to reach any firm conclusion.

7.2.2 *Probable effects of nest predation on distribution*

Pink Pigeon

The Pink Pigeon has long occupied only a fraction of the habitat apparently suitable for it; even in the mid nineteenth century, it was rare and restricted to the south-west (Newton 1861), although extensive native forest then survived in the central east (Cheke 1987a). In the 1980s, the wild Pink Pigeons used only around 60 % of the suitable habitat in the south-west (Jones 1987). The birds were then restricted to the Southern Slopes, leaving the less degraded Macchabé Area vacant; the same was true in 1989-93 (pers. obs.). The last regular breeding site away from Pigeon Wood, used until about 1977, was another *Cryptomeria* grove on a stream feeding the Rivulet des Chevrettes in State Land Declerc, close to Bois Sec Nature Reserve (Jones 1987). I found neither pigeons nor Mauritius Fodies there in 1993.

Jones (1987) explained the pigeons' current restriction to the Southern Slopes by the high plant species diversity in this wetter area. This is debatable, as the vegetation is so much more degraded than that in Macchabé - Brise Fer (even if more plant species may be present); a causal link would be difficult to establish. Jones (1987) suggested that the pigeons stopped using the Macchabé - Brise Fer forests because they were unwilling to cross the plantations of Les Mares or the 400 m deep Grandes Gorges (pigeons do in fact occasionally make this crossing: Jones *et al.* [1992], pers. obs. of ringed birds). These observations do not, however, explain why a population of pigeons could not have survived entirely within this 12-15 km^2 area; Jones & Owadally (1988) also thought that the area could support a small, self-supporting population.

A far more convincing explanation for the restriction of the Pink Pigeon to the forests of the Southern Slopes is that the existence there of Pigeon Wood provides safer nesting cover than is available in the Macchabé Area, and that a population outside Pigeon Wood would not be self-sustaining because of nest predation rather than poor food diversity. The combination of dense, mature *Cryptomeria* and native forest, found in Pigeon Wood, is unique. The rarity of the pigeons' visits to the Macchabé Area may be because they can meet their feeding requirements without leaving the Southern Slopes, as much as due to any supposed unwillingness to cross the plantations and gorges.

The loss of the Bois Sec colony was probably brought about by two factors. Firstly, the area was until the mid 1970s contiguous with a large area of native forest, but forest clearance then left it isolated from foraging habitat, so birds may simply have emigrated rather than died out. Secondly, even in Pigeon Wood, productivity is critically low, and the same was presumably true at Bois Sec: perhaps too much so to maintain the population there, particularly if some birds had indeed emigrated due to the area's isolation.

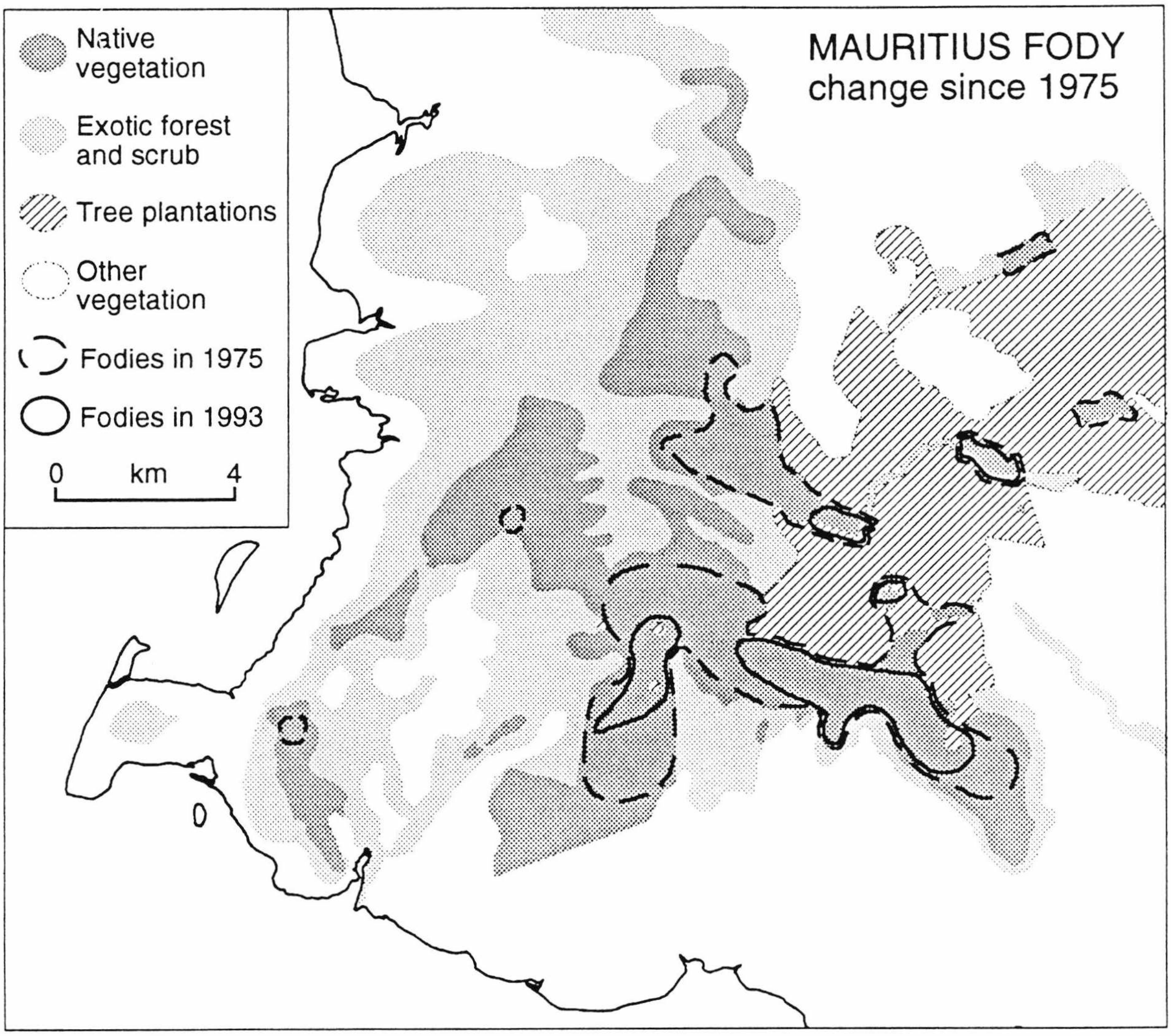
Mauritius Fody

Fig. 7.1 shows the entire distribution of the Mauritius Fody found in 1975 and in 1989-93, in relation to the main areas of native forest, exotic forest and scrub, and tree plantations (nearly all *Pinus* and *Eucalyptus*, with some *Cryptomeria* and other species). In more detail, Fig. 3.9 shows all Mauritius Fody territories found between Alexandra Falls and Combo (out of a total of 73-83 estimated in the same area: Chapter 3). The distribution in 1993 was obviously associated with sites where both native forest and plantations could be included within territories; these were generally either where plantations abutted native forest, or groves were surrounded by native forest. The somewhat isolated population of 20-25 pairs in upper Bel Ombre was in 1993 concentrated around the two *Pinus* plantations and the broken line of conifers along the main track below the plantations. The largely unbroken areas of native forest of lower Bel Ombre, Black River Peak, Plaine Champagne and Macchabé - Brise Fer were all more or less devoid of fodies, although these included some of the best preserved areas. I propose that availability of suitable nesting cover is an important constraint on habitat suitability. For the Pink Pigeon and Mauritius Fody, the variable breeding success in different tree species seems to have large-scale effects on distribution.

Other species

Effects on the distributions of other native land-birds are less obvious than those on the Pink Pigeon and Mauritius Fody; also, fewer data exist. However, all native landbirds experience predation pressure, and several further aspects of bird distribution may be at

Fig. 7.1. Distribution of the Mauritius Fody in 1975 and 1993, in relation to vegetation types. 1975 distribution excludes areas of habitat cleared since then (such as the Kanaka area), and assumes that the Rivière du Poste patch was occupied in 1975.



least partly explained by variation in predation pressure.

Black bulbuls and olive white-eyes are relatively common along much of the southern scarp (especially between Montagne Cocotte and Piton Savanne), but rare in Macchabé - Brise Fer. This pattern is analogous to that for the fody and pigeon, and I suggest a similar explanation. Cheke (1987c) and Safford (1991) could not explain why the only olive white-eyes in the Macchabé - Brise Fer area survive in the dwarf forest around State Land Florin; rainfall and plant species composition in Florin are similar to the contiguous Macchabé forest, where olive white-eyes are absent. Although no plantation trees are available to provide safer nest sites, the dwarf forest may perform the same function: it is so degraded by *Psidium cattleianum* as to be almost impenetrable and may well be unproductive for monkeys and rats, so offering lower predation rates than the tall forest.

Cheke (1978) suggested that the rarity of flycatchers in native forest might be due to predation. They are indeed absent from most areas which appear structurally suitable, and the fact that an exceptional cluster of territories exists in Pigeon Wood, where predation rates on other species are known to be unusually low, provides circumstantial evidence in support of Cheke's hypothesis. The most important area for flycatchers on Mauritius is the area of mixed exotic plantations at Bras d'Eau (Chapter 3). These appear extremely unproductive for most animals, with very few plant species including large stands of *Araucaria*, another spiky, exotic conifer which may well rival *Cryptomeria* for unattractiveness to vegetarian feeders; monkeys are certainly rare there (pers. obs.). As in Pigeon Wood, the flycatchers nest mainly on saplings under the shade-bearing trees (Cheke 1987c, pers. obs.).

Further research on the ecology and abundance of rats and monkeys may yet prove to what extent these latter suggestions are true, and also indicate further effects of introduced nest predators on the native birds. Lowland and transitional forest areas include some of the best-preserved native vegetation (Strahm 1993 & in prep.); could high predation rates in these areas help to explain why native birds are so rare there (Cheke 1987c, pers. obs.)? Are olive white-eyes absent from the Montagnes Bambous but present on Montagne Lagrave (Chapter 3) because of differences in predation rates?

7.2.3 *The rôle of nest predation in the declines of native Mauritian birds*

It has been demonstrated that the present distribution of the Pink Pigeon and Mauritius Fody (and possibly other native species) are consistent with the existence of a link with varying nest predation rates. It seems very likely that predation was the main cause of the extinction of the fody and pigeon over most of the native forest area, by reducing recruitment below mortality. Only in the areas where breeding success was high enough could populations persist. The distributions would therefore be expected to contract towards the areas of highest breeding success, in effect increasing the population's average breeding success. The populations and distributions would stabilize only when the contraction had brought the average breeding success high enough to match recruitment with mortality.

Could the declines be more due to other factors than to nest predation? If the population had been depleted for reasons other than nest predation (such as pesticides, cyclones, food shortage or disease), there is no reason to expect the distribution to centre on areas of areas of high breeding success, unless this were a random effect of redistribution. Since fodies appear faithful to their established territories (Chapter 4), there is no reason to expect them to redistribute. An alternative is that the cause of decline has had the same consequences on distribution as would be expected if the cause were nest predation. This alternative is rejected for the time being, because no cause is apparent which might have such an effect.

The Pink Pigeon population may have stabilized when the breeding range was reduced to Pigeon Wood; without Pigeon Wood, the contraction might not have been halted, resulting in the pigeon's extinction. However the population is so low that many other factors (including a period of unusually severe predation) could cause fluctuations large enough to bring about the pigeon's extinction.

The Mauritius Fody's decline appears to have followed a similar course to that of the Pink Pigeon, but productivity in Pigeon Wood is very much greater, which should cause the population decline to level off at a higher stable population than for the pigeon; this level may indeed already have been reached.

7.3 Modelling of population processes

7.3.1 *Introduction*

In the 1992-93 season (assumed to be a typical season), nine Mauritius Fody nests were seen to succeed in Pigeon Wood and a further approximately four broods were seen, from undiscovered nests, so the actual number of broods was at least 13. Allowing an average of 2.5 fledglings per brood, this indicates that at least 33 juveniles fledged from nine pairs. Surely, no further analysis or computer simulation is needed to show that fody recruitment in Pigeon Wood population is sufficient to maintain the population (nine pairs) there. Fody territories occupy the whole of Pigeon Wood (Fig. 3.10), and so most of these juveniles must disperse outside Pigeon Wood.

Pigeon Wood can therefore be therefore considered as a "source area" for fodies, defined here as a locality where on average enough young are produced to maintain the existing number of pairs and to cause emigration of a surplus. I define a "sink area" as a region where the number of young produced locally is insufficient to compensate for mortality; populations may be maintained, or extinction slowed, by immigration from the source regions. This is another example of the rescue effect described by Brown & Kodric-Brown (1977, cf. Chapter 4). Pure native forest areas are sink areas, as they are believed to have the lowest breeding success. Certain areas may be neither sources nor sinks: recruitment may balance mortality perfectly. Of course, even the most fecund source population is vulnerable to catastrophes and genetic problems.

The distribution of the fody can be considered as a series of source areas and sink areas. The effect of destroying or creating habitat may depend on whether source or sink areas are involved. If a sink area is lost, the long-term effect on the fody population may be small, since the birds lost were contributing little to the viability of the population. If a source area is lost, the effect is likely to be much greater. By the same logic, creation of new source areas, such as a second Pigeon Wood, would be valuable conservation measures, whereas creation of further areas of good foraging habitat without safe nesting sites would be much less helpful to the birds. How viable is a population consisting of sources and sinks likely to be, and can its survival chances be enhanced by adding further sources?

7.3.2 *Modelling methods*

Probability of extinction may be increased or decreased as a result of management measures which alter habitat. This probability needs to be assessed as rigorously as possible. The process of modelling and analysing the forces determining the fate of a population is termed Population Viability Analysis (PVA; Soulé 1987). The demographic and genetic processes in small populations are unpredictable, but the population size, time to extinction and genetic variation can be described by probability distributions, and combine to determine the expected fates of populations (Lacy 1993). PVA requires that these distributions be modelled. This has been attempted using empirical observation of the fates of populations with varying characteristics (Belovsky 1987) or analytical models from probability theory (Goodman 1987). The former is impossible on Mauritius as the empirical data do not exist; the latter was criticized by Lacy (1993) as incorporating only a few of the threatening processes and failing to adjust for interactions between them.

Instead of these methods, in the 1990s, the most common approach to PVA has involved computer simulation. "By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and which cumulatively determine the fates of populations" (Lacy 1993). VORTEX is such a program, which has been used in PVA more widely than any other. It was designed to follow the progress of small, often isolated populations which are vulnerable to the effects of stochastic processes. It has already been used to model an endangered Mauritian bird population in the PVA for the Pink Pigeon (Bruford *et al.* 1991). Details of the structure, assumptions and capabilities of VORTEX are given by Lacy (1993).

Use of VORTEX requires the input of various demographic and genetic parameters (the latter only if inbreeding depression is to be modelled), derived or estimated from autecological study. The number of independent simulations and the timespan over which they are run are specified by the user. The output of the program consists of summary statistics based on the set of simulations; these concern extinction probability (proportion of simulations in which the population went extinct), time to extinction of populations that went extinct, population growth rates and mean sizes and levels of genetic variation for surviving populations.

In this section I use VORTEX (Version 5.1; April 1992) to simulate (more formally than I have done in the foregoing heuristic arguments) the fate of a population of Mauritius Fodies inhabiting sink and source areas, and to demonstrate the changes in extinction probability that would follow the creation or destruction of source and sink areas.

7.3.3 *How VORTEX was used*

The parameters used here are derived from the studies of the annual cycle and nest predation (Chapters 4 and 6). Certain patches of forest (source areas) support elevated breeding success, but a source area can only support a fixed number of breeding pairs (the carrying capacity). I do not attempt to model every detail of the fody population as it was in 1989-93. The assumptions I make about the the main features that need to be modelled are the following:

1. Mortality rates do not differ between source and sink areas.
2. If the total population declines, the source areas remain at carrying capacity while birds are first lost from the sink areas.
3. Birds recruited in source regions in excess of the source area's carrying capacity do not die, but emigrate to the sink areas.
4. Birds recruited in sink regions do not enter source regions.

Reproductive rates are entered in VORTEX as percentages of females in the population that produce litters of a certain size. For birds, "litter size" equates to the number of fledglings per female per year (FFY). Modelling the source and sink as two separate subpopulations is problematic, because of point 3: if populations exceed the carrying capacity, VORTEX introduces a mortality, rather than emigration, to limit the population size. Imposing an emigration rate (from source to sink) calculated to keep the source regions at carrying capacity would be a more accurate model, but VORTEX assumes that the probability of migration is independent of age; migrants are in fact likely to be immatures.

The populations of source regions such as Pigeon Wood have been shown to be robust. It is the survival of the sink region that is in doubt, and whose population processes need to be modelled. The true situation is most closely approached by modelling the sink population only, with supplementation of immatures (from the source). The supplemention rate is calculated using the demographic parameters of the Pigeon Wood (source area) population.

Only the single population on the Southern Slopes from Alexandra Falls to Combo (including the whole Cocotte - Savanne region) is modelled. Inclusion of the small and isolated subpopulations at Bel Ombre, Raoul and around Grand Bassin and Rivière du Poste (comprising 30 % of the population: Chapter 3) would require modelling a metapopulation with five subpopulations. This would be unnecessarily complicated, as well as difficult as migration rates are not known; this is not needed in order to satisfy the stated aim. The parameters used were as follows.

Catastrophes in the form of severe cyclones occur about every 15 years, usually in January to March (the last third of the breeding season). They are assumed to terminate the breeding season, resulting in a 33 % reduction in breeding in the year, but direct mortality of native forest passerines caused by storms on Mauritius does not seem likely to exceed 10 % (see Cheke 1987c).

Age at first breeding is modelled as two years, because 'half-red' (presumed immature) birds were never recorded breeding (Chapter 4). Some birds may attempt to breed at one year, but first-time breeders are anyway often unproductive.

Maximum age and mortality can only be guessed. Maximum age 15 years, adult annual mortality 15 % and juvenile mortality 30 % are used, consistent with data in Prŷs-Jones & Diamond (1984) and Fry (1980).

Reproduction rates. All adult males are assumed to breed. The maximum "litter size" (fledglings produced by one female in one year) is entered as three (the largest brood recorded). Successful rearing of two or three broods is possible (indeed, two broods were regularly reared by pairs in Pigeon Wood), but very unlikely in the sink regions where so few pairs reared even one brood. If each female lays a mean of five clutches per year, with 6 % breeding success (Section 6.3.4), then 30 % of the pairs in the sink region rear one brood, the rest none. This was suspected to be a much higher productivity than the true average breeding success for the sink area (Section 6.4.3) and so simulations were also carried out with 10 % and 20 % of pairs rearing one brood.

The *population* of Mauritius Fodies in the Cocotte - Savanne area (including Alexandra Falls and upper Combo) is 73-83 adult pairs (Chapter 3). The source area (Pigeon Wood) held nine pairs, leaving 64-72 pairs in the sink region. Including immatures, a total of 180 birds is entered.

The *carrying capacity* is defined by Lacy (1993) as the "upper limit for population size within a habitat". It is difficult to interpret this definition for a species possibly declining towards an unknown level. The food resources could probably support many more fodies than exist at present. A stable population size comparable to the number of cuckoo-shrikes or black bulbuls (around 500 birds, or about 200 pairs) is an acceptable target, and this figure is used as the minimum carrying capacity. The food limit is probably much higher than 500 birds; if safe nesting sites were provided, the birds should be able to find sufficient food almost anywhere within the native forest. Under the present conditions, the population is unlikely to reach this level.

Supplementation. As just indicated, an estimated 33 juveniles are assumed to fledge in the source region (Pigeon Wood) each year. Juvenile mortality of 30 % means that 23 reach the age of one year. Annual adult mortality of 15 % implies that three of the 18 breeding birds in Pigeon Wood die each year. If these are replaced by locally reared young, 20 one-year-olds would be free to supplement the population of the sink region each year. The lowest supplementation rate used (ten birds per year) could arise if mortality of the displaced young is 60 % (twice the guessed average), or if only seven broods fledged in Pigeon Wood (that is, if the 1992-93 season in Pigeon Wood was twice as successful as an average year). VORTEX does not allow supplementation until age one; although the young are likely to leave Pigeon Wood and join the sink population before this age, this should not greatly affect the result as they do not breed until aged two years.

Testing different management scenarios

The creation or destruction of sources can be modelled by altering the supplementation rate and the population of the sink region. The single source area of Pigeon Wood is removed by removing the annual supplementation and reverting to a single population of 200 birds with the same reproduction rates as the sink population.

Additional areas like Pigeon Wood are added by subtracting nine pairs from the sink population (to form a new source population), and doubling the supplementation rate. Expansion of existing *Cryptomeria* groves is modelled in the same way.

Assumptions of VORTEX

The model assumes that supplemented birds are unrelated to all other individuals in the population. This is not the case, as the immigrants all come from one small population. There is no evidence of genetic problems in the real population, but it is possible that future genetic effects could cause the results observed in life to deviate from those predicted by the model, even if the demographic factors were perfectly modelled. The model assumes that more genetic diversity will be maintained than is actually likely to be the case. If genetic problems were to arise, they would presumably depress the population. The other main assumptions of VORTEX, listed by Lacy (1993), seem acceptable.

When interpreting summary statistics, it must be noted that a population that is being supplemented annually cannot go extinct. It is easily shown that a population of individuals with maximum longevity m years, annual survival s, supplemented by n individuals each year, without breeding, stabilizes after m years:

$$\text{Final population} = n(s^{m-1} + s^{m-2} + \ldots + s + 1).$$

For $m=15$, $s=0.85$ and $n=20$, this computes to 122 individuals, and is the approximate minimum that the population could reach in any simulation involving these parameters (variance in the parameters causes small departures from this figure); $n=10$ and $n=40$ give respective minima of 61 and 244. Therefore in scenarios involving supplementation, the survival probability (the proportion of simulations that survived) can only be unity. Such scenarios are best compared by charting the population trends during the course of the simulation.

7.3.4 *Results*

The results of the simulations are summarized by the data in Table 7.1 and Fig. 7.2a-c.

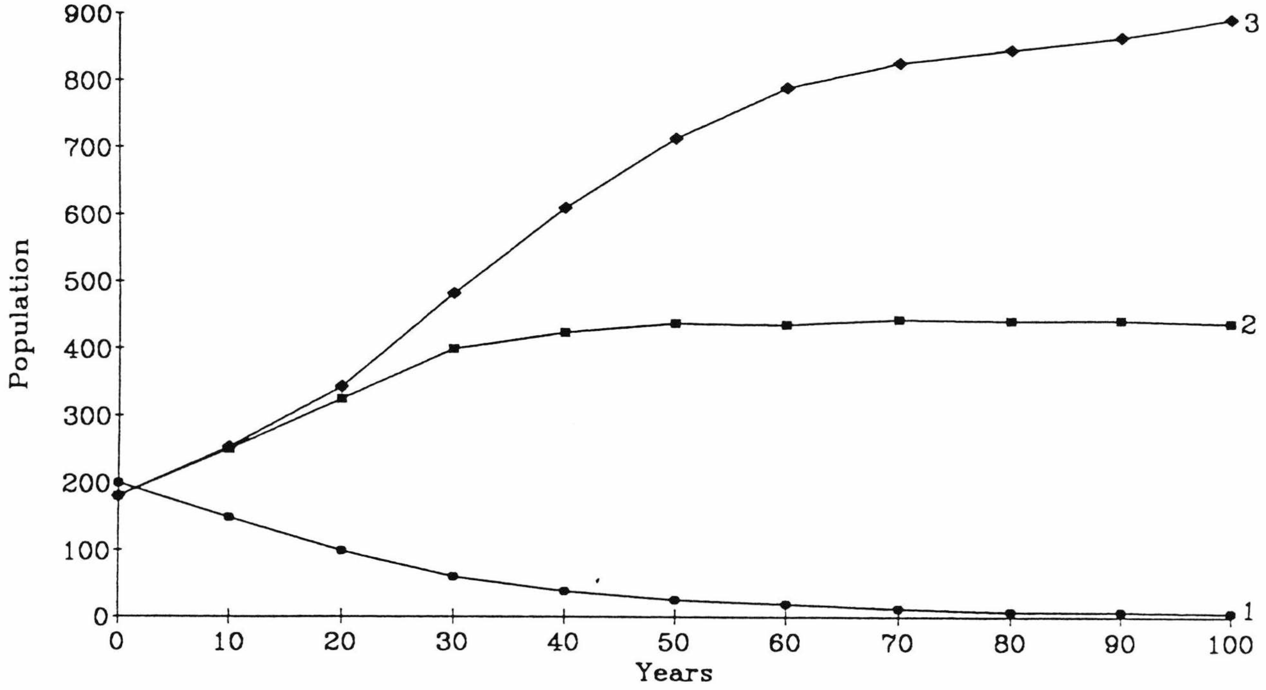
Table 7.1. Input parameters and results of simulations of the fates of Mauritius Fody sink populations using VORTEX.

% success = % of pairs in sink population which rear one brood in any year,
Init. pop. = initial population,
K = carrying capacity,
Suppl. = number of one-year old birds entering sink from source annually,
P(surv.) = probability of survival (% of runs in which population survived),
MFPop. = mean final population in runs where population survived,
MTEx. = median time (years) to extinction (all runs), if relevant,
% MGRate = mean percentage population growth rate.

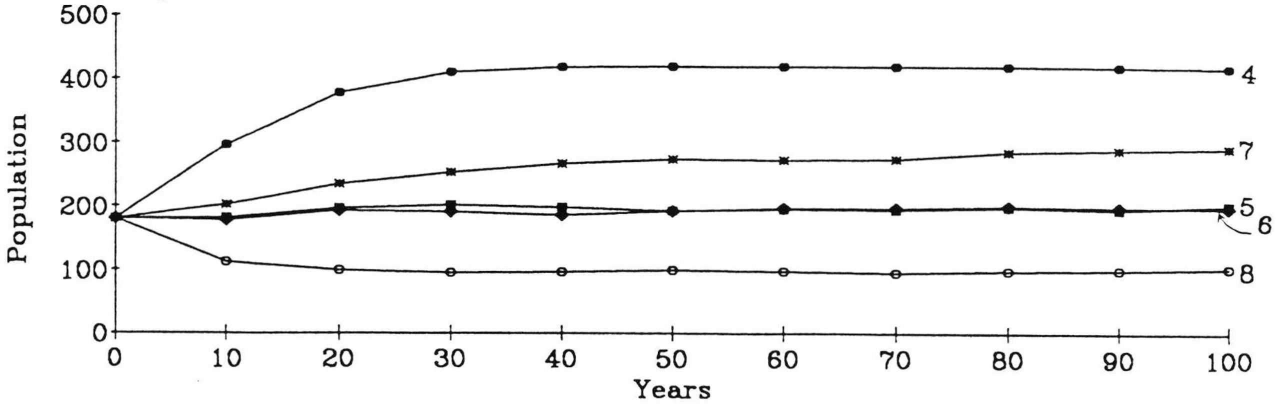
Scenario	1	2	3	4	5	6	7	8	9	10	11
Input											
% success	20	30	30	20	10	10	20	10	10	10	10
Init. pop.	200	180	180	180	180	180	180	180	160	160	12
K	500	500	1000	500	500	1000	500	500	500	1000	500
Suppl.	0	0	0	20	20	20	10	10	40	40	20
Results											
P(surv.)	6	100	100	100	100	100	100	100	100	100	100
MFPop	6	437	893	417	200	196	290	102	388	399	200
MTEx	68	-	-	-	-	-	-	-	-	-	-
% MGR	-6.7	3.1	3.1	1.9	0.1	0.1	0.5	-0.6	1.2	0.9	2.8

Fig. 7.2 a-c. Simulated fates of Mauritius Fody populations modelled using VORTEX. See Table 7.1 for details of each scenario.

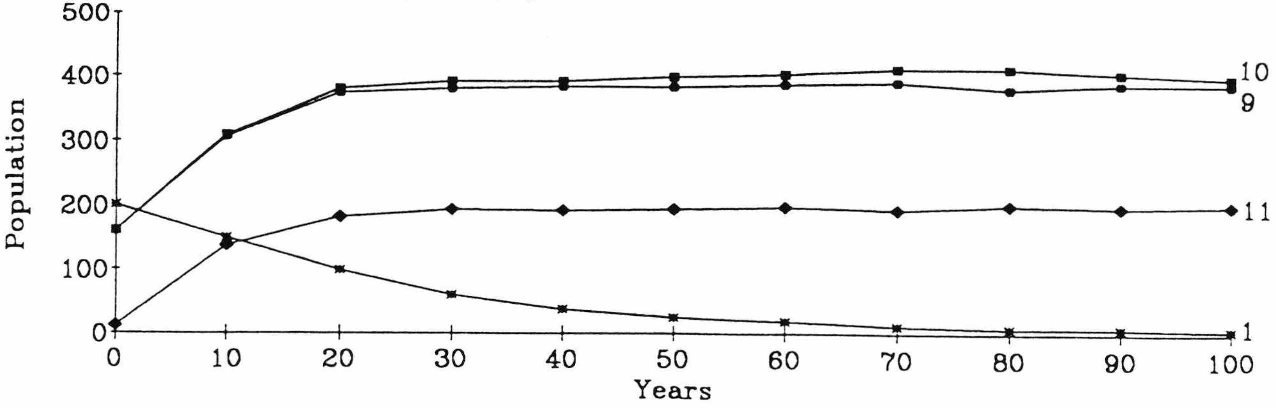
a. Scenarios 1-3: populations without supplementation; varying productivity and carrying capacity.



b. Scenarios 4-8: populations with supplementation at approximately the present level (scenarios 4-6), or half this level (scenarios 7-8); varying productivity and carrying capacity.



c. Scenarios 1 and 9-11: the effects of destruction of the only source (scenario 1), addition of an second source (scenarios 9-10; varying carrying capacity) and addition of a new source to a tiny sink population (scenario 11).



Populations without supplementation by immigration from a source

Any population in which 20 % (or less) of pairs rear one brood per year without supplementation (scenario 1) declines steeply to extinction, and is therefore correctly regarded as a sink population. However, 30 % female productivity causes a steady increase to carrying capacity, with no sign of an equilibrium population other than that imposed by carrying capacity (scenarios 2 and 3). This is consistent with the suggestion that 30 % female productivity was an overestimate (Section 7.3.3). For subsequent simulations 10 % and 20 % productivity was estimated.

Populations supplemented by immigration from a source approximately at present levels

Scenarios 4 and 5 use parameters (so far as known) as close as possible to the present, true situation in the Cocotte - Savanne area. The 130 % increase to a stable population resulting in scenario 4 (20 % female productivity) is not shown by the real population. The stable population close to the initial number resulting from scenario 5 (10 % female productivity) seems close to the observed pattern. In both cases, the population change occurs fairly quickly, soon to reach an equilibrium figure which seems to be independent of the carrying capacity (scenarios 5 and 6), although the latter obviously imposes an upper limit. A lower supplementation rate (if 1992-93 was an exceptionally good season: scenarios 7 and 8) also finally results in a stable (but smaller) population.

Effects of destroying or creating source areas

Destruction of Pigeon Wood leaves a lone sink population, which quickly goes extinct (scenario 1). Increased supplementation resulting from the enlargement of the source area population or the creation of a second source area (scenario 9) again results in equilibration at a level independent of carrying capacity (scenario 10), but this occurs at a larger final population than with a smaller, or single, source. Finally, the addition of a new source population to a tiny remnant sink population of five pairs or 12 birds (scenario 11) results in a final population close in size to that of a similar population comprising a similar source and an initial sink population of 180 birds (scenario 5). Therefore the total equilibrium population appears not to depend on the initial size of the sink population.

7.4 Discussion

7.4.1 *The effect of destruction of sources and sinks*

Consider the progressive destruction of a large area of habitat comprising extensive sink areas and several much smaller source areas. Initially, the whole region is populated by a bird species of interest. The destruction of sink areas causes bird population declines in direct proportion to the area of habitat destroyed, and with each act of habitat destruction, the bird population quickly equilibrates at a successively lower level. Then, without any change in the rate of habitat destruction, a source region is destroyed. The result is not only the loss of a small, dense source population: the entire surrounding sink region is abruptly sent into a decline to extinction, even though its habitat has been untouched by the destruction. However, other source areas survive, and the total population soon equilibrates at a much reduced level. Habitat destruction continues, now taking in the sink area, which is already devoid of birds because of the loss if its source; the bird population does not change. The destruction next reaches an inhabitated sink area, and the steady "background" decline in the bird population resumes, until another source region is struck, when another population crash ensues, and so on. When the last source region is destroyed, leaving only sink regions occupied, the bird quickly goes extinct, even though occupied habitat survives at the time when the fatal deed is done.

Overall, when a bird population of sources and sinks declines because of habitat destruction, the decline may be very far from following the pace of destruction, apart from the trivial fact that habitat destruction causes declines (not increases). Even with a steady rate of destruction, the bird declines are likely to proceed in leaps and bounds, interspersed with much slower declines or periods of population stability.

Thus, a population can go extinct well before all its once-occupied habitat is destroyed, if the productivity of the species varies over its range. The introduction of nest predators which spread over a wide area, but are geographically unevenly distributed, is likely to result in such variation; geographical variation in predation rates is proven for the Mauritius Fody. This study shows how introduced nest predators, combined with habitat destruction, can bring about the extinction of a species over a very long time interval. The notion that introduced nest predators are likely only to affect native animal populations soon after their arrival is a fallacy and must be laid firmly to rest.

It must be stressed that extinction due to the arrival of a new nest predator *can* be rapid, regardless of environmental heterogeneity, if the mortality exceeds recruitment throughout the range area (that is, even in the most productive areas). This was probably the case on the Pacific island of Guam, where the forest-living native avifauna was largely exterminated by the newly arrived snake *Boiga irregularis* (Savidge 1987). In this case, the snake became so abundant throughout the forest (to which the native birds were restricted) that there were no "refuges" (this term, used by Savidge [1987], equates here to my "source area"); the bird declines were fast and apparently terminal.

7.4.2 *The effect of nest predation in homogeneous environments*

Productivity will, in general, depend on various environmental factors. Environmental heterogeneity will often lead to variation in productivity. I suggest that uniform productivity is likely to be very rare in heterogeneous environments. However, the system of source and sink populations may not exist in more homogeneous environments.

Simulations 1 and 2 suggest that if the breeding success is uniform across the population, somewhere between 20 % and 30 % productivity (as defined in Table 7.1) will lie a productivity rate that results in an approximately steady population level. Above this critical productivity rate, populations increase to carrying capacity (if they are not already there). Below it, populations decline to extinction (scenario 1): they do not level off.

In some of these cases, a decrease in mortality rates may balance reduced breeding success to keep populations level, but if breeding success should drop by a few percent without compensatory changes in mortality, extinction would result. This could follow any increase in nest predation, and could be caused by the arrival of a new nest predator. Of concern in these cases is the fact that the difference in breeding success between extinction and survival is small, and unlikely to be resolved by field studies unless sample sizes are very large. For example, in a sample of 154 Kirtland's Warbler *Dendroica kirtlandii* nests (a much larger sample than is available for any Mauritian bird) studied by Mayfield (1961), Johnson (1979) estimated 95 % confidence limits of 47 % and 69 % nest success.

7.4.3 *The destruction of Les Mares: a possible source area*

In Chapter 3, the changes in passerine population and distribution following the destruction of the unique vegetation of Les Mares were described. For the olive white-eye and Mauritius Fody, the declines were far more serious than would have been expected from the area of habitat destroyed. This observation can now be tentatively explained by the influence of geographical variation in breeding success. I speculate that the unique vegetation and physical conditions of Les Mares made it a source area, so that its destruction affected bird populations outside the area clear-felled.

The suggestion cannot be tested because of the complete destruction of this habitat type, but two features of Les Mares could have provided protection from nest predators. Firstly, Les Mares was unique in Mauritius because it contained the last area of native *Pandanus* thickets (Vaughan & Wiehé 1953). *Pandanus* is very often selected for nesting by several Aldabran land bird species and is believed to provide good protection from nest predators (Prŷs-Jones 1979). The only nesting association with *Pandanus* reported on Mauritius is a Pink Pigeon nest in a *Sideroxylon* in a dense *Pandanus* thicket in 1974 (Temple 1978b), before destruction of Les Mares was complete. Secondly, before the 1970s clearances, Les Mares already contained several tree plantation areas, such as at Pétrin (A. S. Cheke & G. A. d'Argent verbally), and gaps had been planted up with conifers and *Eucalyptus* elsewhere in Les Mares (Koenig 1912-1928). The availability to birds of *Pandanus* thickets and/or tree plantations for nesting could have led to higher breeding success in Les Mares than in adjacent native forest, making it a source area.

7.4.4 *Evidence for similar nest site shifts in other island endemic birds*

On Aldabra, introduced Roof Rats have long been present (Atkinson 1985). Coconut *Cocos nucifera* and *Casuarina equisetifolia* have replaced native forest and scrub-forest in certain areas (Fosberg 1971), but these trees, especially coconut, were selected as nest sites by the Aldabran fody in 1972-73 (Frith 1976). This association is very similar to that of Mauritius Fodies with *Cryptomeria*: it arose quite abruptly (few Aldabran fodies were said to be nesting in coconut in the late 1960s: Benson & Penny 1971) and apparently in response to demonstrated lower predation rates in coconut (Frith 1976). On its rat-free islands, the Seychelles Fody *F. sechellarum* seems rarely to nest in the abundant coconut palms (three out of 45 nests on Frégate in 1959: Crook 1961).

In the 1970s, the Rodrigues Fody *F. flavicans* nested in exotic *Araucaria cunninghamii* branch ends almost whenever there was a tree of this species in the territory (Cheke 1987e), although the bird's wider distribution by 1991 included many territories devoid of *Araucaria* (pers. obs.). Cheke (1987e: 391) wrote that "the prickly *Araucaria* is obviously more predator-proof than the other species, though it is not clear what predator the Fody is defending itself against". Monkeys were never introduced to Rodrigues, but the history of the Roof Rat there is uncertain. In the 1970s, Cheke (1987a,e) thought that Roof Rats were rare, but trapping in 1983 and 1993 showed them then to be common (C. G. Jones in Cheke 1987a, B. D. Bell *in litt.* 1994); they were certainly abundant in the eighteenth century (Cheke 1987a). The huge (over 50 cm long) native gecko, *Phelsuma gigas*, might also have been a predator until its extinction (in the 1700s: Vinson & Vinson 1969) on the Rodriguan mainland; it could have brought about selection for inaccessible nest sites in dense, spiky cover.

For the Mauritius Kestrel, Temple (1978c, 1986) claimed that in 1974 a similar tradition shift occurred, when the only pair changed nest site from a tree cavity to a cliff cavity safer from predators. However, Jones (1987: 244) showed that Temple's evidence did not stand up to critical examination and in this case the occurrence of the tradition shift is at best unproven.

In each of these cases (excepting the Mauritius Kestrel), the birds using the introduced nest trees may comprise a source population. Thirty-one land-bird species are endemic to the smaller islands of the western Indian Ocean (Mascarenes, Comoros, Aldabras and granitic Seychelles; excluding Madagascar). All but three (Seychelles Magpie Robin *Copsychus sechellarum*, Warbler *Acrocephalus sechellensis* and Fody *F. sechellarum*) at present coexist with introduced Roof Rats; only the Mauritian species also have monkeys to contend with. The two swiftlets *Collocalia* cannot be victims of much nest predation by mammals, as they nest on cave roofs. Nesting biology has been studied in detail for very few of the remaining 26 species, but nesting tradition shifts have been documented for all three studied fodies and the Pink Pigeon, and are strongly suspected for all the other Mauritian passerines except the cuckoo-shrike. Studies on other endemic, forest-living birds in the region may reveal further examples, especially among species which, like the fodies and pigeon, build large, often conspicuous nests.

7.4.5 *Survival of exotic bird populations*

How do exotics such as the Madagascar Red Fody and Malagasy Turtle Dove survive the predation pressure that is endangering their closely related native counterparts? What little evidence there is does not suggest that the a lower proportion of nests of exotics fail, compared to natives. In other words, for a given nest, the native birds may be little or no more successful than the exotics in avoiding predation. The exotics show two characteristics which may help their populations to compensate for heavy nest predation. Firstly, their catholic habitat choice (pers. obs.) allows them a wide distribution. This may allow them to live in unproductive areas where monkeys and Roof Rats are scarce, and predation pressure is therefore low. They can therefore exploit more source areas than the more restricted native forest birds. Secondly, the exotics tend to be more mobile than the natives (Staub 1976: 33, Cheke 1987c: 191, pers. obs.), quickly spreading to isolated areas. This would allow interchange between distant source and sink areas. The survival of the exotics over wide areas may owe much to their ability to compensate for heavy nest predation in sink areas.

7.4.6 *Implications for studies on single species*

The results of this study highlight two major pitfalls to be avoided in studies on single species, especially rare ones. Firstly, distribution and productivity studies must be carried out at a scale which will allow detection of heterogeneity. For the fody, the enormous variation in population density and recruitment over very short distances meant that nothing less than individual territory mapping sufficed to resolve the patterns. Secondly, a bias may be common in studies on threatened species with variable productivity. Source areas are likely to be more intensively studied than sink areas, as they typically support high densities of the study species. My studies on fodies away from Pigeon Wood were extremely time-consuming; nests took much longer to find outside Pigeon Wood than inside it. Bias was avoided in 1992-93 by setting out to find equal numbers of nests inside and outside Pigeon Wood. In the case of the recent Pink Pigeon breeding studies (1975 onwards), data from only a single site (Pigeon Wood) have been available, because this is the only breeding site. Had these studies occurred when the pigeons were more widespread, variation in breeding success would doubtless have been found. The fody data suggest that, should the pigeon population expand outside Pigeon Wood, its breeding success will be even lower than recent analyses (such as Bruford *et al.* 1991) assume.

7.4.7 *Implications for conservation on Mauritius*

The remaining distribution of the Mauritius Fody has been shown to consist of source and sink areas. The source areas hold the key to their survival, and probably also that of some other threatened native birds on Mauritius (such as the pigeon and flycatcher). The simplest way to assist the birds' long-term survival is to create more source areas. *Cryptomeria* is the critical component of the most important source area (Pigeon Wood). Further planting of *Cryptomeria* is therefore urgently needed.

This is not a new suggestion. Based on the then unexplained concentration of pigeons in Pigeon Wood, Jones (1980), Jones & Owadally (1982) and A. S. Cheke (pers. comm.) (all cited by Collar & Stuart 1985) proposed that creation of further *Cryptomeria* groves would help the Pink Pigeon. The suggestion was not taken up, or even mentioned in subsequent detailed discussions of the conservation of the Pink Pigeon (Jones 1987, Jones & Owadally 1988, Bruford *et al.* 1991, Jones *et al.* 1992); food shortages were considered a greater problem (but see Section 5.7.2). Following preliminary study of the fody, the suggestion was repeated (Safford 1991, Safford & Jones 1993), and its implementation is now planned (C. G. Jones verbally 1994). Appropriate planting régimes are discussed in Chapter 9.

Chapter 8. Additional suggested causes of decline, limiting factors and threats

8.1 Introduction

Adverse influences on the forest-living native birds fall into three categories. Certain factors may have brought about past declines, others may limit the existing populations, and still others may threaten the future survival of populations. Some influences fall into all three categories, others into only one or two. The two factors which have most often been suggested to limit the populations of native birds of Mauritius are nest predation and impoverished food supply. These two subjects were discussed in Chapters 5, 6 and 7. However, other threats have been suggested by various authors. In this chapter, I identify these influences, review previous statements about them, present such new data as I have, and assess the past, present and future effects on bird populations.

The proximate and ultimate causes of extinction may differ (Simberloff 1986), so that "the last gasp of a declining species need not be due to the forces that reduced it to a single, restricted population" (Simberloff 1992: 663). Any factor that can cause the death of individuals is a threat to the survival of such rare species as the Pink Pigeon or Echo Parakeet.

8.2 Suggested influences

8.2.1 *Predation on adults*

No specialist predators of arboreal birds are present. However, monkeys, rats, mongooses, cats and kestrels all seem capable of catching and killing adult birds of certain sizes. The two carnivores are largely terrestrial and so would rarely be expected to reach arboreal birds, but are serious predators of terrestrial birds elsewhere, causing numerous extinctions (Baldwin *et al.* 1952, Lever 1985, Veitch 1985). Many of the records of nest predation probably occurred with an adult sitting, but only one involved the disappearance of an adult (a Pink Pigeon and its squab, May 1992). The often rapid repeat nesting and the survival of ringed birds (pigeons, one flycatcher and one female Mauritius Fody) through many predations suggested that the adults usually escaped before their nests were attacked. Therefore predation on adults of arboreal species is likely to be rare.

This should hold for all species except the Mauritius Kestrel, of which fledglings spend much time on the ground (Jones & Owadally 1988), and the Pink Pigeon, which often feeds on the ground at any age (Jones 1987, pers. obs.). These species are therefore vulnerable to carnivores (cats and mongooses). Kestrel remains have been found in mongoose stomachs and predation by mongooses is suspected to account for the deaths of at least 10 % of kestrels released from captivity (Jones *et al.* 1991a). However, the kestrel population continued to increase after the cessation of mongoose control and so this is unlikely to be a serious threat to the species at its present population level.

At least four wild adult and fledgling Pink Pigeons were killed away from nests in and around Pigeon Wood in 1991-93, apparently by carnivores. The remains (and also the remains of several Malagasy Turtle Doves) were found on paths and consisted of piles of body feathers and snapped off flight and tail feathers, with rings (and once also a mandible) discarded (pers. obs. of all four pigeons and two doves). This differs very strongly from the cat kills described and illustrated by Veitch (1985) and Tomkins (1985), in which the feet, tail, wingtips and bill were left attached to the remains of the body (often called a 'bridle carcass'). Mongooses may therefore have been responsible, but I have been unable to trace a description of a typical bird kill by a mongoose. Malagasy Turtle Dove remains have been found in cat stomachs from Pigeon Wood (T. Liddiard verbally 1993). Therefore it seems that both these carnivores kill adult and young Pink Pigeons.

The number of kills in 1991-93 may have been exceptional, but if it is typical, predation of adult Pink Pigeons may be a very serious and hitherto understated threat to the pigeon population, particularly with such a small population. For other species, predation on adults is unlikely to be a major threat.

8.2.2 *Competition with introduced species for resources other than food*

Evidence for food competition between native and exotic species was reviewed in Section 5.7.2. Other forms of competition affecting native birds have only been suggested for the Echo Parakeet. Competition for nest cavities with mynas, Roof Rats and bees *Apis* sp. has been seen to disrupt Echo Parakeet breeding attempts, including causing nesting failure (Jones 1987, Jones & Duffy 1993); Rose-ringed Parakeets are also likely competitors, although few nest in the Echo Parakeet's range (Jones 1987). With so few pairs of Echo

Parakeets nesting, any force which can cause breeding failure is a threat to the species' survival.

8.2.3 *Cyclones*

Cyclones can have direct and indirect effects on bird populations (Wiley & Wunderle 1993) and are believed to have caused severe declines in bird populations on all the Mascarene islands (Barré & Barau 1982, Cheke 1987e, Jones 1987). The most vulnerable species are those which eat fruit; nest, roost or forage on large, old trees; and have small or localized populations (Wiley & Wunderle 1993). Although native Mascarene birds have survived many cyclones, the remnant populations are at much elevated risk from such catastrophes because of their small size and restricted distribution (Bruford *et al.* 1991, Simberloff 1992). Cyclones must therefore be considered as a threat.

8.2.4 *Pesticide contamination*

Pesticides, in particular organochlorines, have killed large numbers of birds worldwide (Newton 1979, Ratcliffe 1980) and organochlorine residues and breakdown products are present in birds the world over (Stickel 1973). Misuse of organochlorines has been widespread in tropical countries and may have been overlooked as a cause of declines and extinctions (Diamond 1984).

Cheke (1987a; originally in Pasquier 1980) suggested that the post-war decline (almost to extinction) of the Mauritius Kestrel was caused by organochlorine pesticide use for malaria control and to a lesser extent in agriculture. It was suggested that the Black River Gorges became the last refuge of the kestrels in the mid 1970s because it was the only part of the island not sprayed, and that recovery began a decade after widespread spraying ceased in 1965. This has not been proven due to lack of evidence but was accepted as a likely explanation for the disappearance of kestrels from the Montagnes Bambous and Moka Range in the 1940s and 1950s (Jones 1987, Jones & Owadally 1985, 1988).

Precise data on organochlorine spraying before 1970 no longer exist (Anon. 1991: 174; Pesticide Control Board verbally 1993). However more information from various sources deserves to be presented.

DDT spraying for malaria control took place from 1949 to 1965, then at reduced intensity until 1973 (Mamet 1979), when the island was declared malaria-free (Bruce-

Chwatt 1974); it is still applied occasionally, but this is tightly controlled (Dr Ragavoodoo, Malaria Control Unit, verbally 1993). Spraying was largely restricted to buildings, mostly in coastal areas but to a much lesser extent over the whole island (Mamet 1979). It seems doubtful that such a programme would have affected birds largely restricted to native upland forest away from the coast.

Organochlorine pesticides were also used in agriculture. Neither sugar nor tea cultivation has involved use of insecticides on a large scale (Sprinks 1950, Ricaud 1975, Joomaye 1988), yet in 1965 these accounted for 98 % of cultivated land (excluding forestry) on Mauritius (Arlidge & Wong 1975). However, the Ministry of Agriculture recommended the use of a wide variety of organochlorines on vegetables, fruit and tobacco (Orian 1961, 1962), and these were much used in the late 1950s (Joomaye 1988), then decreasingly so until most use was banned by the Pesticide Control Act in 1970 (Ricaud 1975). In 1965, only 2085 ha (1.1 %) of the land area of Mauritius was continuously used for food and other crops besides tea and sugar; however most crops were instead grown inter-line or inter-rotation with sugar cane, and this was not accounted for by the 1965 survey (Arlidge & Wong 1975). It is therefore possible that organochlorines were occasionally used wherever sugar was grown.

The Moka and Bambous Ranges, where kestrels disappeared in the 1940s or 1950s (Jones 1987), both rise from the coastal lowlands where spraying for malaria control was carried out, and foodcrops are cultivated on their lower slopes, immediately below the forest. Therefore it is likely that kestrels inhabiting these mountains were exposed to organochlorine pesticides. However, there is no direct evidence for or against the hypothesis that organochlorine pesticides caused the major decline of the kestrel in the 1950s and 1960s; nor does any evidence seem likely to be forthcoming.

The effect of organochlorine spraying on other native land-birds has not been discussed before, but there seems no reason why passerines should not also have been affected. The cuckoo-shrike may be particularly vulnerable because its diet includes many *Phelsuma* geckoes (Chapter 5) as well as large insects. Lowland habitat in the south-west was devoid of cuckoo-shrikes in 1975 but occupied in 1989-93 (Section 3.4.3). The species disappeared from the Montagnes Bambous at some time between the 1930s and the 1970s (Cheke 1987c) and has not recolonized. It is possible that organochlorine pesticide use was responsible for its disappearance from the Montagnes Bambous and the lowland forests of the south-west. The latter areas were recolonized, perhaps because they are contiguous with upland forests where the species survived; the birds could therefore expand their range into the lowlands when pesticide levels there dropped. The Bambous were not recolonized, perhaps because of their isolation. If this hypothesis is true, the Bambous should now be suitable habitat for cuckoo-shrikes. This species is unlikely to recolonize the Bambous on its own (Chapter 4), and an attempt at reintroduction would be appropriate, as has been carried out successfully for the kestrel.

Organochlorine pesticides could have affected the other passerine species, but there is nothing in their current status which reflects this.

8.2.5 *Disease*

No studies of disease in wild bird populations on Mauritius have been carried out since those in 1973-75 and 1978 (Peirce *et al.* 1977, Peirce 1979, summarized in Cheke 1987a,c), although recently Greenwood (1993) called for further monitoring. The distribution of cases of avian malaria on Mauritius in 1975 suggested that infected birds were more frequent in lowland or disturbed upland forest than in undisturbed upland forest. This distribution was thought to correspond with that of the main vector, *Culex quinquefasciatus* (=*fatigans*), although no data on mosquito distribution or abundance were given. Further blood parasites were identified, but for these and also for malaria, the effect on survival of birds infected was unknown.

If disease made lowland areas uninhabitable for Mauritius Fodies and olive white-eyes, this could have reduced their ranges. However, Pink Pigeons, Echo Parakeets and Mauritius Fodies have all been maintained in the Government Aviaries in Black River for six months or more, with no suggestion of altitude-related diseases (which may manifest themselves rapidly when susceptible birds become exposed: Warner 1968). Blood samples from captive Pink Pigeons gave no indication that disease was a limiting factor for birds living in the lowlands (Jones *et al.* 1989). There is no evidence to implicate disease in the rarity of any Mauritian bird species.

8.2.6 *Habitat fragmentation*

Destruction of native forest has now ceased, apart from occasional, illegal clearances of very small areas of the plateau. Further destruction and fragmentation of native forest should not be a threat, although piecemeal encroachment still occurs.

The most obvious recent example of habitat fragmentation on Mauritius is the separation of the Midlands/Montagnes Bambous area from the south-western forests. The two areas were linked until 1950 by a wide sleeve of degraded forest south of Curepipe (maps in Vaughan & Wiehé 1937, Cheke 1987c). This link was gradually replaced by tea and conifer plantations. It is possible that the Bambous now contain suitable habitat for cuckoo-shrikes (see Section 8.2.4). The birds' failure to recolonize is not surprising because of the expanse of unsuitable habitat that they would have to cross in order to do so.

The Macchabé Area and Southern Slopes were largely isolated from each other by clearance of native forest on Les Mares in 1971-75. Jones (1987) believed that Pink Pigeons stopped using the Macchabé Area at this time because access from the Southern Slopes was cut off, but I have already suggested that the birds keep to the Southern Slopes because they rarely need to leave this area (Section 7.2.2). No data exist on the number of birds crossing between the two areas before and after their separation.

The smaller fragments of the Plateau and Central-east Relicts are variable in their species richness. These patches of partly-exploited forest were left standing when the plateau forests were cleared after 1950 (Cheke 1987a,c), varying in area from a few hectares (such as Bois Sec) to 2.1 km^2 (Montagne Lagrave). Several are richer in birds than might be expected from their areas (for example, the patch north of Rivière du Poste opposite Kanaka: Section 3.4.2). This may be partly because they are often floristically very rich: Lorence (1978) found Lagrave to hold the richest pteridophyte flora on Mauritius. Perhaps more importantly for some species, several of the relict patches are surrounded by plantations, providing the valuable combination (for birds) of good native forest and plantation (Chapter 6).

If a native forest fragment is treated as an island, then the smaller and more remote (from the major native forest areas) a fragment is, the more likely it is to lose species (see MacArthur & Wilson 1967). This is consistent with my failure to find any native forest birds at Le Pouce, Monvert, Montagne Fayence and Montagne Blanche, which are the remotest patches (excepting the ubiquitous Grey White-eye, and provisionally discounting the unlikely cuckoo-shrike report on Le Pouce).

8.2.7 *Altitude and climate*

Altitudinal restriction in island birds can arise as a result of natural specialization, as for several species on the Comoros (Louette & Stevens 1992). Additionally, environmental changes (often anthropogenic) acting only at certain elevations can have the same effect, such as the extinction of certain Hawaiian birds from lowland areas because of disease (Warner 1968, but see van Riper *et al.* 1986). Here, I consider altitude and climate together, as in Mauritius the latter depends considerably on the former (Padya 1989).

All native species except the Mauritius Fody and possibly the Pink Pigeon are known to have occurred, or still do occur, in the dry lowlands as well as the humid uplands where most are now concentrated. For these two, no unequivocal locality records were traced by Cheke (1987a,c) or Jones (1987) until E. Newton's (1861) notes. Before this, these birds could have occurred undocumented anywhere on Mauritius, and I suggest that they did so, because other fodies and pigeons in the region all live at a wide range of available altitudes (Penny 1974, Louette 1988, Langrand 1990, pers. obs.). Therefore there is no evidence for natural altitudinal specialization in any species.

Table 8.1 shows the ranges of altitude and annual rainfall in which native forest birds were found in 1989-93. The isohyets are extremely close together in the south-west (the 4000 mm isohyet is 5 km from the 2000 mm isohyet) and it is not known how precisely they were plotted; the limits of rainfall range in this area are therefore approximate. Although all the extant species were probably once widespread, the distributions of several species appeared partly to be correlated to climatic and altitudinal features.

In 1989-93, the cuckoo-shrike, black bulbul and flycatcher showed no sign of restriction to any altitudinal or climatic zone; the first two were absent below 200 m (excluding accidental records of black bulbuls) because of the lack of suitable vegetation. The kestrel's absence from the highest (and therefore wettest) areas was presumably caused by the rarity of cliffs suitable for nesting. The pigeon and parakeet were so rare that restriction of range was inevitable. Jones (1987) suggested that the pigeons occurred in the wettest area because of its higher plant species diversity. The Mauritius Fody and olive white-eye were both restricted to high rainfall areas above 400 m, and absent in native forest elsewhere, as in 1975 (Cheke 1987c). Cheke (1987c) pointed out that high humidity speeds the rotting of dead wood, so the most humid (therefore wettest) areas would most favour the fody's main feeding technique of chiselling into rotting wood.

Table 8.1. Altitudinal and annual rainfall ranges within which native forest birds of Mauritius occurred in 1989-93. Altitudes given to the nearest 100 m; rainfall to the nearest 0.5 m, the latter from 1961-90 averages.

Species	Altitude range/m		Rainfall range/m	
	Breeding	Feeding	Breeding	Feeding
Kestrel	0-500	0-800	1.0-3.0	1.0-3.5
Pigeon	600	500-800	4.0	2.0-4.0
Parakeet	400-600	200-800	2.0-3.0	1.5-4.0
Cuckoo-shrike	200-800	200-800	1.5-4.0	1.5-4.0
Black bulbul	200-800	200-800	1.5-4.0	1.5-4.0
Flycatcher	0-800	0-800	1.0-4.0	1.0-4.0
Olive white-eye	400-800	200-800	2.5-4.0	2.5-4.0
Fody	400-800	400-800	3.0-4.0	3.0-4.0

Suggested connections between bird distribution and climate or altitude have previously concerned the ability to meet feeding requirements: plant species richness for pigeons and swift rotting of dead wood for fodies. These factors probably do favour the birds, but no difference in resource availability between wetter and drier areas has been demonstrated on Mauritius, nor have these (putative) differences been shown to have sufficient effect to limit ranges. Furthermore, several features of the distributions are inconsistent with the existence of a link with climate or altitude. For example, fodies were absent in 1989-93 from the Bambous - Lagrave area (much of which receives 2500-4000 mm rainfall), and nearly so at Alexandra Falls and on Plaine Champagne (3500-4000 mm rainfall).

The distribution of the pigeon and fody are satisfactorily explained by the presence of exotic tree plantations abutting native forest. This explanation is fully supported by a direct causal link (Chapter 7). The same explanation could account for much of the olive white-eye's range. Tree (rather than sugar cane) plantations were created in the wet uplands partly for reasons of climate, providing an anthropogenic connection between climate and bird distribution.

8.2.8 *Hunting*

Cheke (1987a) considered hunting by early colonists to have been a contributory factor in declines and extinctions of native Mascarene species.

Hunting of native birds is now rare, but was occasionally reported in the 1970s (kestrels shot: Temple 1977; bird-lime found on black bulbuls: Cheke 1987c) and swiftlets nesting in accessible caves are still persecuted (pers. obs.). Human persecution of birds in the native forest was very rare by the 1980s (Jones & Owadally 1988), but for the Pink Pigeon and Echo Parakeet even the loss of one fecund individual could be disastrous. The populations of the native passerines are very unlikely to be affected by direct human persecution at its present levels.

8.2.9 *Hybridization*

Hybridization is most likely to occur between closely related taxa. It is therefore unlikely to occur between native species as all but the two white-eyes are in different taxonomic families, and even the white-eyes are very distinct morphologically and vocally.

The threat of hybridization is most serious when a closely related congener of a native species is introduced. The closest example to Mauritius is the introduction of the nominate race of the Malagasy Turtle Dove *Streptopelia p. picturata* to Seychelles, which has largely or entirely eliminated the endemic *S.p. rostrata* by hybridization (Penny 1974).

McKelvey (1976) reported that a female Malagasy Turtle Dove paired to a male Pink Pigeon laid fertile eggs (which were taken by predators) in 1976. He gave no supporting details to exclude the possibility that a male turtle dove was involved. Such an "unlikely mixed pairing" (Jones 1987) has not been reported before or since, and is unproven.

There is no evidence for hybridization between Mauritius and Madagascar Red Fodies (Safford 1991 *contra* Moreau 1960); the bird with intermediate characters described by Newton (1959) is comfortably within the range of plumage variation of Madagascar Red Fodies. However, hybrids between Seychelles and Madagascar Red Fodies were reported in 1992-93 on Aride island, Seychelles, where only one or two female Seychelles Fodies were present among many Madagascar Red Fodies (C. J. Taylor verbally 1994); hybridization has not been noted on the three islands with larger populations of the Seychelles Fody, and would presumably not have happened on Aride if male Seychelles Fodies had been present. This suggests that hybrid fodies could be produced on Mauritius if individuals of one species became isolated from conspecifics, in the presence of congeners. Hybrid populations should be exterminated if discovered, unless there is no possibility of maintaining pure bred populations.

8.3 Discussion

Table 8.2 lists the main factors suggested as causes of decline, limiting factors and threats to native Mauritian land-birds. For completeness, impoverishment of food supply and nest predation, discussed in Chapters 5 and 7, are included.

Table 8.2. Factors believed to have negative impacts on native Mauritian land-birds.
+ Direct or strong circumstantial evidence exists that this factor is a cause of decline, limiting factor or threat for several (or all) species.
? A question mark indicates that evidence is poorer or lacking, but the factor may have a past, present or future negative influence.
Species-specific factors are indicated for the species affected.

	Cause of decline	Limiting factor	Threat to	
			all populations	very small populations
Nest predation	+	+	+	+
Habitat fragmentation	+			
Human persecution	+			+
Pesticides	+			
Predation on adults	?PP	?PP	?PP	+
Cyclones	?+	?+	?+	+
Reduced food supply	?+	?+	+	+
Competition (not food)		?EP	?EP	EP
Disease				+
Altitude/climate				
Hybridization				

Provided that further habitat destruction and fragmentation is prevented, there is no reason to believe that any of the factors discussed in this chapter present as great a threat to bird populations as nest predation or impoverishment of food supply.

Cyclones and predation by carnivores on adult Pink Pigeons may be the most serious of the problems discussed in this chapter. Vulnerability to cyclones is reduced by increasing bird populations and distributions, and by maintaining native habitats resistent to cyclone damage. On a Caribbean island, predation on turtles by introduced Small Indian Mongooses was reduced following mongoose trapping (Coblentz & Coblentz 1985). Cats and mongooses have been controlled on mainland Mauritius by trapping and poisoning, but offshore islets free of these predators offer better long-term security (also from nest predators).

Of the other factors, the prevalance and pathogenicity of diseases in wild bird populations requires investigation, and close monitoring of Echo Parakeet nest sites allows action to be taken to prevent cavities being lost to competitors (Jones & Duffy 1993).

Chapter 9. Conservation strategies for land-bird conservation on Mauritius

9.1 Introduction

The goals for conservation action were defined in Chapter 1; in short, they are the maintenance or restoration of self-sustaining populations of all species and ecosystems. In this thesis I have presented information on the status, diet, breeding success and the annual cycles of each of the forest-living native passerine species which are threatened with extinction. These aspects were selected for study because they are the key features of the birds' ecology which must be understood in order to produce an effective conservation strategy. Where relevant, I have included data on the three other threatened bird species. As stated in Chapter 1, the strategy needs to comprise the most economical set of measures which, if implemented, would increase the viability of all native bird populations to a sustainable level without compromizing the survival chances of other life-forms. In this chapter, I present this strategy: habitat management.

Most of the forest-living native birds of Mauritius are at present restricted to native forest. This is steadily deteriorating, so that floristic composition is shifting towards exotic species, even in the presently least degraded native forest patches (Lorence & Sussman 1986, 1988, Chapter 2). Certain of the abundant exotics are used by foraging native birds, but spontaneous exotic vegetation is generally poor, if not useless, habitat for native birds. The only important population of any of these birds completely independent of native forest (the flycatchers at Bras d'Eau) is in a managed forestry plantation.

Even if these habitats are strictly protected from deliberate acts of destruction, the vegetation will gradually alter to become unsuitable for native birds. If habitat is not managed in any way to improve its value to the birds, the birds will very probably become extinct.

In Mauritius, habitat management strategies for bird conservation are complicated by the problem of nest predation. Providing sustainable food sources is insufficient; safe nest sites must also be provided. Rather than relying on predator control to conserve species threatened by predators in the Americas, Martin (1992) stressed the need to identify and manage habitat features which impede the effectiveness of predators; the same argument applies in Mauritius.

In this chapter, three main habitat management strategies are considered. First, the current attempt to rehabilitate and preserve the native plant communities on the mainland of Mauritius. Second, the management of mainland forest areas with a combination of carefully selected exotics and preserved native forest. Third, the eradication of introduced animals on offshore islets, followed by the restoration of native habitats there.

Other long-term conservation measures are discussed, namely translocations within the mainland of Mauritius and the oft-suggested introduction to Réunion of endangered Mauritian birds. Short-term conservation measures are identified, distinguished from long-term measures, and briefly discussed. Finally, an action plan for implementation is presented and priorities for research in bird conservation on Mauritius are identified.

Definitions

For clarity, I here define terms to be used in the following sections.

Habitat management is any process by which the development of habitat is manipulated, rather than allowed to proceed spontaneously. It can take many forms: gardening, silviculture and island restoration are all examples. Conservation is not always the objective of habitat management.

Restoration is traditionally defined as the exact reproduction of the community or ecosystem that was previously present (Bradshaw 1987). Anticipating that some would insist that this is almost impossible to demonstrate, Simberloff (1990) offered a more realistic definition: restoration is the production of a system whose structure and function cannot be shown to be outside the bounds generated by the normal dynamic processes of communities and ecosystems that were previously present. *Rehabilitation* is the partial re-establishment, through human intervention, of the original biota and/or ecosystem, but with some change or incompleteness (Magnuson *et al.* 1980, Simberloff 1990). *Enhancement* means increasing or improving some characteristic of the site (Magnuson *et al.* 1980).

Regeneration is the natural process of turnover of vegetation, by which plant species propagate, grow and thus maintain their status in communities. An *invasive* plant species is one which can propagate without human assistance in an existing plant community to which it did not belong before human colonization of the island. In theory, native species can be invasive, but in practice invasive exotics are the problem, as they are a major cause of the degradation of the native forest (Lorence & Sussman 1986, 1988).

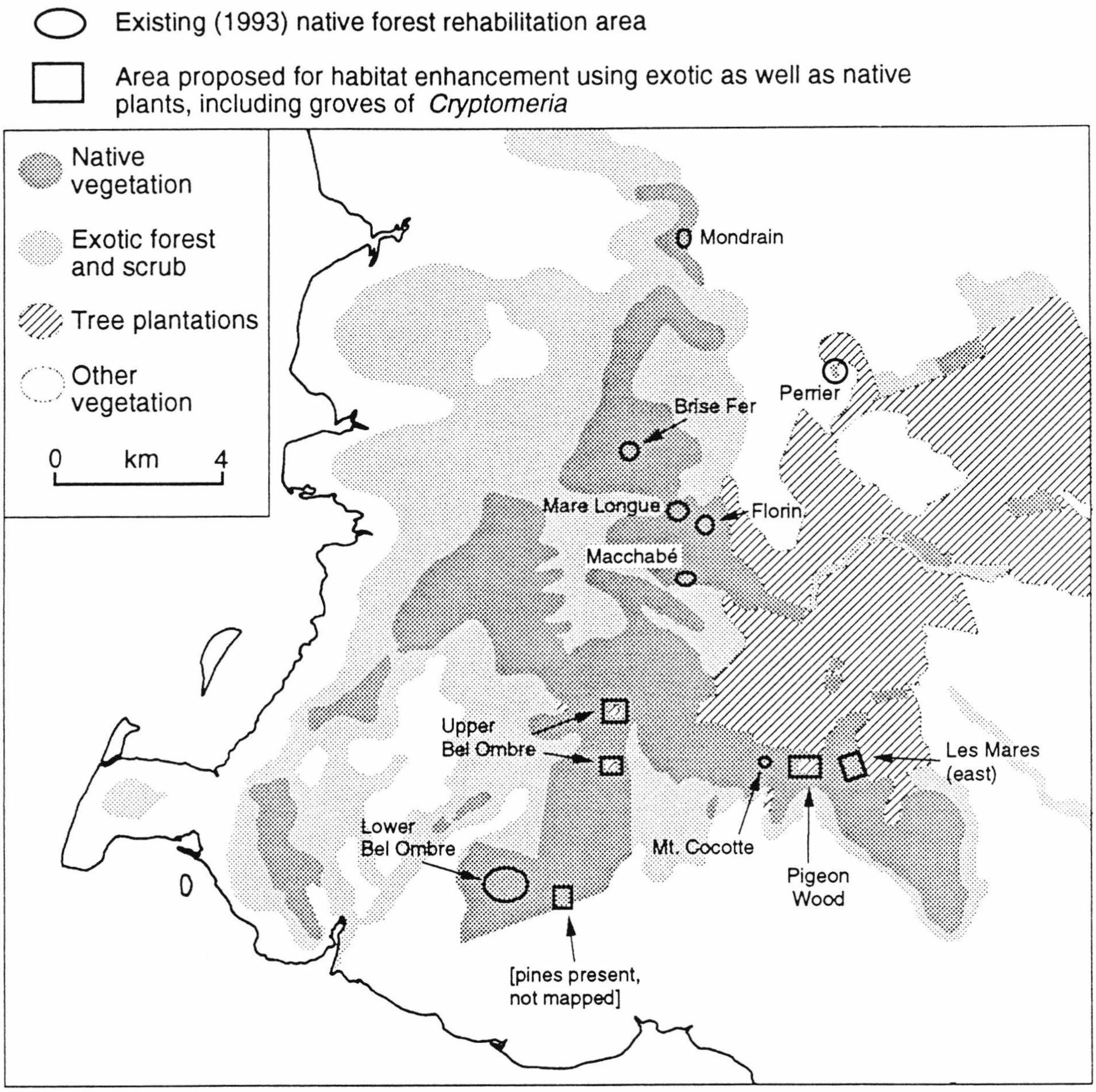
9.2 Rehabilitation and preservation of native plant communities on the mainland

Virtually all the surviving Mauritian native forest is on the mainland, including all upland plant communities. Degradation of the native vegetation is ubiquitous. Spread of the invasive exotic plants is aided by the actions of exotic animal species (Cheke 1987a, Strahm 1988, 1993 & in prep.). To investigate and combat this problem, plots of up to 5 ha (most less than 2 ha) of native forest representing major plant communities have been selected for intensive management (Anon. 1991). These are fenced to exclude deer and pigs, and exotic plants are uprooted manually; herbicide trials began in late 1993. During the study period, such plots existed at Brise Fer, Macchabé, Montagne Cocotte, Mondrain and Perrier (Fig. 9.1). The last two named lacked threatened native birds in 1989-93 because they were outside these birds' main distribution. Unfenced, weeded plots also existed, for example in Bel Ombre. Newly fenced plots were created in 1993-94 at Florin, lower Bel Ombre and Mare Longue (C. G. Jones verbally 1994). Research carried out in these plots is helping to identify the most important causes of the degradation, and has revealed much improved growth and regeneration rates for many native plant species (Strahm 1988, 1993 & in prep.). Strahm (1993) proposes a network of such fenced areas as the main strategy for *in situ* plant conservation in Mauritius.

The plots at Brise Fer, Macchabé and Montagne Cocotte are often visited by native birds (Safford & Jones 1993). No quantitative data exist to confirm that native birds use the plots any more than adjacent forest, but this might be expected, since the high diversity of native plants in the plots is likely to favour abundant native insect prey and foodplants for birds. The plots are smaller than most bird territories and so could hardly benefit more than two pairs of territorial species. However, with increasingly efficient management techniques and availability of labour, the number and size of such plots is increasing rapidly (C. G. Jones verbally 1994).

It is possible, using these methods, to produce patches of habitat containing only native plant species. Although the habitat may superficially resemble a pristine Mauritian forest, it is not merely pedantic to point out that it is far from being so, because the management does not exclude most exotic animals. Of most concern to bird conservation, access to the plots for rats and monkeys (the most dangerous nest predators) is unrestricted. Native birds which rarely breed successfully in existing native forest seem unlikely to do better in the plots, and Mauritius Fodies and Pink Pigeons therefore probably cannot form viable populations based on birds breeding in the plots.

Fig. 9.1. Vegetation of south-west Mauritius, showing existing and suggested habitat management areas



The only way currently known to compensate for the predator problem in such areas is to control nest predators continuously. Rat control at Brise Fer (the site of the release of captive-bred Pink Pigeons since 1987) began in 1992. This, together with the use of monkey-scarers and unlimited supplemental feeding, had resulted in around 30 juvenile pigeons fledging there in late 1993 and early 1994 (C. G. Jones verbally 1994). Although high productivity has resulted, this is not an acceptable long-term conservation strategy.

9.3 Enhancement of the mainland habitat by including exotics

9.3.1 *Background*

The use of exotics is proposed for two reasons. Firstly, for certain purposes, specific exotic plants are of more value to native birds than are any native plants (Chapters 5 & 6). Secondly, certain exotics are capable of surviving and regenerating in spite of the wide range of factors preventing most native plants from doing so. Therefore a habitat containing a well-designed combination of native and exotic plants can be not only more suitable for native birds than are the native forest remnants, but also much simpler and cheaper to manage.

A similar strategy was aired by Cheke (1978). Recognizing the apparently inevitable deterioration of the native forest upon which most native birds depend, he suggested a way of "buffering bird populations from being totally dependent on the native forest". Pointing out the species' occurrence in plantations mixed with depauperate relicts of native vegetation, he proposed the establishment of plantations of mixed evergreen trees selected to provide nesting sites and adequate food. However, few data were available, with which to decide which plant species to use, and in what proportions. The concept was entertained by Jones & Owadally (1982, 1985, the former cited by Collar & Stuart 1985) but apparently then abandoned until resurrected by Safford (1991), Bruford *et al.* (1991) and Safford & Jones (1993). Cheke (1978) hoped that the mixed plantations might be economically viable, providing an additional incentive for their creation, besides conservation. There appears to be no commercial interest in the idea (pers. obs.), and therefore the suggestion stands only upon its conservation merits.

Could such a strategy damage native vegetation? In the most detailed analysis of plant conservation problems and strategies, Strahm (1993) accepts that it would not, so long as it is planned and executed responsibly. Areas selected for intensive rehabilitation of native forest are those which are presently the least degraded. This leaves large areas of forest which are classified as native in Chapter 2, but are considered too degraded to be worth intensive rehabilitation. Such areas (for example, around Piton Savanne) still support important native bird populations (Chapter 3). What remains of the native flora should be preserved and combined with selected non-invasive native and exotic species chosen for specific reasons to help the native birds. To ensure that the conservation of native plants and ecosystems is not compromized, the following guidelines are proposed.

1. Exotics should not be planted within any of the areas retaining the best preserved native forest (such as Macchabé - Brise Fer).
2. No native vegetation should be replaced by exotics: useless exotics should merely be weeded out and replaced with other species which are harmless.
3. No exotic species should be introduced to Mauritius for this purpose, unless there is no doubt whatsoever that it is incapable of spreading.

This strategy does not preserve an entirely native ecosystem. However, nor do the current efforts to restore native plant communities on the mainland, as already pointed out. The inclusion of exotics does not preclude maintenance of the maximum diversity of native species.

9.3.2 *Areas for management*

I propose the following criteria to select areas for management.

1. All these measures should take place within the national park. The park encompasses the native forest of the south-west: the Southern Slopes, Macchabé Area and some of the Plateau Relicts.
2. Most or all of the threatened bird species should initially be present in the area to be managed, so that their populations can increase in step with habitat enhancement.
3. The least degraded native forest areas, where intensive rehabilitation is occurring (for example, Macchabé - Brise Fer) or being considered (for example, parts of the southern slopes of Montagne Cocotte) are unsuitable for this type of management. Patches of exotic habitat adjacent to such areas are, however, acceptable (for example, the exotic plantations in lower Bel Ombre), as are areas of native forest containing a very high proportion of exotics (for example, the area around Piton Savanne).
4. Small, isolated patches of native forest (for example, the Plateau Relicts) are

unsuitable because, even if enhanced for birds, they will always have small carrying capacities.

5. Edaphic and climatic conditions must allow growth of the preferred exotics; dwarf forest (for example, Plaine Champagne) and exposed slopes and summits (for example, Piton Savanne) are unsuitable for *Cryptomeria*, which is a key plant species (Chapters 6 & 7).

6. Human disturbance should be minimal in any refuge for endangered species; popular sites such as Alexandra Falls seem unsuitable.

These criteria eliminate all areas except parts of Bel Ombre and the Bassin Blanc - Combo region. Three specific areas are suggested for management trials (Fig. 9.1): Bel Ombre (in and around the conifer plantations), the immediate surroundings of Pigeon Wood and in the east of State Land Les Mares (on the north-east facing slope above the River Savanne and State Land Le Juge).

9.3.3 *Providing nesting sites*

The conclusions of the breeding success studies for the Mauritius Fody and Pink Pigeon showed that the creation of further "source areas" where nest predation rates are low is necessary if these species are to increase their populations. In this section, I suggest how these could be created.

Tree species to be used

Source areas are characterized by the dominance of tree species in which nest predation rates are lower than the average for the whole population. Of the tree species in which nests were found, predation rates were lowest in *Cryptomeria*; if any other common tree species provided better protection for nests, the birds would presumably be using it. *Cryptomeria* is therefore the obvious choice. It is a major plantation species on Mauritius (Brouard 1963) and so it is cheap and readily available and its management is well understood.

It is of both interest and concern that the *Cryptomeria* in Pigeon Wood itself is not regenerating, as very few young trees are present (Safford & Jones 1993, *contra* Jones 1987, who described it as self-seeding). This provides reassurance that *Cryptomeria* is not invasive and will not spread through the native forest, but management is needed to preserve the nesting cover.

Reliance on one tree species may be risky. The arrival of a disease specific to *Cryptomeria* could result in the loss of all the safe nesting cover, and therefore alternatives need to be considered. Although *Pinus* and *Eucalyptus* are also selected as nests sites by the birds, apparently in the same way as *Cryptomeria* and for the same reasons, the breeding success is not high enough to make them useful alternatives to *Cryptomeria*. A more promising alternative is *Araucaria cunninghamii* (Safford & Jones 1993, Section 7.4.4), but the only *Araucaria* grove in the study area is not within the range of the fody or pigeon and so there is no way of telling whether it would provide more or less safe nesting cover than *Cryptomeria*. Many other tree species from around the world might of course have similar properties, but there seems no justification for introducing further exotics, when a species already present is known to be effective and cheap. In the absence of data for other tree species, I initially propose the planting only of groves of *Cryptomeria*.

Characteristics of the proposed groves

Where, how big and what shape should the new groves be? How should the exotic trees be dispersed in the grove - scattered or clumped? How long would it take for trees to become useful to the birds? How many groves would be needed to guarantee the birds' survival? Answers to these questions can be suggested using empirical data from the few existing areas of *Cryptomeria*, and from theoretical considerations.

Table 9.1 describes the seven areas of *Cryptomeria* and one of *Araucaria* investigated in and around the native forest areas of the south-west. They are mapped in Fig. 2.10 (excepting State Land Dayot). Scattered individual *Cryptomeria* trees occur in parts of the native forest between Montagne Cocotte and Combo, and small plantations exist within the large plantation block of Les Mares. However, only the eight groves listed were considered to be potentially useful to the native birds.

The data in Table 9.1 show that all the groves are, or have been, used by nesting native birds, excepting those on Les Mares and State Land Dayot. The latter, together with my other observations in plantations, indicate that *Cryptomeria* alone does not provide suitable habitat for any of the threatened native birds (as Cheke [1987b] also found on Réunion), presumably because it is very poor for foraging (indeed it is mainly this unproductivity that makes it a refuge from predators: Chapter 6). *Cryptomeria* must therefore be combined with foraging habitat, in order to provide a region avoided by predators, and to retain a productive region so that each bird territory contains foraging areas. Blocks of

Cryptomeria are preferable to scattered trees (as at "Piton Paul"), as predators seem less likely to penetrate the birds' nesting area.

Table 9.1. *Cryptomeria* and *Araucaria* groves in and around the distribution of the Mauritius Fody, listed from north to south. Areas given are those of the smallest convex polygon that encloses the plantation area.

Native birds proven or considered certain to be nesting in the grove, using the plantation trees or the shelter they provide, are marked with an asterisk (*), followed in brackets by the number of pairs. Further native bird species recorded within the grove are also listed; some may also nest. The Grey White-eye is not included. *Cr=Cryptomeria japonica*, *Ar=Araucaria cunninghamii*, *Euc=Eucalyptus robusta*.

Locality, area/ha, age and species	Canopy	Surroundings	Native birds present or nesting	Notes
Dayot >30, old *Cr*	Dense	*Pinus*/clear-felled exotic	none	>1 km from any native forest
Bois Sec 1.5, old *Cr*	Dense, *Pinus* mix	*Pinus*/small native patch	M, OW (PF possible)	Breeding PP and MF in 1970s, until isolated from most native forest
Alexandra Falls 1.5, young *Cr*	Sparse	*Pinus*/*Euc*/ native	MF*(1), OW	degraded, scrubby native forest
Les Mares 2.0, young *Cr*	Sparse	*Pinus*/poor native	OW	degraded, scrubby native forest
Le Juge 2.5, old *Ar*	Dense	*Pinus*/*Euc*/ small native strip	CS*(1), PF*(1), OW	native strip along river; 800 m from big native area
"Piton Paul" 1.5, old *Cr*	Scattered *Cr* trees	native	M, OW, MF*(2)	*Cr* trees poor, ?wind-damaged, mixed with *Euc*
Pigeon Wood 6.0[1], old *Cr*	Mostly dense	native/small *Euc* patch	PP*(5), CS*(1), M*(2), PF*(4), OW, MF*(9)	rich native rain forest, some along rivers through *Cr* grove
Upper Combo 2.5, old *Cr*	Dense	*Pinus*/*Euc*/ native	PF*(1), MF*(1)	part mixed with *Pinus*

Note

[1] The area under *Cryptomeria* in Pigeon Wood is 4.3 ha. Thus the lobed shape increases the geographical extent of the grove by 40 %.

The grove in Bois Sec was the last site away from Pigeon Wood where wild Pink Pigeons nested, before most of Les Mares was cleared of native forest. It (together with the associated native patch surviving in 1993) was then contiguous with the main native forest area, but it is now isolated (Section 7.2.2). The Alexandra Falls plantation was presumably created in the early 1970s (when the native forest in the area was cleared for forestry: Cheke 1987a). Therefore *Cryptomeria* plantations can be ready for use by fodies within 20 years of creation. Pink Pigeons appear to need stouter horizontal branches, which are lacking on these young trees; the smallest trees (of uncertain age) used by pigeons in Pigeon Wood in 1989-93 were around 10 m tall (pers. obs.).

Of the seven groves in or near native forest, Pigeon Wood stands out as having by far the highest diversity and density of birds. It is unique in the following ways:

1. it is over twice the size of the other groves (but no point within it is more than 80 m from native forest),
2. it is almost entirely surrounded by rich native rain forest (*sensu* Lorence 1978), some of which passes through the grove along riverbanks, and
3. it has an irregular, lobed shape, increasing its geographical extent whilst preserving dense *Cryptomeria* areas alongside native patches (Fig. 3.10).

These features are all likely to favour the birds. A bigger grove can contain more territories, but blocks of pure *Cryptomeria* over about 200 m across would probably contain central areas too far from native forest to be used by the birds.

Simply put, Pigeon Wood appears, on current knowledge, to be ideally sited and shaped. There are no data with which to decide whether extending Pigeon Wood or planting additional groves would benefit the birds more. However, either method is certain to be effective. *Cryptomeria* should be planted to create a dense canopy covering at least 2 ha, surrounded by foraging habitat rather than merely abutting it at the edge of a plantation. Lobes of foraging habitat reaching into the grove (or even corridors passing through it) may be beneficial. Therefore areas of patchy, degraded native forest are highly suitable for management, as the native vegetation can be left as foraging habitat and the useless exotic areas (including old groves of *Pinus* or *Eucalyptus*) replaced with *Cryptomeria*. Indeed, Pigeon Wood was created under exactly these conditions, but not for these reasons (Section 2.2).

The number and location of groves

The computer simulations (Chapter 7) suggested that the addition of a further grove similar to Pigeon Wood could lead to a twofold increase in the main population of Mauritius Fodies. I suggest that an aim for the management should be to increase this main population, and to consolidate a second population. Two new groves of similar size and shape to Pigeon Wood in the areas already selected for management (see *Areas for* *management*) should suffice: one within the current Cocotte - Savanne population area (including upper Combo), and one elsewhere (if groves larger than 2 ha cannot be created, a larger number would be needed). This could lead to a stable fody population of over 500 birds. The effect on the populations of the other species is harder to quantify. The most appropriate locations for each of the two groves are the following.

The first grove could be created by extending Pigeon Wood westwards, replacing *Eucalyptus* areas with *Cryptomeria*. Alternatively, a separate, new grove could be created in the east of State Land Les Mares. For the second grove, one or more of the old *Pinus* plantations within Bel Ombre forest should be replaced with *Cryptomeria*. Plantations exist at around 700 m (the edge of Plaine Champagne), 500 m (upper Bel Ombre) and 250 m (lower Bel Ombre, alongside the main track). The native vegetation within these plantations has of course been completely destroyed, but well-preserved forest is present nearby, which would be used by birds nesting in the new groves.

9.3.4 *Foraging habitat*

Although there is no strong evidence that food supply is currently limiting the populations of any of the native birds (Section 5.7.2), forest degradation is certain to reduce food availability in the long term. Habitat management proposals need to address this. I suggest combining what can be preserved of the existing food sources, with an injection of new food sources provided by planting. This strategy relies partly on the preservation of native vegetation, and so may require some of the techniques used in native forest rehabilitation, in particular fencing against deer and pigs, and possibly weeding. However, there would be no need to eradicate every exotic, since several exotic species (see below) could usefully be retained.

In this section, I discuss suitable species for planting. Data are insufficient to propose exactly how the food-producing component of the habitat should be enhanced. I suggest that trials using all the species and management régimes suggested is the most realistic way to proceed.

Animal prey

A primary objective of the habitat management must be to support a rich and diverse invertebrate community, since all the passerine species are to varying extents insectivorous, taking a wide variety of arthropod prey (Chapter 5). The arthropods in turn support *Phelsuma* geckoes, which are important food for kestrels, cuckoo-shrikes and black bulbuls (Jones 1987, Chapter 5), as well as an important component of Mauritius' endemic fauna.

Native vegetation is likely to be richest in invertebrates, since a large proportion of insects are phytophagous, and these are typically both more abundant and more diverse in native trees than in exotics (Southwood *et al.* 1982). This is consistent with the obvious but unquantified predominance of observations of insectivory being in native trees (Cheke 1987c, pers. obs.). Therefore the best way to provide animal prey is to maintain native forest within the managed area. Most exotics, including *Cryptomeria*, appear poor in animal life, but a few, such as *Syzygium jambos*, *Harungana madagascariensis* and *Litsea monopetala* often yield prey items to foraging passerines (Cheke 1987c, Safford & Jones 1993). These last are invasive species and further planting is not suggested although they already form an important component of the vegetation of the area.

Phelsuma geckoes favour palms and various exotic trees (Jones & Owadally 1985). Native palms should be planted, as they once formed an important part of the native flora but are now rare. *Dictyosperma album* and *Acanthophoenix rubra* are cultivated for palm-hearts (Guého 1988, *Flore des Mascareignes*), and were much poached in the wild for the same reason. Measures against poaching may be needed if these are to be planted.

Nectar

The Mauritius Fody and both white-eyes take much nectar if available. They are dominant over exotic birds at nectar sources, and take readily to exotic foodplants. The most widely used exotics are *Syzygium jambos*, *Eucalyptus robusta* and *Callistemon* (Chapter 5). *S. jambos* and *E. robusta* are both common and damaging to native vegetation and so planting is not encouraged (indeed, control may be necessary if they are spreading). However, both provide copious nectar in winter, when it is in short supply, and so some should be left in areas where they will not suppress native vegetation. *Callistemon* appears to be non-invasive, as it has not spread from where it was planted. Further planting of this species is therefore strongly urged, as it was by Jones (1980, cited by Collar & Stuart 1985) and Safford (1991).

Native nectariferous species should also be considered. Strahm (in Safford 1991) suggested that *Trochetia blackburniana* is the most suitable native species, as it flowers all year (mainly in winter, but not only in April and May: pers. obs., *contra Flore des Mascareignes*) and is fast-growing and very rich in nectar (Staub 1988, pers. obs.).

However, this species has not been seen to be used by Mauritius Fodies (Section 5.3.2) and no data are available on the survival of planted individuals. The latter uncertainty exists for most of the native species that might be considered; trials are needed.

Cheke (1978) proposed the introduction of *Fuchsia magellanica*, as this species was absent on Mauritius but naturalized in native forest on Réunion where it was much used for nectar by olive white-eyes (Cheke 1987b), and did not appear to be invasive. Macdonald *et al.* (1991) found that it had become much more damaging to native vegetation on Réunion than Cheke expected, and the proposal to introduce it to Mauritius is not supported (Safford 1991).

Fruit

The Pink Pigeon, Echo Parakeet and Mauritius Black Bulbul all take large amounts of fruit. Few data exist with which to predict which native plant species would be best used to enhance fruit availability in the managed habitat, because of the lack of data on both frugivory and survival of planted specimens. Appropriate species may include *Aphloia theiformis*, *Erythrospermum monticolum*, *Tabernaemontana mauritiana* and *Nuxia verticillata*, as these are much used at present (Chapter 5, Jones 1987). Native palms, already proposed for planting because of their attractiveness for geckoes, would also provide fruit and perhaps also nectar; *Acanthophoenix rubra* palm seeds are dispersed by Réunion Black Bulbuls (Cadet 1980).

Of exotic fruiting trees, starfruit *Averrhoa carambola* and bilimbi *A. bilimbi* are highly attractive to Echo Parakeets. A few individuals of the former, but possibly none of the latter, are naturalized in the parakeets' distribution. The birds gather annually in the area of a small scatter of starfruit trees to feed on their fruit, and take bilimbi provided as supplemental food (Jones & Duffy 1993). I support these authors' suggestion of planting of *Averrhoa* spp. in degraded areas adjacent to Macchabé forest; the Pigeon Wood area may be too humid, as on the Mascarenes they are generally cultivated in lowland areas (*Flore des Mascareignes*).

Exotics of particular value to frugivores and already present in the wettest forest areas are champak *Michelia champaca* and *Homalanthus populifolius*; numerous other exotics are also taken (Chapter 5, Jones 1987). No exotics can yet be proposed as fruit sources for inclusion in planting programmes, apart from *Averrhoa* spp..

9.3.5 *Evaluation of this strategy for the Pink Pigeon and Echo Parakeet*

The foregoing strategy was devised with the passerines primarily in mind, although many of the measures suggested should benefit the Pink Pigeon and Echo Parakeet. It is necessary to consider whether implementation would be likely to guarantee the survival of the latter two species.

The breeding success of the Pink Pigeons in Pigeon Wood without predator control is sufficient to maintain the population at a stable level of up to 20 birds (Jones 1987). Recruitment is insufficient to sustain populations outside Pigeon Wood. If the same proves true of the new groves, it is likely that breeding by pigeons would remain restricted to the groves, rather than being spread throughout the remaining forest. Therefore, even the addition of two new groves would probably not, without additional supplemental feeding and predator control, result in a wild population over 100 individuals. Such a small population would always need close monitoring, and perhaps some further management to ensure its survival.

The Echo Parakeet is unlikely to be helped by the planting of *Cryptomeria*, unless pairs nest (in other trees) within the groves. The maintenance of native vegetation and the provision of additional food plants will benefit the species, but the long-term problems that it faces due to habitat degradation are daunting, because of the large areas it uses during the year and its apparently more specialized diet than the pigeon.

9.3.6 *A totally exotic habitat for native birds?*

The kestrel, flycatcher and Grey White-eye on Mauritius already live in habitats composed almost entirely of exotic plant species. The fact that the other native bird species do not probably stems from the composition and structure of the spontaneous exotic vegetation. The secondary and man-made habitats on the Comoros support native black bulbuls *Hypsipetes parvirostris*, paradise flycatchers *Terpsiphone mutata*, white-eyes *Zosterops maderaspatanus* and fodies *Foudia eminentissima* (Louette & Stevens 1992), all of which seem ecologically similar to the Mauritian species (pers. obs.). The richness of the native avifauna of these areas is in stark contrast to the usual situation in the man-made habitats of Mauritius; the visibly greater structural diversity, with an abundance of apparently productive tree species, of these habitats on the Comoros (pers. obs.) probably contributes to this. On Seychelles, native black bulbuls *H. crassirostris*, white-eyes *Z. modestus* and fodies *F. sechellarum* occur in exotic vegetation, the latter only on rat-free islands (Greig-Smith 1979, Collar & Stuart 1985, Crook 1961).

There appears no reason why all of the native passerines, and also the Pink Pigeon, could not live in such a habitat if it were created and managed correctly. However, such a habitat would be of little interest to the conservation of plants or other groups. While so much of Mauritius' native wildlife is endangered, there appears to be no interest in working intensively with exotic vegetation (pers. obs.), so long as the possibility exists of maintaining populations of native birds in native (or largely native) habitat. Exotic trees typically suffer worse damage from cyclones than do native trees (Vaughan & Wiehé 1937, King 1945), and bird populations in exotic habitats appear more vulnerable to the effects of cyclones than are those in native forest (Cheke 1975a).

For these reasons I have not put forward detailed proposals for the creation of completely exotic habitat for native birds. However, the possibility must not be forgotten, in case the native vegetation proves impossible to maintain in sufficient areas to assure the viability of bird populations. The uses of exotic plants put forward here would apply equally in a completely exotic habitat.

9.4 Ecological restoration of offshore islets

9.4.1 *Background*

Mauritian offshore islets are of actual or potential conservation importance for two main reasons. Firstly, some have by their isolation escaped the adverse effects of at least some of the biological invaders that have destroyed so much of the mainland's biota; Round and Serpent Islands are the outstanding examples, as they have never been colonized by rodents and, as a result, contain the last populations of several reptile and plant species extinct elsewhere (Cheke 1987d). Secondly, islands are often more suited to ecological restoration than are equivalent areas of mainland, because "the boundedness and small size of islands makes removal of exotics more feasible, and the isolation hinders reinvasion" (Simberloff 1990), and also because reintroduced native birds, being sedentary, are unlikely to leave. The predator problem which dogs mainland habitat repair can therefore be addressed if the predators can once be eradicated and their reintroduction prevented. The process of introducing species to islands is often termed marooning (for example, Cade 1993). In the western Indian Ocean, successful inter-island transfers of birds have been carried out on Seychelles (Watson 1989, Komdeur 1994).

In New Zealand, ecological restoration of islands has for decades played a pivotal rôle in conservation for exactly the same reasons as those given above for Mauritius. Techniques for eradication of exotic mammals and plants, translocation of native species (including birds) and many aspects of island management are well developed (Towns *et al.* 1990). Atkinson (1990) and C. R. Veitch (*in litt.* 1991) reported that 35 taxa of indigenous animal have been translocated to 62 New Zealand islands in 195 recognizable actions; more than 85 % were successful and the majority of failures were before 1950. Birds transferred to predator-free islands have often proved to possess a much wider habitat tolerance than could have been expected from their behaviour in their previous refuges; for example, the normally forest-living Saddleback *Philesturnus carunculatus* fared better than before when introduced to Tiritiri Matangi, which lacked mature forest (Craig & Veitch 1990).

It has already been suggested (Section 8.2.7) that all the native birds of Mauritius are capable of living at any altitude. There is no obvious reason why ecologically managed islets should not be suitable habitat for all of the native forest birds. It is possible that some Mauritian birds might, like the Saddleback in New Zealand, live at much higher density and show wider habitat tolerance in predator-free environments than they presently do; densities of Pink Pigeons, flycatchers and Mauritius Fodies already appear higher in predator-poor regions than in predator-rich areas.

Whenever the population of a species becomes concentrated in one location, such as an island, the population is at risk from localized catastrophes (Simberloff 1992). Cyclones may be a particular threat to birds on the Mauritian islets. Whereas larger land masses with varied relief may provide safe areas where bird populations and vegetation can survive an intense storm, a small islet is more vulnerable to a localized gust. Creation of a strong, full canopy is essential to provide protection.

9.4.2 *Mauritian islets*

Islets larger than about 20 ha may be large enough to support viable land-bird populations, as apparently does the 25 ha Cousin, Seychelles (Prŷs-Jones & Diamond 1984). Mauritius has ten islets over 20 ha within 25 km of the mainland. Three (Ile d'Ambre, Ile de l'Est and Ile aux Cerfs) are of little relevance to conservation, being 400 m or less from the mainland and intensively developed for tourism. The remaining seven are detailed in Table 9.2.

Table 9.2. Offshore islets of Mauritius with bird conservation potential. Exotic mammal lists compiled from Cheke (1987a), with additional details from B. D. Bell *per* C. G. Jones (verbally 1993). *Rr=Rattus rattus, Rn=R. norvegicus, Mm=Mus musculus, Sm=Suncus murinus, Ln=Lepus nigricollis.* The latter hare is a grazer not a predator, and is damaging to native vegetation.

Island	Area/ha	km to mainland	Exotic mammals	Key features
Serpent Island	32	24	none	huge seabird colony, no vegetation
Round Island	169	20	none	regenerating native palm savanna
Flat Island	253	11	*Rr,Mm*,cat	degraded, native remnants
Gabriel Island	42	11	*Rr*	degraded, native remnants
Gunner's Quoin	76	4	*Rn*[1],*Ln*	degraded, native remnants
Ile aux Aigrettes	25	0.6	*Sm*	regenerating native lowland forest
Ile aux Bénitiers	65	1.3	*Rr,Mm,Sm*	coconut plantation

Note

[1] Bullock (1986) mentioned only *Rattus rattus* on Gunner's Quoin, but intensive trapping in 1993 revealed only *R. norvegicus* (B. D. Bell *per* C. G. Jones verbally 1993).

The most suitable Mauritian islet for bird introductions is Ile aux Aigrettes. Flat and Gabriel Islands and Gunner's Quoin should next be considered, but will need more restoration first. The reasons are as follows.

Serpent Island is largely bare rock (Safford 1993), unsuitable for any land-bird. Ile aux Bénitiers has a very poor flora, although, unlike most islets, Grey White-eyes occur (pers. obs. 1991); it is run commercially as a coconut plantation and offers little scope for restoration. Restoration is well underway on Round Island, and the vegetation is recovering well from the past influence of goats and rabbits, now eradicated (Merton 1988, North *et al.* 1994). Priority is given to the repair of the unique palm savanna (Merton *et al.* 1989). This is a slow process, and the vegetation is still sparse and depauperate (pers. obs. 1992); even the highly adaptable Red-whiskered Bulbul is only present at very low density, and the islet is unlikely to be able to support native birds. Birds should be introduced as soon as the islet is believed to have become suitable.

Ile aux Aigrettes is well protected and managed as a nature reserve. Native forest rich in ebonies *Diospyros egrettarum* survives (Parnell *et al.* 1989). Roof Rat eradication was attempted and appears to have been successful (pers. obs.) and almost the whole islet had been weeded of exotics by late 1993. It is therefore the first choice for translocation of threatened native birds, as the habitat is probably already suitable for some species. However, eradication of shrews is an essential part of the restoration plan; birds should not be introduced until this has been done, as eradication will require the islet to be saturated with poison.

I have not landed on Flat and Gabriel Islands and Gunner's Quoin. All three support rats but mammal eradication is feasible even on the largest (B. D. Bell verbally 1993). The vegetation is dense in places and very degraded, but enough soil is present to allow rapid enhancement of bird habitat (B. D. Bell verbally 1993). The larger size of these islets gives them the potential to support more pairs of birds than Ile aux Aigrettes, and their more varied relief may provide sheltered areas relatively safe from cyclones.

9.4.3 *Bird species for introduction to restored islets*

All species except the Echo Parakeet could be introduced to islets without seriously damaging existing populations; for the Pink Pigeon, captive-bred birds are available. Although lowland habitat may be suitable for all the native birds, not all are equally suited to translocation to islets. The behaviour and habitat preference of a bird in its mainland refuge is a poor guide to its performance in a new habitat (Craig & Veitch 1990), so that "lateral thinking" is appropriate in deciding which species to translocate, and when to do so (D. V. Merton verbally 1992).

The strongest candidates are species which already occur at higher than average densities in low-predation areas like Pigeon Wood: the Pink Pigeon, flycatcher and Mauritius Fody. These species might live at still higher densities on a predator-free islet. The latter two species are especially suitable in view of their sedentary behaviour; they would not be likely to disperse if the habitat were acceptable.

The cuckoo-shrike shows no elevation in density in Pigeon Wood, and so there is no evidence that it can live at higher density in predator-free areas than the present maximum at Macchabé - Brise Fer. However, lizards (an important part of the diet) may become commoner on mammal-free islets; this could result in more food per unit area for cuckoo-shrikes and also black bulbuls, which might allow these species to live at higher densities than on the mainland.

Species which usually show seasonal movements may be unsuitable for marooning. However, they may only migrate from an area if food becomes scarce there. For example, some olive white-eye pairs (living in what appeared to be rich habitat) were found to be sedentary during 1989-93. If food resources were sufficient, Pink Pigeons, Echo Parakeets, black bulbuls and olive white-eyes (all mobile species: Chapters 3 and 4, Jones 1987) might all remain on the islets. Supplemental feeding may be needed if birds are transferred before restoration is complete; this is planned for the Pink Pigeon in Ile aux Aigrettes (C. G. Jones verbally 1994). The aim must be to establish self-sustaining populations, and so feeding should be discontinued as soon as possible without harming the birds.

9.5 Introduction of endangered Mauritian bird species to Réunion

9.5.1 *Previous proposals*

The closest and most ecologically similar island to Mauritius is Réunion, only 164 km away. Most Mauritian bird species have or had a Réunion analogue (a conspecific, or a very closely related species) (Cheke 1987a). Réunion once supported a kestrel (Cowles 1994) and about three native pigeons, one probably similar to the Pink Pigeon of Mauritius; all have been extinct for perhaps 300 years (Cheke 1987a). The extinct Réunion parakeet is regarded as conspecific with the Echo Parakeet, and has not even been shown to be subspecifically distinct (Jones 1987); its extinction in the eighteenth century may have been caused by a combination of extreme hunting pressure and destruction of lowland forest (A. S. Cheke in Collar & Stuart 1985). The Réunion native fody, whose rapid extinction may have coincided with the arrival of Roof Rats, was probably similar to the Red Forest Fody *F. (eminentissima) omissa* of Madagascar (Cheke 1987a) or indeed the Mauritius Fody; no specimens exist.

Réunion has around 650 km^2 of native forest (over seven times the extent on Mauritius), which is far less degraded than that on Mauritius, and monkeys and mongooses are absent (Cheke 1987a, Doumenge & Renard 1989, Macdonald *et al.* 1991). For these reasons, Cheke (1975b) proposed that the Mauritian pigeon, parakeet and fody should be introduced to Réunion (using captive-bred birds for the former two); Temple (1976, cited by Collar & Stuart 1985) added the kestrel to this list. The concept has been supported, without detailed consideration, by many authors, including Diamond (1985), Jones & Owadally (1985, 1988), Collar & Stuart (1985), Jones (1987) and Safford (1991); the excessive hunting pressure on Reunion was generally regarded as the main threat to introduced populations, especially of the pigeon. Temple (1981) provided the only detailed analysis, using island biogeographic theory to support the proposal; however, he completely ignored the nature of the threats to the birds and Diamond (1985) argued that Temple's analysis was invalid on theoretical grounds. Introduction of the Mauritius Fody was attempted in 1975, but only three birds were finally available for release; the birds were not seen again (Cheke 1987c). The failure of such a small propagule to produce an ongoing population is not surprising on grounds of demographic stochasticity alone (Simberloff 1992).

Jones *et al.* (1991b) reported on the feasibility of introducing the pigeon (and also the kestrel, which is no longer under serious consideration). They concluded that no adverse effects on other Réunion species were likely, but that studies on the abundance, distribution and seasonality of known food plants were needed. Predation of nests and adults by rats and cats was not considered of great concern; local poisoning campaigns around release sites were expected to "deal effectively" with them.

In the light of increased understanding of the ecology of, and threats to, these species on Mauritius, the proposals require re-examination. In particular, the problem of nest predation by rats, virtually ignored in previous assessments, needs careful consideration.

9.5.2 *Reassessment of the proposals*

There is no longer any conservation need to introduce the Mauritius Kestrel to Réunion, since its population is increasing rapidly on Mauritius (Jones *et al.* 1991a, in prep.) and it should soon be considered non-threatened.

During two visits to Réunion (May 1991 and May 1992), I visited several possible release sites for the pigeon, parakeet and fody to gain a qualitative impression of habitat suitability. I also collected preliminary data on rat abundance at one site. The two main aspects in support of the proposal, which I investigated, are now discussed.

Quality and area of habitat on Réunion

I visited seven native forest sites (excluding the high-altitude heath-zone) on Réunion: Bébour, Bélouve, Plaine des Chicots, Plaine d'Affouches, Rivière des Remparts, Vallée Heureuse (Basse Vallée) and the Cirque de Cilaos east of Cilaos town. These sites comprise a representative selection of the humid forests (Cadet 1980), although the richest lowland forest of Mare Longue (above Saint-Philippe) was not visited.

Most of the native forest of Réunion is at higher altitude than that on Mauritius, with frequent winter frosts, unlike Mauritius (Cheke 1987b). The likely effect (if any) of this difference on birds is unpredictable.

The suitability of the habitat on Réunion for pigeons and parakeets depends ultimately on the presence of suitable food-plants. Of the sites visited, Bélouve seemed the least suitable because it was dominated by one endemic tree species, *Acacia heterophylla*, whose usefulness to Mauritian birds is unknown; Jones *et al.* (1991b) doubted its suitability for pigeons. The remaining sites are mixed, humid, evergreen forests, variably invaded by exotics. The humid forests of Mauritius and Réunion share many plant species and genera; numerous known food-plants for these three birds on Mauritius are commoner on Réunion (Cadet 1980, *Flore des Mascareignes*, cf. Jones 1987, Chapter 5). In view of the varied diets of the pigeon, parakeet and fody, other plants, absent on Mauritius, would doubtless be used by the Mauritian birds. Plant food availability studies on Réunion restricted to plant species which are known or probable food-plants on Mauritius (suggested by Jones *et al.* 1991b) might ignore very important new food sources which would be available on Réunion.

The humid, epiphyte-rich forests of Réunion, with abundant rotting wood, superficially appear highly suitable for Mauritius Fodies, but no data exist on invertebrate food availability. The invertebrate fauna of Réunion is, according to entomologists on both islands, poorer in species than that of Mauritius, but higher biomasses are expected to be present in the native forests of Réunion than of Mauritius because of the higher proportion of native plant species (P. Berne, B. Vercambre & J. R. Williams verbally 1991; cf. Southwood *et al.* 1982). Quantitative sampling of food available for fodies on Réunion may be an unrealistic suggestion, because the food selection by fodies introduced to Réunion cannot be predicted.

In short, it may be impossible to predict how much food would be available to pigeons, parakeets and fodies introduced to Réunion, but there is no reason to think that the Réunion native forest would be unsuitable foraging habitat for any of these species.

The parakeet has an additional requirement: large, cavity-forming trees for nesting. For this reason, Cheke (1975b) considered the forest of Mare Longue (not visited by me) to be the only suitable area for this species, but that other areas could be made so by provision of nest boxes; however, Echo Parakeets have not yet used any of the many nestboxes provided for them on Mauritius (Jones & Duffy 1993).

Predators

Nest predation has been shown to be a critical factor determining the distribution and survival of the Pink Pigeon and Mauritius Fody. The Roof Rat and Crab-eating Macaque are both proven nest predators, and are considered to be responsible for most acts of nest predation upon these species (Section 6.3.2). Data on rat abundance at a potential release site on Réunion, compared to the existing ranges on Mauritius, were considered a prerequisite for any planned introductions (C. R. Veitch *in litt.* 1992). Feral cats are known predators of adult pigeons on Mauritius, and are common on Réunion (pers. obs.); for pigeon release, data would be desirable on cat abundance and food habits on Réunion.

I collected no data on the abundance of cats in forest on Réunion. However, rat-trapping trials were carried out at Vallée Heureuse (Réunion, 800 m altitude) on 23-25 May 1992, and in Macchabé forest (Mauritius, 640 m) monthly from June to October 1992. Each month, thirty baited snap-traps were set in pairs for three nights at 15-25 m intervals along a transect passing from *Cryptomeria* plantation into native forest, and rebaited and rechecked daily, following Newman & McFadden (1990). The aims were to confirm the dominant species of rat present in each forest, and to develop a monitoring method for use in the Mascarenes. For the latter reason, the methods were not precisely replicated each month, preventing detailed comparison of samples. However, summarized results are reported, because they suggest strong differences in the small mammal populations on Mauritius and Réunion. Appendix 4 details all animals caught.

On Mauritius, 4-14 Roof Rats were caught in each three-day trial, totalling 28 individuals, along with a single Brown Rat. On Réunion, the single trial produced eight Roof Rats, seven Brown Rats and three House Shrews. Non-systematic trapping at the field camp in Brise Fer forest, Mauritius (close to Macchabé) produced many hundreds of Roof Rats and less than ten Brown Rats during 1989-93 (pers. obs.).

There is no reason to doubt that the Réunion sample is typical. If so, it is confirmed that Roof Rats are abundant in the native forest there, but the small mammal populations of the two islands are very different: abundance of Brown Rats and House Shrews, and total small mammal biomass, may be much higher on Réunion. In addition (but presumably unimportant to the birds), the Roof Rats caught on Réunion included an individual of the brown-and-white phenotype (*"frugivorus"*) as well as the grey phenotype (*"rattus"*), which was the only one found on Mauritius.

9.5.3 *Conclusion*

The hunting threat on Réunion persists (pers. obs.), but could probably be countered by a vigorous education campaign (Collar & Stuart 1985). The presence of large areas of intact native forest on Réunion appears to favour the introduction proposal. However, the abundance of Roof Rats on Réunion may, even in the absence of monkeys, prevent the Pink Pigeon and Mauritius Fody forming viable populations there.

One factor, however, keeps the proposal alive for these two species: the extreme heterogeneity of the vegetation of Réunion may lead to areas of higher than average breeding success, which could keep recruitment high enough to maintain populations of these species. Réunion contains a great variety of native plant communities, and also large areas of *Cryptomeria* plantations abutting native forest. There seems no reason why the increased protection from predators for birds nesting in *Cryptomeria* should not apply equally on Réunion as on Mauritius. Furthermore, other native Réunion habitats (absent on Mauritius) might also give better than average protection against predators, and thus become source regions, as was suggested was the case in Les Mares (Mauritius) before its destruction (Section 7.4.3).

I therefore suggest that the introduction of Pink Pigeons or Mauritius Fodies would have the greatest chance of success if carried out in an area containing several habitats, including *Cryptomeria* plantations adjacent to native forest. Of the localities I visited, Vallée Heureuse (Basse Vallée) met this requirement best; wider surveys may reveal other suitable localities. Bébour may be unsuitable because it is relatively homogeneous native forest: this is, ironically, precisely the reason why it was originally suggested, before the breeding success patterns on Mauritius were understood.

The likelihood of success is uncertain for the introductions of the Pink Pigeon and Mauritius Fody to Réunion. Overall, a combination of current conservation measures and the new strategies on Mauritius presented here seem on current knowledge to offer an equally high chance of success.

Echo Parakeet populations may be less vulnerable to nest predation by Roof Rats than those of the pigeon and fody. Therefore the Roof Rat population of Réunion may not prevent the species' establishment there. Provided that the hunting which is believed to have contributed to their extinction on Réunion can be controlled, and that the lowland forest of Saint-Philippe is preserved, I strongly suggest that the introduction of the Echo Parakeet to the Forêt de Saint-Philippe, Réunion, is included within the overall recovery plan for this species. Of course, the present critically low population of the parakeet on Mauritius prevents this, but the option may become available when the species is established in captivity.

Overall, I suggest that further research on predator distribution, abundance and habits should precede any further development of the proposal to introduce endangered Mauritian species to Réunion.

9.6 Translocation within the mainland of Mauritius

Areas formerly occupied by a species can only be successfully repopulated if the cause of the species' disappearance no longer operates (Black 1991). For Mauritian birds, most of the causes of decline continue to operate all over the island, making translocations within the mainland pointless for most species. However, two sites, the Montagnes Bambous and Bras d'Eau, are isolated from the range areas of most species, and may contain habitat suitable for more native species than currently occur there.

The use of organochlorine pesticides, which may have been the cause of the local extinction the kestrel population in the Montagnes Bambous, ceased in around 1970 (Cheke 1987a, Section 8.2.4). It has already been suggested that the same cause could have eliminated the cuckoo-shrike there, as the Bambous contain apparently suitable habitat unoccupied by this species (Chapter 3). The highly successful reintroduction of the kestrel to the Bambous (Jones *et al.* 1991a, Cade & Jones 1993) suggests that the cuckoo-shrike could follow, as they are unlikely to recolonize naturally (Chapter 4). Reintroduction of this species to the Bambous should therefore be attempted, as Temple (in King 1978-79) has already suggested. There appears no reason why the birds could not occupy all 26 km^2 of this forest area: this would allow a 75 % increase over the present range area, and could double the population. Reintroduction should be achieved by translocation of wild birds from areas of high population density in the south-west, where losses should rapidly be made up. The initial release site should be an area of undisturbed, little-degraded native forest; the valley above Ferney appears suitable.

The black bulbul already occurs in the Bambous. Pink Pigeons, Echo Parakeets, olive white-eyes, flycatchers and Mauritius Fodies were probably more affected by other factors, especially nest predation, than by pesticides, and so are unlikely to be suited to reintroduction to the Montagnes Bambous.

The possibility of translocating native birds to Bras d'Eau has not been mentioned before. This site is around 20 km from the nearest sizeable tract of native forest (the Montagnes Bambous) and the mixed exotic plantations there have apparently been created since 1930 (see Koenig 1912-28), so some native bird species might have been unable to colonize. Floristic composition is very simple, comprising few species and prey diversity may be poor, but this site is the most important on Mauritius for flycatchers (Chapter 3); rarity of predators may be part of the reason (Chapter 7). The abundant mosquitoes which are probably important to the flycatchers (Cheke 1987c) may be of no use to gleaners, and so I suggest that studies on invertebrate diversity and predator and invertebrate abundance should be carried out, in order to investigate introducing other native birds.

9.7 Short-term conservation measures

Two species, the Pink Pigeon and Echo Parakeet, are in danger of imminent extinction in the wild. While the status of these two species remains so precarious, short-term conservation measures may be needed to ensure their survival until such time as long-term habitat management measures come to fruition.

Such measures are described and discussed for the Mauritius Kestrel and Pink Pigeon by Jones *et al.* (1991a, 1992) and for the Echo Parakeet by Jones & Duffy (1993). These measures are now, happily, unnecessary for the kestrel (Jones *et al.* in prep., Chapter 1). They include continuous control of predators on adults and nests, supplemental feeding and release of captive-bred birds. These measures have proved particularly effective for the kestrel and pigeon; actions for the parakeet have been less obviously successful, but this species finally bred in captivity in 1993 (C. G. Jones verbally 1993). For passerines, rat control in Pigeon Wood was the only short-term measure implemented; no increase in breeding success for fodies was found.

It is crucial to acknowledge that many of the successful conservation measures implemented to date are only short-term measures. For example, the current (1993-94) high productivity of the population of Pink Pigeons released from captivity is very likely to be directly attributable to continuous predator control and unlimited supplemental feeding. These measures need not be unduly expensive or time consuming, if carried out efficiently: rat control in Pigeon Wood cost less than £500 per year, and took around five man-hours per month to implement (pers. obs.). Such measures may therefore be continued for pigeons and parakeets for many years. Nevertheless in the long term, a sustainable strategy for providing sufficient food and allowing successful breeding is needed.

No other short-term measures are proposed for the passerine species, unless they show signs of declining much further.

9.8 Discussion

The four main conservation strategies for native birds discussed above are summarized in Table 9.3. Each strategy has unique advantages to both bird and ecosystem conservation. The method of habitat enhancement using exotics has hitherto been the most neglected, and its implementation is urgent, in order to consolidate and increase bird populations on the mainland (D. V. Merton verbally 1993-94).

As already pointed out, no strategy seems to offer any guarantee of long-term security for the Pink Pigeon and Echo Parakeet. This emphasizes the need to pursue all available strategies, with regular appraisal of their progress. In addition, the captive population of the pigeon must be maintained indefinitely (as stressed by Bruford *et al.* 1991) and efforts to establish the parakeet in captivity must continue, with a view to future reintroductions (including introduction to Réunion). Regarding captive breeding, I agree with the view of Simberloff (1988: 504): "Like it or not, many species will survive only with massive intervention that requires captivity, and we can not even always view this as a stopgap measure until reintroduction into the wild will occur. If it only fills a gap, it will surely be a long gap." For the passerines, the measures proposed here do, however, offer a high probability that such massive (and expensive) intervention will not be necessary.

Table 9.3. Summary of the main long-term strategies suggested for the conservation of forest-living native Mauritian birds, their advantages and disadvantages.

Strategy	Main overall advantage	Main drawback for birds	Main drawback for ecosystem restoration
Rehabilitate native vegetation on the mainland	Closest approach to true restoration for most habitats	Predator problem not addressed	Labour-intensive and costly
Enhance degraded native habitats using exotic plants	Large areas manageable; predator problem addressed	Predator problem reduced but not eliminated	Exotic plants maintained in habitat
Restore offshore islets	Predator problem eliminated; lowland habitat may be restored	Populations of larger species likely to be small; all species vulnerable to catastrophes such as cyclones	Not applicable to upland habitats
Introduce pigeon, parakeet and fody to Réunion	Large habitat area, no monkeys	Only three species can benefit; rat and cat problem not addressed	Conservation on Mauritius not addressed

9.9 Action plan for conservation measures

For each strategy, I now propose specific measures for implementation. It is difficult to rank the overall strategies in order of importance, because implementation or continuation of all the first three strategies in Table 9.3 is indispensible. Sufficient resources can certainly be raised to attempt this. Within each overall strategy, recommendations are presented in order of urgency.

1. *Habitat enhancement on the mainland using exotics*

i. The highest priorities are the maintenance of Pigeon Wood by planting new *Cryptomeria* trees, and the creation and maintenance of the two new groves, each covering up to 6 ha: one near Pigeon Wood and one in Bel Ombre, as identified above (Section 9.3.3 and Fig. 9.1). These priorities must be addressed first.

ii. Fence areas of native forest around these groves to exclude deer and pigs.

iii. In the Pigeon Wood area, weed selected plots within the fenced areas to varying extents, leaving some areas of *Michelia*, *Syzygium jambos*, *Eucalyptus*, *Harungana* and *Litsea monopetala* (if present). In Bel Ombre, weeded plots for habitat rehabilitation already exist; additional plots subjected to less intensive management levels (similar to those suggested around Pigeon Wood) need to be set up for comparison.

iv. Plant native species, including palms and *Trochetia*, in the fenced areas. Plant clumps of *Callistemon* inside and outside the plots. Plant *Averrhoa* spp. in degraded areas adjacent to Macchabé forest. Monitor the survival of planted individuals, and the amount of use of each plant species by the birds.

2. *Rehabilitation of native vegetation on the mainland*

i. Continue and expand the current plant conservation programme, including creation of further managed plots, following Strahm (1993).

3. *Island restoration*

i. Eradicate shrews from Ile aux Aigrettes, and then introduce Mauritius Fodies, Pink Pigeons and flycatchers.

ii. Continue rehabilitation of the vegetation of Ile aux Aigrettes and Round Island, with a view to eventual introductions of native birds on to the latter. All native bird species may be considered for future introduction.

iii. Begin rehabilitation or enhancement on Gunner's Quoin, Flat Island and/or Gabriel Island, following the recommendations of surveys carried out by B. D. Bell and others in 1993.

4. *Introductions to Réunion*

i. Carry out parallel studies on Mauritius and Réunion on the distribution, abundance and habits of rats and cats.

5. *Translocations within the mainland of Mauritius*

i. Carry out a carefully-planned and monitored introduction of the Mauritius Cuckoo-shrike to the Montagnes Bambous.

ii. Study invertebrate and predator abundance at Bras d'Eau, in order to investigate this site's suitability for species other than the flycatcher.

9.10 Further monitoring and research

The monitoring of Pink Pigeon and Echo Parakeet populations and breeding success must continue as at present. Simultaneous with the implementation of the above measures, the following aspects of ecology and management are the highest priorities for further research.

1. Wherever management is carried out, the bird, mammal, reptile, invertebrate and plant populations must be monitored, in order to assess the efficacy of the management régime.
2. Quantitative foraging studies are needed on Pink Pigeons and Echo Parakeets, to investigate the suggested existence of seasonal food shortages.
3. Ringing (or marking) studies on parakeets and passerines are needed to establish mortality and dispersal patterns. Such monitoring is already in progress for the Pink Pigeon.
4. Research into methods of control and eradication for all predators must be greatly expanded.
5. As Jones & Duffy (1993) pointed out for the Echo Parakeet, many more data on Mauritius have been collected than analysed. This imbalance must be rectified, and this can only happen if adequate time for sorting data and writing up is set aside in annual timetables.

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Appendix 1. Territory maps from survey work

To help comparisons between my surveys and those of future observers, the most important territory maps from my surveys are reproduced here. Maps for the flycatcher (all territories found) and Mauritius Fody (Alexandra Falls to Combo and Pigeon Wood) have already appeared in the main text (Figs 3.5, 3.6, 3.9 and 3.10).

On all maps, CS = blue, BB = yellow, OW = green, MF = red. Circles enclose territories. Points indicate individual sightings. See Section 3.2 for how territories were identified and mapped. For black bulbuls and olive white-eyes, whose home range is often bigger than the exclusive territory, the approximate extent of the exclusive territory is shown; individuals of these species were often seen outside the territories marked.

Fig. A2.1. The Macchabé - Brise Fer area, showing cuckoo-shrike, black bulbul and olive white-eye territories found in 1989-93. Flycatcher sightings are shown in Fig. 3.5. Mauritius Fodies were not recorded in the area.

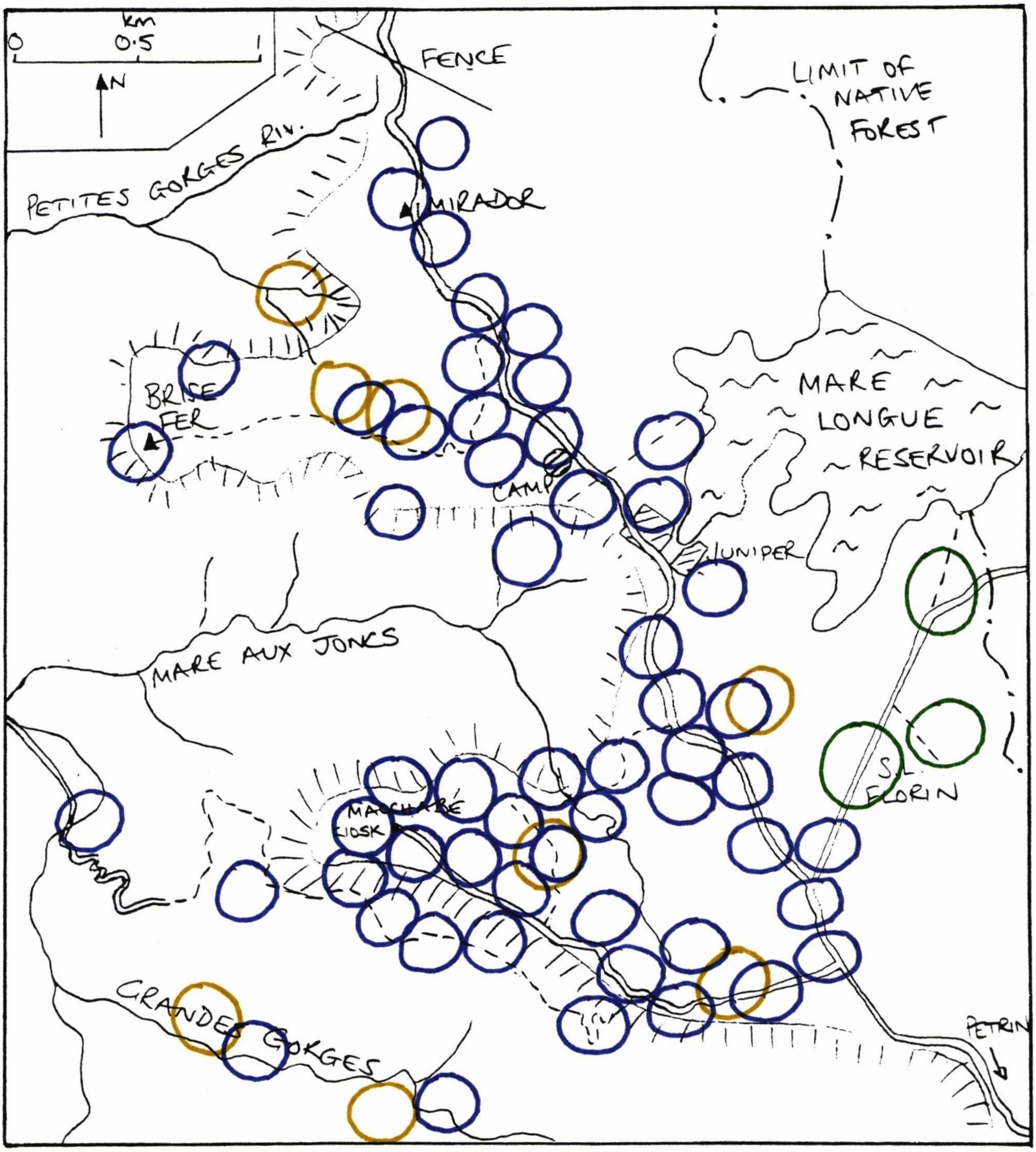


Fig. A2.2. The Pétrin - Raoul area, showing olive white-eye and Mauritius Fody territories found in 1989-93. No other threatened native species was recorded.

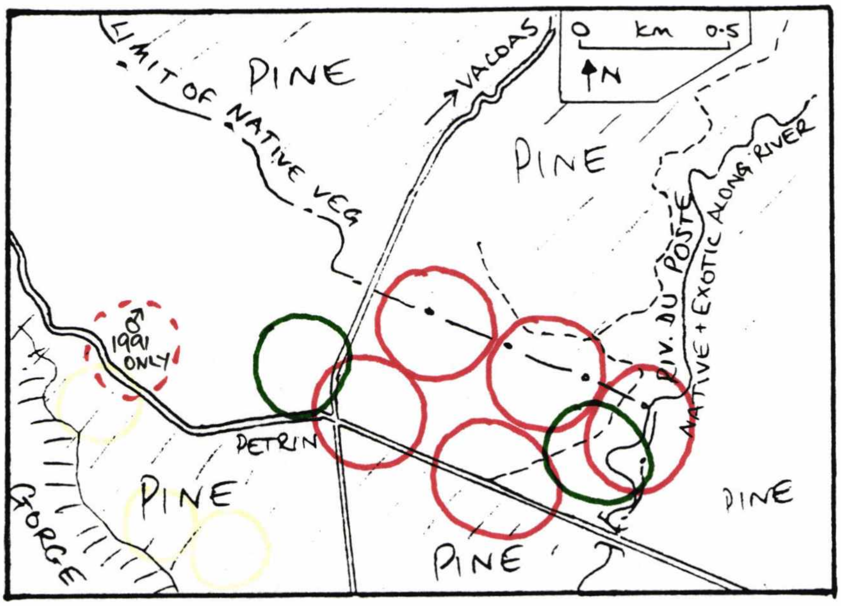


Fig. A2.3. The Bel Ombre - Black River Peak area, showing cuckoo-shrike and olive white-eye territories found in 1989-93. See Fig. A2.4 for Mauritius Fody territories. Black bulbul territories were not precisely mapped.

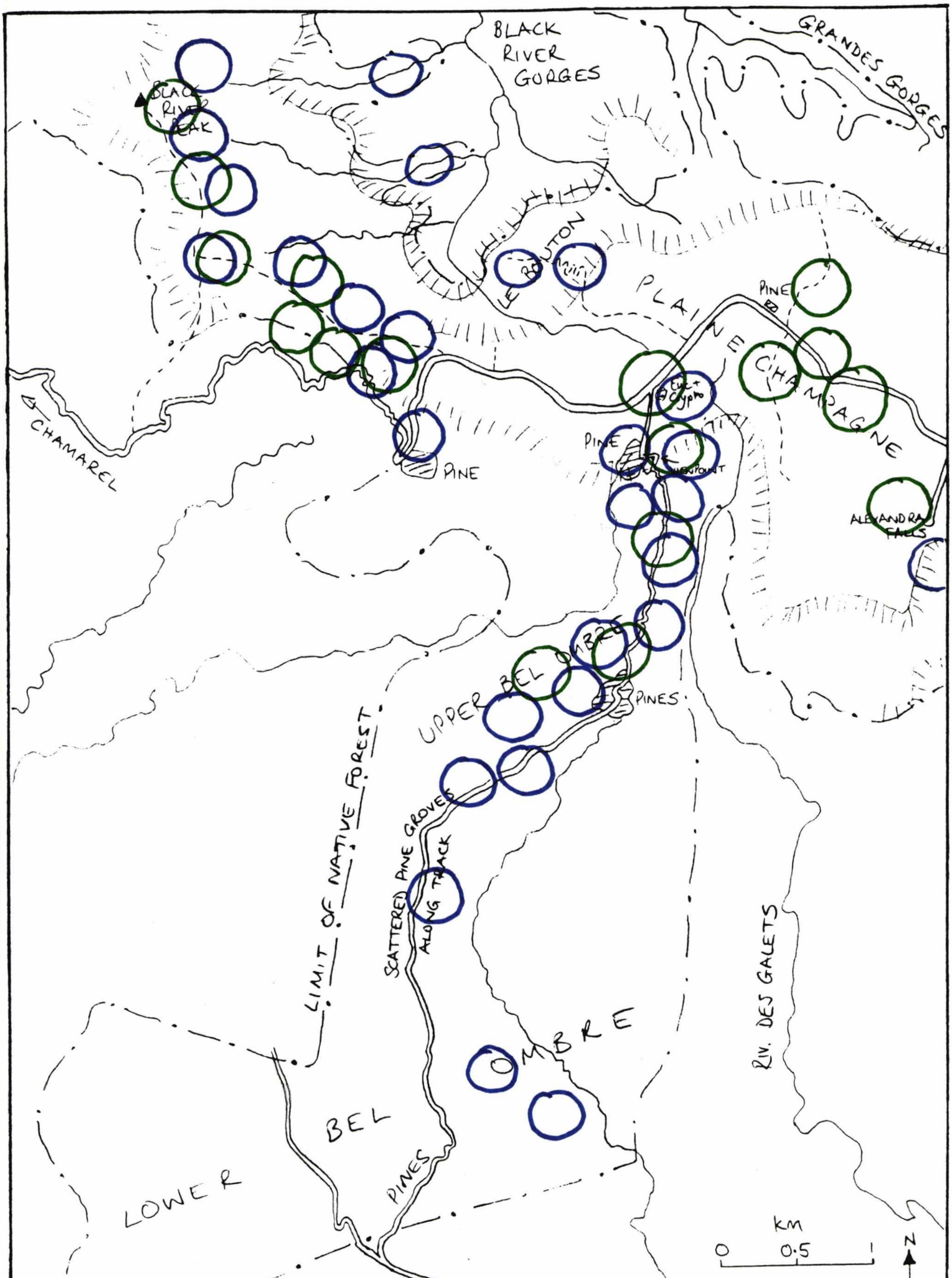


Fig. A2.4. Upper Bel Ombre and west Plaine Champagne, showing Mauritius Fody territories found in 1989-93.

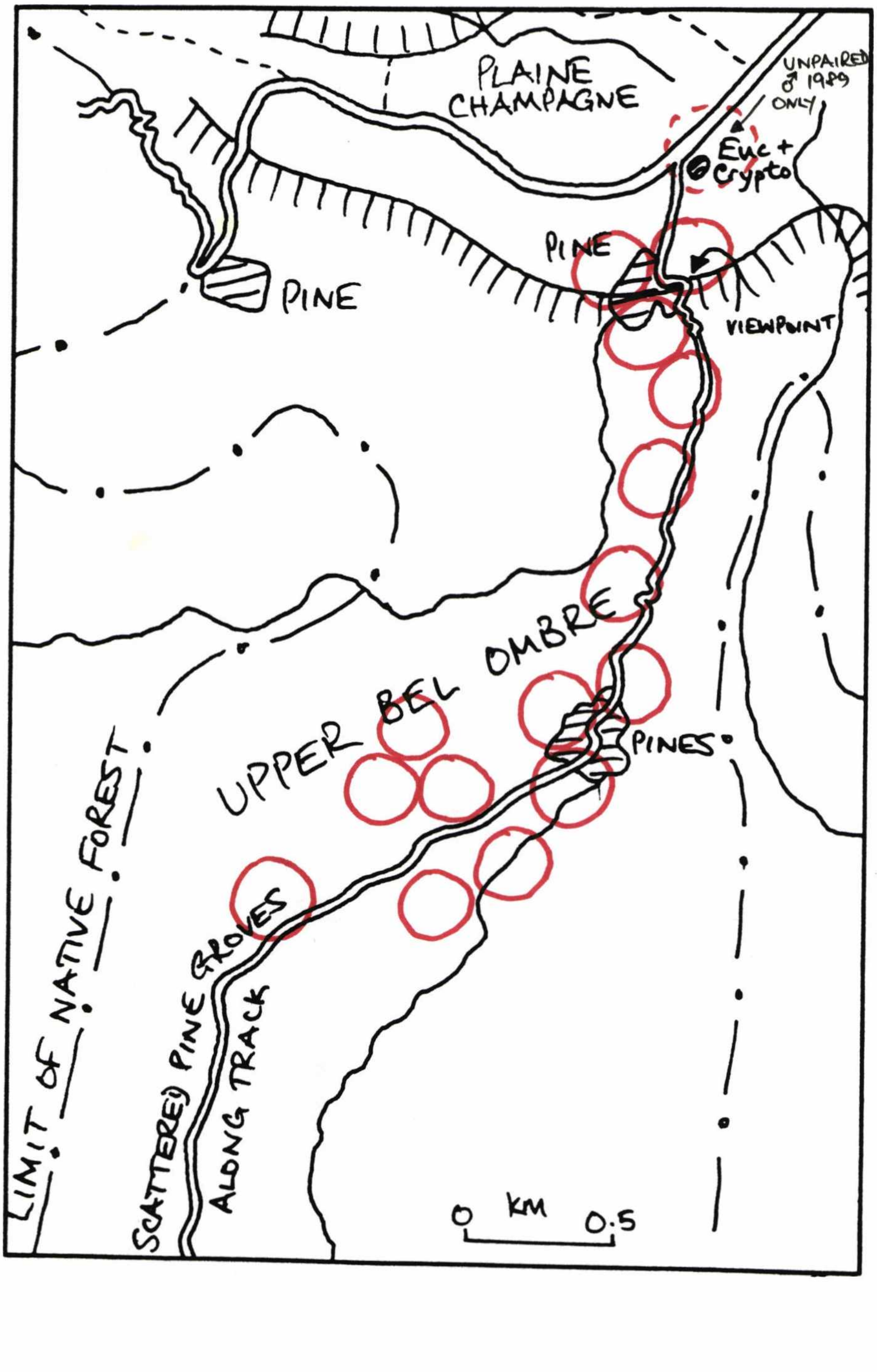


Fig. A2.5. Relict native forest patches by the Rivière du Poste and at Concession Jouanis, showing Mauritius Fody territories and precise locations of all sightings of other threatened native species (except the flycatcher: see Fig. 3.5).

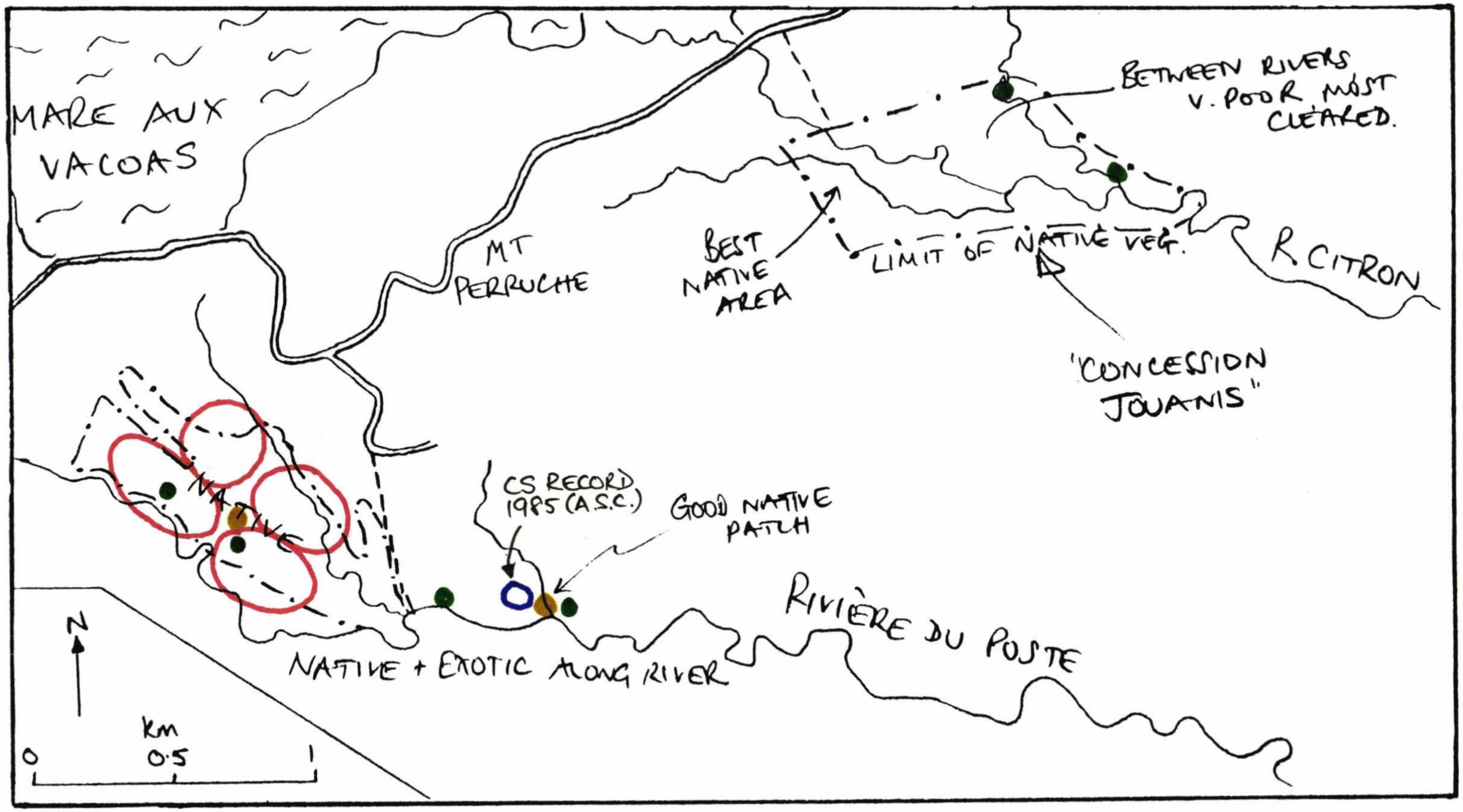


Fig. A2.6. The Montagne Cocotte - Piton Savanne area of the Southern Slopes, showing cuckoo-shrike territories found in 1989-93. See Fig. 2.10 for key.

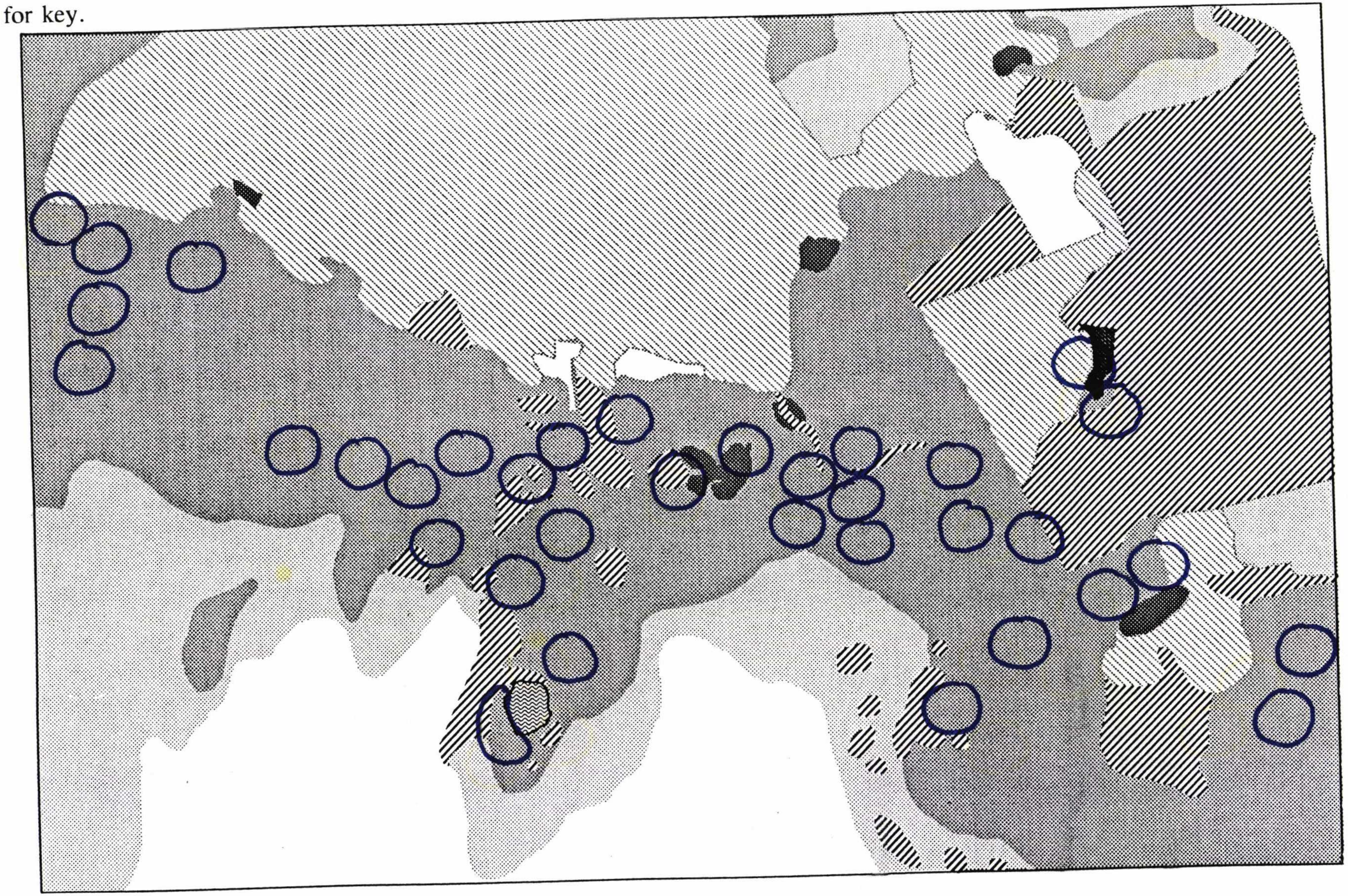


Fig. A2.7. The Montagne Cocotte - Piton Savanne area of the Southern Slopes, showing black bulbul territories found in 1989-93.

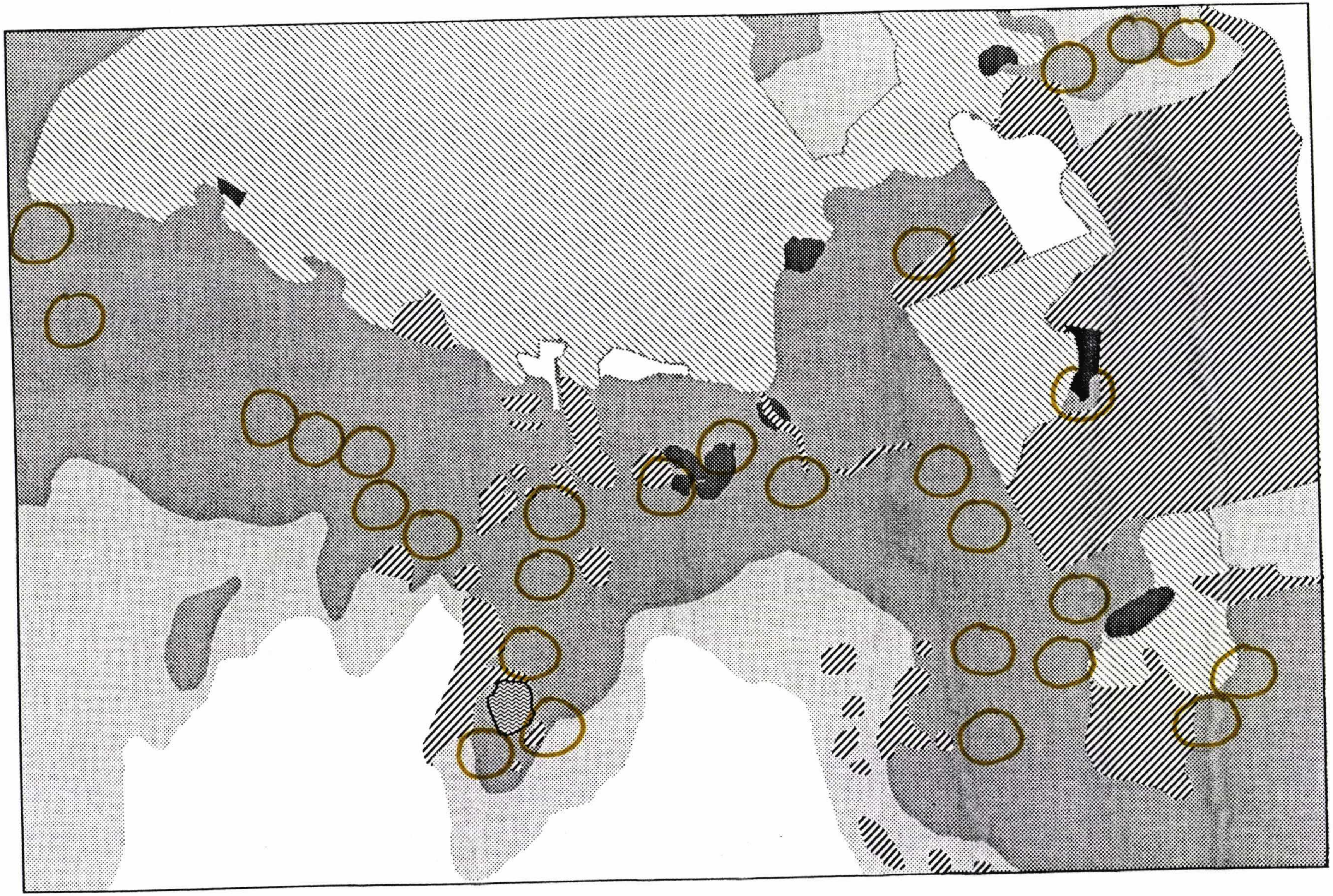
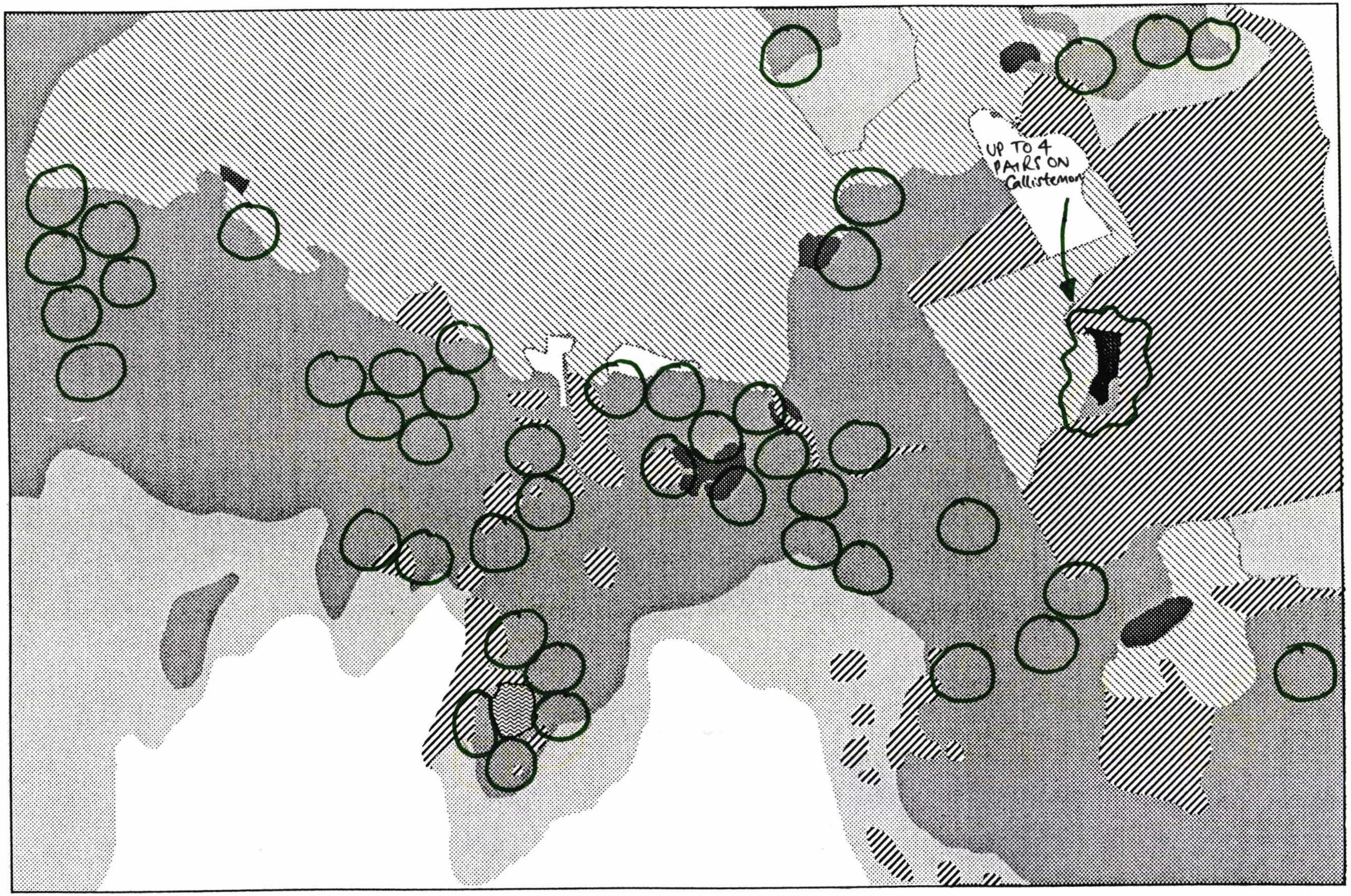


Fig. A2.8. The Montagne Cocotte - Piton Savanne area of the Southern Slopes, showing olive white-eye territories found in 1989-93.



Appendix 2. Database of all records of nests found or monitored in 1989-93

Future workers may wish to re-analyze my nest data-set, compare it with other data, or pool it with the results of future studies on Mauritius. I therefore give the entire database.

Sources

Almost all passerine nests were found and monitored by me.

For the Pink Pigeon, data were extracted from the following sources.

July 1989-June 1991 and July 1992-August 1993: monthly progress reports of the Pink Pigeon project (T. Liddiard, K. Swinnerton & C. Taylor unpubl.; none was written to cover July 1991-June 1992). June 1991-May 1992: field notes of C. Taylor. July 1989-June 1992: nest record cards summarizing field notes of above observers.

These data were supplemented throughout by my own observations.

For the Echo Parakeet, nests were found and monitored by K. J. Duffy, J. Mills and S. Rault. Data were summarized by Jones & Duffy (1993), but note that these authors' Table IV includes fledged broods from undiscovered nests; data presented here were checked by K. J. Duffy and against monthly progress reports.

Key to database

1) Sp (bird species): Nm=*Nesoenas mayeri*, Pe=*Psittacula echo*, Ct=*Coracina typica*, Ho=*Hypsipetes olivaceus*, Tb=*Terpsiphone bourbonnensis*, Zb=*Zosterops borbonicus*, Zc=*Zosterops chloronothus*, Fr=*Foudia rubra*, Pj=*Pycnonotus jocosus*, Fm=*Foudia madagascariensis*.

2) Month: given as the expected month of egg-laying (8912=December 1989). For Mauritius Fodies and Pink Pigeons, the number of the season follows (1=August 1989-July 1990). For fodies, the timing is then given: e=early (September-December), l=late (January-March).

3) Site: PW (y/n)=Pigeon Wood, with (y) or without (n) rat control; B.Blanc=Bassin Blanc; P. Paul="Piton Paul"; Patates=valley of Rivière Patates close to Bassin Blanc track.

4) Pair: for pigeons, ring numbers (male first) are given; for other species in traditional territories, the name of the territory is used (see Fig. 3.10 for Mauritius Fody territories in Pigeon Wood).

5) Plant (species supporting nest): Aphl=*Aphloia theiformis*, Calophyll=*Calophyllum eputamen* var. *grandis*, Cassia=*C. fistula*, Citrus=*C. aurantium*, Crypto=*Cryptomeria japonica*, Diospyros=*D. tesselaria*, Homalium=*H. paniculatum*, Labourd gl/ca=*Labourdonnaisia glauca/calophylloides*, Mimusops=*Mimusops maxima*, Nuxia=*N. verticillata*, Psidium/Psid=*P. cattleianum*, Rubus alc/rosi=*Rubus alceifolius/rosifolius*, Syz glom/jambos=*Syzygium glomeratum/jambos*, Tabebuia=*T. pallida*, Wiks=*Wikstroemia indica*.

6) Ht (height of nest above ground): given in metres.

7) SF/SR (stage found/reached): the stage of the breeding cycle at which the nest was found, and the stage ultimately reached by the nesting attempt. NM=nest-building, INC=incubation, FY=feeding young, FL=fledged young. Followed by the outcome: s=success, f=failed, d=deserted, u=outcome unknown.

8) Damage seen, Why failed and Notes: des=deserted, frag=fragment, inaccess=inaccessible, indet=indeterminate, infert=infertile, pred=robbed by predator, rems=remains, sl=slightly.

10) Pred (inferred identity of predator): RR=Roof Rat, CEM=Crab-eating Macaque.

11) nm, inc, fy: recorded days of exposure during nest-building, incubation and nestling periods (for Mayfield calculations). Nest loss marked with "x".

Sp	Month		Site	Pair	Plant	Ht	SF	SR		Damage seen	Why failed	Pred	Notes	nm	inc	fy
Nm	9102		PW (n)	417xA041	Crypto	?	NM	NM	d	x	x	x				
Nm	9105		PW (n)	A040xA051	Crypto	?	NM	NM	d	x	x	x				
Nm	9111		PW (n)	413xA049	Crypto	?	NM	NM	d	x	x	x				
Nm	9201		PW (n)	A040xA051	Crypto	?	NM	NM	d	x	x	x				
Nm	8912	1	PW (n)	A040xA051	Crypto	10	NM	INC	f	shells below	pred	RR	shells found after thought abandoned	0	7x	0
Nm	9004	1	PW (n)	[pr 5]	Crypto	10	NM	INC	f	shell rems below	pred	RR	poss Pr 7	4	2x	0
Nm	9006	1	PW (n)	417xA041	Crypto	11	INC	FY	f	intact	pred	?	squab killed about FL time, no juv seen	0	1	21x
Nm	9104	2	PW (n)	417xA041	Crypto	?	NM	INC	f	demolished	pred	CEM	small shell fragments below	3	1x	0
Nm	9105	2	PW (n)	UNxA054	Crypto	?	INC	INC	f	intact, shells below	pred	RR	A054 not yet ringed	0	5x	0
Nm	9105	2	PW (n)	417xA041	Crypto	?	NM	FY	f	intact, squab gone	pred	CEM	feathers & CEM faeces in tree	4	12	11x
Nm	9105	2	PW (n)	UNxA054	Crypto	?	NM	FY	f	intact, squab below	?gales	x	pred possible; A054 not yet ringed	2	14	2x
Nm	9105	2	PW (n)	417xA041	Crypto	?	NM	INC	f	intact, shell rems	pred	RR	shell halves below	1	2x	0
Nm	9105	2	PW (n)	417xA041	Crypto	?	NM	INC	f	shell rems	pred	RR	egg remains below	1	1x	0
Nm	9112	3	PW (n)	413xA049	Crypto	10	NM	FY	f	x	dead squab	x	squab deformed bill dead below	17	14	2x
Nm	9102	2	PW (n)	413xA049	Crypto	15	FY	FL	s	x	x	x		0	0	22
Nm	9105	2	PW (n)	413xA049	Crypto	15	FY	FL	s	x	x	x	same nest as previous by same pair	0	2	20
Nm	9111	3	PW (n)	417xA041	Crypto	?	NM	FL	s	x	x	x		16	14	23
Nm	8912		PW (n)	[pr 3]	Crypto	8	NM	INC	u	x	x	x	egg to captivity, dummy disappeared			
Nm	8912		PW (n)	419x418	Crypto	?	NM	INC	u	x	x	x	eggs to captivity, no dummies			
Nm	9001		PW (n)	419x418	Crypto	12	NM	INC	u	x	x	x	eggs harvested, dummies CEM toothmarked			
Nm	9002		PW (n)	419x418	Crypto	9	NM	INC	u	x	x	x	egg harvested, dummy rat-toothmarked			
Nm	9003		PW (n)	A040xA051	Crypto	8	NM	INC	u	x	x	x	egg to captivity, dummy disappeared			
Nm	9004		PW (n)	417xA041	Crypto	10	NM	INC	u	x	x	x	eggs to captivity, dummies inc full-term			
Nm	9005		PW (n)	417xA041	Crypto	12	INC	INC	u	x	x	x	eggs to captivity, dummies inc full-term			
Nm	9005		PW (n)	[pr 5]	Crypto	9	NM	INC	u	x	x	x	eggs to captivity, dummies thrown out			
Nm	9202		PW (y)	A040xA051	Crypto	?	NM	NM	d	x	x	x				
Nm	9204		PW (y)	A040xA051	Crypto	?	NM	NM	d	x	x	x				
Nm	9205		PW (y)	A040xA051	Crypto	?	NM	NM?	d				no details; presumed d so discarded			
Nm	9208		PW (y)	417xA041	Crypto	?	NM	NM	d	x	x	x				
Nm	9208		PW (y)	417xA041	Crypto	?	NM	NM	d	x	x	x				
Nm	9210		PW (y)	A055xA054	Crypto	?	NM	NM	d	x	x	x				
Nm	9211		PW (y)	A055xA054	Crypto	?	NM	NM	d	x	x	x				
Nm	9211		PW (y)	A055xA054	Crypto	?	NM	NM	d	x	x	x				
Nm	9211		PW (y)	A055xA054	Crypto	?	NM	NM	d	x	x	x				
Nm	9301		PW (y)	417xA041	Crypto	?	NM	NM	d	x	x	x				
Nm	9205	3	PW (y)	417xA041	Crypto	8	FY	FY	f	intact, dead squab	squab died	x	also dead egg intact below, not pred	0	0	4x
Nm	9205	3	PW (y)	413xA049	Crypto	?	INC	FY	f	x	indet	?	adandoned: cause unknown (pred possible)	0	3	10x
Nm	9205	3	PW (y)	UNxA054	Crypto	9	INC	FY	f	?	pred	?	male & squab disappeared near FL time	0	3	19x
Nm	9206	3	PW (y)	417xA041	Crypto	10	INC	FY	f	squab gone	pred/fell	?	1 egg still in nest	0	10	5x
Nm	9208	4	PW (y)	413xA049	Crypto	?	NM	FY	f	x	squab died	x		0	19	1x
Nm	9209	4	PW (y)	413xA049	Crypto	?	NM	INC	f	x	dead embryo	x		7	19z	0
Nm	9210	4	PW (y)	A045xA050	Crypto	?	NM	FY	f	intact	indet	?	squab died cause unknown, A050 killed	1	15	17x
Nm	9210	4	PW (y)	413xA049	Crypto	?	NM	INC	f	x	unhatched	x	dead embryo/infert; 413 killed ?9301	2	18z	0

Sp	Month		Site	Pair	Plant	Ht	SF	SR		Damage seen	Why failed	Pred	Notes	nm	inc	fy
Nm	9212		PW (y)	A040xA053	Crypto	?	?	INC	f	shell rems below	pred	RR	nest ?not found, dubious pair, discard	0	0	0
Nm	9212		PW (y)	A040xA053	Crypto	?	?	INC	f	shell rems below	pred	RR	nest ?not found, dubious pair, discard	0	0	0
Nm	9302	4	PW (y)	A055x418	Crypto	?	NM	INC	f	intact, shells below	pred	RR	shell remains 10m off	7	5x	0
Nm	9304	4	PW (y)	A040xA049	Crypto	?	NM	INC	f	demolished, C/2 gone	pred	CEM		2	9x	0
Nm	9304	4	PW (y)	A045xA044	Crypto	?	NM	INC	f	intact	pred	?		12	2x	0
Nm	9305	4	PW (y)	A055x418	Crypto	?	FY	FY	f	squab dead	pred	?	squab below, dismembered near FL age	0	0	4x
Nm	9305	4	PW (y)	A040xA049	Crypto	?	INC	FY	f	squab gone	pred	?	damage to nest not noted (?intact)	0	17	3x
Nm	9305	4	PW (y)	A045XA044	Crypto	?	INC	INC	f	no data	pred	?		0	11x	0
Nm	9306	4	PW (y)	A040xA049	Crypto	?	NM	INC	f	x	bad nest	x	egg fell through nest	1	1z	0
Nm	9306	4	PW (y)	A045XA044	Crypto	?	NM	INC	f	x	infert	x		1	16z	0
Nm	9307	4	PW (y)	A040xA049	Crypto	?	INC	INC	f	x	infert	x	both eggs infertile	0	7z	0
Nm	9307	4	PW (y)	A040xA049	Crypto	?	NM	FY	f	?	pred	?	?RR pred, no details given	3	17	1x
Nm	9202	3	PW (y)	417xA041	Crypto	?	NM	FL	s	x	x	x		8	15	24
Nm	9204	3	PW (y)	413xA049	Crypto	12	INC	FL	s	x	x	x		0	9	20
Nm	9206	3	PW (y)	417xA041	Crypto	?	NM?	FL	s	x	x	x	juv later died	0	0	22
Nm	9207	3	PW (y)	413xA049	Crypto	?	FY	FL	s	x	x	x	records ambiguous; nest ?not found	0	0	5
Nm	9208	4	PW (y)	A045xA050	Crypto	?	FY	FL	s	x	x	x		0	0	22
Nm	9210	4	PW (y)	A052xA044	Crypto	?	INC	FL	s	x	x	x	A052 killed	0	13	20
Nm	9211	4	PW (y)	417xA041	Crypto	?	NM	FL	s	x	x	x		1	15	26
Nm	9212	4	PW (y)	A040xA049	Crypto	?	FY	FL	s	x	x	x		0	0	21
Nm	9301	4	PW (y)	A045xA044	Crypto	?	FY	FL	s	x	x	x		0	0	16
Nm	9301	4	PW (y)	417xA041	Crypto	?	NM	FL	s	x	x	x		7	15	17
Nm	9302	4	PW (y)	A045xA044	Crypto	?	NM	FL	s	x	x	x		1	15	25
Nm	9305	4	PW (y)	417xA041	Crypto	?	INC	FL	s	x	x	x	3Jun: 5 d old; FL 30 Jun; 33d in nest!	0	3	33
Nm	9205	3	PW (y)	A045xA050	Crypto	?	NM		u				outcome?, squab OK age 8d, then no data	3	14	8
Nm	9307	4	PW (y)	417xA041	Crypto	?	NM		u				continuing 9308	35	6	0
Nm	9307	4	PW (y)	A045xA044	Crypto	?	NM		u				continuing 9308	28	15	15
Nm	9307	4	PW (y)	A055x418	Crypto	?	NM		u				continuing 9308	8	0	0
Nm	9211	4	PW (y)	A045xA044	Cyathea	5	INC	FL	s	x	x	x		0	11	22
Nm	9105		PW (n)	A040xA051	native sp.?		NM	NM	d	x	x	x				
Nm	9106	2	PW (n)	UNxA054	Pinus	11	NM	INC	f	intact, eggs below	?gales	?	pred possible; A054 not yet ringed	3	7x	0
Pe	9011		M. Longue	ML1	?	?	<NM	INC	f	egg shells in nest	pred	RR				
Pe	8811		Macchabé	Mac1	?	?	<NM	?FY	f	inaccess	?	?	abandoned nest, cause unknown			
Pe	9111		Macchabé	Mac1	?	?	<NM	FY	f	x	[chick dead]	x	chick rescued moribund; rat control			
Pe	9211		Macchabé	Mac1	?	?	<NM	INC	f	egg shells in nest	pred	RR	rat food cache in nest; rat control			
Pe	8711		Macchabé		?	?	<NM	FY	u	x	x	x	chicks harvested, no repeat seen			
Pe	8911		M. Longue	ML1	Labourd gl	6	<NM	FY	u	x	x	x	chick harvested, no repeat			
Pe	9211		Macchabé	TJunc	Labourd gl	5	<NM	INC	f	x	bees invade	x	clutch 1 harvested, 2 fails; rat control			
Pe	9011		Macchabé	TJunc	Labourd gl	5	<NM	FL	s	x	x	x	2 chicks harvested, 1 left to FL			
Pe	9112		Macchabé	TJunc	Labourd gl	5	<NM	FL	s	x	x	x	clutch 1 harvested, cl 2 FL; rat control			
Pe	8911		Macchabé	Mac2	Mimusops		<NM	INC	u	x	x	x	eggs harvested, no repeat			
Ct	9011		PW (n)		Calophyll	6	FY	FL	s	x	x	x				
Ct	9110		Brise Fer	BF1	Diospyros	7	INC	FY	f	chicks mutilated	pred	RR	nest intact			

Sp	Month			Site	Pair	Plant	Ht	SF	SR		Damage seen	Why failed	Pred	Notes	nm	inc	fy
Ct	9111			Brise Fer	BF1	Diospyros	8	NM	INC	f	shell fragments	pred	RR	nest intact			
Ct	9012			Brise Fer	BF1	Diospyros	7	FY	FL	s	torn apart	×	?	nest found, FL, pred all same day!			
Ct	9202			PW (y)		Eucalypt	7	NM	NM	f	blown out unfinished	gales	×	exposed to cyclonic wind			
Ct	8712			Brise Fer		Labourd gl	7	?	?	u	?	×	?	H.G.Young verbally			
Ct	9112			Brise Fer	BF3	Syz glom	7	NM	INC	f	shell fragments	pred	RR	nest intact			
Ct	9101			Brise Fer	BF2	Syz glom	9	FY	FL	s	×	×	×				
Ho	9302			Combo		Crypto	3	NM	?INC	f	sl dislodged	pred	?				
Ho	9102			PW (n)	PW1	Crypto	8	INC	FY	f	intact, emptied	pred	?				
Ho	9102			PW (n)	PW1	Crypto	8	NM	INC	f	intact, emptied	pred	?	later torn apart			
Ho	9112			PW (n)	PW1	Crypto	6	FY	FY	f	intact, emptied	pred	?	nest sl dropped			
Ho	9211			PW (y)	PW1	Crypto	7	NM	?INC	f	nest on ground	pred	?				
Ho	9302			PW (y)	PW1	Crypto	9	NM	FY	f	intact, chick out	?pred	?	nest intact, inaccess; dead chick below			
Tb	9001			Bras d'Eau		Cassia	6	NM	?	u	×	×	?	lowland			
Tb	9110			PW (n)	PW1	Psidium	1.6	FY	FL	s	×	×	×				
Tb	9210			PW (y)	PW2	Psidium	2	FY	FY	f	intact, emptied	pred	?	lining sl pulled: clinging chicks?			
Tb	9212			PW (y)	PW1	Psidium	1.7	INC	INC	f	intact, emptied	pred	?				
Tb	9210			PW (y)	PW1	Psidium	1.6	FY	FL	s	×	×	×	nest later destroyed			
Tb	9211			PW (y)	PW2	sapling sp	1.8	NM	FL	s	×	×	×				
Tb	9202			Bras d'Eau		shrub sp.	1.7	dis	?	u	×	×	?				
Tb	9110			B.Blanc		Syz jambos	2	NM	NM	f	nest ruffled	NM stolen	×	nest destroyed by Zb taking material			
Tb	9302			Bras d'Eau		Tabebuia	1.5	dis	?	u	×	×	?				
Zb	9301			Gr. Gorge		Harungana	3	dis	?	u	[torn out intact]	×	?				
Zb	9001			B.Blanc		herb sp.	1	NM	?	u	×	×	?				
Zb	9212			Cocotte		Ligustrum	4	dis	?	u	×	×	?	pines abut native forest			
Zb	9001			Pétrin		Pinus	8	NM	?	u	×	×	×				
Zb	9211			Raoul		Pinus	4	NM	?	u	×	×	×	pines abut native forest			
Zb	9212			Raoul		Pinus	8	FY	?	u	×	×	×				
Zb	9301			Raoul		Pinus	5	NM	?	u	×	×	×	pines abut native forest			
Zb	9111			Macchabé		Psid/fern	1.8	NM	INC	f	eggs gone, nest move	pred	?				
Zc	9001			Raoul		Pinus	6	NM	FY	f	torn out intact	pred	CEM	pines abut native forest			
Fr	9211	4	e	Bel Ombre		Calophyll.	7	dis	?	u	?	×	?		0	0	0
Fr	9210	4	e	B.Blanc		Citrus	1.7	NM	NM	f	demolished	pred	CEM	few Eucs in territ	3x	0	0
Fr	9210	4	e	Alex Falls		Crypto	6	NM	FL	s	×	×	×		3	15	16
Fr	9211	4	e	Combo	Combo1	Crypto	7	NM	?	u	?	×	?		0	0	0
Fr	9301	4	l	Combo	Combo2	Crypto	12	NM	?	u	?	×	?		0	0	0
Fr	9212			P.Paul	Paul2	Crypto	5	NM	NM	d	×	×	×				
Fr	9301	4	l	P.Paul	Paul3	Crypto	5	NM	INC	f	disappeared in gale	pred/wind		scattered Crypto sheltered from wind	4	1.5x	0
Fr	9012			PW (n)	central	Crypto	3	NM	NM	d	×	×	×				
Fr	9108			PW (n)	central	Crypto	8	NM	NM	d	×	×	×				
Fr	9109			PW (n)	central	Crypto	9	NM	NM	d	×	×	×				
Fr	9110			PW (n)	central	Crypto	8	NM	NM	d	×	×	×				
Fr	9110			PW (n)	E5	Crypto	10	NM	NM	d	×	×	×				
Fr	9110			PW (n)	stream	Crypto	12	NM	NM	d	×	×	×				

Sp	Month			Site	Pair	Plant	Ht	SF	SR	Damage seen	Why failed	Pred	Notes	nm	inc	fy
Fr	9111			PW (n)	central	Crypto	7	NM	NM	d x	x	x				
Fr	9111			PW (n)	palmiste	Crypto	9	NM	NM	d x	x	x				
Fr	9112			PW (n)	central	Crypto	10	NM	NM	d x	x	x				
Fr	9112			PW (n)	central	Crypto	5	NM	NM	d x	x	x				
Fr	9112			PW (n)	central	Crypto	12	NM	NM	d x	x	x				
Fr	9112			PW (n)	W ridge	Crypto	14	NM	NM	d x	x	x				
Fr	9112			PW (n)	W ridge	Crypto	10	NM	NM	d x	x	x				
Fr	9109	3	e	PW (n)	central	Crypto	5	NM	?INC	f intact, inaccess	pred/other	?	later demolished	9	1x	0
Fr	9110	3	e	PW (n)	stream	Crypto	8	FY	FY	f torn open/apart	pred	?	further attacked next day	0	0	6x
Fr	9110	3	e	PW (n)	E5	Crypto	5	NM	?NM	f torn open/apart	pred	?		30x	0	0
Fr	9110	3	e	PW (n)	central	Crypto	6	NM	FY	f demolished	pred	CEM		7	15	12x
Fr	9111	3	e	PW (n)	W ridge	Crypto	10	INC	INC	f torn open/apart	pred	?		0	7x	0
Fr	9111	3	e	PW (n)	central	Crypto	6	NM	INC	f nest & eggs intact	abandoned	x	eggs fertile	11	14z	0
Fr	9101	2	l	PW (n)	central	Crypto	7	NM	FY	f rat hole	pred	RR	chicks taken later (after hole made)	9	15	1x
Fr	9102	2	l	PW (n)	central	Crypto	3	NM	FY	f intact, emptied	pred	RR	demolished day after	4	15	3x
Fr	9201	3	l	PW (n)	palmiste	Crypto	7	NM	?NM	f torn open/apart	pred	?		5x	0	0
Fr	8911	1	e	PW (n)	central	Crypto	8	FY	FL	s x	x	x		0	0	13
Fr	9011	2	e	PW (n)	central	Crypto	7	INC	FL	s x	x	x		0	2	17
Fr	9011	2	e	PW (n)	stream	Crypto	12	NM	FL	s x	x	x		9	15	18
Fr	9109	3	e	PW (n)	W ridge	Crypto	10	NM	FL	s x	x	x		30	15	16
Fr	9110	3	e	PW (n)	Palmiste	Crypto	7	FY	FL	s x	x	x		0	0	17
Fr	9110	3	e	PW (n)	stream	Crypto	10	NM	FL	s x	x	x		33	15	18
Fr	9112	3	e	PW (n)	central	Crypto	8	NM	FL	s x	x	x		9	15	16
Fr	9001	1	l	PW (n)	central	Crypto	8	NM	FL	s x	x	x		3	15	17
Fr	9110	3	e	PW (n)	G3	Crypto	10	dis	?	u x	x	x		0	0	0
Fr	9102	2	l	PW (n)	stream	Crypto	10	NM	?	u x	x	x		5	0	0
Fr	9112			PW (y)	W ridge	Crypto	14	NM	NM	d x	x	x				
Fr	9202			PW (y)	central	Crypto	5	NM	NM	d x	x	x				
Fr	9202			PW (y)	palmiste	Crypto	14	NM	NM	d x	x	x				
Fr	9202			PW (y)	W ridge	Crypto	10	NM	NM	d x	x	x				
Fr	9208			PW (y)	W ridge	Crypto	8	NM	NM	d x	x	x				
Fr	9209			PW (y)	W ridge	Crypto	8	NM	NM	d x	x	x				
Fr	9210			PW (y)	D2	Crypto	4	NM	NM	d x	x	x				
Fr	9211			PW (y)	central	Crypto	5	NM	NM	d x	x	x				
Fr	9211			PW (y)	central	Crypto	7	NM	NM	d x	x	x				
Fr	9211			PW (y)	central	Crypto	4	NM	NM	d x	x	x				
Fr	9301			PW (y)	central	Crypto	6	NM	NM	d x	x	x				
Fr	9301			PW (y)	W ridge	Crypto	12	NM	NM	d x	x	x				
Fr	9302			PW (y)	central	Crypto	7	NM	NM	d x	x	x				
Fr	9209	4	e	PW (y)	stream	Crypto	5	NM	FY	f torn open/apart	pred	?	N/2 alive on ground below	8	15	1x
Fr	9212	4	e	PW (y)	H	Crypto	7	FY	FY	f torn open/apart	pred	?		0	0	6x
Fr	9202	3	l	PW (y)	palmiste	Crypto	6	NM	INC	f rat hole	pred	RR		5	9x	0
Fr	9301	4	l	PW (y)	H	Crypto	8	NM	?INC	f torn open/apart	pred	?		5	1x	0

Sp	Month			Site	Pair	Plant	Ht	SF	SR		Damage seen	Why failed	Pred	Notes	nm	inc	fy
Fr	9301	4	1	PW (y)	central	Crypto	12	NM	FY	f	rat hole	pred	RR		8	15	6x
Fr	9301	4	1	PW (y)	stream	Crypto	9	NM	FY	f	torn open/apart	pred	?		4	16	1x
Fr	9301	4	1	PW (y)	G1	Crypto	12	NM	INC	f	demolished	pred	CEM	CEMs close by	6	2x	0
Fr	9301	4	1	PW (y)	W ridge	Crypto	7	NM	INC	f	torn open/apart	pred	?		3	15x	0
Fr	9302	4	1	PW (y)	central	Crypto	4	NM	FY	f	intact, emptied	pred	RR		5	15	10x
Fr	9209	4	e	PW (y)	central	Crypto	5	NM	FL	s	x	x	x		6	16	18
Fr	9209	4	e	PW (y)	W ridge	Crypto	8	NM	FL	s	x	x	x		6	15	16
Fr	9210	4	e	PW (y)	stream	Crypto	8	NM	FL	s	x	x	x		10	15	18
Fr	9211	4	e	PW (y)	E5	Crypto	4	FY	FL	s	x	x	x		0	0	6
Fr	9211	4	e	PW (y)	G3	Crypto	4	FY	FL	s	x	x	x		0	0	7
Fr	9211	4	e	PW (y)	W ridge	Crypto	12	NM	FL	s	x	x	x		3	15	16
Fr	9212	4	e	PW (y)	palmiste	Crypto	10	FY	FL	s	x	x	x		0	0	7
Fr	9212	4	e	PW (y)	central	Crypto	7	INC	FL	s	x	x	x		0	10	16
Fr	9212	4	e	PW (y)	E5	Crypto	4	NM	FL	s	x	x	x		10	15	16
Fr	9201	3	1	PW (y)	W ridge	Crypto	14	NM	FL	s	x	x	x		12	15	15
Fr	9202	3	1	PW (y)	stream	Crypto	12	NM	FL	s	x	x	x		0	0	10
Fr	9210	4	e	PW (y)	D2	Crypto	9	NM	?	u	x	x	x		0	0	0
Fr	9212	4	e	PW (y)	E5	Crypto	5	NM	NM	u	[roof lifted]	pred/des	x	deserted (loose) or rat predation	0	0	0
Fr	9202	3	1	PW (y)	central	Crypto	10	NM	NM	u	x	x	x	deserted or failed due to bad weather	4	0	0
Fr	9302	4	1	PW (y)	stream	Crypto	8	NM	?	u	x	x	x	?FL but juvs not found	4	15	10
Fr	9301	4	1	P.Paul	Paul2	Eucalypt	8	NM	INC	f	torn open/apart	pred	?		9	5x	0
Fr	9301	4	1	P.Paul	Paul3	Eucalypt	5	NM	NM	f	demolished	pred	CEM		1x	0	0
Fr	9301	4	1	P.Paul	Paul3	Eucalypt	6	NM	NM	f	torn open/apart	pred	?		2x	0	0
Fr	8912	1	e	Patates	Pat1	Eucalypt	16	NM	INC	f	disappeared in gale	pred/wind		Strong wind	7	14x	0
Fr	8912	1	e	Patates	Pat2	Eucalypt	11	NM	INC	f	rat hole	pred	RR	on ground next day	4	13x	0
Fr	9011	2	e	Patates	Pat2	Eucalypt	12	NM	FY	f	intact, inaccess	pred/other	?	later pulled apart	9	15	6x
Fr	9012	2	e	Patates	Pat2	Eucalypt	12	NM	INC	f	torn open/apart	pred	?		9	8x	0
Fr	9210	4	e	Patates	Pat2	Eucalypt	7	NM	INC	f	rat hole	pred	RR	Lonicera in single Caloph in Euc grove	9	11x	0
Fr	9212	4	e	Patates	Pat4	Eucalypt	6	NM	?NM	f	torn open/apart	pred	?		14x	0	0
Fr	9001	1	1	Patates	Pat3	Eucalypt	12	NM	?INC	f	torn open/apart	pred	?	?inc	11	4x	0
Fr	9001	1	1	Patates	Pat2	Eucalypt	10	NM	FY	f	torn open/apart	pred	?		6	15	12x
Fr	8812	1	e	W of PW	?	Eucalypt	?	NM	?	u	x	x	x		0	0	0
Fr	9211	4	e	Cocotte		Homalium	3	NM	NM	f	torn open/apart	pred	?	no plantn in territ	1x	0	0
Fr	9302			NW of PW		Labourd ca	6	NM	NM	d	x	x	x				
Fr	9211	4	e	Savanne		Nuxia	4	NM	NM	f	torn open/apart	pred	?	no plantn in territ	2x	0	0
Fr	8912	1	e	Bel Ombre		Pinus	?	NM	?	u	?	x	?		0	0	0
Fr	9111			N of PW		Pinus	5	NM	NM	d	x	x	x				
Fr	9209	4	e	P.Paul	Paul1	Pinus	7	NM	NM	f	torn open/apart	pred	?		4x	0	0
Fr	9209	4	e	Patates	Pat1	Pinus	7	NM	FY	f	torn open/apart	pred	?		9	15	10x
Fr	9301	4	1	PW (n)	stream	Pinus	5	NM	INC	f	nest fell out intact	fell out	x	poor attachment	8	11z	0
Fr	8912			Raoul	Rao1	Pinus	10	NM	NM	d	x	x	x				
Fr	8911	1	e	Raoul	Rao1	Pinus	10	NM	INC	f	disappeared	Pred	?		4	9x	0
Fr	9011	2	e	Raoul	Rao1	Pinus	9	NM	?NM	f	demolished	pred	CEM	?inc	3x	0	0

Sp	Month	Site	Pair	Plant	Ht	SF	SR	Damage seen	Why failed	Pred	Notes	nm	inc	fy
Fr	9211 4 e	Raoul	Rao1	Pinus	15	NM	INC	f rat hole, egg frag	pred	RR	nest later blown out	8	9x	0
Fr	9301 4 l	Raoul	Rao2	Pinus	5	NM	?INC	f disappeared in gale	pred/wind			6	1x	0
Fr	9301 4 l	Raoul	Rao1	Pinus	10	NM	NM	f torn open/apart	pred	?		1x	0	0
Pj	9102	PW (n)		Crypto	6	dis	?	u x	x	x	terminal frond			
Pj	9212	PW (y)		Crypto	6	dis	?	u x	x	x	terminal frond			
Pj	9212	PW (y)		Crypto	10	dis	?	u x	x	x	terminal frond			
Pj	9301	PW (y)		Crypto	5	dis	?	u x	x	x	terminal frond			
Pj	9301	PW (y)		Crypto	3	dis	?	u x	x	x	terminal frond			
Pj	9301	P.Paul		Cyathea	2.5	dis	?	u x	x	x				
Pj	9212	P.Paul		fern	0.1	INC	INC	f gone, few tatters	pred	CEM				
Pj	9001	Savanne		fern	0	INC	?	u x	x	x	touching ground on embankment			
Pj	9301	Savanne		fern	0.1	INC	?	u x	x	x				
Pj	9001	Cham rd		grass	0.3	FY	?	u x	x	?				
Pj	9211	Monvert		grass	0.5	INC	?	u x	x	x				
Pj	9101	Patates		grass	0.2	INC	INC	f torn apart, emptied	pred	CEM				
Pj	8912	Patates		grass	1	INC	?	u x	x	x				
Pj	9101	Patates		grass	0.2	?	?	u ?	x	x				
Pj	9002	W of PW		grass	0.3	FY	?	u x	x	x				
Pj	9212	Patates		Ligustrum	1	INC	?	u x	x	x				
Pj	9301	P.Paul		Psid/Aphl.	0.8	INC	?	u x	x	x				
Pj	9212	NW of PW		Psid/grass	0.2	INC	FY	f intact, emptied	pred	?				
Pj	9212	Patates		Psid/grass	0.5	INC	?	u x	x	x				
Pj	9212	Bel Ombre		Psid/Wiks	0.2	FY	?	u x	x	?				
Pj	9012	NW of PW		Rubus alc	0.3	INC	FY	f brood taken in day	pred	?	N/2 taken between AM & PM visits			
Pj	9301	P.Paul		Rubus alc.	0.5	INC	INC	f gone, few tatters	pred	CEM				
Pj	9001	Patates		Rubus alc.	0.3	INC	?	u x	x	x				
Pj	9001	Bras d'Eau		shrub sp.	0.3	INC	?	u x	x	?				
Pj	9101	Réduit		shrub sp.	?	dis	?	u [on ground, ruffled]	x	x	down & adult tail feathers about			
Fm	9301	Pétrin		Bambusa	3	dis	?	u x	x	x				
Fm	9203	PW (y)		Bambusa	3	dis	?	u x	x	x	dense 5m tall bamboo thicket			
Fm	9201	PW (y)		Crypto	3	NM	INC	f on ground with C/3	?	?	nest torn into 2, unexplained			
Fm	9302	PW (y)		Crypto	4	FY	FY	f torn out & apart	pred	?	blood in nest remains			
Fm	9211	PW (y)		Crypto	3	NM	?	u [rat hole]	x	x	pred by RR poss after FL			
Fm	9212	Savanne		Crypto	7	dis	?	u x	x	x	?deserted			
Fm	9112	Bénarès		Dracaena	3	dis	?	u intact	x	x	inacc, disused when found			
Fm	9103	Cocotte		grass	0.3	INC	FY	f torn apart in situ	pred	?				
Fm	9103	Raoul		grass/fern	0.6	dis	?	u [torn apart in situ]	x	x	area trampled (CEM?), poss after FL			
Fm	9302	Pétrin		Pinus	?	INC	INC	f blown out intact	gales	x				
Fm	9103	Cocotte		Psid/grass	2	INC	INC	f rat hole	pred	RR				
Fm	9212	Lagrave		Ravenala	5	dis	INC	f torn out, rat hole	pred	RR	shell fragments			
Fm	9302	NW of PW		Ravenala	4	dis	?	u [torn apart & out]	x	x				
Fm	9104	Kanaka		Rubus rosi	1	dis	?	u x	x	x	empty when found			

Appendix 3. GENSTAT programme used to analyze the Mauritius Fody nest data, written by Dr L. G. Underhill, University of Cape Town.

```
 1 units [16]
 2 output [print=dots] 1
 3 vari nests,success
 4 factor [levels=2] crypto,ratc,earlate
 5 fact [levels=4] year
 6 read year,crypto,ratc,earlate,nests,success

Identifier   Minimum    Mean     Maximum     Values    Missing
nests        1.000      3.812    11.000      16        0
success      0.000      1.250     9.000      16        0          Skew

24 print year,crypto,ratc,earlate,nests,success

   year     crypto     ratc     earlate     nests     success
     1         1         1         1          1          1
     1         2         1         1          3          0
     1         1         1         2          1          1
     1         2         1         2          2          0
     2         1         1         1          2          2
     2         2         1         1          3          0
     2         1         1         2          2          0
     3         1         1         1         10          4
     3         1         1         2          1          0
     3         1         2         2          3          2
     4         1         1         1          1          1
     4         1         1         2          1          0
     4         2         1         1          8          0
     4         2         1         2          6          0
     4         1         2         1         11          9
     4         1         2         2          6          0
25 model[link=logit;dist=bin]success;nbin=nests
26 fit year,crypto,ratc,earlate
27 fit crypto,ratc,earlate
28 fit crypto
29 fit rate
30 fit year
31 fit earlate
32 fit crypto,ratc
33 fit ratc,earlate
34 fit crypto,earlate
35 stop
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Appendix 4. Details of small mammals caught on Mauritius and Réunion

Captures resulted from systematic snap-trapping in native forest on Mauritius (Macchabé) and Réunion (Vallée Heureuse) in 1992. The methods are given in Section 9.5.2. Dates given are the first day of the trial. All linear measurements are in millimetres, weights in grammes. HBL=head and body length, HF=hind foot length, Wt=weight, Rr=*Rattus rattus*, Rn=*Rattus norvegicus*, Sm=*Suncus murinus*. Shrews are easily identified by eye. Rats are identified as *R. rattus* if tail length > 110% of HBL, as *R. norvegicus* if tail length < 90 % of HBL (see Moors *et al.* 1989). The remaining five rat specimens (tail 90-110 % of HBL) were identified by a combination of the features in Moors *et al.* (1989). All measurements taken by myself and K. J. Duffy. ND=not done.

Locality and date	HBL	Tail	Ear	HF	Wt	Pelage	Sp.
Réunion	170	145	17	33	ND	br/wh	Rn
23 May 92	155	138	17	36	ND	br/gr	Rn
3 nights	163	143	17	36	ND	br/gr	Rn
	153	137	18	35	ND	br/wh	Rn
	173	142	19	36	ND	br/wh	Rn
	143	117	17	32	ND	br/wh	Rn
	160	157	18	36	ND	br/wh	Rn
	147	175	21	32	ND	grey	Rr
	180	210	22	37	ND	br/wh	Rr
	175	202	24	35	ND	grey	Rr
	179	188	24	33	ND	grey	Rr
	155	167	23	34	ND	grey	Rr
	165	208	25	34	ND	grey	Rr
	175	185	24	33	ND	grey	Rr
	190	195	23	34	ND	grey	Rr
	105	66	13	19	ND		Sm
	90	55	14	17	ND		Sm
	110	67	14	18	ND		Sm
Mauritius	150	160	19	28	106	grey	?Rr
2 Jun 92	120	162	18	30	55	grey	Rr
3 nights	110	133	18	27	41	grey	Rr
Mauritius	147	197	24	31	138	grey	Rr
6 Jul 92	157	182	24	33	131	grey	Rr
3 nights	95	119	20	27	ND	grey	Rr
	139	165	22	31	77	grey	Rr
	139	166	18	32	79	grey	Rr

Mauritius 2 Sep 92 4 nights	155	197	23	33	103	grey	Rr
	130	178	22	34	88	grey	Rr
	145	169	22	32	83	grey	Rr
	160	205	23	31	140	grey	Rr
	150	216	24	33	147	grey	Rr
	135	165	22	32	76	grey	Rr
	160	205	22	32	115	grey	Rr
	170	220	24	33	136	grey	Rr
	140	180	23	33	82	grey	Rr
	135	185	24	32	80	grey	Rr
	125	177	22	31	72	grey	Rr
	125	172	22	32	67	grey	Rr
	130	162	22	30	72	grey	Rr
	140	177	23	32	84	grey	Rr
	185	163	18	37	234	brown	Rn
Mauritius 8 Oct 92 3 nights	170	196	24	34	112	grey	Rr
	155	198	23	35	113	grey	Rr
	153	193	24	33	109	grey	Rr
	155	213	24	34	149	grey	Rr
	164	204	22	33	116	grey	Rr
	158	177	22	31	70	grey	Rr