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Rescue of the Seychelles warbler on Cousin Island, Seychelles: The role of habitat restoration

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Abstract

Management policies to save threatened species are not always successful, often due to the lack of a scientific basis and evaluation of the species response. We describe the ecological studies and the conservation actions taken between 1985 and 1992 on Cousin Island (29 ha, Seychelles) to safeguard the future of the highly threatened Seychelles warbler (*Acrocephalus sechellensis*), which until 1988 only occurred on this island. A detailed field study was designed to (1) identify the key processes influencing warbler demography, (2) identify appropriate management techniques to increase the warbler population, and (3), assess the influence of the resulting habitat management. Since 1980 the island has been saturated with c. 115 territories and c. 320 birds. The warbler is purely insectivorous. *Morinda* (*Morinda citrifolia*), the most insect rich tree, is preferred for foraging. The higher the insect abundance (and *Morinda* cover) in territories the higher the reproductive success and survival of warblers. Insect numbers were highest in the central part of Cousin and decreased towards the coast. Coastal territories protected by a salt tolerant hedge of *Scaevola* (*Scaevola taccada*) had more insects and higher reproductive success than unprotected territories. Between 1990 and 1992 *Morinda* trees were planted on the island and *Scaevola* along the coast. Although these habitat restoration measures have not resulted in higher numbers of adult warblers and territories due to habitat saturation, they have been successful in terms of improving the quality of existing breeding territories and with that the reproductive success of breeding birds (including the number of territories producing recruits), and the exchange of individuals (genetic material) between territories. We provide evidence that the high reproductive potential of this species is likely to improve the resilience of the species to catastrophic events.

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Keywords: Seychelles warbler; Habitat restoration; Population saturation; Demography; Effective breeding population; Buffer population; Genetic resilience

1. Introduction

Faunas on oceanic islands and mountain peaks are rich in endemic species, and represent a disproportionately large contribution to global biodiversity (Collar and Stuart, 1985, 1993; Collar and Crosby, 1995; Cronk, 1997; Stattersfield and Capper, 2000). Over the last sev-

eral hundred years these faunas have become among the most restricted and threatened in the world, mainly because of human disturbances such as habitat deterioration (e.g., Achard et al., 2002; Brooks et al., 1997, 1999), climate change (e.g., Pounds and Puschendorf, 2004; Thomas et al., 2004) and introductions of predators or competitor species (e.g., Clark and Dingwall, 1985; King, 1985; Stattersfield and Capper, 2000). Calls for management policies to save threatened species have been made in recent years (Collar and Stuart, 1985, 1993; Collar and Crosby, 1995; Cronk, 1997; Stattersfield and Capper, 2000; Overpack et al., 2002; Thomas

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et al., 2004). However, the management options are not always clear, as they need to combine scientific aims with technical feasibility and value judgements (Micol and Jouventin, 1995). To prevent a conservation failure, conservation actions should be based on detailed scientific studies carried out a priori. Until now, few conservation policies have been based on the outcome of scientific studies (Clemmons and Buchholz, 1997). This paper presents the scientific basis and evaluates the management actions taken to conserve the endangered Seychelles warbler (*Acrocephalus sechellensis*).

The Seychelles warbler is endemic to the Seychelles islands in the Indian Ocean, and its current IUCN red list status is vulnerable (IUCN, 2004). It is assumed that the Seychelles warbler originally occurred on most of the Seychelles islands, as they still constituted a single large island during the last ice age (Collar and Stuart, 1985). Between 1910 and 1920, most of the islands were planted with coconut palms (*Cocos nucifera*). This policy left very little suitable natural habitat for the warblers, resulting in their disappearance from all islands from 1920 onwards, with the sole exception of Cousin (29 ha) (Vesey-Fitzgerald, 1940; Collar and Stuart, 1985). Since that time the entire world population of

Seychelles warblers was confined to a tiny patch (c. 1 ha) of mangroves (predominantly *Avicennia maritima*), and oscillated around a dangerously low number of between 26 and 30 birds (Vesey-Fitzgerald, 1940; Crook, 1960; Loustau-Lalanne, 1968). Alien predator species, such as cats (*Felis catus*) and rats (*Rattus* spp.), and alien competitor species have never found their way onto the island. The introduction of these species would create by far the greatest threat to the future of the warblers. In 1968 Cousin was purchased by a consortium including Christopher Cadbury, the Royal Society for Nature Conservation and BirdLife International (then International Council for Bird Preservation) with the express aim of saving the warbler. Between 1968 and 1970, the young coconut trees were cleared and the native vegetation was allowed to regenerate from the tiny remnants (Fig. 1). By 1982 most of the island was covered in tropical forest (Fig. 1) which consisted mainly of indigenous *Pisonia* (*Pisonia grandis*; 47% of trees), *Morinda* (*Morinda citrifolia*; 15% of trees) and *Ficus* (*Ficus luea*; 12% of trees) trees, and the warbler population had grown to nearly 320 birds (Bathe and Bathe, 1982). Since that time numbers of birds have fluctuated around that level and the warbler population has reached carrying capac-

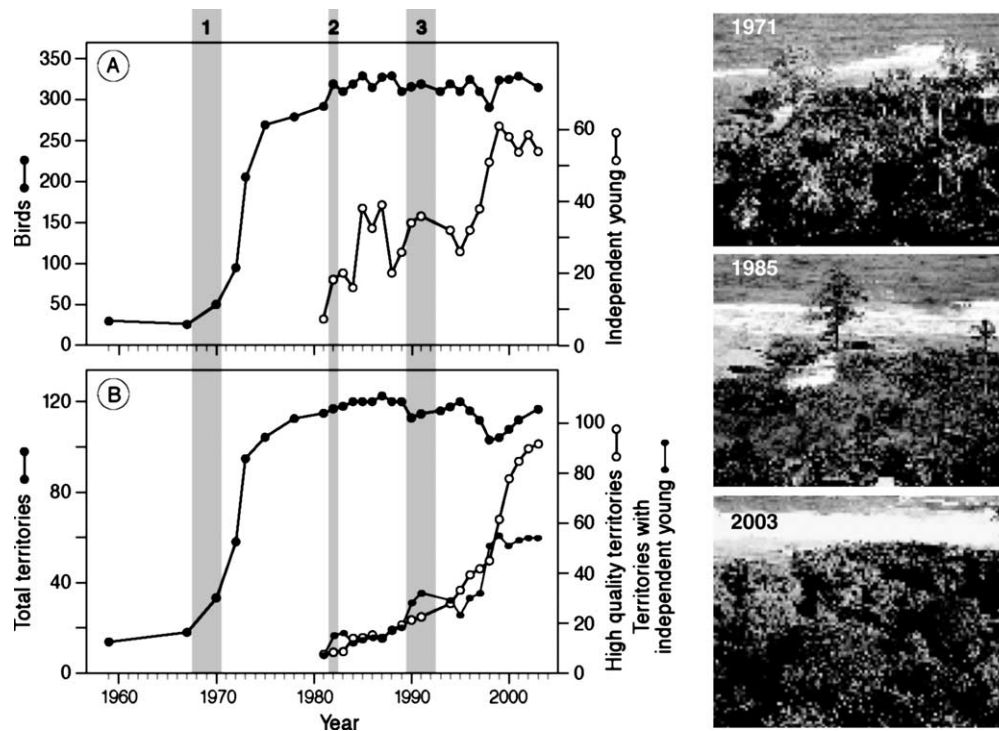


Fig. 1. Vegetation development of the south-eastern part of Cousin Island from 1970 to 2003. Photographs taken from the same position (photographs: 1970 from Fiedler, K., 1985 from Komdeur, J., 2003 from L. Brouwer), (a) the increase in number of fledged young and total number of Seychelles warblers, and (b) the increase in number of high-quality territories (tq > 30), total number of territories, and number of territories with independent young on Cousin Island since 1959 (sources for data in different years: 1959: Crook, 1960; 1967: Loustau-Lalanne, 1968; 1970, 1972, 1973, and 1975: Diamond, 1980, 1981; 1978: Brooke unpublished; 1982: Bathe and Bathe, 1982; 1983: Phillips and Wood, unpublished; 1984: Owen, unpublished; 1985–1991, 1993–2003: this study). Main ecological events indicated in blocs: (1) Young coconuts cleared (1968–1970); (2) tropical forest re-established (1982); (3) mature coconuts cleared, *Morinda* planting all over the island, and *Scaevola* planting along shoreline (1990–1992).

ity (Fig. 1(a)). The number of territories reached its saturation level of c. 115 territories in 1978 (Fig. 1(b)). In each of the years from 1978 onwards the island was completely covered by territorial groups with no empty spaces and there has been a surplus of non-territorial adult birds. As a consequence, young, but sexually mature birds remained on their natal territories and assisted their parents to raise subsequent broods (Diamond, 1980; Komdeur, 1992).

Until 1985 almost nothing was known about the ecology of the Seychelles warbler and the question was whether or not numbers of warblers could increase beyond the 320 birds if adequate conservation strategies were used. Our specific tasks were to study the ecology of the Seychelles warbler and to design and implement a conservation plan to increase the warbler population on Cousin. In this paper we describe the ecological studies and the conservation actions taken between 1985 and 1992 on Cousin in an attempt to safeguard the future of the Seychelles warbler on this island. Second, we document the short- and the long-term response (until 2003) of the warblers to the restoration strategies.

2. Methods

2.1. Study area

Seasonal climatic variation on Cousin Island (04°20' S, 55°40' E) is determined by changes in the direction of the winds. From May/June until October/November a strong (often force 5 at Beaufort scale), steady south-east trade wind blows. Between December and March the north-west monsoon predominates with lighter (force 3–4) and less persistent winds. Between the two main seasons transition periods are interpolated characterised by light winds (Diamond, 1980; see Section 3).

2.2. Factors influencing Seychelles warbler demography

2.2.1. Breeding behaviour

All Seychelles warblers on Cousin Island were studied from December 1985 to September 1990. Additional monitoring of the warbler population was conducted during the main breeding period (May to August) from 1981–1984 and from 1994–2003. Every week all territories were checked for the presence of colour-ringed birds and breeding activity. If a colour-ringed bird was missing from its territory, the rest of the island was searched for it. Off-island migration by warblers is negligible (0.13% per annum; Komdeur et al., 2004), so birds that have disappeared were considered to be dead. Breeding activity was assessed by following each female continuously for 30 min and recording whether she was nest-

building, incubating, or feeding young. The minimum number of records of these behaviours per 30-min interval was two (Komdeur, 1991). As many nestlings as possible (on average 74%) were individually colour-ringed. Young were independent by three months of age and sexually mature by one year of age (Komdeur, 1996) and remained on the natal territory for at least one year after birth (Komdeur, 1992, 2003). Most data were based on individually colour-ringed adults and young. The average yearly percentage of individually colour-ringed warblers varied from 70%–96%.

2.2.2. Foraging ecology

Foraging behaviour was studied (January 1987–March 1988) by walking a fixed transect (1.5 km) twice each week, once in the morning (0600–0830 h) and once in the afternoon (1630–1900 h), stopping for 2-min periods at 30 points, each 50 m apart. During each 2-min period we searched for a foraging warbler and for each half minute (up to four observations per bird) we noted the plant species in which the bird was foraging, part of the plant involved (stem, branch or leaf (upper- and under-side)), and prey taken (insect, fruit or seed). To assess prey availability during the foraging study, insect counts were conducted at 41 randomly chosen sites along the transect between the 15th and 20th of each month. At every site, 50 leaves per plant species (12 dominant species) were searched for insects and spiders, counting the totals on the upper- and under-sides separately. In the remainder of this manuscript we use the term 'insects' to refer to insects and spiders combined. During the foraging studies, the amount of foliage cover was measured along the transect monthly (January 1987–March 1988). At each fifth meter the presence or absence of foliage and plant species was noted in the following height bands: 0.0–2.0, 2.1–4.0 and at 2-m intervals thereafter. The foliage cover of plant species x is the total number of 'presence' scores at all height bands along the transect per 100 measure points on the ground. Percentage foliage cover of plant species x is foliage cover for plant species x divided by foliage cover of all plant species combined times 100. The significance of the various plant species for foraging was revealed by dividing percentage feeding observations in plant species x by percentage foliage cover of plant species x recorded on the transect.

2.2.3. Territory quality and foliage studies

Because the warblers are insectivorous, taking insect food from leaves (see Section 3) the quality of a territory depends on the insect prey available, amount of foliage and territory size. Territory quality (tq) was determined by measuring these variables and calculating territory quality following Komdeur (1994a). Territory quality of each of the 115–123 warbler territories was measured monthly between May 1986 and June 1991, and between

May and September from 1994 to 2003. Territories were divided into three categories: low- ($tq = 0.0\text{--}15.0$), medium- ($tq = 15.1\text{--}30.0$), and high-quality ($tq > 30.0$). For each plant species, insect density per unit leaf area was assessed by measuring the area of 250 leaves at 50 random sites on the island (five leaves per site). The quality of territories present in each year from 1981 to 1985 was assessed as high or low/medium combined ($tq = 0.0\text{--}30.0$) by using the territory and vegetation maps made each year.

Foliage development for *Pisonia* (the most abundant tree species on the island) was recorded monthly at three trees in each territory from January 1987 to February 1988. For each tree three shoots were tagged with a piece of string and the number of new leaves and total leaves counted each month, then indelibly marked with a waterproof marker, so that subsequent growth could be recorded. Monthly net foliage production was assessed as total leaves present per shoot minus total leaves present per shoot in previous month. Values for monthly net foliage production and monthly new leaves produced per shoot are corrected to 30-day-month. During the above period daily weather records were kept of rainfall (to the nearest 1 mm), wind direction and force (using the Beaufort scale). Rainfall frequency is the number of days per month that 0.1 mm or more was recorded, corrected to a 30-day-month. Once a fortnight wind direction and force was recorded in each territory between 0800 and 1000 h.

2.3. Data analyses

Reproductive success was calculated per breeding pair without helpers, because the presence of helpers significantly affected reproductive success of the breeding pair (Komdeur, 1994b). Territories were categorized in six habitats comprising woodlands of different heights and of different vegetation compositions (Table 1). For each warbler territory seven fitness components were calculated over the period December 1985 to September 1990, and averaged per year: (1) mean group size, (2) mean number of young fledged, (3) reaching independence, and (4) surviving to one year of age, (5) first year survival, (6) mean annual adult survival and (7) mean adult life expectancy. Survival is expressed as $12b/cm$ where c is number of birds present in year y , b is number of ringed birds still present in year $y + 1$, m is number of months between counts in year y and $y + 1$. Mean adult life expectancy is the length of time at which 50% of the population alive at one year will have died. Statistical analyses were performed using SPSS 11.0 (2001) and were two-tailed. Mean values are expressed with standard errors; probability values are two-tailed and the level of significance was set at $P < 0.05$.

Table 1

Categorisation of Seychelles warbler territories on Cousin Island in habitat types comprising woodlands of different heights, and of different vegetation compositions (*Pisonia* woodland, *Morinda* woodland, or *Morinda-Pisonia* woodland), area of habitat types during 1985–1990 and 2002–2003, and the effect of habitat type on mean (\pm SE) annual territory quality and demography of Seychelles warblers (group size, number of fledged young, independent young, and one-year-old young, first year survival, annual adult survival, and adult life expectancy) during December 1985–September 1990

| Habitat type | Height (m) | Tree cover (%) | Area (ha) 1985–1990 | Area (ha) 2002–2003 | Territory size (ha) | Territory quality | Group size | Young fledged | Young independent | One year old young | First year survival | Annual adult survival | Adult life expectancy | N |
|--------------------|---|----------------------|---------------------|---------------------|---------------------|--------------------|---------------------|---------------------|---------------------|---------------------|---------------------|-----------------------|-----------------------|----|
| I | Coastal <i>Pisonia</i> woodland with tall herbs | 30–70 <i>Pisonia</i> | 7.5 | 1.6 | 0.30 (± 0.07) | 3.3 (± 0.8) | 2.44 (± 0.55) | 1.00 (± 0.23) | 0.64 (± 0.20) | 0.48 (± 0.14) | 0.48 (46) | 0.66 (20) | 1.3 | 72 |
| II | Tertiary <i>Pisonia</i> woodland | >70 <i>Pisonia</i> | 5.4 | 3.4 | 0.24 (± 0.04) | 1.3 (± 0.5) | 2.15 (± 0.34) | 0.59 (± 0.13) | 0.15 (± 0.07) | 0.15 (± 0.05) | 0.25 (16) | 0.79 (40) | 2.1 | 52 |
| III | Secondary <i>Morinda</i> woodland | >70 <i>Pisonia</i> | 2.1 | 6.3 | 0.18 (± 0.04) | 28.3 (± 4.9) | 3.67 (± 0.71) | 1.11 (± 0.26) | 0.96 (± 0.19) | 0.96 (± 0.21) | 0.86 (14) | 0.90 (20) | 6.4 | 24 |
| IV | Secondary <i>Morinda</i> woodland | 30–70 <i>Pisonia</i> | 3.2 | 11.5 | 0.24 (± 0.11) | 17.0 (± 3.4) | 2.78 (± 0.43) | 1.10 (± 0.32) | 0.83 (± 0.16) | 0.83 (± 0.13) | 0.75 (14) | 0.90 (20) | 6.4 | 36 |
| V | Secondary <i>Pisonia</i> woodland | >70 <i>Pisonia</i> | 6.9 | 2.2 | 0.29 (± 0.10) | 4.8 (± 3.1) | 2.20 (± 0.38) | 0.83 (± 0.31) | 0.38 (± 0.09) | 0.38 (± 0.09) | 0.29 (17) | 0.58 (20) | 1.7 | 60 |
| VI | Primary <i>Pisonia</i> woodland | >70 <i>Pisonia</i> | 3.9 | 4.0 | 0.46 (± 0.12) | 18.5 (± 4.1) | 2.67 (± 0.33) | 0.67 (± 0.24) | 0.54 (± 0.11) | 0.54 (± 0.12) | 0.80 (7) | 0.86 (72) | 4.4 | 36 |
| Mean (I–VI) | | | 0.29 | 8.3 | 2.51 (± 0.08) | 0.80 (± 2.4) | 0.53 (± 0.45) | 0.49 (± 0.24) | 0.52 (± 0.14) | 0.90 (± 0.12) | 4.2 (114) | 280 (172) | | |
| Mean (III, IV, VI) | | | 0.29 | 21.3 | 3.04 (± 0.10) | 0.96 (± 4.0) | 0.78 (± 0.46) | 0.74 (± 0.28) | 0.80 (± 0.15) | 0.89 (± 0.15) | 5.1 (35) | 96 (112) | | |

All demography variables, except for adult life expectancy, were based on annual means of data collected from December 1985 to September 1990. N = number of territory years.

3. Results

3.1. Influence of vegetation composition and territory quality on demography

The Seychelles warbler is purely insectivorous. Of all food items taken ($N = 4512$), 99.8% consisted of insects, 98.2% were taken from the under-sides of leaves, and 93.6% of feeding occurred through gleaning behaviour. The preference for under-sides of leaves cannot be explained by higher prey density, as the latter was the same for both sides (ratio insects under- to upper-sides for all plant species combined was 1.02). There was no sexual difference in foraging behaviour (Mann–Whitney U -test: $z = 1.329$, 62 males, 68 females, $P = 0.184$). Therefore data from both sexes were combined in further analyses. Even within a small island such as Cousin insect numbers varied locally during the period from 1986 to 1990 (Fig. 2). Mean yearly insect number for the three most common tree species combined (*Pisonia*, *Morinda* and *Ficus*) was highest in the central part of Cousin and decreased gradually towards the coast (Fig. 2). The difference in insect numbers between the central

part and the coastal area can be explained by wind force. Mean insect numbers was negatively correlated with mean wind force ($r^2 = 0.22$, $N = 123$, $P < 0.001$). Mean wind force in the central part of the island was very low, and increased gradually towards the coast where the mean wind force was greatest (Fig. 2). Due to these spatial differences in insect availability, Seychelles warblers occupying territories in the central area of the island had access to significantly more food than warblers occupying the coastal area. Insect numbers not only varied locally, but also per plant species. The insect numbers on the different plant species were compared using the insect abundance on the underside of leaves because nearly all feeding by the warblers was from the underside of leaves. The greatest abundance of insects was found on *Morinda*, which exactly matched the warbler's preference for foraging in *Morinda* (Fig. 3(a)). *Pisonia*, other trees and herbs had lower insect numbers and were not preferred for foraging (Fig. 3(a)).

The differences in insect numbers between plant species and at the island scale were important determinants of reproductive success and survival of Seychelles warblers. The higher the cover of *Morinda*, which is rich

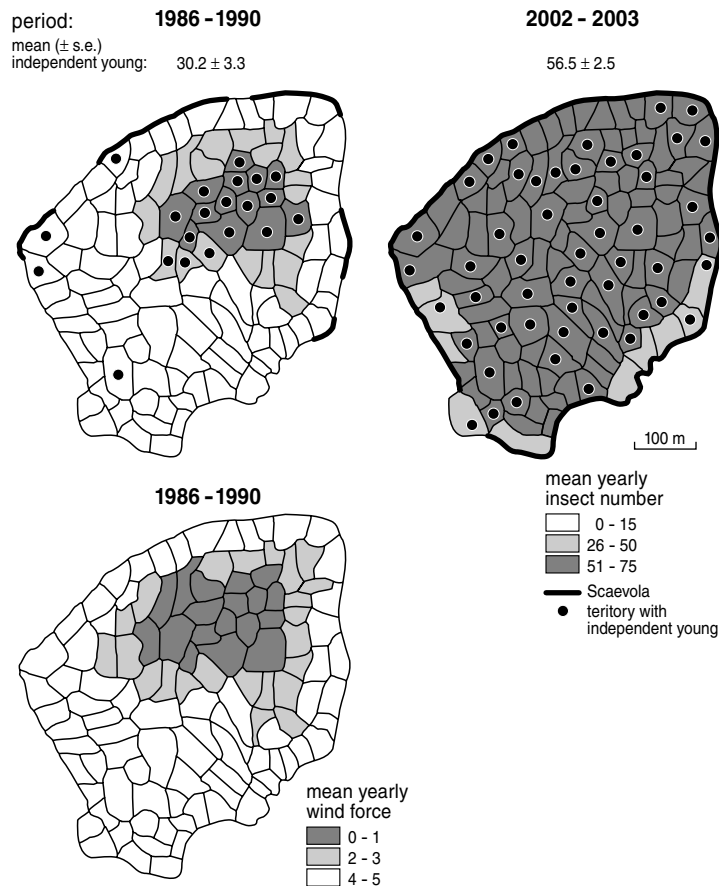


Fig. 2. Mean yearly insect number for three tree species combined (*Pisonia*, *Morinda* and *Ficus*), the production of independent young in each Seychelles warbler territory, and the presence of *Scaevola* along the coast line during the periods January 1986 to September 1990 and January 2002 to September 2003 on Cousin Island. Mean yearly wind force (Beaufort scale) in each territory during the period January 1986 to September 1990.

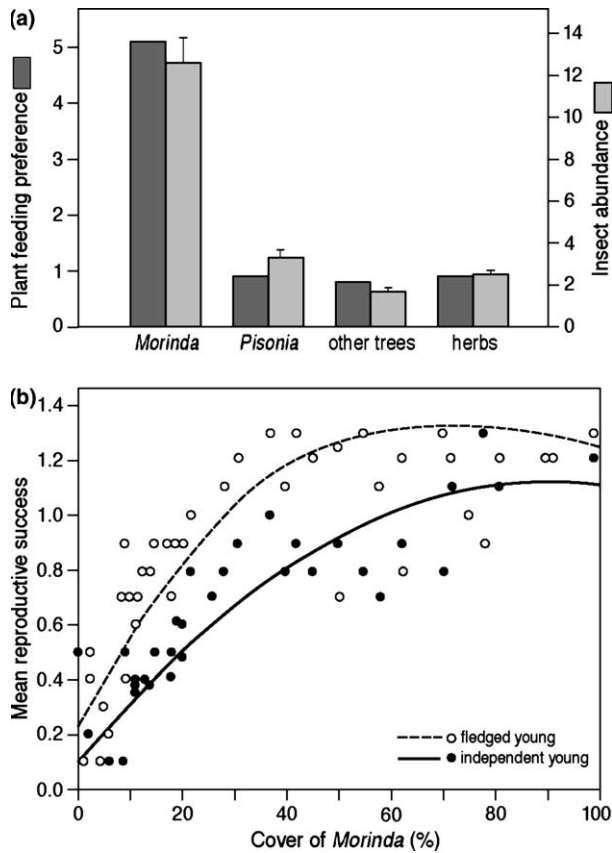


Fig. 3. (a) Plant species preference for feeding by Seychelles warblers (ratio percent feeding observations in plant species x to percent cover of plant species x), and insect abundance for different plant species (mean insects on the under-sides of leaves per dm^2 (January 1987–March 1988; $N = 4512$ feeding observations). Other trees include *Ficus rubra*, *F. lutea*, *F. reflexa*, *Casuarina equisetifolia*, *Ochrosia oppositifolia*, *Phyllanthus pervilleanus*, and *Scaevola taccada*. Herbs include *Achyranthes aspera*, *Gossypium hirsutum*, and *Amaranthus dubius*. For each plant species a total of 30,750 leaves were searched for insects. (b) Mean annual reproductive success of unassisted Seychelles warbler pairs in relation to percentage cover of *Morinda* (x) in territories measured from December 1985 to September 1990. Fledged young = $0.038x - 2.91 \times 10^{-4}x^2 + 0.248$; $r^2 = 0.81$, $N = 53$, $P < 0.001$; Independent young = $0.023x - 1.34 \times 10^{-4}x^2 + 0.103$; $r^2 = 0.88$, $N = 53$, $P < 0.001$. Each point refers to one breeding pair. If the breeding pair received assistance during part of the study period, numbers were corrected to a one-year unassisted period.

in insects, in territories, the more young fledged and reached independence (Fig. 3(b)). The increases were not linear, but levelled off to a maximum for territories with c. 50% or higher cover of *Morinda* (Fig. 3(b)). Furthermore, warbler pairs occupying higher quality territories built more nests and produced more fledged young, independent young and yearlings compared with pairs of lower quality territories (Fig. 4). The number of insects in a warbler territory thus depends on its abundance of *Morinda* and positioning on the island. Most habitats comprising primary *Pisonia* woodland (type VI) and secondary woodland (types III, IV, and V) were situated in the central part of Cousin with hardly any

wind. Territories situated in primary *Pisonia* woodland (VI), secondary *Morinda* woodland (III), and secondary *Pisonia* woodland with *Morinda* (IV) were rich in insects (high quality), but territories in secondary *Pisonia* woodland without *Morinda* (V) were low in insects (Table 1). The other habitat types (I and II) were mainly situated close or along the windy coast and had low insect numbers. The territories in woodland types III, IV, and VI were on average seven times higher in quality as those in other woodland types (mean $tq = 21.3$ vs. 3.1 ; Table 1). The reproductive success and survival of warblers occupying territories in either primary *Pisonia*, secondary *Morinda*–*Pisonia* or secondary *Morinda* woodlands were similar, but significantly higher than those of warblers occupying territories in other woodland types (Table 1).

3.2. Influence of halophytic shrubs on reproductive success

There is a seasonal variation in the growth of vegetation. Both monthly net foliage production and monthly new leaves produced for *Pisonia* showed two peaks in a year, which coincide with the transition periods between both monsoons (Fig. 5). During the south-east trade winds (June–August) leaf loss was higher than leaf production (negative net foliage production) resulting in defoliation of *Pisonia*, which (with 88% cover, the most dominant species on the island during 1985–1990) resulted in lower food supply for the warbler. There was a significant correlation between frequency of rainfall and both net foliage production and new leaves produced two months later ($r^2 = 0.46$, $N = 12$, $P = 0.007$ and $r^2 = 0.46$, $N = 12$, $P = 0.004$, respectively). However wind driven salt spray was also important. A significant negative correlation existed between wind force and both net foliage production and new leaves produced one month later ($r^2 = 0.40$, $N = 12$, $P = 0.018$ and $r^2 = 0.29$, $N = 12$, $P = 0.046$, respectively). Monthly net foliage production and monthly new leaves produced were not correlated with weather variables measured in any other month ($P > 0.2$). The halophytic shrub *Scaevola* (*Scaevola taccada*) with thick fleshy leaves, which dominates the beach crests (40% presence), is very salt and wind tolerant. Immediately after the onshore winds had set in, *Scaevola* was significantly less defoliated by wind driven salt spray than coastal *Pisonia* woodland either protected or not protected by *Scaevola* (Fig. 6). On average monthly net foliage production of *Scaevola* during this period was five times as high as *Pisonia*. As soon as the wind had changed to onshore, *Pisonia* woodland protected by *Scaevola* was significantly less defoliated than unprotected woodland (Fig. 6). On average monthly net foliage production of protected coastal *Pisonia* was two times as high as unprotected coastal *Pisonia* woodland. In the absence of onshore wind driven saltspray, during the north-west

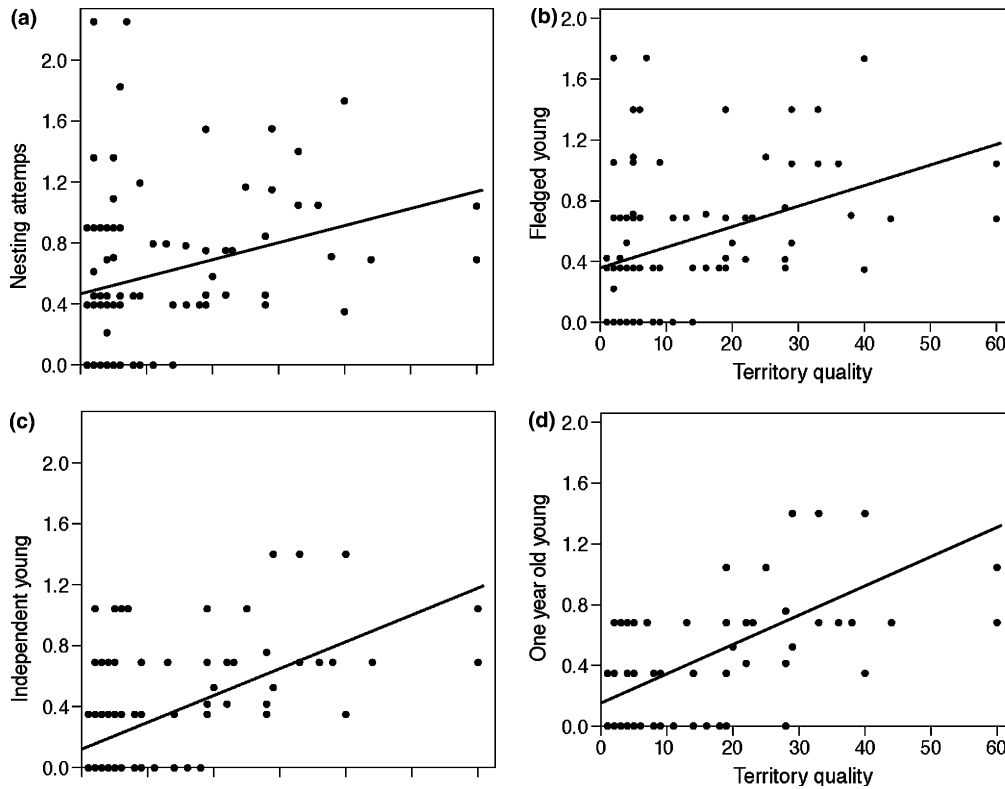


Fig. 4. Mean annual reproductive success of unassisted Seychelles warbler pairs in relation to mean territory quality (tq) measured from December 1985 to September 1990. (a) Nesting attempts = $0.011tq + 0.482$; $r^2 = 0.08$, $N = 101$, $P < 0.006$; (b) Fledged young = $0.015tq + 0.356$; $r^2 = 0.15$, $N = 101$, $P < 0.001$; (c) Independent young = $0.017tq + 0.116$; $r^2 = 0.37$, $N = 101$, $P < 0.001$; (d) One-year-old young = $0.019tq + 0.17$; $r^2 = 0.036$, $N = 101$, $P < 0.001$. Each point refers to one breeding pair.

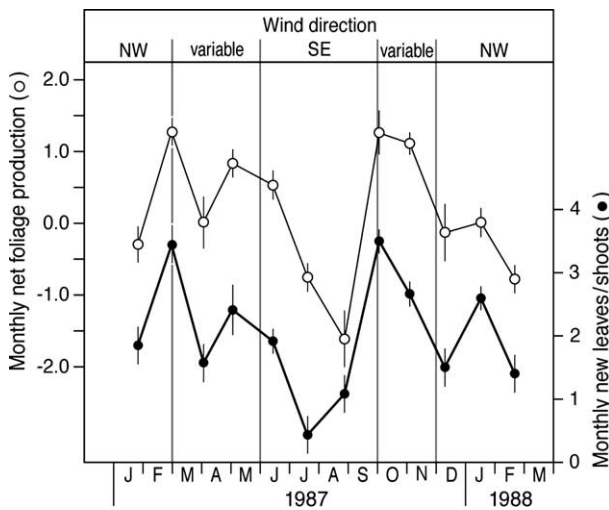


Fig. 5. Mean (\pm SE) monthly net foliage production and mean (\pm SE) monthly new leaves produced per shoot of *Pisonia* during the period January 1987 to February 1988 (values corrected to 30-day month; $N = 437$ shoots).

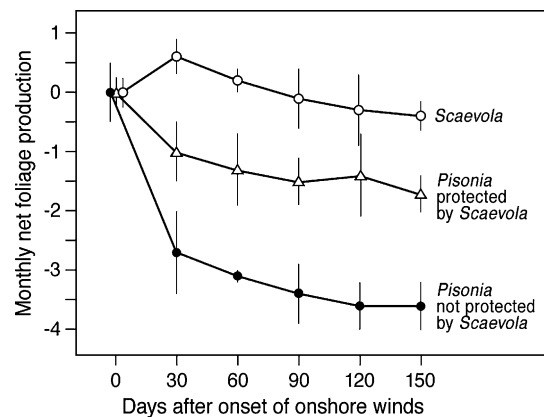


Fig. 6. Mean (\pm SE) monthly net foliage production per shoot of coastal *Scaevola* ($N = 107$ shoots), and of coastal *Pisonia* protected ($N = 42$ shoots) and not protected ($N = 56$ shoots) by a *Scaevola* hedge after the onset of wind driven onshore salt spray (day 0 which is 1 June 1987; values corrected to 30-day month; day 0 is 1 June).

season, reproductive success of unassisted warbler pairs occupying territories on the south-east coast protected by a *Scaevola* hedge was the same as that of unprotected territories (Fig. 7(a)). Breeding success of unassisted

warbler pairs in territories protected by a *Scaevola* hedge was the same during the north-west season without onshore winds (Fig. 7(a)) as during the south-east season with onshore winds (Fig. 7(b)). However, in the presence of onshore winds there was a significant decrease in reproductive success of warblers occupying unprotected

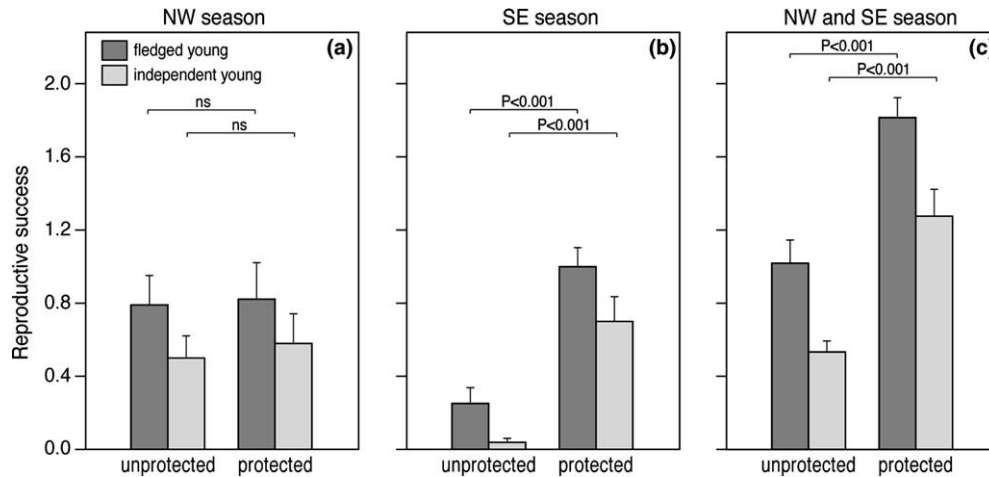


Fig. 7. Effect of protection by a *Scaevola* hedge along coastal territories on the south-east coast on the breeding success (\pm SE) of unassisted Seychelles warbler breeding pairs during (a) the four-month north-west season (December 1987–March 1988), (b) the four-month south-east season (June–September 1987), and (c) both seasons combined. Data were based on the same pairs occupying the same territories during 1987–1988 (24 unprotected territories, 40 protected territories).

territories compared to warblers occupying territories protected by a *Scaevola* hedge; producing, on average, four times fewer fledglings and 18 times fewer independent young (Fig. 7(b)). The overall effect of a *Scaevola* hedge during both seasons combined on reproductive success remained significant with warblers occupying protected territories producing two times more fledglings and two times more independent young than warblers occupying unprotected territories (Fig. 7(c)).

3.3. Habitat management and its long-term effect on demography

The above results showed clearly that both reproductive success and survival of Seychelles warblers were positively influenced by the abundance of insects. Therefore, since 1990, habitat management has been directed towards increasing the number of insects on the island with the aim to increase the Seychelles warbler population. This had been accomplished in three ways. First, through enhancement of vegetation cover. This required no human intervention because the forest was still in succession (Bathe and Bathe, 1982). From 1990 to 2002 the total area of coastal and tertiary *Pisonia* woodland had decreased from 12.9 to 5.0 ha (Table 1) and most (c. 90%) had developed into secondary woodland (Dekker, A and van de Crommenacker, J., personal communication). The vegetation maps constructed each year showed that the cover of woodland had also steadily increased from c. 21.5 ha (74% of the island) in 1990 to 27.4 ha (95% of the island) in 2002. Second, through improving the growth of *Morinda*, the most insect-rich tree species on the island. Originally it was thought that secondary *Morinda* and *Morinda-Pisonia* woodlands would be succeeded by primary *Pisonia* forest without *Morinda*, because *Morinda* is neither a pio-

neer nor a climax species (e.g., heavy fruits, regeneration in shady places, Bathe and Bathe, 1982). However, there was good evidence for primary *Pisonia* woodland to be diverted into desirable mixed secondary woodland naturally. *Pisonia* thins itself naturally after being weakened by standing water in the forks of branches and as a result *Morinda* can grow up again (Phillips, 1984a). Therefore it was decided not to interrupt the succession, which was a good decision: from 1990 to 2002 the total area of primary *Pisonia* woodland remained unchanged (Table 1). To speed up the process towards the development of *Morinda* woodland c. 400 young *Morinda* were planted between 1990 and 1992, especially in places where *Morinda* was absent or rare. *Morinda* is a fast growing tree species and it takes 5–7 years to maturate (Bullock, 1989). Yet it was not until suitable *Morinda* woodland was re-established by the mid 1990s that the warblers showed a sudden increase in reproductive success (Fig. 1(a) and (b)). The area of secondary *Morinda* and *Morinda-Pisonia* woodlands had increased from 5.5 ha in 1985/1990 to 17.8 ha in 2002/2003 (Table 1). The fraction of secondary *Morinda* and *Morinda-Pisonia* woodlands within the total area of secondary woodlands had increased from 0.45 (5.5/12.2 ha) in 1990 to 0.89 (17.8/20.0 ha) in 2003 (Table 1). Third, through minimisation of defoliation by wind driven salt spray. This was achieved by allowing *Scaevola* and other salt tolerant species (e.g., *Suriana maritima* and *Cordia subcordata*) to extend to provide a continuous salt-resistant barrier along the coast line. As from 1990 onwards *Scaevola* was planted along the coast, and the percentage coastline with *Scaevola* increased from 35% in 1990 to 93% in 2003 (Fig. 2).

These measures combined have caused a significant increase in insects on the island. The area with high insect numbers (51–75 per dm^2 leaf area) has increased

from 3.1 ha in 1986/1990 to c. 27.1 ha in 2002/2003 (Fig. 2). As a consequence the mean (\pm SE) number of high quality territories had increased from 17.2 ± 1.3 to 91.0 ± 1.0 , mean annual production of independent young from 30.2 ± 3.3 to 56.5 ± 2.5 , and the total number of territories producing independent young from 19 to 51 (Figs. 1 and 2). Also the mean annual number of territories producing recruits (young that fill breeding vacancies) had increased from 5.6 ± 1.2 in 1986/1990 to 18.5 ± 2.5 in 2002/2003. However, the total number of territories and warblers had remained the same during this period (Fig. 1). Given the increase of recruits on the one hand, and the presence of a static population and sporadic dispersal of young to other islands (Komdeur et al., 2004) on the other hand, there must be an increase in adult mortality.

4. Discussion

4.1. Species response to habitat management

Our study showed that *Morinda* was the most insect rich tree on the island and that warblers preferred this tree for foraging. The higher the abundance of *Morinda* trees in warbler territories the higher the reproductive success. Moreover, the presence of a salt tolerant *Scaevola* hedge along the coast resulted in increased growth of other tree species and higher reproductive success of warblers in coastal territories. Between 1990 and 1992 young *Morinda* trees and *Scaevola* shrub were planted on the island, which resulted in a threefold increase in *Morinda* woodland and six times more high-quality territories present on the island a decade later due to low/medium quality territories becoming high quality. After implementation of habitat management (1990–1992), the total number of young warblers produced on the island each year had increased nearly twofold as a consequence of higher reproductive success per warbler territory and more territories producing successfully, but the total number of territories and warblers did not increase. Most young failed to establish a territory due to habitat saturation and remained on their natal territories or died (Komdeur, 1992, 2003). Habitat management through planting critical tree species has also been conducted for other endangered species, but in contrast to the warbler, this resulted in a population increase due to an increase in breeding territories and not to an increase in reproductive success (Solomon, 1998; Brandeis et al., 2002).

It has been stated that the ultimate measure of success for an endangered species program is whether or not a species has been recovered (Solomon, 1998). One could argue that the habitat restoration program was of no effect on the recovery of Seychelles warblers, because despite its positive effect on reproductive success,

population size did not increase. However, not only the increase in population size of a species but also the increase in young birds should be taken into account as measure of conservation success, especially for island species. The pool of surplus birds can be used as a buffer against extreme events (see Section 4.2) and as reservoir for transplants. Nowadays translocations of part of populations to new islands are employed as successful conservation tools to save species (Griffith et al., 1989). New populations of Seychelles warblers were established by moving 29 surplus birds to Aride Island (68 ha, 9 km from Cousin) and to Cousine Island (26 ha, 1.6 km from Cousin) in 1988 and 1990, respectively (Komdeur, 1994a), and 58 birds to Denis Island (140 ha, 35 km from Cousin) in 2004 (Richardson, D.S., Brouwer, L. and Eikenaar, C., unpublished data). This was based on the vulnerability of a single isolated population, the presence of surplus birds on Cousin and the extremely small chance of successful establishment on unoccupied islands by unaided warblers. These translocations were highly successful, with the founder populations expanding to a combined population of c. 1750 individuals on three islands by 1996 (Komdeur, 2003).

4.2. Numerical and genetic resilience of island populations towards catastrophic events: the role of the non-breeding pool

Island species make up 75% of all animal extinctions recorded since 1600 (World Conservation Monitoring Centre, 1992), including 90% of bird extinctions (Diamond, 1984). Populations on islands are much more vulnerable to extinction due to demographic and environmental stochasticity than mainland populations (Pimm, 1991; Whittaker, 1995). Seychelles warblers have very low reproductive productivity. They usually have a one-egg clutch (Komdeur, 1996) and low annual reproductive success (0.49 yearlings per breeding group, this study). This does not need to present a conservation management problem if the constraints on reproduction are only temporary. Seychelles warblers are long-lived (the oldest bird recorded died at 21 years of age and mean adult life expectancy in this study was 4.2 years) and therefore can tolerate periods of low recruitment. Although the warbler population on Cousin Island has evidently been thriving and secure from 1982 onwards, it may be still vulnerable to factors leading to a sudden increase in adult mortality or a prolonged reduction in recruitment. The benefit of a higher reproductive potential of the population may be improved resilience towards catastrophic events. In case of sudden high mortality of breeders, a surplus of young non-breeding birds and the high rate of juvenile recruitment may form a buffer against sudden population decline (e.g., Kokko and Sutherland, 1998; Heg et al., 2000; Ekman et al.,

2001). Extreme events, such as sudden disease outbreaks, wild fires, and hurricanes and cyclones, commonly occur on tropical islands and contribute to species threats or extinctions, especially on small islands of only a few square kilometres or less (e.g., Lugo, 1995; Whittaker, 1995). In the Seychelles warbler three such events have been reported. In 1982 there was a considerable loss of Seychelles warbler breeders (c. 15% of breeders) and nests due to a heavy storm lasting only two days (Phillips, 1984b), in 1997 nearly all breeding attempts on the entire island failed due to torrential rains, and in 1999 circa one fifth of the breeding population died due to an extreme storm lasting only a couple of days (Richardson, D.S., unpublished data). However, soon after the events the opened up space became quickly occupied by formerly surplus birds. Other support for the buffer role of surplus birds comes from the translocations of breeding birds from Cousin to the islands of Aride and Cousine. The 38 breeding vacancies created on Cousin were filled immediately (some within hours) by formerly non-breeding birds born on Cousin (Komdeur, 1992).

The presence of surplus birds as a buffer against extreme events is especially important for island species that have lost the ability to re-establish populations on other islands. The majority of island species are prevented from re-establishing on other islands (Abbott and Black, 1980), because they have lost their 'morphological' flight capacity or refuse to fly across water (e.g., Diamond, 1981; Mayr and Diamond, 2001). This is also the case for the Seychelles warbler. Despite the over-production of warblers on Cousin in the last decades, only two warblers (0.13%, $N = 1599$ banded birds) have crossed the small stretch of sea (1.6 km) between Cousin and Cousine unaided (Komdeur et al., 2004).

Recent empirical evidence has indicated that the viability of small, dwindling populations may be reduced by the loss of genetic variation as a result of inbreeding (Jimenez et al., 1994; Frankham, 1995). The size of the breeding population can be small enough to raise the possibility of a permanent loss of wild-type alleles as deleterious mutations drift to fixation, thereby reducing the populations ability to cope with diseases or habitat change (e.g., Olivieri et al., 1990; Nunney and Campbell, 1993; Lynch and O'Hely, 2001). The potential consequences of loss of genetic variation for population viability have often been dismissed by conservation biologists and should be taken into account in the evaluation of conservation programs (Parker and Waite, 1997). Even in a stable population, such as the Seychelles warbler, the genetic resilience to stochastic factors can be improved through a higher reproductive potential. The larger the effective breeding population the greater the scope for exchange of recruits (young that become breeders) between territories and the higher the chance that beneficial alleles remain present and can

be returned to high frequency through selective advantage (Keller et al., 1994). In the Seychelles warbler habitat restoration has caused a near threefold increase in the effective breeding population and a threefold increase in number of territories producing recruits. Apart from the exchange of recruits between territories, there is no exchange of established breeding birds between territories (Komdeur, 1991).

5. Conclusion

This study showed that habitat restoration has not resulted in higher adult numbers of Seychelles warblers and territories due to habitat saturation. However, it has been successful in terms of improving the quality of existing breeding territories and hence the reproductive success of breeding birds, and the size of the effective breeding population. We have provided evidence for the role of higher reproductive potential on improved resilience towards catastrophic events, but resilience against deleterious genetic mutations needs further investigation.

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References

- Abbott, I.J., Black, R., 1980. Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography* 7, 399–410.
- Achard, F., Eva, H.D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.-P., 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* 297, 999–1002.
- Bathe, G.M., Bathe, H.V., 1982. Territory size and habitat requirements of the Seychelles brush warbler *Acrocephalus (Bebrornis) sechellensis*. International Council for Bird Preservation, Internal Report, Cambridge, UK.
- Bullock, I.D., 1989. Aride Island, Nature Reserve. Scientific report, Part 1: Climate, Vegetation and Insects. Royal Society for Nature Conservation, UK.
- Brandeis, T.J., Newton, M., Filip, G.M., Cole, E.C., 2002. Cavity-nester habitat development in artificially made douglas-fir snags. *Journal of Wildlife Management* 66, 625–633.
- Brooks, T.M., Pimm, S.L., Collar, N.J., 1997. Deforestation predicts the number of threatened birds in insular Southern Asia. *Conservation Biology* 11, 382–394.
- Brooks, T.M., Pimm, S.L., Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* 13, 1140–1150.
- Clark, M.R., Dingwall, P.R., 1985. Conservation of Islands in the Southern Ocean. A Review of the Protected Areas of Insular Antarctica, IUCN. Cambridge University Press, Cambridge.
- Clemmons, J.R., Buchholz, R., 1997. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, UK.
- Collar, N.J., Crosby, M.J., 1995. Birds to Watch 2: The World List of Threatened Birds. IUCN/Birdlife International, Smithsonian Institution Press, Washington, D.C.
- Collar, N.J., Stuart, S.N., 1985. Threatened birds of Africa and related islands. The ICBP/IUCN Red Data Book, Part 1. International Council for Bird Preservation, Cambridge.
- Collar, N.J., Stuart, S.N., 1993. Threatened birds of Africa and related islands. The ICBP/IUCN Red Data Book, Part 1. Smithsonian Institution Press, Washington, D.C.
- Cronk, Q.C.B., 1997. Islands: stability, diversity, conservation. *Biodiversity and Conservation* 6, 477–493.
- Crook, J. H., 1960. The present status of certain rare landbirds of the Seychelles Islands. *Seychelles Government Bulletin*, 1960.
- Diamond, A.W., 1980. Seasonality, population structure and breeding ecology of the Seychelles Brush Warbler *Acrocephalus sechellensis*. In: *Proceedings of the Fourth Pan-African Ornithological Congress*, pp. 253–266.
- Diamond, J.M., 1981. Flightlessness and fear of flying in island species. *Nature* 293, 507–508.
- Diamond, J.M., 1984. Historic extinctions: their mechanisms, and lessons for understanding prehistoric extinctions. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions, Conservation for the Twenty-first Century*. Oxford University Press, University of Arizona Press, Oxford, Tucson, pp. 824–862.
- Ekman, J., Eggers, S., Griesser, M., Tegelström, H., 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. *Journal of Animal Ecology* 70, 317–324.
- Frankham, R., 1995. Inbreeding and extinction: a threshold effect. *Conservation Biology* 9, 792–799.
- Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocations as a species conservation tool: status and strategy. *Science* 245, 477–480.
- Heg, D., Ens, B.E., Jeugd, H.P. van der, Bruinzeel, L.W., 2000. Local dominance and territorial settlement of nonbreeding oystercatchers. *Behaviour* 137, 473–530.
- IUCN, 2004. 2004 IUCN Red List of Threatened Species. Available from: <http://www.iucnredlist.org>.
- Jimenez, J.A., Hughes, K.A., Alaks, G., Graham, L., Lacy, R.C., 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266, 271–273.
- Keller, L.F., Arcese, P., Smith, J.N.M., Hochachka, W.M., Stearns, C.S., 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 373, 356–357.
- King, W.B., 1985. Island birds: will the future repeat the past?. In: Moors, P.J. (Ed.), *Conservation of Island Birds*, 3. ICBP Technical Publication, Cambridge, pp. 3–16.
- Kokko, H., Sutherland, W.J., 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist* 152, 354–366.
- Komdeur, J., 1991. Cooperative breeding in the Seychelles warbler. PhD dissertation, University of Cambridge, UK.
- Komdeur, J., 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358, 493–495.
- Komdeur, J., 1994a. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousine. *Biological Conservation* 67, 143–152.
- Komdeur, J., 1994b. Experimental evidence for helping and hindering by previous offspring in the cooperative breeding Seychelles warbler. *Behavioural Ecology and Sociobiology* 34, 175–186.
- Komdeur, J., 1996. Influence of age on reproductive performance in the Seychelles warbler. *Behavioral Ecology* 7, 417–425.
- Komdeur, J., 2003. Daughters on request – about helpers in the Seychelles warbler. *Proceedings of the Royal Society of London B, Biological Sciences* 270, 3–11.
- Komdeur, J., Piersma, T., Kraaijeveld, K., Kraaijeveld-Smit, F., Richardson, D.S., 2004. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there?. *Ibis* 146, 298–302.
- Loustau-Lalanne, P., 1968. The Seychelles, Cousin Island Nature Reserve. International Council for Bird Preservation, Internal Report, Cambridge, UK.
- Lugo, A.E., 1995. Reconstructing hurricane passages over forests: a tool for understanding multiple scale responses to disturbance. *Trends in Ecology and Evolution* 10, 98–99.
- Lynch, M., O'Hely, M., 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2, 363–378.
- Mayr, E., Diamond, J., 2001. *The birds of Northern Melanesia*. Speciation, Ecology, and Biogeography. Oxford University Press, New York.
- Micol, T., Jouventin, P., 1995. Restoration of Amsterdam Island, South Indian Ocean, following control of feral cattle. *Biological Conservation* 73, 199–206.
- Nunney, L., Campbell, K.A., 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* 8, 234–239.
- Olivieri, I., Couver, D., Gouyon, P.H., 1990. The genetics of transient populations: research at the metapopulation level. *Trends in Ecology and Evolution* 5, 207–210.
- Overpack, J., Whitlock, C., Huntley, B., 2002. In: Alverson, K., Bradley, R., Pedersen, T. (Eds.), *Paleoclimate, Global Change and the Future*. Springer, Berlin, pp. 81–103.
- Parker, P.C., Waite, T.A., 1997. Mating systems, effective population size, and conservation of natural populations. In: Clemmons, J.R., Buchholz, R. (Eds.), *Behavioral Approaches to Conservation in the Wild*. Cambridge University Press, Cambridge, UK, pp. 243–261.
- Phillips, N.J., 1984a. Spatial relationships of *Pisonia grandis* and *Cocos nucifera*. International Council for Bird Preservation, Internal Report, Cambridge, UK.
- Phillips, N.J., 1984b. Seasonal and locational differences in the breeding success of the Seychelles brush warbler *Bebrornis*

- seychellensis*. International Council for Bird Preservation, Internal Report, Cambridge, UK.
- Pimm, S.L., 1991. *The Balance of Nature: Ecological Issues in the Conservation for Species and Communities*. University of Chicago Press, Chicago.
- Pounds, J.A., Puschendorf, R., 2004. Clouded futures. *Nature* 427, 107–108.
- Solomon, B.D., 1998. Impending recovery of Kirtland's warbler: case study in the effectiveness of the endangered species act. *Environmental Management* 22, 9–17.
- SPSS 11.0., 2001. SPSS Inc. Chicago, USA.
- Stattersfield, A.J., Capper, D.R., 2000. *Threatened Birds of the World*. Birdlife International, Lynx Editions and BirdLife, Barcelona and Cambridge, UK.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Siqueira, M.F., de Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Petersen, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Vesey-Fitzgerald, D., 1940. The birds of the Seychelles 1: the endemic birds. *Ibis* 14, 480–489.
- Whittaker, R.J., 1995. Disturbed island ecology. *Trends in Ecology and Evolution* 10, 421–425.
- World Conservation Monitoring Centre, 1992. *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, London.