

Population dynamics of insular vertebrates, examples from the Seychelles islands

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Abstract

The populations of four vertebrate taxa restricted to the Seychelles islands were modelled. Basic population models provided accurate predictions of the populations of Seychelles Warbler *Acrocephalus sechellensis*, Seychelles Sunbird *Nectarinia dussumieri*, Seychelles Magpie Robin *Copsychus sechellarum* and Aldabra Giant Tortoise *Dipsochelys dussumieri*. A number of general trends were apparent in the modelled populations; all species had the potential for rapid population increase but the larger taxa were constrained by territorial limitations on small islands. This results in population instability and local extinctions, suggesting that large taxa will survive on small islands only in a metapopulation system. These population processes may drive adaptation to island conditions towards flexible reproduction (including precocious reproduction) and two alternative evolutionarily stable strategies: size reduction to minimise the area constraint on population size or gigantism to promote individual resistance to over-population through resource storage and extended longevity.

Key words: bird, island, metapopulation, modelling, population, Seychelles, tortoise

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INTRODUCTION

Many conservation reviews have noted the disproportionately high levels of extinction in island ecosystems (e.g. King 1979, Stattersfield 1987, Johnson & Stattersfield 1990, Stattersfield et al. 1998). High extinction rates of insular taxa may result from a combination of factors, including small population sizes derived from geographical restriction, ecosystem instability reflecting the imbalance between colonisation and extinction, and stochastic processes (MacArthur & Wilson 1967). To these has to be added the major influence of human mediated disturbance through habitat destruction and the introduction of alien taxa. Despite their inherent vulnerability and the anthropogenic threats faced by insular taxa, there are several remarkable success stories concerning the conservation of insular species (e.g. Mauritius Kestrel *Falco punctatus* - Jones et al. 1994 and Chatham Island Black Robin *Pterodroma traversi* - Butler & Merton 1992); these suggest that the population processes of some taxa include highly adaptable elements. Examination of these processes in insular species recovering from population contractions may identify key factors in their adaptations to island life.

The vertebrate fauna of the Seychelles islands has been studied in detail for over 100 years; monitoring studies and introduction programmes have compiled extensive data on population processes in vertebrate species covering a range of basic biological processes. Four of these are analysed below: two small insectivorous birds (the Seychelles Warbler *Acrocephalus seychellensis* and the Seychelles Sunbird *Nectarinia dussumieri*), a medium sized omnivorous bird (the Seychelles Magpie Robin *Copsychus seychellarum*) and a large, slow-breeding reptile (the Aldabra Giant Tortoise *Dipsosaurus dorsalis*).

The Seychelles Warbler is assumed to

have been widely distributed throughout the granitic Seychelles islands (Gerlach 1997) although historical records are restricted to Cousin, Cousine, Marianne and Mahé (Komdeur 1994a), and by 1965 it survived only on Cousin (Penny 1967), although there was a temporary colonisation of Cousine in 1974 (Diamond 1980). Following purchase of Cousin by The Royal Society for Nature Conservation, the population increased from 50 birds in 1965 to 200-300 in 1974 (Diamond 1980). The species was reintroduced to Aride island in 1988 and Cousine 1992, with the release of 29 birds on each island (Komdeur 1994a). In both cases populations have grown rapidly and in 1999 the total population stood at some 2000 birds. Research carried out during the reintroductions has demonstrated that the reproductive biology of this species is highly adaptable with flexible nest-helping (Komdeur 1994b) and brood sex ratio manipulation (Komdeur et al. 1997).

The Seychelles Sunbird is one of the most abundant and widely distributed of all the native birds. It remains present on almost all islands but ceased to breed on Aride in the mid 1900s. Only single birds colonised Aride until 1986 when a pair was recorded (Bullock 1989); breeding started in 1990. The resultant population has grown rapidly and the presence of full-time wardens has allowed close monitoring of this natural re-colonisation.

The Seychelles Magpie Robin is one of the larger native Seychelles birds. Historically it was present on all the larger islands but by 1965 was restricted to Fregate island due to causes assumed to include habitat destruction (Newton 1867, Gerlach 1996), hunting (Newton 1865 & 1867, Gerlach 1996) and predation (Newton 1867, Watson et al. 1992). The introduction of cats to Fregate in 1958 was accompanied by a decline in the Seychelles Magpie Robin population,

falling to 18 birds in 1970s. Eradication of cats in 1986 did not result in an increase in the Magpie Robin population. A recovery programme was initiated in 1990 by BirdLife International using a variety of techniques (Komdeur 1996). Population recovery started in 1992 with initial rapid growth (McCulloch 1996). Reintroductions to Cousin and Cousine were carried out successfully in 1994-5, although demographic problems have since reduced the viability of these small populations (Gerlach & Le Maitre 2000). Attempts to reintroduce the species to Aride in 1978, 1979, 1992, 1993 and 1996 failed. A further attempt was made in 2000. The Seychelles Magpie Robin population has been stable at 75-80 birds since 1997 when operation of the recovery programme was passed to BirdLife Seychelles.

The Aldabra Giant Tortoise is naturally restricted to Aldabra atoll. Hunting by humans eliminated all other wild populations of giant tortoise in the Indian Ocean with the exception of a remnant population of Seychelles Giant Tortoise *Dipsochelys hololissa* on Cerf island. The Aldabra population was brought close to extinction in the 1890s and there were local extinctions on some of the islets (Gerlach & Canning 1996). Protection of the surviving populations from the early 1900s has resulted in rapid population growth and current population levels are estimated at approximately 100,000 (Bourn et al. 1999). This is significantly less than estimates from the 1970s (Coe et al. 1979, Bourn et al. 1999) and it is believed that the Aldabra giant tortoise population has already exceeded its carrying capacity and is now declining to a stable level. This species was introduced to Curieuse island in 1978 but this introduction was followed by significant declines due to poaching (Samour et al. 1987). Poaching levels have reduced and the practice of rearing hatchlings for five

years prior to release has allowed the population to start increasing since 1990.

METHODS

Data on population parameters and changes in population levels were compiled from published accounts (Table 1). These were combined into population dynamics models taking the basic form (after May 1978 and Comins & Hassel 1979):

$$N_{1t} = N_{t-1}s_1(e^{(r-r/K)})(1+aP/k)^{-k}$$

$$N_{i>1t} = N_{i-1t-1}s_i(1+aP/k)^{-k}$$

where N = number of prey, P = number of predators, $r = \ln(\lambda+1)$, λ = annual rate of production of female offspring per female, K = carrying capacity (numbers per hectare), k = clumping parameter (May, 1978), i = year group, t = year, s = survival from $i-1$, a = predator attack rate. The estimated mean values used are shown in Table 1.

For the bird species carrying capacity (K) is not known explicitly but as these species are territorial K can be calculated as:

$$K=AB/T$$

where A = area occupied, B = average number of birds per territory at carrying capacity and T = territory size (hectares). T varies between years with a strong correlation with invertebrate numbers and rainfall (Table 1).

For tortoises K was taken as the maximum number of tortoises recorded in each major habitat type.

Predation levels have not been studied directly for these species and are estimated from predator dietary data. The two major bird predators in the studied system are cats *Felis catus* and Barn Ols *Tyto*

Table 1. Population parameters used in models. F = feeding levels (proportion of food provided by supplementary feeding); V = invertebrate abundance in absence of insectivorous birds; R = rain (1000mm; Fregate data prior to 1988 is estimated at 80% of Mahé values); for other abbreviations see text

Parameter	Seychelles Warbler AB/T	Seychelles Sunbird AB/T	Seychelles Magpie Robin AB/T	Aldabra Giant Tortoise
carrying capacity (K)				grassland = 23.5/ha mixed scrub = 20/ha dense scrub = 7/ha <i>Pemphis</i> scrub = 1.6/ha
clutch size (C)	2	2	1	2.1057-0.0584N/A
λ (number of hatchlings)	0.93+0.0011R(4.87-0.44lnNA)	1.9	(1.163/0.8)X	ln(0.5CR(8.25-0.175N/A))
carrying capacity (K)	4.51R/e(0.011/A - 1.6)	110/ha	T.A/(e(3.57-(0.6lnR)-(0.3ln(IF))-1))	9.52N/A
number per territory (B)	0.291e(4.87-(0.44ln(N/A)))	3	{e(3.57-0.6ln(R+1))-0.3ln(1+1)}-1	-
Invertebrate availability (I)	0.9VR	-	-	-
sex ratio (X)	-	-	$\bar{X}_{L,r} - 1 + 1/(1.411 - 1.014ln(N/A))$	-
clumping parameter (k)	0.1	0.1	0.1	-
survival (s)	$s_1 = (0.15ln) - 0.28$ $s_{2,10} = 0.58 + 0.08 \ln I$	$s_1 = 0.4$ $s_{2,10} = 0.95$	$s_1 = 1/X$ $s_2 = 1 - (0.46 + (0.439lnX))$ $s_3 = 0.52$ $s_4 = 0.7$ $s_5 = 0.8$ $s_6 = 0.85$ $s_7 = 0.89$ $s_{8,16} = 0.9$	$s_{1,5} = 0.2284 - (0.0062N/A)$ $s_{5,10} = 0.75$ $s_{10,100} = 0.997$
cat attack rate (a)	-	-	-	-
owl attack rate (a)	370.0	370.0	370.0	-
Parameter source	Diamond 1980, Komdeur 1994a, b, 1997, Komdeur et al. 1997	Unpublished data	Komdeur 1988-90, 1996, Gretton 1990-2, 1993, Watson et al. 1992, McCulloch 1992-5, 1996, Parr 1998-9, Gerlach & Le Maitre 2000	Frazier 197, Grubb 1971, Bourn & Coe 1978, Swingland & Coe 1978, 1979, Swingland 1978, Coe et al. 1979, Swingland & Lessells 1979, Gibson & Hamilton 1984, Bourn et al. 1999

alba. Cat diet on Fregate in 1981-2 is known and can be used to estimate predation levels. On Fregate 18% of cats that were trapped at any one time contained bird remains (8% with land-bird remains). These made up 25% of items eaten (14% land birds) (Todd 1982). This would give 65.7 birds or 29.2 land birds eaten by each cat each year. The selection of different prey will depend upon the relative abundance of each species, so the attack rate can be calculated as $65.7B/N$ where B = number of a specific bird species and N = total number of birds. The average rate of Barn Owl predation on birds is given by the daily rate of pellet production (2; Taylor 1994) and the number of birds per pellet. Data from Aride and Cousin give 0.511 and 0.502 birds per pellet for full year data (Gerlach & Lambert 1997). This gives 370 birds per owl per year; an attack rate of $370B/N$. These parameter values are in broad agreement with data from other island groups.

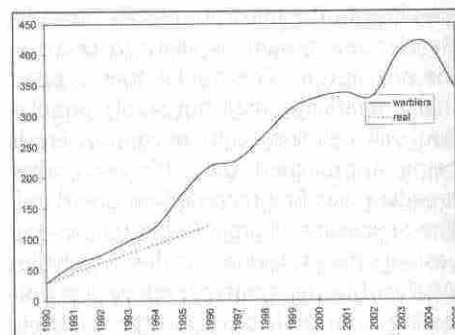
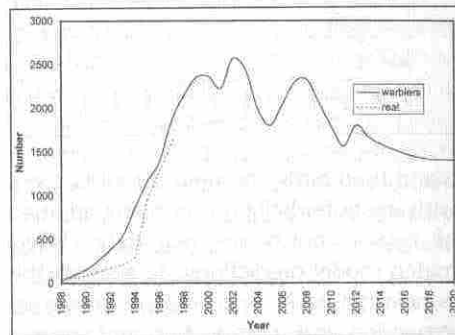
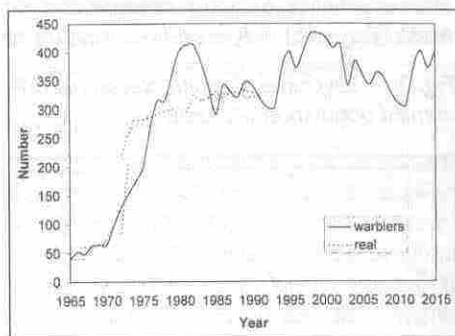
Predation levels on Aldabra Giant Tortoises have not been evaluated but the quantified survival rate includes the impact of predation by the presumed predators cats, rats *Rattus rattus*, crabs and birds. These are all present on Aldabra and on Curieuse (with the exception of the birds).

RESULTS

The predictions of the models for the four species show very close correspondence to the population monitoring data (Figure 1 - 4). Each species is considered individually below.

In the Seychelles Warbler (Figure 1) population establishment and growth are entirely dependent on food availability; as territory size can be extremely small (0.25 ha; Komdeur 1997), island area is not a significant factor in any of the studied systems. At present both the introduced populations are in phases of growth and

Fig. 1. Populations of Seychelles Warbler
a). Cousin
b). Aride
c). Cousine

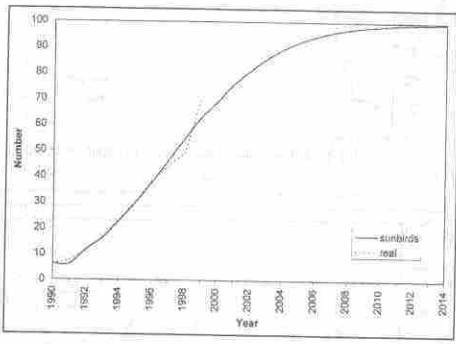


the precise model predictions of density dependent processes cannot be fully analysed. Data for Cousine suggest lower population growth rates than predicted by the model; however, census data from this island are not reliable and the true figures may be much higher. The warbler populations are highly susceptible to changes in food supply and are thus affected by density dependent food reg-

ulation and by external climatic influences on food. The dynamically stable population level is reached 14 years after introduction.

The Seychelles Sunbird colonisation of Aride (Figure 2) may contain a mixture of

Fig. 2. Seychelles Sunbird *Nectarinia dussumieri* population on Aride



island bred birds and new colonists. Even with the potentially confounding addition of new colonists the real data closely match model predictions. At present this population is in a phase of maximum expansion and reproduction and survival are close to the maximum levels possible. Decelerated growth is likely to occur in the near future. The model does suggest that a relatively small but stable population will develop, with maximum levels being approached only 10 years after breeding was first recorded on the island. The Seychelles Magpie Robin follows the basic patterns found in the Seychelles Warbler but the greater territory size, following from body size, and the relatively

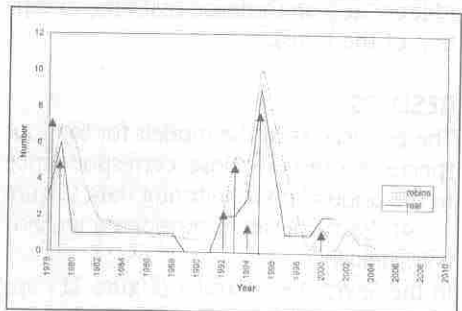
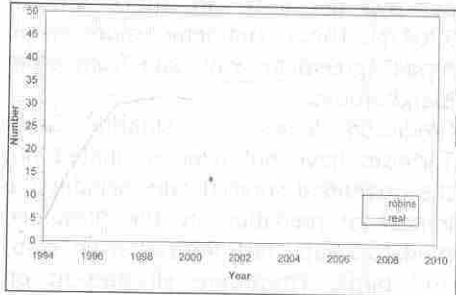
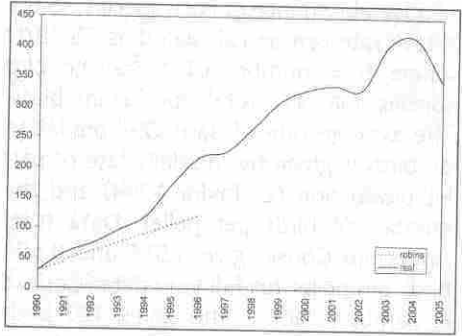
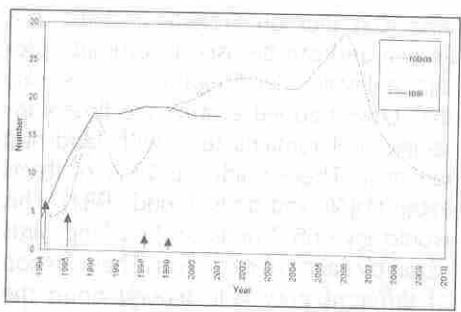
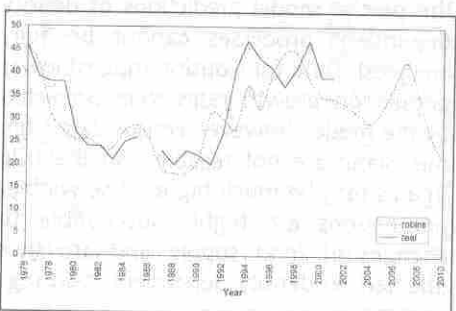


Fig. 3. Seychelles Magpie Robin *Copsychus seychellarum* populations

- a). Frigate
- b). Cousin
- c). Cousine
- d). Cousin and Cousine metapopulation
- e). Aride

scarcity of terrestrial prey compared to foliage inhabiting prey results in a greater sensitivity to island area. The primary limitation on population growth is food availability, this factor being most pronounced on Aride island (Gerlach 2000). The instability of constrained populations on small islands is shown by the discrepancies in the models for Cousin and Cousine. As there has been significant movement between the two islands (23% of the birds fledged on Cousine in 1997-8 have moved from the island) there is justification for considering the islands to be part of a single system. Combining the two islands into a single model gives a closer fit to the combined data (Figure 3d). In this species population maxima are reached within five years of the introduction or the start of population growth. Emigration of juvenile males to Praslin island in 2000-2001 results in suppression of the sex ratio imbalance and stabilisation of the population model.

The Seychelles Giant Tortoise model (Figure 4) repeats the rapid growth of the other models but a delay in density dependent feedback results in long-term population oscillations. Under a stable system these are damped oscillations. However, stochastic rainfall results in perturbation of the oscillations. For Aldabra, the population data are in accordance with predictions (Figure 4a); it should be noted that juveniles (<5 years old) are difficult to locate in the wild (Swingland & Coe 1979) and census data are effectively numbers of adult and sub-adult tortoises only. For the population introduced to Curieuse initial losses due to poaching have delayed population growth. Most of the island is characterised by relatively poor habitat and the carrying capacity of Curieuse is probably below 300 adult tortoises (assuming that lowland forest, the island's best habitat, can be equated to Aldabra's mixed scrub habitat). Recent increases of giant tortoises, resulting from

a reduction in poaching and the effective implementation of juvenile 'headstarting', are close to predicted patterns of fast population growth. The virtual elimination of juvenile mortality by headstarting results in a much higher population growth rate than that predicted.

DISCUSSION

The potential for rapid population growth was found in all four systems studied. Although insular species are often reported to have a low reproductive potential (Lack 1970, Williamson 1981) this would be a maladaptive trait for insular colonists. Although many species have been studied at stable population levels, instability might be expected to be the norm on small islands. This would be expected to be associated with an evolutionary potential to respond to instability. In the taxa studied here this response is manifest in the dynamic reproductive potential already noted in the Seychelles Warbler (Komdeur et al. 1997) and Aldabra Tortoise (Swingland 1978), although not noted as a general trait. The counter-balance to high reproductive potential could be a need to be able to tolerate high levels of mortality when subject to density dependent processes. Density dependence would be expected to be most severe when geographical area is a major constraint. Accordingly, density dependence is a relatively minor influence on the Seychelles Warbler and sunbird when compared to the other species.

Tolerance of the high mortality levels resulting from density dependent stresses may be effected by a combination of longevity and a lack of reproductive senescence masking juvenile mortality, or precocious reproduction compensating for adult mortality. Great longevity is well known for giant tortoises; longevity in the wild is not known but in captivity an age in excess of 152 is possible (Gerlach

1998); the Seychelles Magpie Robin may reach 16 years (McCulloch 1996). In contrast the Seychelles Warbler mortality increases after six years of age (Komdeur 1997). Precocious reproduction may occur in the Seychelles Magpie Robin, although available evidence suggests that reproduction rarely occurs before two years (McCulloch 1996). The earliest reproduction in giant tortoises is estimated to be 15 years (derived from data in Gibson & Hamilton 1984) whilst the Seychelles Warbler is capable of breeding from seven months (Komdeur 1994b & 1997). Longevity and maturity data on the sunbird are lacking. Further tolerance of high density dependence stresses may be achieved in the Seychelles Warbler through a highly adaptive mating system with cooperative nesting, kin-selected nest helping and brood sex ratio manipulation also being detected (Komdeur 1994b & 1997, Komdeur et al. 1997). Nest helping has also been recorded in the Seychelles Magpie Robin but does not appear to be a regular or stable feature (McCulloch 1996).

These data indicate that insular species are more adaptable than is conventionally suggested. The relatively unstable nature of islands means that insular faunas must be adaptable in order to survive; this adaptability is derived firstly from a flexible and rapid reproductive potential. This reproductive capability is evolutionarily advantageous for small populations with stochastic risk and relatively high levels of juvenile mortality. This mortality derives from a high frequency of stochastic events, density dependent factors and intense predation. Although the insular vertebrate systems are often stated to be naturally predator free (e.g. Johnson & Stattersfield 1990), this is only true with respect to mammalian predators. On most island groups the predatory niche is occupied by reptiles, birds or invertebrates. In Seychelles, birds are vulnerable

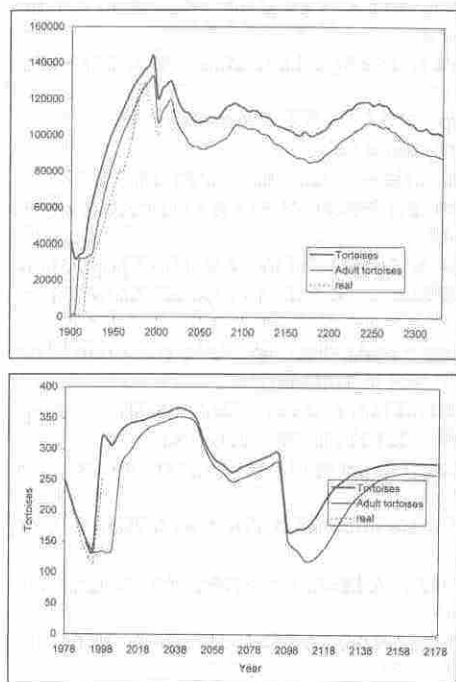
to predation by other native birds, skinks and snakes (Honegger 1966, McCulloch 1996) and juvenile giant tortoises to birds and crabs, all of which are highly abundant.

A critical factor in population establishment and stability are population sizes. These, in turn, are primarily determined by resource availability in terms of feeding levels, breeding sites and the area of potential habitat. These constraints are most severe for large taxa; for example, comparison of the taxa studied here shows that, of the birds, Seychelles Warblers can survive at 15.4-25.0/ha but Seychelles Magpie Robins at only 1.2/ha. The energetics and carrying capacity of the poikilothermic herbivorous giant tortoises are not directly comparable with those of endothermic insectivorous birds. The tortoises reach 19.6/ha in optimal habitats.

For a population to achieve dynamic stability an evolutionarily stable strategy (ESS) is required in the form of self-limitation or release from the resource and area constraints. Self-limitation is provided by extended longevity combined with resource storage, a combination tending to promote gigantism. This is most apparent in the tendency for insular giant tortoises to converge on a giant morphology (Bour 1984) but is also seen in a variety of other insular reptiles (e.g. *Mabuya wrightii*, *Macrosclincus coctei*, *Gallotia* spp.). It has also been recorded in some birds (e.g. *Raphuls cuculatus*, Dinornithidae, *Aepyornis* spp.), mammals (e.g. insular rodents) and invertebrates (e.g. giant tenebrionid beetle *Pulposipes herculeanus*, giant wetas *Deinacrida* spp.). Previous studies have noted the connection between large size and liberation from resource limitation (e.g. *Mabuya wrightii* - Brooke 1983) or enhancing reproductive potential (*Gallotia* spp. - Barahona et al. 2000). The alternative strategy, that of release

Fig. 4. Aldabra Giant Tortoise populations

- a). Aldabra
b). Curieuse



from constraints, is facilitated by size reduction as is seen in many insular avifaunas (Lack 1947). Where the ESS is not attained, insular populations may remain unstable on small islands. This is further exacerbated by sex specific mortality factors leading to behavioural disruptions and sex ratio instability (Gerlach & Le Maitre 2001). These circumstances exist in the Seychelles Magpie Robin where a relatively large size is retained and small island populations can only persist as a metapopulation.

The failure of certain island species to reach such an ESS is likely to result in population instability and contribute to the high extinction rates of insular taxa. The restriction of the adaptive zone imposed by even the successfully attained ESS may further contribute to the vulnerability of island ecosystems to human disturbance.

REFERENCES

- BUTLER, D. & MERTON, D. 1992: The Black Robin: saving the world's most endangered bird. Oxford University Press, Auckland.
- BARAHONA, F., EVANS, S.E., MATEO, J.A., GARCIA-MARQUEZ, M. & LOPEZ-JURADO, L.F. 2000: Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary islands. *J. Zool.* 250: 373-385.
- BOUR, R. 1984: Les tortues terrestres géantes des îles de l'océan Indien occidental. *Stud. Geol. Salamanticensia* 1: 17-76.
- BOURN, D. & COE, M.J. 1978: The size, structure and distribution of the giant tortoise population of Aldabra. *Phil. Trans. R. Soc. Lond. B.* 282: 139-175.
- BOURN, D., GIBSON, C., AUGERI, D., WILSON, C.J., CHURCH, J. & HAY, S.I. 1999: The rise and fall of the Aldabran giant tortoise population. *Proc. R. Soc. Lond. B* 266: 1091-1100.
- BROOKE, M. de L. 1983: The biology and biomass of the skinks, *Mabuya sechellensis* and *Mabuya wrightii* on Cousin Island, Seychelles (Reptilia: Scincidae). *Journal of Zoology* 200: 179-195.
- BULLOCK, I.D. 1989: Aride Island Nature Reserve. Scientific Report April 1987 - April 1989. RSN, unpublished.
- COE, M.J., BOURN, D. & SWINGLAND, I.R. 1979: The biomass, production and carrying capacity of giant tortoises on Aldabra. *Phil. Trans. R. Soc. Lond. B.* 286: 163-176.
- COMINS, H.N. & HASSEL, M.P. 1979: The dynamics of optimally foraging predators and parasitoids. *Journal of Animal Ecology* 48: 335-351.

- DIAMOND, A.W. 1980: Seasonality, population structure and breeding ecology of the Seychelles Brush Warbler *Acrocephalus sechellensis*. Proc. 4th Pan-Afr. Orn. Congr.: 253-266.
- FRAZIER, J.G. 1971: Behavioural and ecological observations on giant tortoises on Aldabra Atoll. Unpublished DPhil. thesis, Oxford.
- GERLACH, J. 1996: Rainfall patterns - an overlooked ecological influence. *Phelsuma* 4: 75-80.
- GERLACH, J., ed. 1997: Seychelles Red Data Book 1997. NPTS, Seychelles.
- GERLACH, J. 1998: Famous Tortoises. J. Gerlach, Cambridge.
- GERLACH, J. 2000: Aride's invertebrates and the magpie robin. *Birdwatch* 35: 16-17.
- GERLACH, J. & CANNING, K.L. 1996: Evolution and history of the giant tortoises of the Aldabra island group. *Testudo* 4: 33-40.
- GERLACH, J. & LE MAITRE, S. 2001 in press: Sex ratio variation in small island populations of an endangered bird, the Seychelles Magpie Robin (*Copsychus sechellarum*). *Ostrich* 71.
- GERLACH, R. & LAMBERT, T. 1997: Analysis of barn owl pellets. In: Betts, M. Aride Island Nature Reserve, Scientific Report 1997. RSNC Unpublished.
- GIBSON, C.W.D. & HAMILTON, J. 1984: Population processes in a large herbivorous reptile: the giant tortoises of Aldabra Atoll. *Oecologica* 61: 230-240.
- GRETTON, A. 1990-2: The Seychelles Magpie Robin Recovery Plan. Progress Reports 1-8. ICBP, unpublished.
- GRETTON, A. 1993: Ecology of the Seychelles Magpie Robin *Copsychus sechellarum*. Proc. VIII Pan-Afr. Orn. Congress: 165-172.
- HONEGGER, R.E. 1966: Beobachtungen an der Herpetofauna der Seychellen. *Salamandra* 1: 20-36.
- JOHNSON, T.H. & STATTSFIELD, A.J. 1990: A global review of island endemic birds. *Ibis* 132: 167-180.
- JONES, C.G., HECK, W., LEWINS, R.E., MUNGROO, Y., SLADE, G. & CADE, T. 1994: The restoration of the Mauritius Kestrel *Falco punctatus* populations. *Ibis* 137: 173-180.
- KING, W.B. 1979: Red Data Book, Vol. 2 Aves. IUCN, Morges.
- KOMDEUR, J. 1988-90: The Seychelles Magpie Robin *Copsychus sechellarum*: Progress Reports 1-13. ICBP unpublished.
- 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: The effects of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proc. R. Soc., Lond B.* 256: 47-52.
- KOMDEUR, J. 1996: Breeding of the Seychelles Magpie Robin *Copsychus sechellarum* and implications for its conservation. *Ibis* 138: 485-498.
- KOMDEUR, J. 1997: Inter-island transfers and population dynamics of Seychelles Warblers *Acrocephalus sechellensis*. *Bird Cons. Int.* 7: 7-26.
- KOMDEUR, J., DAAN, S., TINBERGEN, J. & MATEMAN, C. 1997: Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* 385: 522-525.
- LACK, D. 1947: Darwin's Finches. Cambridge University Press, Cambridge. 208pp.
- LACK, D. 1970: The endemic ducks of remote islands. *Wildfowl* 213: 5-10.
- MacARTHUR, R.H. & WILSON, E.O. 1967: The theory of island biogeography. Princeton University Press, New Jersey.
- MAY, R. 1978: Host-parasitoid systems in patchy environments in a phenomenological model. *Journal of Animal Ecology* 47: 833-843.

- McCULLOCH, N. 1992-5: The Seychelles Magpie Robin Recovery Plan. Reports 9-20 ICBP/BirdLife International, unpublished.
- McCULLOCH, N. 1996: The Seychelles Magpie Robin Recovery Plan. Recovery Plan Revision 1996: Discussion document. RSPB, unpublished.
- PARR, S.J. 1998-9: Seychelles Magpie-Robin Recovery Plan. Quarterly Report 31-3 BirdLife Seychelles, unpublished.
- NEWTON E. 1865: On an apparently undescribed bird from the Seychelles Islands. Ibis (New Series) 1: 335-337.
- NEWTON, E. 1867 : On the land birds of the Seychelles Archipelago. Ibis (New Series) 3: 335-360.
- PENNY, M.J. 1967: A new sanctuary in the Seychelles. Oryx 9: 214-216.
- SAMOUR, H.J., SPRATT, D.M.J., HART, M.G., SAVAGE, B. & HAWKEY, C.M. 1987: A survey of the Aldabra giant tortoise population introduced on Curieuse island Seychelles. Biological Conservation 41: 147-158.
- STATTERSFIELD, A.J. 1987: A systematic list of birds presumed to have become extinct since 1600. In: Mountfort, G. Rare Birds of the World. Collins, London.
- STATTERSFIELD A.J., CROSBY, M.J., LONG, A.J. & WEGE, D.C. 1998: Endemic Bird Areas of the World. BirdLife Conservation Series 7. BirdLife International, Cambridge.
- SWINGLAND, I.R. 1978: Reproductive effort and life history strategy of the Aldabra giant tortoise. Nature 269: 402-404.
- SWINGLAND, I.R. & COE, M.J. 1978: The natural regulation of giant tortoise population on Aldabra Atoll: reproduction. Journal of Zoology 186: 285-309.
- SWINGLAND, I.R. & COE, M.J. 1979: The natural regulation of giant tortoise population on Aldabra Atoll: recruitment. Phil. Trans R. Soc. Lond. B. 286: 177-188.
- SWINGLAND, I.R. & LESSELLS, C.M. 1979: The natural regulation of giant tortoise population on Aldabra Atoll: movement polymorphism, reproductive success and mortality. Journal of Animal Ecology 48: 639-654.
- TAYLOR, I. 1994: Barn Owls. Predator -prey relationships and conservation. CUP, Cambridge.
- TODD, D.M. 1982: Seychelles magpie robin - cat eradication on Fregate island. ICBP Emergency Project Report. ICBP unpublished.
- WATSON, J., WARMAN, C., TODD, D. & LABOUDALLON, V. 1992: The Seychelles magpie robin *Copsychus sechellarum*: ecology and conservation of an endangered species. Biological Conservation 61: 93-106.
- WILLIAMSON, M. 1981: Island Populations. Oxford University Press, Oxford.