ORIGINAL ARTICLE

Demography and conservation of the White-tailed Tropicbird *Phaethon lepturus* on Aride Island, Western Indian Ocean

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Abstract The White-tailed Tropicbird *Phaethon lepturus* breeding population of Aride Island, Seychelles, has experienced a strong decline in the recent past. To predict the future trends of the White-tailed Tropicbird population on Aride Island and understand the urgency of applying management procedures, we developed a population matrix model. We estimated White-tailed Tropicbird adult survival rate over a 12-year period and investigated whether oceanographic conditions (El Niño Southern Oscillation, ENSO, and inter-annual climate variability in the Indian Ocean, Indian Ocean Dipole, IOD) or local factors (*Pisonia grandis* fruiting events) potentially affect adult survival. Annual adult survival could not be linked to inter-annual variability in oceanographic conditions, but may be more influenced by *Pisonia* fruiting events, which, overall, accounts for 23.2% of the adult mortality. The growth rate of the population, primarily influenced by annual adult survival, was estimated to be 0.946, which indicates an annual population decline of 5.4%. At the current rate, the probability of extinction of this population would be 99% in 170 years. Management scenarios studied through Monte Carlo simulations, assuming small increments in adult survival and/or breeding success, dramatically reduce the risk of extinction of White-tailed Tropicbirds. Habitat management, in order to maintain an open canopy and little understorey vegetation, appears to be crucial for the conservation of White-tailed Tropicbirds on Aride Island, as has already been shown for other ground-nesting tropical seabirds nesting on forested islands.

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Introduction

Assessing the dynamics of an animal population is a major contribution to understanding the evolution of its life history and represents an important tool in both evolutionary and conservation biology (Weimerskirch 2001). For long-lived birds with low fecundity, characteristics typical of most seabirds, adult survival is the main parameter explaining population dynamics (Doherty et al. 2004). Adult survival is less sensitive to environmental variability

than other demographic parameters, but the effect of some stochastic environmental events on adult seabird survivorship, such as the El Niño Southern Oscillation (ENSO; Doherty et al. 2004) and the North Atlantic Oscillation (NAO; Sandvik et al. 2005) has recently been demonstrated, whereas others, such as the Indian Ocean Dipole (IOD), have been poorly investigated (but see Monticelli et al. 2008a).

White-tailed Tropicbirds breed in forested areas on several islands of the Indian Ocean (Fishpool and Evans 2001), such as in the Seychelles archipelago (Aride, Cousin, Cousine, Mahé, Silhouette), Christmas Island, Mauritius and Maldives. On Aride Island, Seychelles, they breed all year round, mostly under a tree canopy dominated by Mapou trees *Pisonia grandis*, and were very abundant in the recent past (ca. 10,000 pairs in 1975–1976; Warman and Todd 1984). In the period 1987–2000, Bowler et al. (2002) estimated this tropicbird population at only 600–1,500 pairs and showed that the species suffered an apparent decline of 60% between 1989 and 1998, although the main causes for this decrease were never identified. The severity of this decline in numbers highlighted the need for investigation into its causes in order to identify appropriate conservation action (Bowler et al. 2002). In 1995, ringing and nest-monitoring programs started on Aride Island, primarily to estimate tropicbird adult survival and investigate the relationship between population trends and adult survival. Later, Ramos et al. (2005) studied annual variation in tropicbird productivity and the influence of local factors (ectoparasitism of chicks by hard ticks *Amblyomma loculosum*, and possible interspecific competition for nest-sites) and large-scale (ENSO) factors in explaining productivity between 1989 and 2002. Productivity of White-tailed Tropicbirds showed little annual variation (between 0.21 and 0.37 chicks/pair) and was significantly correlated with the El Niño Multivariate Index, but apparently not influenced by local factors (Ramos et al. 2005). Mean productivity of tropicbirds on Aride Island was only slightly lower than that found on the smaller (27 ha) neighbouring island of Cousin (0.36; Phillips 1987), where tropicbirds breed at higher densities and where the population apparently increased from 700 pairs in 1981 (Phillips 1987) to at least 1,446 pairs in 2000 (northwest monsoon census; Burger and Lawrence 2000). Hence, productivity was insufficient to explain the opposite trends of the breeding White-tailed Tropicbird populations on Aride and Cousin Islands.

Since 1999, the breeding population of White-tailed Tropicbird of Aride Island seems to have undergone considerable oscillations, with several increases and declines (B. Sampson and G. Rocamora, unpublished). However, given the absence of consistent and accurate annual censuses in recent years, it is difficult to delineate the trend of the White-tailed Tropicbird breeding population of Aride Island. This fact underlines the need of a demographic study that elucidates the present and future scenarios for this population.

The main objective of this study was thus to predict the future trends of the White-tailed Tropicbird population on Aride Island and to assess the urgency for the implementation of conservation measures. Specific goals include: (1) estimating White-tailed Tropicbird adult survival rate and investigating which large-scale environmental factors (ENSO and IOD) and local factors (fruiting events of *Pisonia grandis*) potentially affect this parameter, (2) developing a matrix model to estimate the growth rate (λ) of the White-tailed Tropicbird breeding population and predict the future trends of this species under different simulated management scenarios, and (3) proposing management measures for the conservation of White-tailed Tropicbirds on Aride Island.

Methods

Study area

This study was carried out on Aride Island (4°10′S, 55°40′E), the most northerly of the granitic islands of Seychelles, Western Indian Ocean. Aride (72 ha) is a rocky and steep-sided island mainly covered with native Mapou *Pisonia grandis* trees, with only one flat coastal plateau.

Data collection for the survival model

To estimate White-tailed Tropicbird adult survival rate we modelled survival (ϕ) and recapture (p) probabilities from live capture–recapture histories of individual adult White-tailed Tropicbirds ringed at their nests and re-sighted in the study area over a 12-year period, and used Cormack–Jolly–Seber (CJS) open-population models (Cormack 1964; Jolly 1965; Seber 1965) as implemented in Program MARK (White and Burnham 1999).

Between 1995 and 2005, 80 White-tailed Tropicbird nests have been marked and 238 adult tropicbirds were captured and ringed with metal rings. To estimate age of first breeding, 95 chicks from these nests were ringed between 1997 and 2005. Marked nests were monitored weekly between 1997 and 2000 and 2003 and 2006 (several non-systematic visits were done during 2001–2002) in order to record nest occupancy, adult identity and breeding success. Although White-tailed Tropicbirds are known to show strong nest-site fidelity (Phillips 1987; Schreiber et al. 2004), in June–August of 2004, 2005 and 2006, the whole area of marked nests and the other four most important nesting areas for tropicbirds on Aride Island

(M. Moller-Holtkamp, unpublished) were inspected to assess possible movements of birds from marked nests to non-marked nests and locate breeding birds that were ringed as fledglings.

Data selection for the survival model

Given the highly asynchronous breeding cycle of White-tailed Tropicbirds on Aride Island, population monitoring was carried out all year round. For each year, the whole capture–recapture dataset was plotted on a monthly basis. In most of the study years, capture–recaptures were spread over 12 months. However, one of the underlying assumptions of capture–recapture models is that the recapture occasions are of negligible length relative to the time-interval between them (White and Burnham 1999). Thus, to obtain discrete capture–recapture sampling periods, we only selected two recapture periods for each year (bi-monthly periods, except in 2002, with only one period; see Table 2). The criteria used during the selection procedure was a best compromise between (1) the necessity to include months of peak capture–recapture observations, and (2) the need for an acceptable time-interval between recapture occasions whenever possible (J. Hines, personal communication). During data analysis in MARK, the time-interval considered between two successive recapture occasions was that between the mid-points of these two periods. Individuals for which recaptures did not fall within the sampling periods were discarded from the analyses and for individuals included, the recapture data between the bi-monthly sampling period was not used during the modelling. Although the time period between recapture events considered in the modelling is uneven and is not 1 year, survival between recapture periods is annualised (to calendar years) in the modelling procedure.

Modelling survival rate

Following the CJS approach, we first fitted models where survival and recapture probabilities were time-specific [$\phi(t)$, $p(t)$]. Three restricted versions of the CJS model were also used: the constant survival model [$\phi(c)$, $p(t)$], the constant capture model [$\phi(t)$, $p(c)$], and the constant survival and capture model [$\phi(c)$, $p(c)$]. We also investigated whether oceanographic conditions could contribute to explain annual changes in tropicbird adult survival. We considered two variables, the El Niño Southern Oscillation (described by the Multivariate El Niño Index—MEI; http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html) and the Indian Ocean Dipole (described by the Dipole Mode Index-DMI, http://www.jamstec.go.jp/frsgc/research/d1/iod/). MEI and DMI values corresponding to each sampling (recapture) period were calculated as the mean of the monthly (or bi-monthly) values for the period between each recapture event and the previous one. Each oceanographic variable was entered into a further survival model as an annual covariate [ϕ(MEI), p] and [ϕ(DMI), p].

To select the most parsimonious model among our set of candidate models, we used Akaike's Information Criterion corrected for small sample sizes (AICc) and goodness-of-fit tests (GOF) following the procedures described by Burnham and Anderson (2002) and Cooch and White (2005).

Emigration rate

The survival probabilities estimated by the CJS model represent an "apparent" survival because they include an unknown component of permanent emigration from the study area (animals that emigrate from the study area are not available for recapture and so appear to have died in the model; White and Burnham 1999). With data from marked-nests and from systematic searches of ringed birds outside the study area (see above), we calculated the mean percentage of birds recaptured, each year, in a different nest from the nest where it was in the previous breeding attempt. Assuming that emigration rate is constant through time, then the bias-adjusted adult survival rate (S) can be estimated as ϕ/p (site fidelity), where ϕ is the survival rate estimate and p (*site fidelity*) is the probability that a bird remains faithful to the breeding site at which it was breeding in the previous breeding attempt (Shealer et al. 2005).

Effects of *Pisonia* fruiting events on White-tailed Tropicbird adult survival

Pisonia grandis covers most of Aride Island. Periodically, these trees produce extremely sticky multi-seeded infructescences that fall to the ground when ripe and can then easily adhere to bird feathers. Birds commonly become entangled in the infructescences of *Pisonia* and in many cases lose their flying capacity and consequently die of starvation (Ogden 1993; Burger 2005). Episodes of *Pisonia* fruiting occur every year on Aride Island, but frequency, duration and intensity of such events are highly variable. *Pisonia* fruiting events could not be included as a covariate in the adult survival or in the population matrix modelling because data on fruiting frequency and intensity in most study years is only qualitative.

In order to estimate the annual impact of *Pisonia* on the adult survival of White-tailed Tropicbirds, we followed six fruiting events (randomly chosen; April 1998, April and September 1999, December 2000, July 2004, February 2007). In each event, we counted the number of adult tropicbirds affected by *Pisonia* (either dead or alive) and,

for live birds, we recorded whether the bird was able to fly. In 1998, 1999 and 2000 we focused exclusively on ringed birds breeding at the marked nest sites area. In 2004 and 2007, we prospected a larger pre-defined area, including non-ringed birds. For each of the earlier 3 years, we estimate a minimum adult mortality rate, considering the ratio between the number of dead or flightless birds found entangled in *Pisonia* infructescences and the number of birds that bred annually in the prospected areas (estimated from our own data records and from unpublished Aride Island Annual Reports). We consider this mortality rate as a minimum estimate because we assumed that, during the 5 years, the sole *Pisonia* events that occurred were those recorded in this study. Furthermore, we only include in the estimation dead or flightless birds. However, it is possible that tropicbirds found entangled in the *Pisonia* infructescences and still able to fly at the moment of capture, would have died later and that some tropicbird corpses were missed during the searches.

Population matrix model

We constructed a population matrix model for the White-tailed Tropicbird, using program ULM, based on the general formulation for a matrix projection model structured by population stages (Legendre and Colbert 1995). White-tailed Tropicbirds typically start breeding at 4 years of age (Schreiber and Burger 2001; authors' unpublished data). From 89 chicks ringed as fledglings on Aride Island between 1997 and 2003, only 6 (ca. 7%) were later found breeding. The age of these birds varied between 32 and 73 months, being on average 52.5 months (approximately 4 years old). Consequently, we developed a female-based, post-breeding census model with five age stages.

The demographic parameters used in our model were obtained both from the literature and from our own work on Aride Island. The number of adult females was calculated based on the number of breeding pairs estimated for the period 1989–2000 and 2003 (Bowler et al. 2002, M. Betts, unpublished). Breeding success (0.33 ± 0.08) followed data presented by Ramos et al. (2005) for several periods between 1989 and 1991 and 1996 and 2002, and our own estimations for 2003–2004 ($n = 52$). White-tailed Tropicbirds breed all year round on Aride Island with a mean interval of 226.38 ± 38.38 days between breeding attempts (either successful and unsuccessful; authors' unpublished data), so that annual breeding frequency is 1.61. Adult survival probability was derived from the capture–recapture model presented in this study (corrected with data on emigration rates). To our knowledge, there are no estimations of immature White-tailed Tropicbird survival. Thus, we assumed pre-breeding survival (from fledging to first breeding) to be 0.80, as was estimated for

Red-tailed Tropicbird *P. aethereus* in the Johnston Atoll, central Pacific Ocean (Doherty et al. 2004).

Apart from the deterministic model, we also build a stochastic model, which is a more realistic model that incorporates variation in demographic rates (Legendre and Colbert 1995). Demographic parameters can be subjected to demographic and/or environmental stochasticity; however, environmental stochasticity is generally considered to dominate demographic stochasticity in populations larger than 100 individuals (Lande 1988). Therefore, in our model, we incorporate exclusively environmental stochasticity, considering fecundity and adult survival as stochastic variables (Legendre and Colbert 1995). Estimates of the stochastic growth rate and of the probability of extinction were obtained by running 1000 Monte Carlo simulations during 150 years (Legendre and Colbert 1995). Possible management scenarios were simulated for the same period.

Results

Adult survival model selection and estimates

Adult survival and recapture probabilities were estimated by using the capture–recapture histories of 191 White-tailed Tropicbirds (80% of the initial dataset) followed between 1995 and 2006. The parametric bootstrap GOF test performed on the fully parameterised CJS model [$\phi(t)$ $p(t)$] gave rise to a variance inflation factor $\hat{c} = 3.551$, suggesting the presence of some over dispersion in the data, but no major need to re-think our global model. This value of $\hat{c}$ was applied to adjust AICc values.

The AICc results comparing different parameterisations of survival and recapture probabilities are shown in Table 1. Two models with survival being either time-invariant [$\phi(c)$ $p(t)$] or a function of annual variations in DMI [$\phi(DMI)p(t)$] had the lowest QAICc values. However, the former model was two-times more supported by the data than the latter (QAICc weights of 0.53 vs 0.26, respectively), and the analysis of deviance (ANODEV) indicated that DMI did not explain a significant proportion of the difference in deviance between the time-specific survival and constant survival models ($F_{1,20} = 2.534$, $P = 0.1271$). The model that incorporated annual variations in ENSO (MEI) did not fit the data well (ΔQAICc > 2 units; Table 1).

The adult White-tailed Tropicbird survival estimate from our most parsimonious model [$\phi(c)$ $p(t)$] was 0.76 (SE = 0.02; 95% CI = 0.71, 0.80), while estimates for probability of recapture ranged from 0.00 (SE = 0.00) to 0.57 (SE = 0.07; Table 2).

Between 2004 and 2006, the period for which we carried out systematic searches for ringed birds outside the study's

Table 1 Selection of adult survival models for the White-tailed Tropicbird *Phaethon lepturus* on Aride Island, Seychelles, based on corrected Quasi-AIC (QAICc) with variance inflation factor $\hat{c} = 3.55139$ (model deviance is also adjusted with $\hat{c} = 3.55139$)

Model	QAICc	ΔQAICc	QAICc weight	No. of parameters	QDeviance
$\phi(c)\,p(t)$	**340.21**	**0.00**	**0.53**	**23**	**143.33**
ϕ(DMI) $p(t)$	341.65	1.44	0.26	24	142.48
ϕ(MEI) $p(t)$	342.59	2.38	0.16	24	143.43
$\phi(c)\,p(c)$	344.69	4.48	0.06	2	192.95
$\phi(t)\,p(c)$	366.71	26.5	0.00	23	169.83
$\phi(t)\,p(t)$	383.64	43.43	0.00	44	135.79

Survival rate (ϕ) and recapture probabilities (p) were modelled as constant over time (c), time dependent (t), or as an annual function of the Multivariate El Niño Index (*MEI*) and the Dipole Mode Index (*DMI*). The model that best explained the data (lower QAICc) is highlighted in bold

Table 2 Recapture probabilities of White-tailed Tropicbird on Aride Island between 1995 and 2006

Year	Period	$\bar{x}$	SE	95% CI Lower	95% CI Upper
1995	Sep–Oct	0.55	0.13	0.31	0.77
1996	May–Jun	0.56	0.10	0.36	0.75
	Oct–Nov	0.13	0.07	0.04	0.34
1997	Jun–Jul	0.11	0.07	0.03	0.35
	Oct–Nov	0.31	0.11	0.14	0.55
1998	Apr–May	0.57	0.07	0.43	0.70
	Oct–Nov	0.35	0.07	0.23	0.49
1999	Mar–Apr	0.34	0.07	0.22	0.48
	Nov–Dec	0.26	0.06	0.17	0.39
2000	Mar–Apr	0.13	0.04	0.07	0.23
	Sep–Oct	0.20	0.05	0.13	0.31
2001	Jan–Feb	0.01	0.01	0.00	0.08
	Apr	0.00[a]			
2002	Dec	0.08	0.04	0.03	0.20
2003	Feb	0.02	0.02	0.00	0.14
	Jul–Aug	0.02	0.02	0.00	0.14
2004	Mar–Apr	0.09	0.04	0.03	0.21
	Oct–Nov	0.10	0.05	0.04	0.24
2005	Jun–Jul	0.32	0.09	0.17	0.51
	Oct–Nov	0.28	0.09	0.14	0.47
2006	Feb	0.10	0.06	0.03	0.28
	Jul–Aug	0.42	0.12	0.23	0.65
$\bar{x}$		0.23	0.06	0.13	0.38

No birds were recaptured in the period January–February 1995. The $\bar{x}$ is a weighted average

[a] No standard error estimate available (parameter on a boundary)

Table 3 Annual mortality of adult White-tailed Tropicbird on Aride Island due to *Pisonia* fruiting events

	Number of birds affected by *Pisonia* (dead or flightless)	Annual number of breeding birds (in prospected areas)	Mortality rate (%)
1998	2	66	3.0
1999	3	66	4.5
2000	1	100	1.0
2004	17	200	8.5
2007	10	200	5.0
Average			4.4 ± 2.8

be extremely rare because, despite systematic searches on some neighbouring islands (Cousin and Cousine), tropicbirds ringed on Aride Island were never recorded breeding elsewhere (R. Bristol, personal communication; authors' unpublished data). Considering emigration rate to be constant through time, we estimate the bias-adjusted survival rate as 0.81 (SE = 0.02; 95% CI = 0.76, 0.85).

Effects of *Pisonia* fruiting events in White-tailed Tropicbird adult survival

We estimated annual adult tropicbird mortality due to *Pisonia* to be 4.4% (1–8.5%, SD = 2.8; Table 3), accounting on average for 23.2% of the total annual adult mortality.

Population matrix model

The deterministic model predicted a long-term annual growth rate of 0.946, indicating an average population decline of 5.4% per year. The sensitivity analysis performed shows that adult survival is the demographic parameter with largest impact on the tropicbird population growth, followed by fecundity (Table 4).

marked nests, we recaptured 51 ringed tropicbirds, 48 in the marked nests and three breeding in new non-marked sites. These data suggested that site-fidelity is high (94%) but a permanent emigration rate of 6% is not negligible. Permanent emigration to other neighbouring islands must

Table 4 Sensitivities and elasticities of the demographic parameters (survival and fecundity) of White-tailed Tropicbird population showing which parameters have the largest impact on population growth
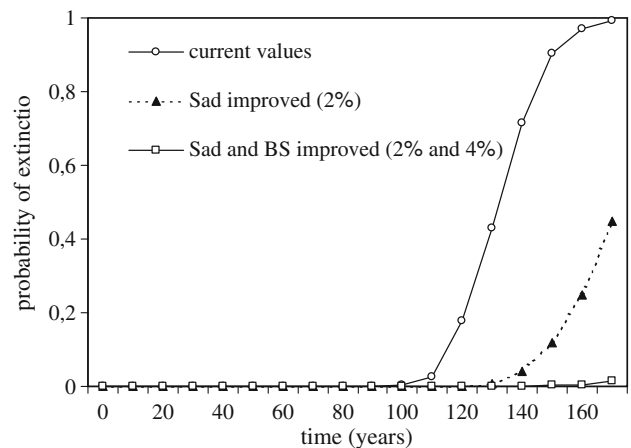
Parameter	Sensitivity	Elasticity
S_0	0.1079	0.0912
S_1	0.1079	0.0912
S_2	0.1079	0.0912
S_3	0.1079	0.0912
S_{Ad}	0.6350	0.5438
F	0.3249	0.0912

Elasticity is similar to sensitivity but takes the size of the parameter into account
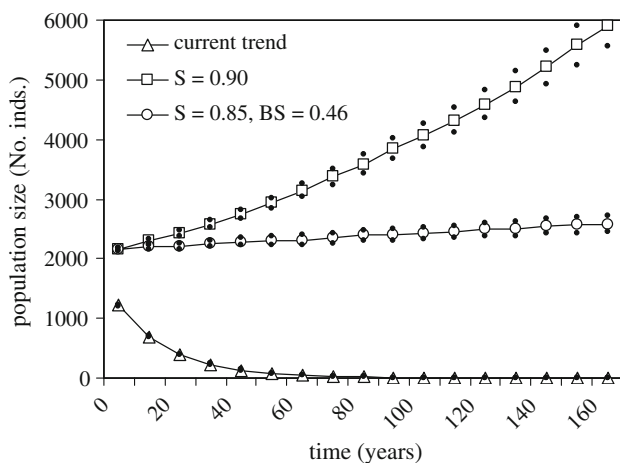
Fig. 1 Simulated Monte Carlo population trajectories of White-tailed Tropicbird for the whole population at the current growth rate, and for increases in adult survival (+9%) and in both adult survival (+4%) and breeding success (+13%) that reverse negative growth rate. *Black dots* represent 95% confident intervals

Fig. 2 Monte Carlo simulations of the probability of extinction for the White-tailed Tropicbird breeding population of Aride Island in the time-period of 170 years under current values, improved adult survival (2%), and improved adult survival (2%) and breeding success (4%) values (management scenario)

SE = 0.0002 and λ = 1.000, SE = 0.0002, respectively; Fig. 1).

Discussion

Adult survival

Despite the large number of studies on seabird demography, to our knowledge, no previous studies focused on survival of non-seasonal breeding species such as the White-tailed Tropicbird. Our estimate of 0.81 for adult White-tailed Tropicbird survival is well within the range found for other oceanic seabirds (0.74–0.97; Schreiber and Burger 2001) but rather lower than that estimated for the Red-tailed Tropicbird (0.85–0.90; Schreiber and Burger 2001; Doherty et al. 2004; Schreiber et al. 2004).

Our study provides no evidence that tropicbird adult survival is influenced by inter-annual variability in environmental oceanographic conditions, either ENSO or IOD, a pattern previously found in another pelagic seabird breeding at a tropical location, the Brown Booby *Sula leucogaster* at the Johnston Atoll (Beadell et al. 2003). Although other studies have shown the existence of a negative effect of environmental anomalies on adult seabird survival (e.g. Doherty et al. 2004; Jenouvrier et al. 2003; Sandvik et al. 2005), it is known that survival rates of adult seabirds are relatively less sensitive to annual fluctuations in food availability compared to other demographic parameters such as breeding success (Weimerskirch 2001). Lower susceptibility of adult survival to reduced food availability might be due to seabird ability, especially in

The stochastic model gives a mean growth rate of 0.943 (SE = 0.002), which is close to the value predicted by the deterministic model. Monte Carlo simulations show that population trajectories decrease rapidly with time (Fig. 1) and that at the current rate, the probability of extinction of this population would be 99% in 170 years (Fig. 2). Two management scenarios (see "Discussion"), one that assumes an increment of 2% in the estimated adult survival (as a reduction in mortality due to *Pisonia*), and another that also assumes an increment of 4% in productivity (from 0.33 to 0.37, which seems realistic once the maximum value recorded was 0.50), would reduce the probability of extinction of this population to 44.9 and 1.4% in 170 years, respectively (Fig. 2). However, only an increase of 9% in the estimated adult survival or both an increase of 4% in adult survival and of 13% in breeding success would reverse the negative growth of this population (λ = 1.006,

pelagic species, to move to more profitable foraging areas, even when this involves the abandonment of the breeding areas.

Mortality of seabirds due to entanglement in *Pisonia* infructescences has been previously described (Ogden 1993; Burger 2005). Ogden (1993) estimated adult mortality of Black Noddies *Anous minutus* due to *Pisonia* fruit clusters to be 0.1% per annum on Heron Island (Great Barrier Reef), and assumed it had a negligible effect on the population. In our study, however, adult tropicbird mortality due to *Pisonia* fruiting events averages 4.4% per year, but might account for as much as 8.5%, being presumably an important factor in explaining adult mortality (averaging 23.2% of total adult mortality). On Aride Island, other seabird species, mainly those that spend considerable time on the ground, such as Sooty Terns *Sterna fuscata*, Roseate Terns *Sterna dougallii* and Lesser Noddies *Anous tenuirostris*, appeared to be affected by *Pisonia* (Monticelli et al. 2008b; personal observations).

Population projections and management

Results from this study suggest that the White-tailed Tropicbird breeding population of Aride Island is declining and would be extinct in approximately 170 years at the current trend. Adult survival and, to a lesser extent, fecundity, were the most sensitive parameters of population growth rate. Either adult survival or fecundity should increase significantly in order to reverse the actual negative growth rate of the White-tailed Tropicbird population on Aride Island. However, different scenarios that simulate a small increment in adult survival or in both adult survival and breeding success, drastically reduced the risk of extinction of the population in the next 170 years. This fact demonstrates that management can still play an important role in the future of the White-tailed Tropicbird population of Aride Island. The only source of adult mortality identified in this study was directly linked to *Pisonia* fruiting events. It is virtually impossible to eliminate *Pisonia* as a mortality factor, but it might be possible to reduce its impact through management procedures. Surveillance of the areas with higher tropicbird nest density by the island staff, especially during strong *Pisonia* fruiting events, to search and "clean" entangled birds might be reasonably successful in reducing adult mortality (personal observations).

On the other hand, both adult survival and breeding success of White-tailed Tropicbirds can possibly benefit from habitat management. Aride Island was in the past a coconut plantation, where natural vegetation was coppiced annually (Warman and Todd 1984). Annual coppicing ceased in 1967 when the island was converted into a nature reserve. Aride was one of the few islands that

remained rat-free and this status led the island to be the target for the re-introduction of some of the Seychelles endemic landbirds, such as the Seychelles Warbler *Acrocephalus sechellensis* and Magpie Robin *Copsychus sechellarum*. Such species require bush and tall trees and hence the cessation of coppicing of the native vegetation. Nowadays, apart from a minority of bare rocky areas, Aride Island is covered by a mature woodland dominated by *Pisonia* trees ca. 15–20 m tall with dense canopy cover, while the understorey is dominated by a small number of low trees ca. 2–6 m high (e.g. *Ficus reflexa*, *F. nautarum*, *Euphorbia pyrifolia*) and ferns *Nephrolepsis biserrata* (Martin, unpublished; Hunter 2005). Habitat changes, especially in relation to vegetation structure, seem to be important in explaining distribution and abundance of seabirds on Aride Island. Increasing canopy cover was an important factor in understanding the spatial distribution of breeding Roseate Terns on Aride Island and explained why forest areas with high canopy closure were readily abandoned (Monticelli et al. 2008b). Sooty Terns, although breeding in high numbers under an enclosed tree canopy on Aride Island, are present at significantly lower densities compared to other islands of the archipelago with an open habitat, and Aride's population size might be constrained by canopy and understorey density (Feare et al. 1997). We hypothesise that massive changes in the island habitat could be an important factor explaining the significant decline in the tropicbird population that occurred between 1975–1976 and 1989.

Throughout their range, tropicbirds (*Phaethon* sp.) may nest under the shelter of a tree canopy or under shrubs including *Pisonia* (Clark et al. 1993; Burger and Lawrence 2000), which to a greater or lesser extent may influence their demographic parameters (this study). Most tropicbird species land beside the nest-site, and a closed canopy as well as a large number of stems and/or ferns severely impedes movement (Clark et al. 1993). It is possible that the large increase in canopy and understorey cover that occurred over the whole island restricted the suitable White-tailed Tropicbird breeding areas. Although to a lesser extent than in the past, the continuous recovery of the native vegetation of Aride Island could still be affecting tropicbirds in the present. This idea is supported by the abandonment of several marked nests in the recent years, as a result of dense vegetation cover, mainly fast-growing ferns. Habitat management, in order to maintain some open areas both at canopy and ground level, should be very important for the conservation of the White-tailed Tropicbird population on Aride Island. Specifically, if tropicbirds are attracted to more open areas, where the density of *Pisonia* trees is lower, the likelihood of birds becoming entangled in *Pisonia* infructescences will also decline and, as a consequence, adult survival might increase.

Habitat management can also presumably improve breeding success of White-tailed Tropicbirds. Approximately 23% of the study nest-sites on Aride Island are used by two tropicbird pairs (authors' unpublished data) and an unknown number are also used by Wedge-tailed Shearwaters *Puffinus pacificus*. Inter and intra-specific nest-site competition is known to be an important cause of breeding failure among tropicbirds (Stonehouse 1962). On Aride Island, tropicbird chicks are commonly pecked to death by adult shearwaters or tropicbirds (Ramos et al. 2005; personal observations) and violent fights between adult tropicbirds at nest-sites often result in the loss of the egg. Stonehouse (1962) suggested that the tropicbird (*Phaethon* spp.) population of Ascension Island is limited by nest-site availability, through the high losses of eggs and young caused by competition for sites. If habitat quality on Aride Island is improved and nest-site availability increases, we should expect a decrease in nest-site competition and an increase in breeding success.

Another demographic parameter that could increase with habitat management is recruitment rate. In this study, we were not able to accurately estimate this parameter. Nevertheless, the fact that only ca. 7% of the ringed chicks were found breeding in subsequent years on Aride Island, which represents approximately 17% of the birds that would reach breeding age (assuming the survival rates used in the matrix model), raises the suggestion that recruitment rate on Aride Island could be unusually low for a philopatric species. Once again, low nest-site availability and high nest competition can presumably explain the value of this demographic parameter. Low recruitment rates, associated with high nest competition, were recorded for other seabird species (Crespin et al. 2006).

Further studies on White-tailed Tropicbird demography, focusing mainly on immature survival and recruitment rate, will help to support our conclusions and to delineate a strong-based management strategy. Nevertheless, this study highlights the conflict between habitat management for reintroduced endemic landbirds and the restoration of seabird populations. It seems that the habitat return on Aride Island to a predominantly native climax forest, following its designation as a nature reserve, has contributed to a decline of some seabird species (Feare et al. 1997; Monticelli et al. 2008b; this study). Habitat management, such as the maintenance of canopy gaps, with the consequent decline of fern density, has been already shown to be an important conservation tool for other breeding seabirds of Aride Island, such as the Roseate and Sooty Terns (Feare et al. 1997; Monticelli et al. 2008b), and it may be crucial for the White-tailed Tropicbird. Although endemic landbirds depend on the presence of a native forest to survive, habitat management for seabirds might, presently, have positive impacts on such birds. Maintenance of canopy gaps would be important for maintaining a healthy distribution of early successional plant species and their attendant biota, which would presumably benefit the conservation of native landbirds such as the Seychelles Warbler (Hunter 2005).

Zusammenfassung

Demographie und Schutz des Weißschwanz-Tropikvogels *Phaethon lepturus* auf Aride Island im westlichen Indischen Ozean

Die Brutpopulation des Weißschwanz-Tropikvogels auf Aride Island, Seychellen, hat in der jüngsten Vergangenheit einen starken Rückgang erfahren. Um die zukünftigen Trends der Weißschwanz-Tropikvogel-Population auf Aride Island vorhersagen und die Dringlichkeit der Anwendung von Managementverfahren verstehen zu können, entwickelten wir ein Populationsmatrix-Modell. Wir schätzten die Überlebensrate adulter Weißschwanz-Tropikvögel über einen Zeitraum von zwölf Jahren und untersuchten, ob die ozeanographischen Bedingungen (El Niño-Südliche Oszillation, ENSO, und die interannuale Klimaschwankungen im Indischen Ozean, Indian Ocean Dipole, IOD) oder lokale Faktoren (Fruchttragen von *Pisonia grandis*) möglicherweise das Überleben der Altvögel beeinflussen. Das jährliche Überleben der Altvögel konnte nicht mit der interannualen Variabilität in den ozeanographischen Bedingungen in Verbindung gebracht werden, sondern dürfte stärker durch das Fruchttragen von *Pisonia* beeinflusst werden, das insgesamt 23,2% der Altvogelmortalität erklärt. Die Wachstumsrate der Population, die vorwiegend durch das jährliche Überleben der Altvögel beeinflusst wird, wurde auf 0,946 geschätzt, was auf einen jährlichen Populationsrückgang von 5,4% hinweist. Bei der gegenwärtigen Rate wäre die Aussterbewahrscheinlichkeit für diese Population 99% in von 170 Jahren.

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