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Research Paper

Combining monitoring data from multiple sites to assess population status and trends of White-tailed Tropicbirds (*Phaethon lepturus*) in the Seychelles

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ABSTRACT. Seabirds, being long-lived top-level marine predators, are often considered to be valuable environmental indicators. With growing evidence of seabird declines worldwide, it is essential to monitor changes in populations and determine drivers of change. The Seychelles Archipelago supports the greatest abundance of seabirds in the tropical Indian Ocean, but regional seabird population breeding success and trend data are not readily available despite multi-year data collection at several locations. Here we use monitoring data on White-tailed Tropicbirds (*Phaethon lepturus*) in the Seychelles to present the first nation-wide assessment of the status and trends of breeding success at five key sites. Mean annual breeding success was 15% for Aldabra Atoll in the southern Seychelles and 33–55% in the inner islands (Aride, Cousine, Denis, and Cousin). In the inner islands there are indications of potential population declines (inferred from declining nesting activity rates at Aride), despite stable and comparatively high breeding success. This contrasts with Aldabra where nesting activity has been relatively stable, but a decline in breeding success is causing concern. Our study highlights clear priorities for management of *P. lepturus* populations in the Seychelles; the causes of the declines in *P. lepturus* breeding population at Aride and breeding success at Aldabra should be a focus of future research and monitoring. We propose the adoption of standardized monitoring programs and increased site coverage across the Seychelles and the broader Western Indian Ocean. This, coupled with increased pooling of data and regular analysis, will strengthen the collective effort toward the conservation management of this and other seabird species within this global seabird hotspot.

Regroupement de données de suivis provenant de plusieurs sites pour évaluer l'état et la tendance des populations de Phaétons à bec jaune (*Phaethon lepturus*) aux Seychelles

RESUME. Les oiseaux marins, prédateurs de haut niveau trophique et de longue durée de vie, sont souvent considérés comme de précieux indicateurs environnementaux. Compte tenu de l'accumulation d'indications penchant vers la diminution des oiseaux marins dans le monde entier, il est essentiel de surveiller les changements dans les populations et de déterminer leurs facteurs sous-jacents. L'archipel des Seychelles abrite la plus grande abondance d'oiseaux marins de l'océan Indien tropical, mais il y a peu de données régionales sur le succès de reproduction et la tendance des populations d'oiseaux marins malgré la collecte de données pluriannuelles à plusieurs endroits. Dans le présent article, nous avons utilisé les données de suivis des Phaétons à bec jaune (*Phaethon lepturus*) aux Seychelles pour présenter la première évaluation à l'échelle nationale du statut et de la tendance du succès de reproduction à cinq sites clés. Le succès annuel moyen de reproduction était de 15 % pour l'atoll d'Aldabra dans le sud des Seychelles et de 33-55 % dans les îles intérieures (Aride, Cousine, Denis et Cousin). Dans les îles intérieures, des indications laissent entrevoir une baisse potentielle de la population (déduite de la baisse du taux d'activité de nidification à Aride), malgré un succès de reproduction stable et comparativement élevé. Ce résultat contraste avec Aldabra, où l'activité de nidification a été relativement stable, mais où la baisse du succès de reproduction est préoccupante. Notre étude révèle des priorités claires pour la gestion des populations de *P. lepturus* aux Seychelles; les causes de la baisse de la population nicheuse de *P. lepturus* à Aride et du succès de reproduction à Aldabra devraient faire l'objet de recherches et de suivis. Nous préconisons l'adoption de programmes de suivis normalisés et une couverture accrue de sites aux Seychelles et dans l'ensemble de l'océan Indien occidental. Cette proposition, associée à une mise en commun accrue des données et à leur analyse régulière, renforcera l'effort collectif pour la gestion de la conservation de cette espèce et d'autres espèces d'oiseaux marins dans ce lieu d'intérêt mondial pour les oiseaux marins.

Key Words: *breeding success; Indian Ocean; population trends; seabird monitoring*

INTRODUCTION

The evidence for declines in both ocean health and seabird populations is unequivocal; just 13% of the world's oceans are relatively unaffected by human activity (Jones et al. 2018), and seabirds are now considered more threatened than any other comparable group of birds (Dias et al. 2019). Being long-lived top marine predators, seabirds are considered valuable environmental indicators (Einoder 2009). When monitored, they provide both a measure of health of that species as well as an indication of the overall state of the surrounding ecosystem (Piatt et al. 2007, Parsons et al. 2008).

The Western Indian Ocean (WIO) region has recently been identified by scientists as a key area to prioritize for the conservation of global marine biodiversity in the face of the climate crisis (Ramírez et al. 2017). The Seychelles support the greatest abundance of tropical seabirds in the Indian Ocean: the total is estimated to be approximately 3.4 million pairs (Le Corre et al. 2012) of 16 breeding species. The Seychelles islands are the main breeding ground for White-tailed Tropicbirds (*Phaethon lepturus*), with an estimated 6500 breeding pairs, and 56% of the WIO breeding population (Le Corre et al. 2012). Breeding populations of this species are monitored on a number of Seychelles islands, primarily because *P. lepturus* is one of the most ubiquitous seabird species and easily accessible to monitor. In addition, it is considered by conservation practitioners to be an important indicator species (Burger and Lawrence 2000a), whose status reflects or predicts the condition of the broader marine environment.

Phaethon lepturus are pelagic seabirds that undertake long foraging trips, feeding mainly on surface-dwelling prey, such as flying fish and squid (Schreiber and Clapp 1987, Catry et al. 2009). Its niche foraging strategy limits its rate of provisioning when these food sources are scarce (Schaffner 1990) and therefore directly relates to chick rearing (or breeding) success. Additionally, *P. lepturus*' ground-nesting breeding strategy is highly dependent on habitat integrity and is susceptible to environmental perturbations such as climatic events (Ancona et al. 2011) and invasive alien species (Russell and le Corre 2009). To use *P. lepturus* as an indicator of broader scale environmental changes, the factors influencing adult survival and breeding success must be identified and understood by those designing and conducting monitoring programs. Consolidating *P. lepturus* breeding population monitoring data therefore has the potential to be a valuable tool for managers of marine ecosystems.

With 115 islands stretching across an exclusive economic zone of 1.4 million km², the Seychelles form a substantial part of the WIO region. Biodiversity monitoring programs are widely used across the Seychelles and can form an integral role in informing conservation management. However, despite the intensive efforts on various Seychelles islands, region-wide coordination of monitoring efforts is challenging on account of the high number and range of management authorities with varying management priorities. Determining broader trends, e.g., at national and regional scales, in population and breeding success, rather than island-by-island trends, of such a key seabird species is an essential step to facilitate effective management of this species and ultimately to provide better insight into the health of the surrounding ocean.

Although *P. lepturus* is listed as of "Least Concern" on the International Union for Conservation of Nature and Natural Resources (IUCN) red list, the species is suspected to be in decline on account of predation by invasive alien species at nesting sites (IUCN 2016). Seabird populations in the Seychelles have been threatened by habitat loss, invasive alien predators, and over-utilization of seabirds and their eggs as a food source. Expanding fisheries activity and climate change also pose threats (Rocamora and Skerrett 2001, Bristol 2007). Here, for the first time, we compile multi-site monitoring data of *P. lepturus* in the Seychelles to (1) establish and compare breeding success between different islands; (2) assess nation-wide trends in breeding success and nesting activity as a proxy for population trends; and (3) identify breeding seasonality. We use these results to determine the population status of *P. lepturus* in the Seychelles and make recommendations to both improve monitoring effectiveness at a national level and establish whether the species is truly an indicator of broader ecosystem health.

MATERIAL AND METHODS

Study sites and species

We analyzed data from five sites in the Seychelles (Fig. 1, Table 1), including the four main monitoring sites for *P. lepturus* (Aldabra Atoll, Cousin Island, Cousine Island, and Aride Island) as well as Denis Island, where little was known about the *P. lepturus* population. The islands vary in size, geomorphology, elevation, protection status, management type, predator threats, and estimated *P. lepturus* population size (Table 1). Although *P. lepturus* also breed on other islands in the Seychelles (e.g., Frigate Island, Silhouette Island, North Island, and Bird Island; Skerrett et al. 2001), most are not routinely monitored. Each of the monitoring programs was managed independently, although they were based on locally developed guidelines (Burger and Lawrence 2000b), and they vary in duration, area covered, and methods (Table 2).

On rat- and cat-free islands (i.e., all sites except Aldabra), *P. lepturus* prefer to nest on bare, scratched patches inside rock or log cavities or next to vertical structures such as trees, boulders, or cliffs, laying one egg that both parents take turns to incubate (Prys-Jones and Peet 1980, Phillips 1987). On Aldabra, tropicbird nesting is restricted to limestone islets in the lagoon or coastal outcrops, and nest sites are predominantly crevices in the limestone. Although cats are present on some of Aldabra's islands, they are not present on or close to the tropicbird nesting areas. On Cousin Island, egg incubation is 40–41 days, with a mean incubation shift length by parents of 6.6 days and fledging age of 67–89 days (mean 76.5 days; Phillips 1987).

Monitoring

On all islands, monitoring areas were visited and new nests searched for every 2–14 days. The area surveyed, the monitoring program duration, and the methods varied between islands (Table 2). Specifically, on Cousin Island, an annual or bi-annual snapshot survey was conducted whereby 100 nests at egg stage were chosen and followed to record nesting outcome. We focused on two metrics: breeding success (% nests that fledged a chick) and nesting activity (the number of new nests). A nesting *P. lepturus* was defined as an adult incubating an egg or brooding a chick.

Table 1. Details of the five *Phaethon lepturus* breeding study sites in the Seychelles.

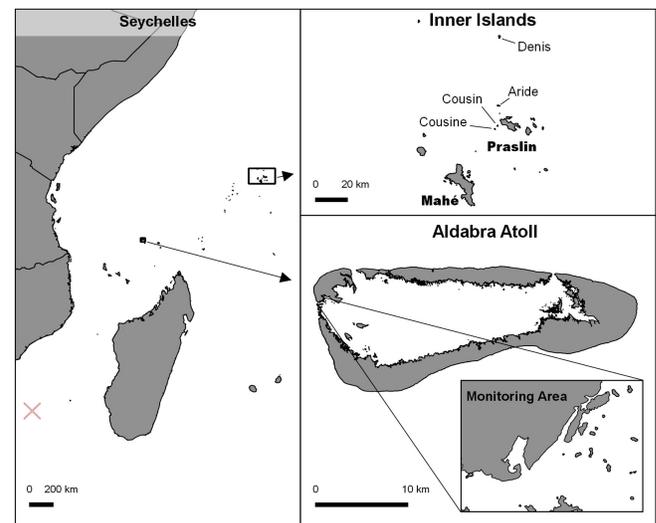
Site	Protection status	Land area (ha)	Geomorphology	Location	Management	Population estimates	Potential nest predators	Other disruptive [†] species or factors
Aldabra	UNESCO World Heritage site (1982); Special Reserve (1975)	15,254	Coralline	9.2255°S, 46.1310°E	Public Trust	2000 pairs (Diamond 1975)	All able to access the islets: black rat (<i>Rattus rattus</i>), Gray Heron (<i>Ardea cinerea</i>), Aldabra Drongo ^A (<i>Dicrurus aldabranus</i>), coconut crab ¹ (<i>Birgus latro</i>), Pied Crow (<i>Corvus albus</i>)	Red-tailed Tropicbirds ^A (<i>Phaethon rubricauda</i>); occasional tidal inundation of nest sites
Aride	Special Reserve (1979)	74	Granitic	4.2000°S, 55.6667°E	NGO	1446 pairs (Bowler et al. 2006)	Wright's skink ^B (<i>Trachylepis wrightii</i>), Seychelles Fody ^B (<i>Foudia sechellarum</i>), house mouse (<i>Mus musculus</i>)	Bird-catcher tree ² (<i>Pisonia grandis</i>), ticks, shearwaters ^B
Cousin	Nature Reserve (1969) Special Reserve (1975)	27	Granitic	4.3314°S, 55.6631°E	NGO	2110 pairs (Burger and Lawrence 2000b)	Wright's skink ^B , Seychelles Fody ^B , ghost crabs ³ (<i>Ocypode</i> spp.)	<i>Pisonia grandis^B, shearwaters^B</i>
Cousine	None, private resort island	26	Granitic	4.3500°S, 55.6333°E	Private	450-850 pairs (Malan et al. 2009)	Wright's skink ^B , Seychelles Fody, ghost crabs, Seychelles Magpie-Robin ^B (<i>Copsychus sechellarum</i>)	<i>Pisonia grandis</i> , giant tortoises ^B (<i>Aldabrachelys gigantea</i>), shearwaters ^B
Denis	None, private resort island	140	Sand cay	3.8000°S, 55.6667°E	Private	~40 pairs (this study)	None perceived; cats removed in 2000, rats removed in 2002	

^AUnpublished camera trap images, ^BStaff personal observations; published observations: ¹Diamond 1975, ²Catry et al. 2009, ³Phillips 1987
[†]Observed or thought to hinder *P. lepturus* breeding success by increasing nest desertion or causing parent mortality

Because clutch size is one egg in this species, we calculated breeding success as the proportion of nests encountered with an egg that resulted in a fledgling. Nest status was determined by comparing the nest stage of two consecutive visits. For example, if a nest was observed to have been occupied by an egg or a young (partially feathered) chick and was subsequently observed empty or with signs of predation/death, it was recorded as unsuccessful. Unsuccessful nests were scored as to whether failure occurred at egg or chick stage. We acknowledge that the gaps between nest checks may therefore over-estimate the number of attempts failing at egg stage if an egg hatched and the chick died before the next nest check, but observers searched the nest area for signs of chick predation or egg remnants to inform decisions on nest failure stage. Conversely, if a nest was observed to be occupied by a near-fledged (fully feathered) chick and found empty in a subsequent visit, without signs of predation/death, it was assumed that the chick had fledged and was recorded as successful.

Nesting activity was defined as the number of new nests encountered per month; we used “new nest” rather than “total active nests per month” to avoid potential pseudo-replication from one nesting attempt being included across several months. Although we use “new nests” as a proxy for population trends, we acknowledge that this dynamic between number of new nests and failed nests is sensitive to patterns of re-nesting behavior. We calculated nesting activity per month for the sites in which all nests were monitored within a specific area (Aride, Aldabra) or for a set number of known nesting sites (Cousine). For these sites, observers checked all known nesting sites/cavities within the specified area to ensure survey/observer effort remained constant; nesting attempts (sites/cavities) were marked for ease of following (Burger and Lawrence 2000a). This nesting activity can be used as a proxy for breeding population size, assuming that the area monitored and the effort remained constant over time. All nests were dated from the first record. To avoid introducing potential bias, new nests were only included in the breeding success dataset if they were first found at incubation stage (i.e., nests found at chick stage were excluded). Nevertheless, across all sites, more than 95% of the nests were first encountered at egg stage.

Fig. 1. Seychelles islands in the Western Indian Ocean region (left), the four *Phaethon lepturus* monitoring site locations in the inner Seychelles (Cousin, Aride, Cousine, and Denis; top right), and Aldabra Atoll (bottom right) in the southern Seychelles, with specific monitoring area of Aldabra shown (inset).



Data analysis

We treated breeding success as a binomial variable (successful nest = 1; unsuccessful = 0) and calculated the mean breeding success as the percentage of successful nests at each site. We also calculated the proportion of unsuccessful nests that failed during egg stage compared to those that failed during chick stage. At the three sites where monitoring effort was continuous for 4–10 years (Aldabra, Aride, and Cousine), we also investigated long-term and seasonal trends using a set of generalized additive models (GAM) with a binomial error structure and breeding success as

Table 2. Details of *Phaethon lepturus* monitoring programs at the five study sites in the Seychelles, including the most recent published assessment of breeding success.

Site	Area monitored (ha)	Monitoring data included	Frequency of monitoring	Methods	Nest distribution	Nest description and habitat type	Last assessment
Aldabra	0.4	Feb 2009–Nov 2016	Continuous year-round monitoring, every 2 weeks	Entire monitoring area searched, all new nests recorded and tagged; nests visited on subsequent surveys until nest outcome determined	Only on limestone islets or coastal outcrops; monitored on 13 small lagoon islets and an outcrop of Picard Island	Limestone cavities or cavities in dense vegetation on small islets and coastal outcrops	Prys-Jones and Peet 1980
Cousin	20	1999, 2009–2016	1–2×/year beginning Feb and/or July, nests visited every 3–4 days	Survey effort defined by a set number of nests rather than a specific area; ~100 nests at incubation stage tagged; nests visited on subsequent surveys until nest outcome determined	Ubiquitous, predominantly monitored on plateau along coast and inland	Bare scratched patches inside rock or log cavities or against tree roots or boulders	Phillips 1987
Aride	5	Jan 2011–Dec 2016	Continuous year-round weekly monitoring	Entire monitoring area searched, all new nests recorded and tagged; nests visited on subsequent surveys until nest outcome determined	Ubiquitous, only monitored on coastal plateau along coastal and inland areas of forest	Bare scratched patches inside rock or log cavities or against tree roots or boulders	Ramos et al. 2005
Cousine	~3.5	Jan 2007–Dec 2011	Continuous year-round weekly monitoring	90 fixed nest sites monitored continuously; all new nests tagged and visited on subsequent surveys until nest outcome determined	Ubiquitous, only monitored on accessible eastern side	Bare scratched patches inside rock or log cavities or against tree roots or boulders	Malan et al. 2009
Denis	20	Nov 2015–Sept 2016	Continuous year-round monitoring, every 2 weeks	Entire monitoring area searched, all new nests recorded and tagged; nests visited on subsequent surveys until nest outcome determined	Ubiquitous, more abundant in forest; monitored in all areas except coconut plantation	Mostly in tree cavities or on forked branches/trunks, some on ground amongst tree roots or boulders	n/a

the response variable. At the remaining two sites (Cousin and Denis) we only calculated annual breeding averages because monitoring efforts were seasonal (Cousin) or monitoring was of short duration (< 1 year; Denis). To quantify temporal trends, we included “date” as a continuous smooth variable. This date (year and month) allowed us to explore potential non-linear changes in breeding success over time.

We followed a similar approach when analyzing the nesting activity on Aldabra, Aride, and Cousine. Here, we used a set of GAMs with a Gaussian error structure in which the response variable was the number of new nests recorded per month at a particular site. As in the breeding success models, date was included as a smooth variable. Because seabird nesting patterns generally have a strong seasonal component (Diamond and Prýs-Jones 1986, Šúr et al. 2013), we included month as a continuous smooth variable to control for seasonal variation in nesting activity. All models were fitted using the MGCV package in R 3.2 (R Core Team 2013).

Model diagnostics indicated that the dimensions used for the smooth terms were adequate in all sites for both breeding success and nesting activity. On Aride and Cousine where breeding success was aggregated on a monthly basis and therefore possible to analyze residual plots, we found no patterns that would suggest a violation of model assumptions. The residuals of the nest activity models suggest that there might be small amounts of overdispersion and therefore we are cautious in interpreting the results.

RESULTS

Mean annual breeding success was 15% for Aldabra and 33–55% in the inner islands (Aride, Cousine, Denis, and Cousin; Table 3). The values from Denis are based on 11 months of monitoring and are therefore a monthly mean rather than annual mean. At all sites, nests were more likely to fail during egg than chick stage (Table 3). Breeding success did not show strong seasonality and remained constant over the years of monitoring at all sites except Aldabra, where a significant decline was observed between 2009 and 2016 ($df = 1$, $x^2 = 7.61$, $p < 0.05$; Fig. 2A, Table 4).

Nesting activity showed no significant variation between years at Aldabra (Table 4), whereas it increased on Cousine ($df = 1.9$, $x^2 = 29.2$, $p < 0.05$; Fig. 2A, Table 4) and strongly declined on Aride ($df = 1.6$, $x^2 = 35.2$, $p < 0.001$; Fig. 2B, Table 4). Aride’s nesting activity also showed significant seasonal variation ($df = 3.8$, $x^2 = 49.1$, $p < 0.001$; Fig. 3, Table 4) with clear peaks during September–October and April–June, and a low in December–January. Seasonality in nesting activity showed a similar, though weaker pattern on Cousine ($df = 3.1$, $x^2 = 12.7$, $p = 0.003$; Fig. 3, Table 4) and was virtually non-existent on Aldabra.

DISCUSSION

Breeding success and temporal trends

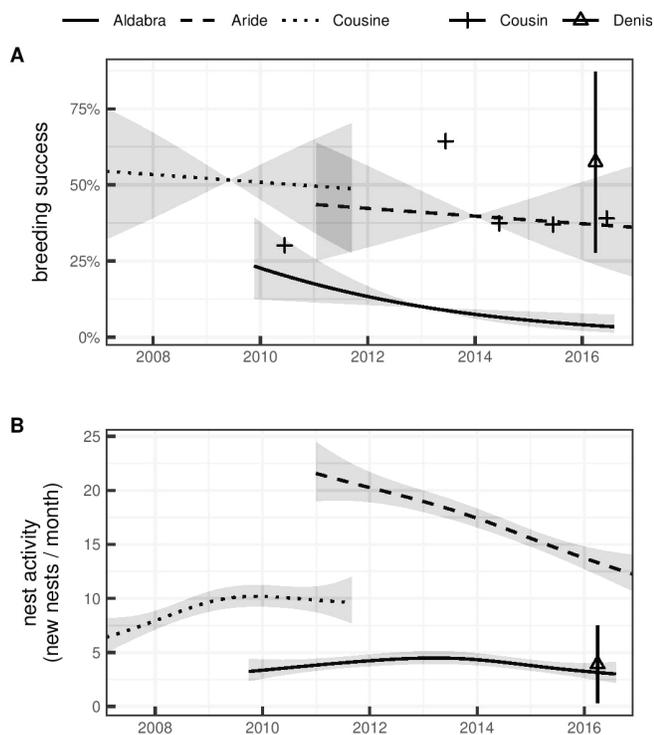
Phaethon lepturus have been monitored continuously on four islands across the Seychelles for up to 13 years. Monitoring duration varied by island and additional programs have been

Table 3. Success of *Phaethon lepturus* nests monitored annually at each study site: total and annual nests monitored, mean annual breeding success (% successful nests), and the proportion of nests that failed at egg or chick stage at each site.

Site	Monitoring duration	Total nests monitored	Total # nests successful	Annual mean # nests monitored (\pm StDev)	Annual mean # nests successful	Of failed nests, % failed at egg/chick stage	Annual mean breeding success (\pm SE)
Aldabra	Feb 2009–Nov 2016	308	47	42 (\pm 9.8)	6.4	66/34 (1.9:1)	15.2% (\pm 2.29)
Aride	2009–2016	1033	416	172 (\pm 35)	69	62/38 (1.6:1)	40.2% (\pm 3.8)
Cousin	1999, 2009–2016	880	318	97 (\pm 3)	35	64/36 (1.7:1)	34.6% (\pm 4.04)
Cousine	Jan 2007–Dec 2011	537	261	107 (\pm 25)	52.2	72/28 (2.6:1)	51.6% (\pm 2.9)
Denis [†]	Nov 2015–Sept 2016	39	21	(39)	(21)	11/7 (1.6:1)	53.8% (\pm 9.3)

[†]Denis Island nest monitoring was conducted for 11 months so the data shown (in parentheses) is the 11-month mean.

Fig. 2. Long-term trends in (A) probability of breeding success on five islands in Seychelles and (B) nesting activity of new *Phaethon lepturus*. Grey bands indicate the corresponding standard error of the model predictions. Vertical bars indicate standard deviation for Denis Island.

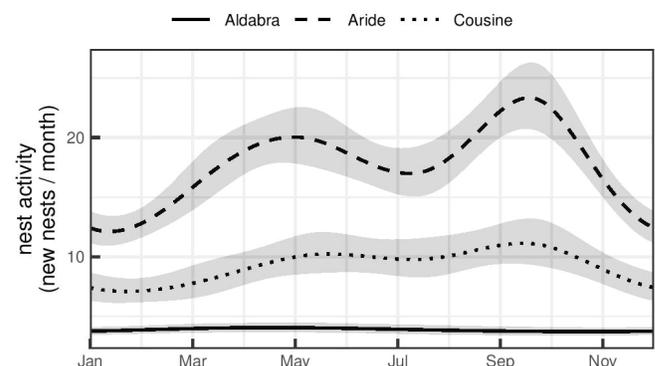


implemented on other islands more recently. We pooled these data to provide the first national assessment of breeding success and population trends for *P. lepturus* in the Seychelles. There was considerable variation in breeding success across sites (15–55%), with the Aldabra population showing the lowest annual breeding success. Breeding success of *P. lepturus* in the inner Seychelles (33–55%) is relatively high compared with records from elsewhere: 30% on Ascension Island (Stonehouse 1962) and 21% on Cayo Luis Peia, Puerto Rico (Schaffner 1991). The highest breeding success recorded globally is in Bermuda, where success across eight islands averaged 70.6%, and all sites are managed as nature reserves with active exclusion of mammalian predators (Madeiros

Table 4. Generalized additive model output for nesting rate and breeding success of *Phaethon lepturus* on three of the five islands included in this study. Term column: trend refers to change between years, and season refers to changes observed on an annual cycle (seasonality). Significant statistics are in bold. Note that the lack of year-round data collection on Cousin Island and the short duration of monitoring on Denis Island excluded them from this type of analysis.

Model	Island	Term	e.d.f.	X ²	p
Success	Aldabra	season	0.60	1.13	0.141
		trend	1.00	7.61	0.006
	Aride	season	0.00	0.00	0.467
		trend	1.00	0.14	0.706
Cousine	season	0.00	0.00	1.00	
	trend	1.00	0.06	0.802	
Nests	Aldabra	season	0.64	1.17	0.151
		trend	2.11	5.68	0.090
	Aride	season	3.78	49.1	<0.001
		trend	1.60	35.2	<0.001
	Cousine	season	3.09	12.7	0.003
		trend	1.99	9.25	0.014

Fig. 3. Seasonality in nesting activity of *Phaethon lepturus* on Aldabra, Aride, and Cousine. Shaded areas indicate the standard error of the model predictions.



2008). Aldabra, despite its high protection status, has among the lowest records of *P. lepturus* breeding success worldwide, similar to that at Fernando de Noronha archipelago, also a UNESCO

World Heritage site and protected area, in Brazil, the largest colony of *P. lepturus* in the South Atlantic (Leal et al. 2016). At Fernando de Noronha, between August 2011 and January 2012, only 14.3% of nests were successful, and predation at egg stage accounted for 50% of nest outcomes. The low success was attributed by the authors mainly to predation by native and non-native predators, although this was not confirmed in their study, in which only one chick was observed to be predated by a crab (Leal et al. 2016). The lowest breeding success for *P. lepturus* has been recorded at Europa Island, also in the WIO, at 6.9% for non-rat-controlled habitats (Ringler et al. 2015), and local eradication of rats on one of Europa's islets increased breeding success of Red-tailed Tropicbirds (*Phaethon rubricauda*) to 79%, i.e., 15 times higher than on the non-rat-controlled main island. Aldabra is the only site within this study that has invasive black rats (*Rattus rattus*) and many additional potential nest predators (Table 1) that may account for the low breeding success. This could be confirmed by setting camera traps at nest sites to observe nest failure events. The low breeding success recorded at Aldabra conforms to results from other studies where invasive predators are present and supports the claim that, in the case of White-tailed Tropicbirds, predation by invasive species, primarily rats (Russell and le Corre 2009, Sarmento et al. 2014), as well as native species (Phillips 1987, Schaffner 1991), is the main cause of nest failure in the Seychelles. We therefore conclude that for stable populations, it is likely that the differences observed in breeding success amongst the Seychelles islands are primarily due to the composition and abundance of local predators.

Breeding success trends in the inner Seychelles were stable over the monitoring period (Aride, Cousine, and Cousin), but Aldabra shows not only low annual breeding success but also a concerning decline over time. Earlier studies of *P. lepturus* at Aldabra reported breeding success to be much higher 30–35 years ago in the same area (47.5% in 1975, $n = 40$; [Diamond 1975]; 46% in 1980, $n = 39$ [Prys-Jones and Peet 1980]). For Aldabra, all the known and potential predators listed (Table 1), except rats and Pied Crows (*Corvus albus*), are also monitored and none have shown increasing trends (SIF unpublished data). An increase in drought periods has been reported for Aldabra (Haverkamp et al. 2017); this may influence nest site conditions via reduced shading from vegetation, but is unlikely to have directly impacted *P. lepturus* breeding success on account of their choice of limestone crevices as sheltered nest sites rather than vegetation cover, which is preferred by the sympatric *P. rubricauda*. Sheltered nests like limestone crevices have more stable ambient temperatures (Hart et al. 2016), and site selection offsets difficulties imposed by the weather. However, the low-lying islets on which they nest may be increasingly impacted by tidal inundation because of increased storm surge and eventually sea-level rise (Rabbani et al. 2010). For Aldabra, we conclude that the monitoring program was sufficient to detect a decline in breeding success and, in combination with other monitoring, rules out several potential drivers of the decline. Further investigation into nest site competition, predation, and in particular food availability, should be prioritized to understand the drivers of breeding success decline on Aldabra.

The stable breeding success trends detected in the inner Seychelles islands from this study were reinforced when comparing breeding success records from previous studies at those sites. For example,

we recorded an annual mean of 51.6% nesting success on Cousine compared to 25% during 2003–2005 (Malan et al. 2009), showing a large increase, possibly as a result of forest habitat rehabilitation. Cousin averaged 33% breeding success in this study, compared to 36% in 1981–1983 (Phillips 1987), and Aride averaged 40.2% here, compared to 21–37% in 1989–2002 (Ramos et al. 2005).

Trends in nest activity

At sites where the number of nests monitored was delineated by a set area (or number of cavities) that remained constant across monitoring years, we assessed trends in nesting activity over time. Nesting activity remained stable at Aldabra (2009–2016), showed a slight upwards trend at Cousine (2007–2011), and a continuous negative trend on Aride (2011–2016). A decline on Aride was previously reported; the nesting population of *P. lepturus* suffered an apparent decline of 60% between 1989 and 1998 (Bowler et al. 2006). Our results, along with unpublished census data (Island Conservation Society Seychelles), show that this decrease has continued, with a rapid decline of 65% in nesting activity between 2011 and 2016.

The islands of Aride, Cousin, and Cousine are less than 15 km apart, and therefore their *P. lepturus* populations are likely to be affected by similar external factors, such as climate and food availability. The differences in monitoring periods used in this study between Cousine and Aride make it difficult to determine, without additional data, whether the decline in nesting activity on Aride is mirrored in these nearby populations. We recorded a slight upward trend in nesting activity at Cousine but this was during the four years prior to the data analyzed for Aride. One would expect, if the population decline—via adult mortality and/or lack of recruitment to population—is caused by local factors on Aride itself, such as from nest-site predation, e.g., by skinks, fodies, or mice, or by poor food provisioning for chicks, e.g., frigatebird kleptoparasitism, that these would also influence breeding success. Previous studies at Aride have shown that breeding success was correlated with the El Niño Multivariate Index, i.e., El Niño events resulted in lower fledging success (Ramos et al. 2005), and there was little evidence that productivity, i.e., breeding success, was influenced by local factors such as hard tick infestations or intra- and inter-specific competition. This coincides with our findings; breeding success on Aride remains relatively high and stable but this is evidently not enough to support population stability. Adult survival is considered the vital rate to which population dynamics for long-lived species like *P. lepturus* are most sensitive (Souchay et al. 2013). The decline in nesting activity previously recorded was attributed to annual adult survival, which was suggested not to be linked to inter-annual variability in oceanographic conditions, but potentially influenced by fruiting events of the coastal shrub, *Pisonia grandis*, which, overall, accounted for 23.2% of adult mortality (*P. grandis* produces sticky seeds that can accumulate on and eventually kill seabirds; Catry et al. 2009). Based on adult survival rates, the probability of extinction of this population was predicted to be 99% in 170 years (Catry et al. 2009). Active management was proposed and carried out by maintaining some areas free of *P. grandis*.

However, *Pisonia grandis* is native to the Seychelles and thrives in acidic, guano-enriched soils. It is common across Aride, Cousin, and Cousine, causing mortality in all seabird species that nest in

its vicinity. Cousin, for example, has 69% *P. grandis* coverage (Hill 2002) and likewise suffers some *P. grandis*-induced mortality of *P. lepturus* adults. Management of *P. grandis* is fairly similar across these sites and includes raking away the seeds from certain areas. On Aride, a 1170-m² coastal strip was cleared of *P. grandis* between 2009 and 2011 and planted with other native trees. This management action appears to have had no positive impact on the nesting activity rate for Aride. It is therefore reasonable to conclude that, if *P. grandis* was the major cause of rapid adult mortality and subsequent reduction in nesting activity on Aride, it would have had similar effects on Cousin and Cousine, although little data exists to compare *P. grandis* extent and impact across these three sites. It is also unclear whether *P. grandis* affects fledged chicks (after they have left the nest but before they have left the island), which would result in lower population recruitment but not be detected by nesting success monitoring. Without additional evidence of site-driven mortality at Aride and data on *P. lepturus* population status on Cousine and Cousin for recent years, a precautionary approach is prudent. The decline in nesting activity on Aride is likely to be an indication of the health of the broader environment and may be similarly affecting the populations on Cousine and Cousin. To conclude, it remains unclear why the Aride breeding population is in decline; however, comparing data from multiple sites enables us to rule out several potential causes. Further collaborative research across the same time period is required to compare populations at Aride, Cousine, and Cousin to disentangle the factors influencing adult mortality and identify the driver of the declines on Aride, and possibly on other islands. Specifically, additional research into post-fledging survival, e.g., via mark and recapture and recording numbers of adults/fledglings affected by *P. grandis*, and comparisons of levels of *P. grandis*-induced mortality across these sites would be valuable, as well as compiling long-term census data.

Nesting rate seasonality

Marked seasonality in seabird nesting is often related to prey availability at certain times of year (Le Corre 2001, Jaeger et al. 2010). However, we found no nesting seasonality for *P. lepturus* on Aldabra, concurring with previous studies (Diamond 1975, Prys-Jones and Peet 1980), whereas inner island populations show varying levels of seasonality. Breeding seasonality differences between the inner Seychelles islands and Aldabra have been recorded previously for tern species (Diamond and Prÿs-Jones 1986); differences were associated with seasonal latitudinal movement of the divergence zone between the South Equatorial Current and the Equatorial Counter-Current, acting via correlated latitudinal shifts of prey species and surface-dwelling tuna abundance. The lack of seasonality at Aldabra suggests there may be an additional or alternative driver to nesting seasonality in the inner granitic islands. One potential factor is the level of shade at nest sites. Phillips (1987) reported that *P. lepturus* nesting against tree roots were sometimes exposed to direct sunlight, causing noticeable heat stress. Birds at these sites may have developed nesting seasonality to counteract the effects of this, avoiding heat stress during the dry season when shade cover is lowest. Our data supports this on Cousine and Aride, with peak nesting activity in October, which coincides with the start of the rainy season. If shade cover is indeed driving seasonality in nesting *P. lepturus*, the lack of nesting seasonality on Aldabra is likely because the species nests almost exclusively in well-sheltered

limestone crevices, rather than the forest cover areas that dominate nesting sites on Cousine and Aride. In contrast, the *Phaethon rubricauda*, which nest in the same locations on Aldabra but in vegetation rather than limestone crevices, do exhibit pronounced nesting seasonality with peaks coinciding with the rainy season (SIF unpublished data). Whether the breeding seasonality differences between these two sympatric species at Aldabra is on account of nest site choice as suggested by Prys-Jones and Peet (1980) or driven by seasonal differences in prey availability as a result of different target prey is unclear. Another possibility is that *P. lepturus* is forced to breed year-round because the larger more dominant *P. rubricauda* is monopolizing the best breeding window. Data from other sites concur with *P. lepturus* breeding year-round (Stonehouse 1962, Le Corre 2001), but seasonal peaks vary from site to site (e.g., Raine et al. 2020).

National conservation status and monitoring

The five *P. lepturus* breeding sites in this study demonstrate the high level of commitment and resources allocated to monitoring this species in the Seychelles. Despite differences in methods and effort, the individual long-term monitoring programs fulfil the aim of determining temporal trends in breeding success at each site. Furthermore, the continuous year-round monitoring carried out at Aride, Aldabra, and Cousine, and recently begun on Denis Island, provide data on breeding seasonality as well as a continuous measure of nesting activity over time within the surveyed area. Although there was no overall consensus in breeding success trends, on account of the decline at Aldabra, the inner Seychelles populations show overall stable breeding success. However, population trends based on nesting activity over time were difficult to interpret with the current data because of the differences in monitoring methods and time frame across the sites. Although annual (some bi-annual) population censuses are conducted at Aride, Cousin, and Cousine, as well as other islands, these datasets have not yet been compiled and analyzed collectively. The information from these census trends would enable more accurate assessment of the current population status and trends of *P. lepturus* in the Seychelles, especially whether the nesting activity decline on Aride is seen on neighboring islands. Additionally, capture-mark-recapture methods should be added where possible because of the species' high fidelity to nesting areas (Leal et al. 2016) to provide information on adult survival.

This research provides information that can feed directly back into management decisions, such as where to focus research efforts and conservation resources. The causes of the declines in *P. lepturus* breeding population at Aride and breeding success at Aldabra should clearly be priorities for future research. Other actions that support tropicbird survival and breeding success, such as rat and cat eradications, should be prioritized.

We also highlight an important consideration when using species monitoring as an indicator of broader environmental changes; the effects of local drivers of breeding success and activity should, where possible, be distinguished from external factors such as climatic changes impacting prey availability. This could be achieved for *P. lepturus* by measuring local impacts such as predation levels, e.g., by setting up a camera trapping study to identify causes of nest failure and/or monitoring predator species trends, and habitat changes, e.g., by including a measure of nest site quality/type such as exposure level. Additional studies can be costly, but when set up collaboratively they are often more feasible;

for example, cameras used to monitor nests can be passed on to other sites, bringing overall costs down and being more attractive for potential funders than a one-site project.

Based on the challenges we faced in compiling and analyzing these data, we can make several specific *P. lepturus* monitoring recommendations to managers. First, we strongly recommend survey effort to be delineated not by a fixed number of nesting attempts or nesting sites but by a set area that is representative of the main island habitat, and as large as is feasible to ensure monitoring effort consistency. Area-delineated monitoring is the most widely applied method in the Seychelles and enables a broader scope for analysis, resulting in a greater understanding of the changes in nest activity and nesting success over time. Second, maintaining continual year-round monitoring is preferential to snap-shot (seasonal) monitoring to ensure direct comparability across sites, to understand seasonal nuances, and to detect anomalies or changes. Finally, data storage/format varied greatly across sites and required substantial cleaning to enable analysis, therefore we highly recommend that analysis-friendly data spreadsheets or databases are adopted across sites, coupled with the development of an analysis script to facilitate regular on-site data visualization and analysis.

To build upon existing knowledge, maximize the investment of effort and resources, and improve the value of data for *P. lepturus* throughout the Seychelles and across the WIO region, we propose the adoption of a nation-wide monitoring plan with consideration for the spectrum of resources available across sites; regular reviewing and analysis of datasets to detect changes, implement actions, and monitor the effects of those actions; clear monitoring questions (e.g., What is the population status of *P. lepturus*? Does the implementation of this intervention have a positive impact on nesting success? What are the main causes of nest failure?) and objectives (e.g., detect trends in nesting success/activity; identify the main causes of nest failure; increase breeding success by reducing nest predation by rats); and a strong understanding of the factors influencing the ecosystem or population (Lindenmayer and Likens 2018), for example, climate, food availability, disturbance, and habitat changes. Although this study focuses on five sites, *P. lepturus* nests occur on many other Seychelles islands. Utilizing existing practitioner networks, such as the Seychelles and Indian Ocean Seabird Groups (Nature Seychelles 2021) to extend monitoring coverage to other sites and develop comparable monitoring programs will greatly strengthen the collective efforts of site managers to understand and protect this and other seabird species within this seabird hotspot.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/1858>

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