**Status and trends of White-tailed Tropicbirds *Phaethon lepturus* in the Seychelles.**

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**Abstract**

The successful design and implementation of monitoring programmes is an important tool in the effective management of biodiversity, especially in developing nations with limited resources and serious threats. Here we use the monitoring of white-tailed tropicbirds (*Phaethon lepturus*) in the Seychelles to present the first nation-wide assessment of the status and trends of breeding success at each of the sites. At Aldabra Atoll on average 15.2% of nests were successful compared with 33% on Cousin Island, 40.2% on Aride Island, 51.6% on Cousine Island and 55% on Denis Island. In addition, at Aldabra there was a negative temporal trend in breeding success. Nest density a continuous negative trend on Aride and an increase on Cousine. The strengths and weaknesses of the current programmes are discussed and recommendations are made to improve the effectiveness of these conservation efforts and streamline the monitoring programmes for *P. lepturus* across the Seychelles and elsewhere.

Keywords: Seychelles, Tropicbirds, Management, Ecology, Breeding

**Introduction**

Seabirds, as long-lived top marine predators, possess several attributes that make them useful as environmental indicators (Einoder, 2009), as they provide both a measure of health of the species as well as an indication of overall state of the surrounding ecosystem (Piatt *et al.*, 2007; Parsons *et al.*, 2008). The Seychelles supports the greatest abundance of tropical seabirds in the Indian Ocean, estimated to be ca 3.4 million pairs (Le Corre *et al.*, 2012). It is the main breeding ground for white-tailed tropicbirds (*Phaethon lepturus)*, with anestimated 6500 breeding pairs (56% of the Western Indian Ocean breeding population and 13% of the global population (est. ca 50,000) (del Hoyo, J., Elliot, A. and Sargatal, 1992; Le Corre *et al.*, 2012). This species is monitored on a number of Seychelles Islands primarily because it is one of the most ubiquitous seabird species, easily accessible to monitor; and secondly because it is considered an important indicator species, whose status reflects or predicts the condition(s) of the broader marine environment.

*P. lepturus* is a pelagic seabird that undertakes long foraging trips and feeds mainly on surface-dwelling prey, such as flying fish and squid (Schreiber and Clapp, 1987; Teresa Catry *et al.*, 2009). Their specific foraging strategy limits their rate of provisioning when these food sources are scarce (Schaffner, 1990) and therefore directly relates to chick rearing success (breeding success). Additionally, *P. lepturus* is ground nesting (Burger and Lawrence, 2000) and therefore breeding success is highly susceptible to habitat integrity and environmental perturbations such as climatic variations (Ancona *et al.*, 2011) and invasive alien species (Russel and Le Corre, 2009).

﻿Seabirds are more threatened than other comparable groups of birds and their status has deteriorated faster over recent decades (Croxall *et al.*, 2012). The Western Indian Ocean (WIO) region has recently been prioritized for the conservation of global marine biodiversity in the face of climate change (Ramírez *et al.*, 2017). With 115 islands stretching across an exclusive economic zone of 1.4 million km2,the Seychelles forms a substantial part of the WIO region but is a challenging location for coordinated monitoring efforts. Biodiversity monitoring programmes are widely used across the Seychelles and can form an integral role in informing conservation management. Determining trends in breeding success of such a key seabird species at a national and regional scale is an essential first step to inform effective management of this species. To use *P.lepturus* as an indicator of broader scale environmental changes, the factors influencing breeding success must also be distinguished.

Although P. lepturus is listed as ‘Least Concern’ on the IUCN red list, the species is suspected to be in decline owing to predation by invasive species at nesting sites (IUCN Red List). Seabird populations in the Seychelles have been threatened by habitat loss, alien predators, and over-utilisation as a food source; with expanding fishery activity and climate change also posing threats (Bristol, 2007). However, despite the monitoring programmes in place across the Seychelles, the current trend status of *P. lepturus* is unknown. Here, for the first time, we compile multi-site monitoring data of P. lepturus in the Seychelles to: (1) identify the level of and trends in breeding success; (2) assess trends in nesting rate; and (3) identify trends in breeding seasonality. We use these results to determine the population status of *P. lepturus* in the Seychelles and make recommendations to improve monitoring effectiveness.

**Material and methods**

**Study sites and species**

We analysed data from five islands in the Seychelles: Aldabra Atoll, Aride Island, Cousin Island, Cousine Island, and Denis Island (Figure 1), which include the four main monitored breeding sites in Seychelles for *P. lepturus* (Aldabra, Cousin, Cousine, Aride) as well as Denis island, where little is 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 other Seychelles islands also have *P. lepturus* breeding populations (e.g. Fregate, North, Bird) most are not monitored.

All the monitoring programmes were developed independently, although they were based on locally developed guidelines (Burger and Lawrence, 2000) and they varied in size and type of area covered and methods (Table 2).

﻿ *P. lepturus* are ground nesting with a habitat preference of bare scratched patches inside rock or log cavities or next to vertical structures (Prys‐Jones and Peet, 1980; Phillips, 1987a). An in-depth study of breeding biology of *P.Lepturus* on Cousin Island (Phillips, 1987a) determined egg incubation to last 40–41 days, with a mean incubation shift length by parents of 6.6 days. Fledging periods varied between 67 and 89 days (mean 76.5 days). ﻿The mean age at which they were first left alone at night was 11.8 days (range 6-13 days) and as chicks grew older, visits by parents became rapidly shorter until, by about Day 25, parents were mostly arriving, feeding the chick and leaving again in less than ten minutes, very rarely staying as long as half an hour. ﻿A high proportion of total egg losses seems likely to have been due to desertions by adults which had been stressed during incubation, with failures becoming increasingly frequent towards hatching, after repeated intervals of fasting and (at many sites) exposure to the sun.

**Monitoring**

To evaluate the status and trends of *P. lepturus* we focus on two particular metrics: the breeding success and the number of nesting attempts (or nesting rate). A nesting *P. lepturus* was defined as an adult incubating an egg or brooding a chick. First, we define breeding success the percentage of successful nests at each site. We determined whether the nest was successful or not, by comparing the nest stage of two subsequent visits. If a nesting attempt was observed to have been occupied by an egg or a partially feathered chick and was subsequently observed empty or with signs of predation/death, it was recorded as unsuccessful. If the nest was unsuccessful we also recorded whether failure occurred at the egg or chick stage. Conversely, when a nest observed to be occupied by a fully feathered chick and found empty in a subsequent visit without signs of predation/death it was recorded as successful as we could assume the chick had fledged.

Second, to estimate the nesting rate, sites were visited (and new nests searched for) every 2–14 days, depending on the site (see Table 2 for details). We calculated nesting rate for the three sites in which all nests were monitored within a specific area (Aride, Aldabra, and Cousine). Specifically, we define nesting rate as the number of nests encountered per month. This nesting rate is particularly informative as it can, in turn, be used as a proxy for breeding population size (ADD REF). All nesting attempts were characterised by the date of the first record. To avoid introducing potential bias on our monitoring metrics, new nesting attempts were only included in the dataset if they were first found at an incubation stage. Nevertheless, this was relatively rare and in all sites, more than 95% of the nest were first encountered before reaching the chick stage.

**Data analysis**

To analyse breeding success, we treated it as a binomial variable (successful nest = 1; unsuccessful = 0) and calculated the mean breeding success as the percentage of successful nesting attempts at each site. We also calculated the proportion of unsuccessful nesting attempts that failed during the egg stage compared to those that failed during the chick stage. In three sites () we were also able to investigate long term and seasonal trendsTo do that, we used a set of Generalised Additive Models (GAM) with a binomial error structure and breeding success as the response variable. In the remaining two sites () we were only able to calculate annual averages of breeding visits were only performed seasonally the .To quantify the temporal trends we included ‘date’ as a continuous smooth variable. This date (year and month), corresponded to the time and allowed us to explore potential non-linear increases or declines in breeding success over the years. , and other potential sources of variation among the areas surveyed, *formally*

We followed a similar approach for the nesting rate in 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 nest attempts recorded per month in a particular site. As in the breeding success models, date was included as a smooth variable. Because nesting patterns have a strong seasonal component in multiple seabird species in Seychelles (REFS), we also included the month of the year as a continuous smooth in order to control for possible seasonal variation in nesting attemps.

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**Results**

Mean breeding success was 15% for Aldabra Atoll and ranged between 33 and 55% in the granitic islands (Aride, Cousine, Denis, and Cousin; Table 3). The values are not directly comparable as success rates in Denis were calculated in a monthly basis. In all islands, nesting attempts were more likely to fail during the egg than during the chick stage. Breeding success remained constant over the years of monitoring on all sites except Aldabra, where a significant decline was observed (df=1, x2=7.61, p=<0.05; Fig 2A; Table 4).

Nesting rates showed no significant variation over the years at Aldabra, while they increased on Cousine (df=1.9, x2=29.2, p=<0.05; Fig 2A; Table 4) and strongly declined on Aride (df=1.6, x2=35.2, p=<0.001; Fig 2B; Table 4). Aride’s nesting rate also showed significant variation over the year (df= 3.8, x2=49.1, p=<0.001; Fig 3; Table 4) with clear peaks during Sept–Oct and Apr–June and a low in Dec–Jan. Seasonality in nest rate was present though weaker on Cousine (df= 3.1, x2=12.7, p=0.003; Fig 3; Table 4) and virtually nonexistent on Aldabra.

**Discussion**

**Breeding success/Breeding success temporal trends**

*P. lepturus* have been monitored at several sites across Seychelles for a number of years, we provide the first compilation of monitoring data to assess national breeding success and population trend status of *P. lepturus* in Seychelles. The results show variation in average breeding success rates across sites but Aldabra shows a worryingly low annual breeding success (15%) relative to the other sites. The granitic Seychelles sites have breeding success averages that aligned with records from elsewhere; 30% in Ascension Island (Stonehouse, 1962), 21% Cayo Luis Peia, Puerto Rico (Schaffner, 1991). The highest breeding success recorded globally is across eight islands in Bermuda where success averaged 70.6% and all sites are managed as nature reserves with active exclusion of mammal predators including rats, cats and dogs (Madeiros, 2008). Aldabra infact has one of the lowest records of breeding success for *P.lepturus* worldwide, though similar to that found at Fernando de Noronha archipelago, in Brazil – the largest colony of *P. lepturus* in the South Atlantic. Here 14.3% of nesting attempts were successful and predation at egg stage accounted for 50% of the attempts with the low success being attributed mainly to predation by crabs and nest exposure (Leal *et al.*, 2016). The lowest fledging success for *P.Lepturus* has been recorded at Europa Island at 6.9% (also SW Indian Ocean) for non-rat controlled habitats (Ringler and Le Corre, 2015). Aldabra is the only site within this study that has invasive rats present and a different cast of potential nest predators (Coconut crabs, rats, grey heron, drongo) that may account for the lower overall breeding success, though the only way to determine the cause of breeding failure would to be set camera traps at nest sites. The lower breeding success conforms to results obtained from other studies where invasive predators are present and supports the claim that in the case of Tropicbirds, predation by invasive species (mainly rats – Russel & Le Corre, 2009; Sarmento, Brito, Ladle, da Leal, & Efe, 2014) and native species (Phillips, 1987b; Schaffner, 1991) is likely the main cause of mortality during breeding. It is reasonable to conclude that for stable populations, the differences observed in breeding success amongst sites are mostly due to the level and combination of predators at site level.

Breeding success in the granitic Seychelles has been stable over the monitoring period (Aride, Cousine and Cousin), but again Aldabra shows not only worryingly low annual breeding success but also a decline over time. This low breeding success does not account for why breeding success has been decreasing on Aldabra over this study period. This decline is reinforced by the earlier studies of *P.lepturus* at Aldabra, which found breeding success to be much higher 30–35 years ago (47.5% recorded by Diamond in 1975; and 46% recorded by Prys-Jones in 1980). Of all the known and potential predators listed for Aldabra, all except rats are also monitored and none have shown increasing trends (SIF unpublished data). An increase in drought periods reported for Aldabra (Haverkamp *et al.*, 2017) is unlikely to have directly impacted *P.Lepturus* breeding success due to their choice of limestone crevices as sheltered nest sites rather than vegetation cover. Sheltered nests have more stable ambient temperatures (Hart, Downs and Brown, 2016) and site selection offsets difficulties imposed by the weather. In conclusion for Aldabra; this monitoring programme was sufficient to detect a trend and to some extent rule out several factors that may have caused such a trend but overall it was not possible to distinguish the drivers of a decline in breeding success. Further investigation into both internal factors such as nest site competition and predation as well as external factors such as food availability are required.

The stable trends detected at the granitic sites within this study is reinforced by comparisons of breeding success from earlier (individual) studies; on Cousine 51.6% nesting success was recorded compared to 25% by Malan, Hagens, & Hagens (2009); Cousin averaged 33% in this study compared to the 36% recorded by Phillips in 1987, Aride averaging 40.2% compared to the 21-37% recorded by Ramos et al. in 2005.

**Trends in nest density**

At the sites where the number of nests monitored was defined by a set we were also able to assess nesting density over time. Nest density remained stable at Aldabra, showed a slight upwards trend at Cousine but we observed a continuous negative trend on Aride. This decline on Aride was previously reported; Bowler et al. (2002) showed that the nesting population of *P. lepturus* suffered an apparent decline of 60% between 1989 and 1998. Our results and unpublished census data also support the continuation of this decline. There are two key factors that suggest population decline on Aride is caused by adult survival at the site; firstly that Aride continues to maintain relatively high and stable breeding success and secondly, that neighbouring island Cousin maintains a stable population trend (1987 to 2014, unpublished census data) and Cousine island shows an increasing population trend (this study and 2003 to 2017 unpublished census data). For these islands that are within close geographical proximity (<15km) it is reasonable to expect *P. lepturus* to be under similar influence of external factors (climatic variations and food availability) indicating that the Aride breeding population decline is not linked with external factors.

Additional work by Ramos et al., 2005 found that fledging success on Aride was significantly correlated with the El Niño Multivariate Index (i.e El Niño resulted in lower fledging success) but there was little evidence that productivity was influenced by local factors (hard tick infestations and intra and inter-specific competition) in general. Further to this, T. Catry et al., (2009) determined that annual adult survival could not be linked to inter-annual variability in oceanographic conditions, but may be more influenced by *Pisonia grandis* fruiting events, which, overall, accounted for 23.2% of the adult mortality (*P.grandis* produces sticky seeds which trap and kill seabirds). Based on survival rates they predicted that the probability of extinction of this population would be 99% in 170 years and suggested some active management by maintaining some open areas both at canopy and ground level. *P. grandis* is native to Seychelles and thrives in acidic guano enriched soils. It is common across Aride, Cousin and Cousine, causing mortality across all seabird species that nest in its vicinity. Cousin for example has 69% *P. grandis* coverage (Hill, 2002), and despite *P. grandis* induced adult mortality of *P.lepturus,* no decline in population has yet been recorded. One possible interpretation is that, although *P. grandis* is native to the archipelago, its fast post‐restoration establishment (Aride, Cousin and Cousine were all once coconut plantations) has led to possibly higher density than pre-plantation levels, because slower growing climax vegetation is yet to mature, though this doesn’t explain the differences observed between Aride and Cousin/Cousine. However, internal management of *P.grandis* does vary across these sites; Cousine island actively raking *P.grandis* seeds during fruiting events and Cousin raking all pathways regularly. On Aride the pathways are also raked weekly but not actively targeting *P. grandis* like on Cousine. A 1170m2 costal path area was cleared on Aride between 2009 and 2011 and planted with native trees. The 2017 vegetation management plan set up by the Island Conservation Society (Aride management) is planning to further clear 1.5 Ha of *P. grandis* in different areas to assess the seabird entanglement issue. If during the first year the areas are successfully cleared and maintained, the clearing effort can be increased in targeted areas for *P. lepturus*. Continuous monitoring of *P. lepturus* will continue in order to assess the beneficial effect of *P. grandis* removal on the breeding population. Raking *P. grandis* seeds in the monitoring area (5 Ha of plateau) should also be considered and included in the vegetation management plan. To conclude; it still remains unclear why the Aride breeding population is in decline, however comparing data from multiple sites has allowed us to make better sense of the findings. Further investigation is required into site specific internal factors influencing adult mortality.

**Nesting rate seasonality**

Marked seasonality in seabird nesting is often related to favorable prey availability at certain times of year (Le Corre, 2001; Jaeger *et al.*, 2010). However, our study shows no nesting seasonality apparent for P.lepturus on Aldabra, concurring with previous studies (Diamond, 1975; Prys‐Jones and Peet, 1980) whereas the granitic sites show varying levels of seasonality. Breeding seasonality differences between the inner granitic Seychelles islands and Aldabra have been recorded previously for Tern species (Diamond and Prŷs‐Jones, 1986) being 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 game-fish abundance. The lack of seasonality recorded at Aldabra suggests there may be an alternative driver to nesting seasonality in the inner granitic islands though. One possible factor which could influence seasonality in breeding among sites is the level in which shade from vegetation influences nest sites. Phillips (1980) reported that *P.Lepturus* nesting against tree roots where sometimes exposed to direct sunlight causing noticeable heat stress. Birds at these sites may have developed some seasonality to counteract the effects of this, minimizing the chances of heat stress during the dry season when shade cover is lowest. The seasonality found in this study on Cousine and Aride shows a peak in nesting rate in October which directly coincides with the end of the dry season. In this case the lack of seasonality on Aldabra is likely due to P.lepturus nesting almost exclusively in well sheltered limestone crevices, though this is not investigated further in this study.

**National conservation status**

The five monitoring programmes for P. lepturus used in this study demonstrate the high level of commitment and resources allocated to this species within the Seychelles. We have demonstrated that the individual monitoring programmes, with monitoring over multiple years, fulfil the aim of establishing temporal trends in breeding success despite differences in methods and effort. The continuous year-round monitoring carried out at Aride, Aldabra and Cousine provided information on the breeding seasonality as well as a continuous measure of nesting rate over time, within the surveyed area. The benefit of which, is that in essence you can ‘kill two birds with one stone’ establishing the status of the breeding population and measuring the breeding success of that population within one survey effort. There was no overall consensus in breeding success trends due to the decline seen at Aldabra, though overall the inner granitic Seychelles population have stable breeding success. Population trends are also at odds with stability in nesting rate observed except at Aride. Further data comparisons of long-term census data (currently unpublished) would be beneficial in cementing the current national population status.

This study has provided us with information that can feed directly back into management decisions on where to focus research efforts and conservation resources. It is clear that we now need to investigate the causes of decline in breeding population of P. lepturus at Aride and the decline in breeding success at Aldabra.

Our study also highlights an important consideration when linking the monitoring of a species as an indicator of broader environmental changes; that it is important to be able to disentangle the effects of local impacts on breeding success and nesting rate and those external factors such as climatic changes impacting prey availability. This could be achieved in the case of P.lepturus by having a measure of local impacts such as predation levels and habitat changes.

To build upon current knowledge and efforts and improve the value of data for *P. lepturus* throughout the Seychelles werecommend that anationwide monitoring plan should be implemented with consideration for the spectrum of resources available at each site. The major characteristics of effective monitoring programs typically include carefully posed questions and objectives and a conceptual model of the ecosystem or population (Lindenmayer and Likens, 2018).

Conclusions

The Western Indian Ocean has recently been identified as a key area to prioritize for the conservation of global marine biodiversity in the face of climate change (Ramírez *et al.*, 2017). The Seychelles Archipelago supports the greatest abundance of seabirds in the tropical Indian Ocean (Le Corre *et al.*, 2012). Regional seabird population success and trend data is not readily available despite data being collected for many years at several locations. A greater effort must be made to streamline regional data and utilise the results to steer management practices and channel research resources towards the most critical areas. This study highlights a decline in breeding success at Aldabra atoll and a decline in nest abundance at Aride, both require further understanding and therefore management should focus research efforts and conservation resources at establishing likely causes of these declines. This will be most effective by establishing an ecosystem approach to monitoring and implementing adaptive management across the region.

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

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Site** | **Protection status** | **Land area (ha)** | **Geomor-phology** | **Location** | **Max height asl (m)** | **Management** | **Population estimates** | **Nest predators** | **Other disruptive\* species** |
| Aldabra Atoll | UNESCO World Heritage site (1982); IUCN class 1A Special Reserve (1975) | 15,254 | Coralline | 9.2255**°**S, 46.1310**°**E | 8 | Public Trust | 2000 pairs 1 | Black rat*,* grey heron, Aldabra drongo4, coconut crab1, pied crow | Red-tailed tropicbirds4 |
| Aride | Special Reserve (1979) | 74 | Granitic | 4.2000**°**S, 55.6667**°**E | 134 | NGO | 1446 pairs 2 | Seychelles skink, Wright’s skink, Seychelles fody5 | *Pisonia grandis* 6 (bird-catcher tree), ticks |
| Cousin | Nature Reserve (1969)  IUCN class 1A Special Reserve (1975) | 27 | Granitic | 4.3314**°**S, 55.6631**°**E | 69 | NGO | 2110 pairs 3 | Seychelles skink, Wright’s skink, Seychelles fody, ghost crabs7 | *Pisonia grandis*4 |
| Cousine | n/a | 26 | Granitic | 4.3500**°**S, 55.6333**°**E | 72 | Private | 450–850 pairs9 | Seychelles skink, Wright’s skink, Seychelles fody, ghost crabs 8, Seychelles magpie-robin5. | *Pisonia grandis*,giant tortoise5 |
| Denis | n/a | 140 | Sand cay | 3.8000**°**S, 55.6667**°**E | <4 | Private | ca. 40 pairs (this study) | None perceived, cats removed in 2000, rats removed in 2002. |  |
| 1Diamond 1971, 2Burger and Lawrence 2000, 3Bowler et al. 2002, 4Unpublished camera trap images, 5Licia Calabrese (pers.obs), 6(T. Catry *et al.*, 2009) 7Phillips 1987, 8Malan et al. 2010, 9Skerrett et al. 2001; \*Observed to or thought to hinder *P. lepturus* breeding success by increasing nest desertion or causing parent mortality. | | | | | | | | | |

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

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Site** | **Area monitored (ha)** | **Monitoring period** | **Frequency of monitoring** | **Methods** | **Nest distribution** | **Nest description and habitat type** | **Last assessment** |
| Aldabra Atoll | ?? | 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 lagoon islets and an outcrop of Picard Island. | Limestone cavities or cavities in dense vegetation on small islets and coastal outcrops. | Prys-Jones et al. 1980 |
| Cousin Island | 20 | 2005–2007, 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. Ca. 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 Island | 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 Island | James?? | 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, 2010 |
| Denis Island | 65 | 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 |

**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. \*Denis island nest monitoring was conducted for less than a year so the figures shown (in parentheses) are monthly means.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Site** | **Total nests monitored** | **Annual mean # nests monitored** | **Annual mean # nests successful** | **(%) of failed nests failed at egg/chick stage** | **Annual mean breeding success (± SE)** |
| Aldabra Atoll | 333 | 42 | 6.4 | 66 / 34 (1.9:1) | 15.2% (± 2.29) |
| Aride | 1033 | 172 | 69 | 62/38 (1.6:1) | 40.2% (± 3.8) |
| Cousin | 854 | 93 | 37 | 64/36 (1.7:1) | 33% (± 4.04) |
| Cousine | 537 | 107 | 52.2 | 72/28 (2.6:1) | 51.6% (± 2.9) |
| Denis\* | 39 | (39) | (55) | 61/39 (1.6:1) | (55% (± 9.3)) |

**Table 4.** Generalised additive model output for nesting rate and breeding success of *P. lepturus* on five islands in Seychelles. Trend refers to temporal change and season refers to changes observed on an annual cycle (seasonality).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **Island** | **Term** | **e.d.f.** | **χ2** | ***p*** |
| Success | Aldabra | trend | 1.00 | 7.61 | 0.006 |
| Aride | trend | 1.00 | 0.14 | 0.706 |
| Cousine | 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 |

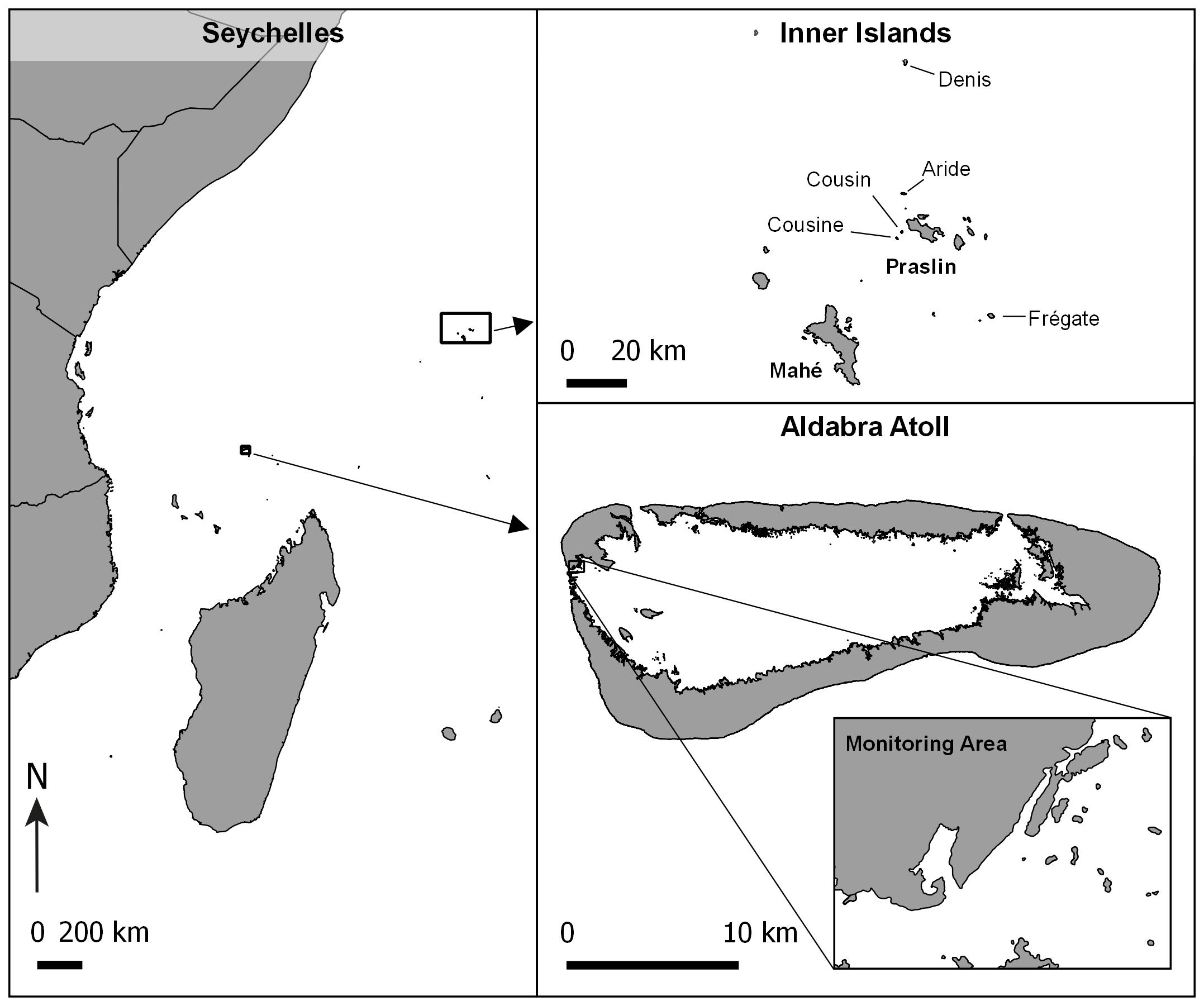
**Figure legends**

**Figure 1.** Seychelles islands in the Western Indian Ocean region (left), the four *P. 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).

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

**Figure 3.** Seasonality in rate of *P. lepturus* at Aldabra, Aride and Cousine Islands. Shaded areas indicate the standard error of the model predictions.

**Figure 1**



**Figure 2**

******

**Figure 3**



**Supplementary Material**

Additional Island Information

*Aldabra Atoll*

Aldabra Atoll is a raised coral atoll, approximately 1150km southwest of the main Seychelles island of Mahé (Figure 1), and consists of four main islands totalling 155 km2 area around a central 195.9 km2 lagoon. *P. lepturus* nest predominantly on islets within the lagoon. The habitat of the islets (area between 41 and 570 m² (mean 249 m²) consists of pitted limestone crevices and salt tolerant vegetation with varying degrees of coverage.

*Aride Island*

Aride is the northernmost granitic island of the Seychelles Archipelago and is situated 15 km away from Cousin Island and 50 km from the main island of Mahé (Figure 1). Aride’s 74 ha consist of 5 ha of flat plateau and 69 ha of mountainous terrain. The island has been restored from a degraded coconut plantation. A colony of *P. lepturus* nests across the island but monitoring is consistently conducted on the plateau along coastal and inland areas of forest.

*Cousin Island*

Cousin is 2 km from Cousine Island and 35km from the main island of Mahé (Figure 1). Cousin’s 27 ha consist of 21.6 ha of flat plateau and 5.4 ha of mountainous terrain. The island has been restored from a degraded coconut plantation. A colony of *P. lepturus* nests throughout this habitat but are predominantly monitored on the plateau both along the coast and inland.

*Cousine Island*

Cousine Island, 2 km west of Cousin and 32 km NE of the main island of Mahé (Figure 1). The island is close in proximity, size and habitat to Cousin Island and likewise has been restored from a degraded coconut plantation. A colony of *P. lepturus* breeds across the island but monitoring has concentrated throughout the accessible plateau on the eastern side.

*Denis Island*

Denis Island is ca. 43 km north of Aride Island and 80 km north-east of the main island of Mahé (Figure 1). Denis holds a small population of *P. lepturus* which nest across the island.