Coral Reefs
https://doi.org/10.1007/s00338-022-02341-9

REPORT

Sex-based divergence in tidal, lunar and seasonal cycles of activity in the olive sea snake, *Aipysurus laevis* (Elapidae, Hydrophiinae)

Tim P. Lynch[1] · Ross A. Alford[2] · Richard Shine[3]

Received: 27 June 2022 / Accepted: 19 December 2022

Abstract Marine environments show strong cycles at daily (tidal), monthly (lunar) and seasonal timeframes, and the behavioural responses of marine organisms to such cycles may depend upon ecological and behavioural traits that differ between the sexes. Underwater observations of free-ranging olive sea snakes (*Aipysurus laevis*, Hydrophiinae, Elapidae) at a site on the southern Great Barrier Reef revealed sex-based divergences in the effects of abiotic cycles on snake activity. Female snakes were active primarily on high and rising tides that allowed access to shallow-water sites for foraging. In contrast, male snakes were active primarily on low and falling tides, especially near the time of the full moon (when tidal range is highest), conditions that may restrict a female snake's ability to evade a courting male. Males were common on the coral-reef site during winter (the mating season), but were rarely seen during summer, whereas females remained on the reef year-round. This highly sexually dimorphic species shows strong temporal separations between the sexes in patterns of activity.

Keywords Elapidae · Foraging · Hydrophiidae · Hydrophiinae · Mating system · Tidal rhythm

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-022-02341-9.

✉ Richard Shine
rick.shine@mq.edu.au

[1] CSIRO, Castray Esplanade, Hobart, TAS 7000, Australia

[2] College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

[3] School of Natural Sciences, Macquarie University, Sydney, NSW 2109, Australia

Introduction

Rhythmic changes such as tides exert a pervasive effect on marine organisms, because those cycles affect a diverse suite of parameters (including water depth, turbidity, temperature, and current speed) that in turn modify biologically significant attributes of an animal's environment. For example, tidal stage can affect an individual's access to food, its exposure to predators, and its ability to disperse among habitats (for reviews see Palmer 1973 and Naylor 1985). Those impacts may be lessened or exacerbated by lunar cycles that modify both illumination levels and the magnitude of tidal variation (Hampel et al. 2003). As a result, one of the most fundamental questions we can ask about any marine species is how its activity is affected by tidal conditions (e.g., Gibson 1992)?

Sea snakes play important ecological roles within marine ecosystems (Heatwole 1999; Ineich et al. 2007) and have experienced enigmatic population declines in several areas (Goiran and Shine 2013; Lukoschek et al. 2013). Nonetheless, the natural history of marine snakes has remained poorly known until recent years (e.g., Udyawer et al. 2018). Most data on sea snake biology have come from prawn-trawler bycatch (Fry et al. 2001; Ward 2001), with only anecdotal observations to document foraging responses of shallow-water species to tidal levels (e.g., Sweet 1989; Guinea et al. 1993). More recently, behavioural analyses have provided quantitative evidence that rising tides stimulate inshore movement of one species (*Emydocephalus annulatus* – Goiran et al. 2020a), and a retreat to safer (shark-free) habitats in others (*Hydrophis elegans*, *H. major* – Kerford et al. 2008; Wirsing and Heithaus 2009). Acoustic telemetry suggests that foraging occurs primarily on falling tides in *Hydrophis major* (Udyawer et al. 2020).

In the present paper, we extend these analyses to another species of sea snake, based on standardised time-series underwater observations at a single study site. Specifically, we ask whether snake behaviour is linked to tidal variation at three timescales: diel (i.e., low-to-high tide), lunar (i.e., neap-to-king tide) and seasonal (i.e., summer to winter); and whether such associations differ between conspecific males and females. The sex-based comparison is of interest not only in its own right, but because it may clarify underlying reasons for associations between snake activity and environmental cycles.

Material and methods

Study species

Olive sea snakes (*Aipysurus laevis*) (Fig. 1) are large (to 2 m, 3 kg) heavy-bodied elapid snakes that are widely distributed across tropical oceans from northern Australia, New Guinea and the IndoPacific (Cogger 2014). The sexes differ in body sizes (females are larger than males; at our study site, maximum body masses of 2.3 vs. 0.7 kg), colour (females are blue-grey, males are brown), scale rugosity (females are smooth-scaled, males are rugose) and rates of approach to SCUBA divers (males approach more often) (Lynch 2000; Lynch et al. 2021). The species has been reported at depths from the reef shallows to > 130 m (Greer 1997). These snakes are entirely aquatic, with females producing a small litter of large offspring on a biennial cycle (Burns and Heatwole 2000). Diets are diverse, including the eggs of gastropods and fish as well as crustaceans and many types of fish (Voris and Voris 1983; Lynch 2000). Analysis of digestion rates of gut contents suggests that *A. laevis* forage continuously, preying on sleeping nocturnal fish during the day and sleeping diurnal fish at night (McCosker 1975). Regurgitated stomach contents from 34 recently-captured snakes during our own study consisted primarily of gastropod egg masses (N = 24), with 9 records of fishes and one of a crab (Lynch 2000).

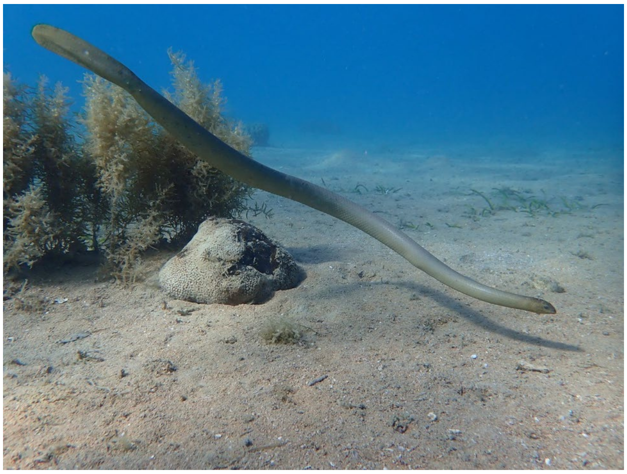

Fig. 1 Olive sea snake (*Aipysurus laevis*). Photo by Aline Guemas

Study area

Our study site was located within the Keppel Group (23°10'S, 150°57'E), continental islands inside the Great Barrier Reef Lagoon on the east coast of Australia. At this southern extremity of the lagoon, the actual barrier reef is far from the coast. This means that sea conditions have a strong oceanic component with sizeable swells even in non-cyclonic conditions. During most of the year warm northerlies dominate the weather system, but the prevailing winds switch during winter, often abruptly, to a southern weather pattern that brings cold sou-westers and rain during the dry season (April–September).

The main study reef, Passage Rocks, is 20 km offshore between South (Great) Keppel Island (GKI) and Middle Island. The area was off-limits to fishing from 1961 through to 1994, and hence supported high and then lower abundances of many reef-associated fish species at the time of the present study (1993 to 1995).

Sampling methods

One of us (TPL) undertook sampling for 10 days per month from April 1993 to July 1995. He made two dives each day, separated by at least 3 h. The start time for each dive was randomly selected, with the proviso that all daylight hours (0800–2000 h) were covered. Due to safety constraints, only diurnal sampling was conducted. The reef was divided into a grid of 10-m squares marked with 154 numbered stakes. Start location for each search was randomly selected from a grid number, without replacement, until the entire grid was searched, after which the randomisation recommenced. During each search the observer both scanned the reef surface for active snakes and searched under coral overhangs for resting snakes. Once a snake was located it became the focal animal for the next 30 min, but other animals seen were recorded during that period. All of our data pertain to adult snakes.

A total of 204 dives were conducted, and snakes were observed on 159 of these dives. To investigate relationships between snake activity, tide quadrant and moon phase, we conducted contingency tables with Vassar stats (http://vassarstats.net/). Each snake was scored as either active or inactive (resting) based on its behaviour when first sighted. At the conclusion of focal observations, snakes were captured and individually marked by scale-clipping. To avoid pseudoreplication, the unit of analysis was per dive not per individual snake. Thus, if we saw an active female and an active male on a dive during a high incoming tide, one count was recorded for active females and one for active males in the "high incoming" category. If two active females were observed the count would still be one, because the sampling unit was the dive not the snake. Few inactive male snakes were recorded (N = 8), so we did not include this group in the analyses. Thus, we looked only at the numbers of observations of active males, and both active and inactive females.

To investigate our time-series of observations of all snakes counted (i.e., all animals observed per dive), we also recorded each animal's sex and the dive time. We plotted these as observations per hour of dive time per month. We then compared the probabilities of encounters with male versus female snakes over this time-series with a binomial generalized additive model (see Wood 2006).

Results

Tidal cycle

Female snakes used the high incoming part of the tide more, and the low outgoing part of the tide less, than would be expected under the null hypothesis of no bias (Fig. 2a; $\chi^2 = 11.06$, 3 df, $P < 0.015$). Male snakes showed the reverse pattern (i.e., tended to be most active on the low outgoing parts of the tide and least active on high incoming and outgoing tides), but this trend fell short of statistical significance (Fig. 2a; $\chi^2 = 7.65$, 3 df, $P = 0.054$). Like active male snakes, inactive female snakes were recorded primarily on outgoing tides (against the null hypothesis, $\chi^2 = 13.23$, 3 df, $P < 0.005$).

Contingency-table analysis thus showed strong differences between the sexes in their activity relative to tidal phase (active snakes only; $\chi^2 = 73.01$, 3 df, $P < 0.0001$). The relative frequencies at which we recorded inactive females at different tidal phases were similar to those at which we recorded active male snakes ($\chi^2 = 2.39$, 3 df, $P = 0.50$) but differed from the tidal distribution of records of active females ($\chi^2 = 81.61$, 3 df, $P < 0.0001$).

Lunar cycle

Male snakes were most active around the time of the full moon and least active during the last quarter of the moon ($\chi^2 = 10.10$, 3 df, $P < 0.02$; see Fig. 2b). The numbers of females seen did not differ significantly between lunar phases, either for active females (vs. a random model, $\chi^2 = 3.43$, 3 df, $P = 0.33$) or inactive females ($\chi^2 = 0.79$, 3 df, $P = 0.85$). Thus, active males were seen at different moon phases than were active females ($\chi^2 = 57.75$, 3 df, $P < 0.0001$) or inactive females ($\chi^2 = 11.68$, 3 df, $P = 0.0009$). Sightings of active and inactive females were similarly distributed among moon phases ($\chi^2 = 7.04$, 3 df, $P = 0.071$).

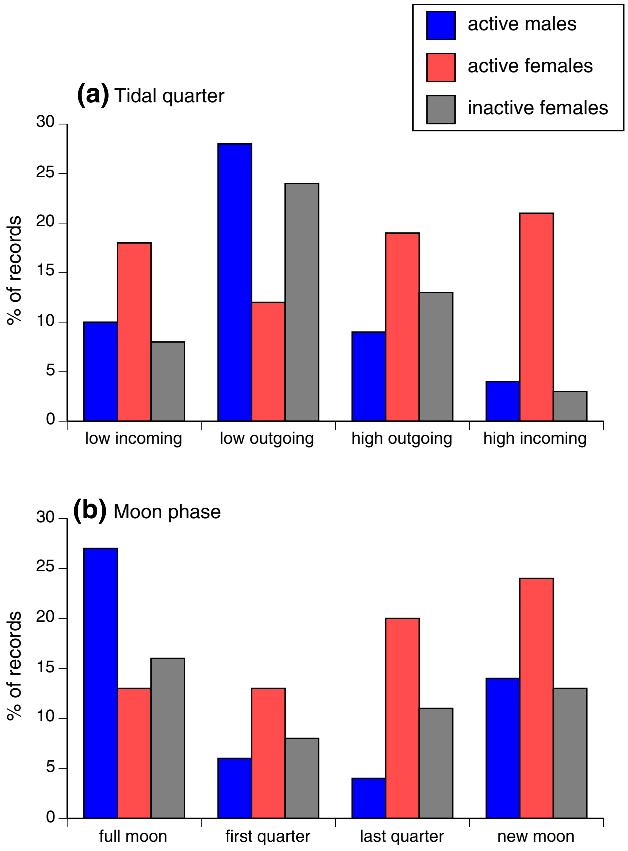

Fig. 2 Percentage of dives in which male and female olive sea snakes (*Aipysurus laevis*) were observed to be active in relation to the tidal cycle (**a**) and the lunar phase (**b**)

Seasonality

Female snakes were seen year-round, whereas males were seen primarily during the breeding season in winter (Fig. 3). There was a strong ($\chi^2 = 36.94$, $P < 0.0001$) difference in the relative probabilities of encountering a female vs. male snake over the time-series of observations. This pattern was seasonal, with four crossover points (i.e., when probabilities of encountering a male were similar to those of encountering a female) followed by divergences (Supplementary Information Fig. S1). Males appeared in March in 1993 and in April in 1994, and in both of those years most of the males left during August. Many of these (individually-marked) male snakes were recaptured at the reef the following year (Lynch 2000). In May–June 1994, after no males had been seen for 6 months, 12 of 17 males found were recaptures from the previous year. Similarly, 5 of 8 males captured in April–May 1995, after 6 months when no male snakes were seen, were

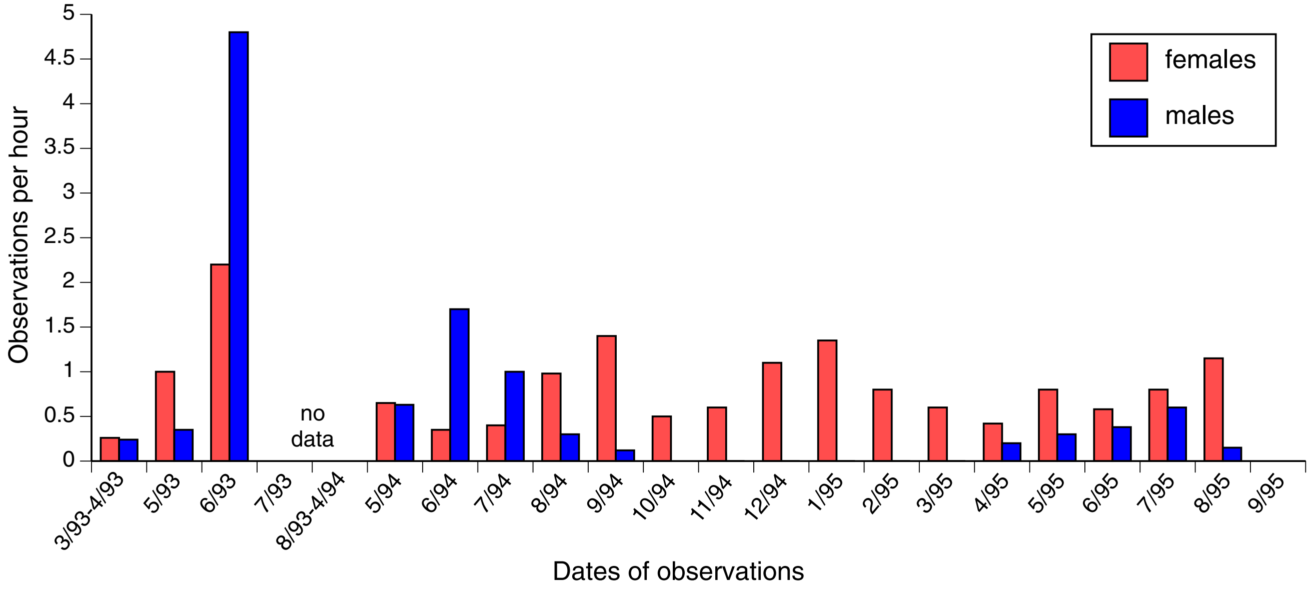

Fig. 3 Seasonal abundance of male and female olive sea snakes, *Aipysurus laevis*, at the Passage Rocks study area

previously-marked animals. Thus, the disappearance of male snakes from the reef post-breeding was due to dispersal not mortality.

Discussion

Activity in adult olive sea snakes was associated with particular tides, lunar phases and seasons, and these associations differed between the sexes. Males were most active on low outgoing tides, whereas females were most active on high incoming tides. The trend for male snakes to be most active on low falling tides was especially marked at the time of the full moon, when tidal range is maximised. Lastly, the sexes showed a strong divergence in the seasons at which they were encountered on the reef: females were present year-round, but males were seen primarily during winter.

The scarcity of records of inactive male snakes may be due to their use of areas off-reef and/or in deep water, and their higher overall activity levels (i.e., less time spent resting within 30-min focal observation periods, than for females: Lynch 2000). The sex difference in responses to tidal rhythms likely reflects similar underlying differences between males and females in behaviour and habitat use. At our study site, female snakes utilised shallower water than did males, and their activity on incoming high tides was associated with movement onto the reef crest (exposed or near-exposed at low tide; Lynch 2000). Females may traverse these shallows to reach coralline sites separated by shallow water, for foraging on gastropod eggs (Lynch 2000). In contrast, we saw male snakes primarily during the winter breeding season, when males combine foraging with mate-searching (Lynch 2000; Lynch et al. 2021). As a consequence, males travelled faster and swam for longer periods of time and over more zigzag paths than did females (Lynch 2000). Many courtship attempts were unsuccessful, with females fleeing from male harassment (Lynch et al. 2021) as described for other snakes (e.g., Shine et al. 2005). A falling low tide may constrain a female's ability to evade males, rendering it easier for a male to obtain a mating. Alternatively or additionally, male activity during low outgoing tides may increase rates of encounter with inactive females (generally found in specific habitats at the interface between coral and sand) that may be easier to find when low tide reduces the area over which females are distributed. Those hypotheses fit well with two other patterns that we observed. First, male snakes tended to be active at times when female snakes were inactive (resting within coral crevices). A male may be more likely to find a female and to obtain a copulation in this situation, than if the female is in open water and can flee. Second, male snakes were especially active on the full moon, when tidal range is at its maximum. The ability of males to locate females and for females to evade males would be lowest at that point, because of lower-than-usual water levels. In the extreme, a female would be trapped in a small and shrinking pool among coral, with no avenue of escape.

In a telemetry-based analysis of activity patterns in another large species of sea snake (the greater sea snake, *Hydrophis major*), Udyawer et al. (2020) reported that snakes (both sexes combined for analysis, but mostly males [N = 15] not females [N = 4]) were most active on falling tides, at relatively low water levels – the same pattern as detected for male but not female olive sea snakes in our own study. Udyawer et al. (2020) attributed that pattern to the availability of scent cues from catfish prey, as water from prey-containing crevices flowed out into the broader water column with falling water levels. Consistent with that hypothesis, captive snakes increased activity when exposed to scent cues from catfish. However, the availability of scent cues from female snakes is unlikely to work in the same way; as on land, sea snakes depend primarily upon substrate-bound lipid molecules for locating females, rather than detecting waterborne chemical cues (Shine 2005). The sex difference in tidal activity in *A. laevis* suggests that future work could usefully look for similar divergence in *H. major*.

Lunar cycles in activity are common in aquatic as well as terrestrial animals, and may have many causes. In the freshwater filesnake *Acrochordus arafurae*, reduced activity on moonless nights may protect the snakes from visually-hunting predators (Houston and Shine 1994a). In contrast, Madsen and Ostercamp (1982) attributed reduced activity of the aquatic colubrid *Lycodonomorphus bicolor* on moonlit nights to fish being more able to detect and evade an approaching snake. In our own study system, shifts in tidal range likely are the most important correlate of lunar cycles (see also Udyawer et al. 2015 for a similar example and interpretation with *Hydrophis curtus*).

A seasonal shift in adult sex ratios on the reef has previously been reported for olive sea snakes at our study site (Burns and Heatwole 2000), and for a similarly-large hydrophiine, *Hydrophis major*, at a shallow bay in New Caledonia (Goiran and Shine 2019). In contrast, a smaller aipysurine species at the same New Caledonian site, *Emydocephalus annulatus*, shows no overt shift in seasonal sex ratio (Goiran et al. 2020b; RS, unpubl. data). In both *A. laevis* and *H. major*, the season when males appear on the reef corresponds to the period of maximal courtship and mating activity. Apparently, then, males (and perhaps, some females) utilise a different habitat during the non-breeding season. That inference is supported by records of snake bycatch from prawn-trawlers, with *A. laevis* often captured in deep water (Ward 2000). An increase in activity levels and home ranges during the breeding season is widespread in reproductively active males of many species of snakes (e.g., Brown and Weatherhead 1999; Lind and Beaupre 2015) including terrestrial taxa within the lineage containing the sea snakes (Elapidae - Shine 1987; Whitaker and Shine 2003). However, an abrupt sex-specific seasonal shift in habitats is less common. The closest analogies of which we are aware involve differential selection of deep versus shallow waterbodies during the breeding season by male and female filesnakes (*Acrochordus arafurae* – Houston and Shine 1994b) and seasonal aggregation of reproductive females for communal oviposition (in oviparous taxa) or effective thermoregulation (in viviparous taxa) in many species of snakes (Graves and Duvall 1995). Because female snakes often forego feeding while they are gravid, it is not unusual for reproductive females to remain close to overwintering sites while males disperse out more widely through surrounding habitats (e.g., Webb and Shine 1997; Shine and Wall 2005). In this sense, such taxa resemble *A. laevis*: females are more sedentary and site-attached than are conspecific males.

Sex-based differences in vulnerability to different predators may also influence the behaviour of *A. laevis*. Juvenile tiger sharks (*Galeocerdo cuvier*) feed on cephalopods, teleosts and sea snakes before switching to larger prey (Simpfendorfer et al. 2001). Male *A. laevis* might be less vulnerable to sharks because of their smaller size and greater agility, allowing them to occupy the more exposed reef-edge and deeper off-reef areas. In shallow waters, sea snakes that surface to breathe are at risk from white-bellied sea-eagles *Haliaeetus leucogaster* and ospreys *Pandion haliaetus* (Smith 1985; Lynch 2000; Corbett and Hertog 2011) with the smaller males potentially at greater risk.

The result that environmental cycles affect behaviour of sea snakes is unsurprising, although our data are the first to show such strong sex-based divergences in those responses. Few species of marine snakes have been studied to date in this respect, but a diversity of patterns already is apparent. Some semi-terrestrial mangrove-dwelling taxa such as *Hydrelaps darwiniensis* exploit falling tides to access prey (fishes) trapped within their burrows (e.g., Sweet 1989; but see Guinea et al. 1993 for an account of *Hydrelaps* emerging to feed on a rising tide). Other semi-terrestrial species move between land and sea when tidal conditions facilitate that movement (*Laticauda colubrina* – Shetty and Shine 2002). Within purely aquatic taxa, a rising tide may enable snakes to move into foraging areas too shallow for use at lower tides (*Emydocephalus annulatus* – Goiran et al. 2020a) or into habitat (seagrass beds) where predatory sharks pose less risk (*Hydrophis elegans*, *H. major* – Kerford et al. 2008; Wirsing and Heithaus 2009) or for both of these reasons (*Hydrophis curtus* – Udyawer et al. 2015). Current strength driven by tidal cycles also may affect movements and habitat use (e.g., of *Enhydrina schistosa* – Heatwole 1999). In short, tidal cycles have a pervasive effect on marine habitats, and alter many characteristics that influence the availability, as well as the costs and benefits, of alternative habitat types. The diversity of hydrophiine sea snakes, both morphologically and ecologically (e.g., Voris and Voris 1983; Sherratt et al. 2018) means that such factors will modify organismal responses to tidal cycles differently in different species.

Understanding that complexity may be an important step towards planning for the effective conservation of these imperilled marine predators (Udyawer et al. 2018). For example, we cannot manage populations of *A. laevis* effectively without knowing more about where males spend the warmer (non-breeding) months. Anthropogenic threats may well differ between reef and non-reef habitats (e.g., coral bleaching vs. trawler bycatch), such that the two sexes will be differentially vulnerable to different threats. Degradation of reef habitats likely will be more deleterious for adult female olive sea snakes than for conspecific males, potentially affecting population viability. Low rates of genetic exchange among populations of *A. laevis* (Lukoschek et al. 2007), despite the wide distribution and high vagility of individuals of this species, suggest that destruction of reef habitats may imperil local populations of snakes. The strong trend for males to return to the same reef in successive breeding seasons (present study) is consistent with the genetic differentiation among reef systems reported by Lukoschek et al. (2007). Hence, populations of olive sea snakes may be vulnerable to anthropogenic sources of mortality not only on the reef, but also at open-water sites used by some segments of the population for at least part of the year.

Acknowledgements We thank Scott Foster for advice on statistical analyses. We also thank Rob Sherrington for helping to set up the study site grid and Bob, Caroline, Vince and Peter from Great Keppel SCUBA Dive Adventures for their technical support. Funding was provided from a scholarship from the Lions Club of Australia for investigations into venomous Australian species. TPL's parents, Dan and Catherine, also provided financial support.

Author contributions TPL and RAA designed the study. TPL gathered all data. All authors conducted statistical analyses. RS drafted the manuscript, which was then modified by TPL and RAA. All authors approve the final version.

Data availability Data is available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.sf7m0cg9v.

Declarations

Conflict of interest All authors declare no conflict of interest.

Ethics approval All procedures were designed to minimise stress to the animals, were carried out in accordance with relevant guidelines and regulations (including ARRIVE guidelines), and were approved by the James Cook University animal care and ethics committee, and by Queensland National Parks and Wildlife Service Permit A185.

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