Running head: Appoo et al.Coconut crab population dynamics on Aldabra

**Population demographics and dynamics of the coconut crab, *Birgus latro,* on Aldabra Atoll, Seychelles**

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ABSTRACT

Aldabra Atoll (Seychelles) hosts a significant and unexploited *Birgus latro* population. We present for the first time the demography and spatial and temporal dynamics of this population on Aldabra, studied from 2007 to 2016 (nine years). We found that Aldabra has a population size of 65,480 ± 3126 (mean ± SE) *B. latro* which has remained largely stable over the study period. The population exhibited high spatial and temporal variability in density, size and sex ratio over this time period. Aldabra’s *B. latro* population is heavily male-biased (sex ratio 3:1 male to female) and is sexually dimorphic, with males attaining larger sizes than females. Overall, our results indicate that Aldabra represents an important refuge for *B. latro* and holds the potential to repopulate other protected areas in the Western Indian Ocean where populations have declined substantially. Our study contributes to much needed information to revise the IUCN Red List threat status of *B. latro*, currently listed as Data Deficient and to leverage conservation efforts for this species.

KEY WORDS: *Birgus latro*, population size, spatial variability, seasonal dynamics, moulting, reproductive season, Aldabra Atoll.

INTRODUCTION

Around 14,600 species are classified as data deficient on the IUCN Red List (IUCN 2018), meaning that their threat status cannot be assessed due to uncertainties in species taxonomy, distribution, population status or threats (Veron et al. 2016). These uncertainties impact the likelihood of active conservation measures being adopted. Unless directly targeted for monitoring, species classified as data deficient can become extinct or locally extinct before protective measures can be put in place (Bland et al. 2014). New information on data deficient species may therefore help fill data gaps in biodiversity indicators, as well as conserve poorly known taxa (Bland et al. 2014). The conservation attention paid to invertebrates generally lags far behind that of vertebrates (Collen et al. 2012) and it is crucial to understand the conservation status and trends of invertebrates, since these species are essential for ecosystem functioning (Baillie et al. 2010).

In tropical island ecosystems, crabs, in particular, play a crucial role in nutrient cycling and food chains. The largest land arthropod, the coconut crab (*Birgus latro*)*,* is classified as data deficient by IUCN (Eldredge 1996) due to limited information on the status of the different populations (Drew et al. 2010). Although *B. latro* has a broad geographical range across the tropical Indo-Pacific region, the size and distribution of the populations have substantially reduced in human-inhabited areas (Schiller 1992). This decline is mostly attributed to loss of habitat, predation in juvenile stages by invasive species such as rats and unmanaged harvesting for human consumption (Laidre, 2018). Despite being abundant across the Indo-Pacific (Drewet al. 2010), in the Indian Ocean the distribution is now largely confined to three populations; Aldabra Atoll, the Chagos Archipelago and Christmas Island (Lavery et al. 1996). *Birgus latro* is locally extinct in Mauritius (Eldredge 1996) and is believed to no longer occur on Mayotte and the Comoros Islands, although the species has recently been re-discovered on Glorieuse for the first time in more than a century (Poupin et al. 2013). In the Seychelles, *B.latro* has been historically overexploited for food on the granitic inner islands and inhabited outer islands. With the exception of Aldabra Atoll, *B.latro* occurs throughout Seychelles in low incidence with recent opportunistic records on two granitic islands and has only been occasionally recorded on some of the outer Seychelles islands (Poupin et al. 2013). Information on the species’ life-history, behaviour and ecological requirements is too limited to assess its status and design potential conservation measures (Drew et al. 2010).

*Birgus latro* has important ecological roles on island ecosystems (Paulay & Starmer 2011, Laidre 2017). Owing to characteristics of their life history, they contribute to transfer of energy and material from sea to land and vice versa. Highly omnivorous, *B. latro* feeds on a variety of plants and animals and actively scavenge (Krieger et al. 2016). As scavengers they remove rotting material, help to decompose leaf litter and their consumption of seeds and seedlings control plant numbers (Alexander 1979). *B. latro* has also been observed hunting (Krieger et al. 2016, Laidre 2017), suggesting they may even function as top predators in their island ecosystems (Laidre, 2018). Furthermore, *B. latro* are a food source for birds in their juvenile stage and they contribute to soil aeration and erosion through their burrowing activities (Alexander 1979).

One of the three remaining key sites for *B. latro* in its Indian Ocean range is Aldabra Atoll (Seychelles) where the species has benefited from complete protection since Aldabra's designation as a Special Reserve in 1981 and UNESCO World Heritage Site in 1982. *Birgus latro* is relatively abundant and widely distributed across the atoll, inhabiting rock crevices, deep pot-holes, vegetation and sandy areas (Grubb 1971). On Aldabra, *B. latro* is an important scavenger of dead giant tortoises, and preys on marine turtle eggs and hatchlings (Haig 1984). Although one of the last remaining viable populations in the Indian Ocean, the status and ecological characteristics of Aldabra’s *B. latro* population have population have never been reported.

Here we investigate the demographics and dynamics of *B. latro* on Aldabra and present the results of a nine-year study where fortnightly counts and biometric data were collected on *B. latro* individuals between 2007 and 2016. Due to its isolation and protection, we hypothesise that Aldabra hosts a large *B. latro* population and acts as a key natural source population for other protected areas within its known historic range. For this population we therefore aim to: (1) estimate the density and size of the population; (2) quantify spatial (habitat) and temporal (inter- and intra-annual, and lunar phase) variability; (3) assess sex ratio and size; and (4) assess moult cycles (to determine whether there is synchronous seasonal moulting) and the timing of breeding and whether this is related to lunar phase. In addressing these questions we define baseline information on the structure and dynamics of a *B. latro* population in a relatively undisturbed site, provide insights into reproductive triggers and ecological parameters that will contribute towards monitoring and conservation strategies on Aldabra and other islands in its range.

MATERIALS AND METHODS

*Study site*

Aldabra Atoll (9°25′0″ S, 46°24′59″ E; land area 155 km2) is a large (34 km × 14 km) raised atoll in the Western Indian Ocean, which forms part of the Seychelles archipelago. It is ca. 1100 km south-west of Mahé, the main island of the Seychelles, and ca. 400 km from Madagascar (Fig. 1). Aldabra is composed of a characteristic and irregular coral limestone formation called ‘champignon’. The terrestrial environment is dominated by dense scrub of varying height, either continuous or in a mosaic with open rocky ground (Hnatiuk & Merton 1979). Aldabra’s climate is determined by two distinct seasons: the wet season of the north-west monsoon from November to April (Stoddart & Mole 1977), while between May to October there is lower rainfall resulting from the south-east trade winds.

*Survey design and sampling*

The distribution of *Birgus latro* is thought to be structured by distance from the coastline (Schiller 1992). Therefore we conducted *B. latro* population surveys along two transects established on existing walking trails at different distances from the shore (Fig. 1) on the island of Picard, one of the four islands of Aldabra. Both transects were divided into 50-m sections. The ‘shore’ transect was 1.4 km long and separated from the shore (high water mark) by distances of 1–26 m. The ‘inland’ transect was 1.8km long and 38–177 m from the shore. We surveyed both transects simultaneously after sunset (give approx. times of surveys), every two weeks between January 2007 and May 2016.

All *B. latro* individuals encountered within 5 m on either side of the mid-transect line were recorded. For each individual encounter, we recorded the following parameters: (i) distance to the mid-transect line (estimated to nearest meter); (ii) sex (female *B. latro* possess three large, feathery pleopods on the ventral surface of their abdomen to support their egg-masses; Fletcher 1993), and for females, whether carrying eggs or not; (iii) thoracic length (linear distance between anterior and posterior borders of the thoracic groove, measured with vernier calipers; Helfman 1973); (iv) moult, measured as the degree of pleonal expansion (Amesbury 1980, Fletcher et al. 1990, Held 1963 cited by Drew et al. 2010) using a four-level categorical scale: category: (1) all tergal plates touching each other or only a small gap between the most posterior tergal plate (first plate) and the second plate; (2) pleon slightly swollen and fleshy abdomen visible between first and second plates, and somewhat visible between second and third plates; (3) pleon swollen and fleshy abdomen clearly present between first, second and third plates, and somewhat visible between third and fourth plates; and (4) strongly swollen pleon with fleshy abdomen visible between all tergal plates.

*Habitat classification*

We considered the habitat along the transects to be representative of the dominant landscape on Aldabra. However, to control for potential habitat effects, we determined habitat composition using high resolution satellite imagery (Walton 2015), which was classified into eight different habitat types (open mixed scrub, exposed surface, standard mixed scrub, grasses, mangrove, sand, dense *Pemphis acidula* bush, and champignon; Walton 2015). In each 50-m transect section we calculated the percentage of area occupied by the different habitat types by counting the number of pixels of each habitat type that overlapped with the transect area.

*Data analysis*

*Density and abundance*

We estimated the density of *B. latro* during each survey using the hierarchical distance sampling model of Royle et al. (2004) implemented in the R package ‘unmarked’ (Fiske & Chandler 2011). We used the numbers of individuals within five distance categories 0−1, 1−2, 2−3, 3−4, and 4−5m from the mid-transect line to estimate the overall density and evaluated the association between habitat with both the detectability and abundance of *B. latro*.

To maximise differentiation between transect sites and reduce the dimensionality of the data, we transformed habitat composition percentages using a principal component analysis. Finally, we included the two components, explaining the largest proportion of the variance as covariates in the distance sampling model. Due to the large number of surveys, we used a fixed effects meta-analysis approach to ascertain the importance of the covariates. A covariate was determined to affect *B. latro* detectability if its effect was significant and consistent over a majority of surveys, and to affect abundance if its effect was either consistent over surveys or variable but according to the seasons. We used the Akaike Information Criterion (AIC) to determine whether the detection process was better approximated by a half-normal, a negative exponential, a hazard-rate, or a uniform distribution function.

Next, we used a generalised additive model (GAM) to determine whether *B. latro* densities varied significantly (i) over the years, (ii) over the yearly cycle, and (iii) over the lunar cycle. We fitted the models using the R package ‘mgcv’ (Wood 2006a), and assessed the model parsimony by comparing their AIC values. We back calculated the phase of the moon during the survey using the R package ‘oce’ (Kelley & Richards 2015) and defined it as a continuous variable from zero to one with both extremes corresponding to new moon, 0.25 for first quarter, 0.5 for full moon, and 0.75 for last quarter (Meeus 1982). To analyse abundance patterns at a finer spatial and temporal scale, we used a set of GAMs to quantify the relative effect of the aforementioned variables on the counts of both male and female individuals. This was possible after initial analysis indicated that *B. latro* detectability did not change over time and was not influenced by habitat composition (see Results) and consequently direct counts provide an accurate index of *B. latro* abundance. As it is plausible that environmental factors interact with habitat requirements, the interaction between day of the year and distance from shore was included in the model (Wood 2006b).

*Sex ratio and size*

We calculated observed sex ratios from the individual counts. Because of the relevance for reproduction, we also calculated the sex ratio of only sexually mature individuals. We assumed sexual maturity based on size: individuals with a thoracic length > 28mm were considered adults (Fletcher et al. 1990, Sato & Yoseda 2008, Drew et al. 2010). We used thoracic length to determine whether the Aldabra population exhibits size sexual dimorphism. We evaluated the difference by visually inspecting the size distribution for both sexes and Mann–Whitney tests on the thoracic length measurements. We used a set of GAMs to infer the effects that time of year, distance from shore, and lunar phase may have on the sex ratio and sizes of individuals encountered. Competing models were compared using their AIC.

*Moulting and reproduction*

We constructed two additional GAMs, one for each sex. In these models the response variable was the index of pleonal expansion (treated as a numeric variable) and the predictor was time of year. To determine the reproductive season of *B. latro* on Aldabra, we constructed a GAM with a binomial error distribution with the response variable being whether a female was seen carrying eggs during a survey transect or not, with time of year and lunar phase as response variables.

RESULTS

*Density over time and population estimate*

Overall, we performed 265 surveys over the study period with 8145 individual *B. latro* encounters. *Birgus latro* density in the study area was 3.2–189.4 ind. ha-1, with an overall average density of 35.4 ± 1.69 ind. ha-1 (mean ± SE). The overall density showed small variations between years, but no long-term trend is observable (Fig. 2A). Since habitat type did not have an effect on *B.latro* density, we extrapolated the value over an area taking into account the furthest distance of our transect from the shore (177 m) and the total perimeter of the outer rim of the atoll (104.5 km). We estimate that Aldabra has a population size of 65,480 ± 3126 (mean ± SE) *B. latro.*

*Effect of season, habitat and lunar phase*

The number of *B. latro* encountered was above average between February and June, with a clear peak in April, and below average between July and December (Fig. 2B). The abundance of *B. latro* males and females was strongly affected by the time of year and the distance from shore. In general, more males were encountered during January–June than July–December. In March and April, males were concentrated away from the shore (Fig. 3A) and more females were encountered closer to shore. In contrast, during July-December, when fewer males were seen, female density was higher in both shore and inland areas, particularly between October and November (Fig. 3A).

The two principal components of the habitat composition analysis explained 81% of the variance among transect sections (Fig. S1 in Supplement 1). The first component was strongly correlated with a decrease in exposed surface and an increase in open mixed scrub. The second component was largely correlated with an increase of grass and a decrease of standard mixed scrub. These habitat differences did not affect the detectability or abundance of *B. latro* (Figs. S2 and S3 in Supplement 2). Among the functions we used to describe the detection process (half-normal, negative exponential, hazard-rate, or uniform) we found that the negative exponential function performed the best as it had the smallest AIC values among the alternatives.

There was no variation in density with moon cycle (p = 0.916). Although moon phase did not affect overall *B. latro* densities, it had distinct effects on males and females (Fig. 4A), with females being most abundant during periods of full moon, and males during new moon.

*Sex ratio and size*

The overall *B. latro* sex ratio of observed individuals was approximately 3:1 (76% male; n = 6536), and approximately 4:1 (82% male; n = 5582) for only sexually mature individuals. This ratio shows temporal and spatial variation, ranging from 57% of individuals encountered being male during November in areas close to shore to 86% during March in inland areas.

Marked size sexual dimorphism was observed (Fig. 5), with males being larger (mean male thoracic length: 40.9 mm; range: 9–78 mm; n = 6536) than females (mean: 30.6 mm; range: 6–76 mm; n = 2071). Although the distributions of males and females did not differ (n1 = 6182, n2= 1994; p = 0.725), large males were significantly larger than females (Mann–Whitney of upper decile, n1 = 666, n2 = 197; p < 0.001). The mean size of both male and female individuals encountered showed two distinct and synchronous peaks during the year, one between October and December, and another more pronounced between March and May (Fig. 3B).

Mean size was also affected by the distance to shore, with females encountered close to shore being larger than those encountered inland. In contrast, males encountered inland were larger than those close to shore. This difference in males encountered, however, becomes inconspicuous in December and January and from June to August (Fig. 3B). Furthermore, males encountered close to new moon were larger than males encountered close to full moon, while females showed no size variation over the lunar cycle (Fig. 4B).

*Moulting and reproduction*

Males over 30mm exhibited an annual cycle in pleon size, with a peak in April and May (Fig. 6), while female pleons were largest in November with a less conspicuous peak of pleon expansion between May and July (Fig. 6). Throughout the monitoring period, only 14 *B. latro* females (of 2071 individuals in 12 of 484 transect surveys) were ovigerous, but our data indicate a reproductive season between December and March with an increased probability of encountering females carrying eggs just before new moon (Fig. 7).

DISCUSSION

Our study is to our knowledge the longest study on *Birgus latro* and shows that Aldabra might potentially have one of the most significant *B. latro* populations worldwide (65,480 ± 3126 individuals), likely as a consequence of decades of protection. Data on unharvested populations is rare and outdated, the only other two studied unexploited populations of *B. latro* (Drew et al 2010) are estimated at 41,865 ± 4728 crabs on Taiaro, French Polynesia (Chauvet & Kadiri-Jan 1999) and 300-1200 crabs on Ikuren Islet, Enewetak Atoll, Marshall Islands (Reese 1987 cited by Fletcher 1991). The Chagos Archipelago, Palmyra Atoll and Christmas Island are also key strongholds of *B. latro* (Laidre, 2018). The population on Christmas Island however experiences limited exploitation and Drew & Hansson (2014) reported significant decline. Despite our study focussed on the island of Picard, this is representative of Aldabra as a whole and Aldabra’s other islands are uninhabited and even less disturbed so we do not expect *B. latro* populations to be declining on any of them.

We found substantial spatial and temporal heterogeneity on *B.latro* density, size and sex. *B.latro* are not sessile animals but are in constant movement locally around their home site and undertake long-distance movements (Krieger et al. 2012). This is most likely linked with a complex life cycle associated with reproductive migrations, moulting requirements, availability of resources and behavioural variations associated with environmental conditions at a site (Drew & Hansson 2014). From February to May, the overall number of crabs observed was higher than average. This is largely due to an increase in the number of active males present in the study area. During this time, large dominant males favoured areas inland, presumably richer in resources, while females and smaller males were mostly encountered in near-shore habitats. Drew & Hansson (2014) noted that large males often actively exclude females and potentially smaller males from desirable feeding locations. Afterwards, roughly from June to December, the overall number of *B.latro* was lower than average, again largely due to a decrease on the number of males, particularly of large ones, which are potentially undergoing moulting during the drier months of the year (Fletcher et al.1991). *B. latro* undergoes moulting in shallow burrows to minimize their vulnerability to predation and desiccation during the moulting process (Drew et al. 2010). Contrastingly, female counts increased on the second half of the year both in the shore and inland areas, likely opportunistically exploiting the available resources left by dominant males (Drew & Hansson 2014). Female densities peaked between September to December close to shore which coincided with a period in which males of sexually active sizes are commonly encountered. This suggests a breeding migration of female *B. latro* involving females moving to the shore to release larvae into the ocean (Schiller et al. 1991). Tracking studies from Christmas Island shows that male *B. latro* also move closer to shore for reproductive purposes but remain for a shorter period (Krieger et al. 2012).

At the spatial scale of this study, sex ratio appears to be biased towards males, most likely as a result of the sampling design. Transect studies typically report male bias ratios compared to grid sampling and are sensitive to variations in habitat use between sexes (Drew et al. 2012). Female *B.latro* have been shown to have affinity to denser vegetation and are therefore less likely to be encountered on transects along existing paths (Drew et al.2012). Furthermore, James (2008) suggested a more sedentary behaviour of female *B. latro* outside of the breeding season, suggesting that the males are wider ranging, increasing their chances of being encountered in surveys along pathways.

All studied island populations of *B. latro* to date show males to be consistently larger than females (Anagnostou & Shubart 2014, Drew et al.2010). Similarly, *B. latro* on Aldabra is sexually dimorphic, with males attaining larger sizes than females. Interestingly, the mean thoracic length of *B. latro* recorded on Aldabra is considerably smaller than all other studied populations (see Drew et al. 2010). In the wild, *B. latro* are known to have extremely slow growth rate due to factors such as sex, size and injury and negative or zero growth is common for this species (Drew et al. 2013). On Aldabra, the slow growth rate might be further influenced by resource limitation. *B. latro* compete intensively with hermit crabs of the genus *Coenobita*, which are abundant on Aldabra (Grubb 1971). In areas with high abundance of *Coenobita*, the amount of scavengeable material available to *B. latro* may be limited, as well as the availability of gastropod shells for the glaucothoe stage (Amesbury 1980). The interspecific competition might be compounded by the drought frequency on Aldabra, which is reported to have increased from two to six months per year between 1970 and 2013 (Haverkamp et al.2017). *B. latro* is suggested to exhibit a decrease in the frequency of their foraging activity during the dry season compared to the wet season (Fletcher 1993), thereby resulting in a much slower growing population on Aldabra.

Based on encounters with ovigerous females, the reproductive season on Aldabra occurs with most likelihood between December and March, during the rainy season. This also corresponds with the period of highest peak of female pleonal expansion in November to December, which is believed to be related to gonad development (Fletcher et al. 1991, Sato & Yoseda 2009). This period coincides with the reproductive seasons observed in other *B. latro* populations in the southern hemisphere (Drew et al.2010). Moreover, signs of synchrony with the moon cycle were found as ovigerous females were mostly encountered during surveys performed close to new moon. This synchrony is likely related to the timing of spawning or egg extrusion (Sato & Yoseda 2009). The few studies detailing mating behaviour in *B. latro* indicate that copulation is brief and not preceded by elaborate courtship (Brown & Fielder 1991). The timing between mating and egg extrusion is unknown. As female individuals don't possess a seminal receptacle, it is believed that egg extrusion occurs shortly after mating (Sato & Yoseda 2009, Drew et al. 2010). The period of egg maturation from egg extrusion to hatching is estimated to be about 25 to 45 days with the majority of eggs maturing 27 to 29 days after extrusion (Schiller et al. 1991, Sato & Yoseda 2009). This means that if female *B. latro* extrude their eggs around the new moon phase, the females will be able to hatch its larvae into the sea around the next new moon phase (Sato & Yoseda 2009).

Although some additional research regarding life history and ecological requirements are required, altogether our results show that Aldabra appears to be a key natural source population for other protected areas within its known historic range. We hope similar long term studies under natural conditions are prioritised for other *B. latro* populations especially in locations where the species is exploited. Although the seasonal variability might complicate monitoring, more studies are essential to revise the IUCN Red List threat status of *B. latro* and leverage conservation efforts for this remarkable species.

CONCLUSION

This study used one of the longest continuously recorded data sets on *Birgus latro* populations and provides additional insight into the ecology of this species. *B. latro* on Aldabra is highly dynamic due mainly to their life history traits and resource availability. With a significant, stable and unexploited *B. latro* population, Aldabra Atoll represents a refuge for this species recorded to be on decline elsewhere throughout its range and potentially a crucial reservoir for repopulating other suitable islands in the Western Indian Ocean (Poupin et al. 2013). Aldabra as a research base is in a privileged position to unravel long held questions on *B. latro*. Its strict protection from human disturbance provides the opportunity to investigate the potential for this species to persist in the face of global climatic changes and provide important lessons for other managed and unmanaged populations elsewhere.

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SUPPLEMENTARY MATERIAL

The supplementary materials for this article can be found online at:

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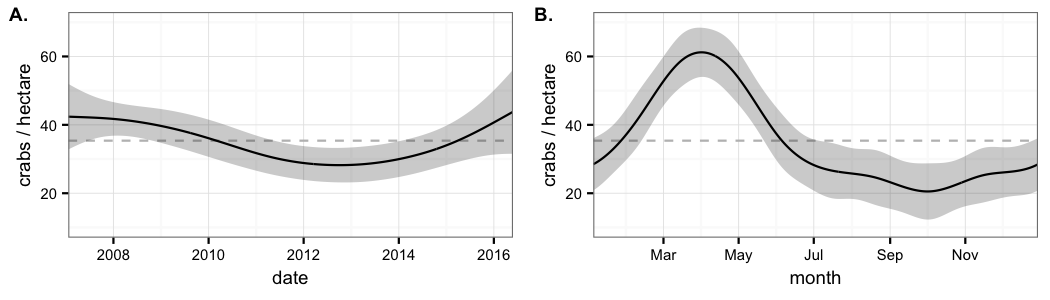
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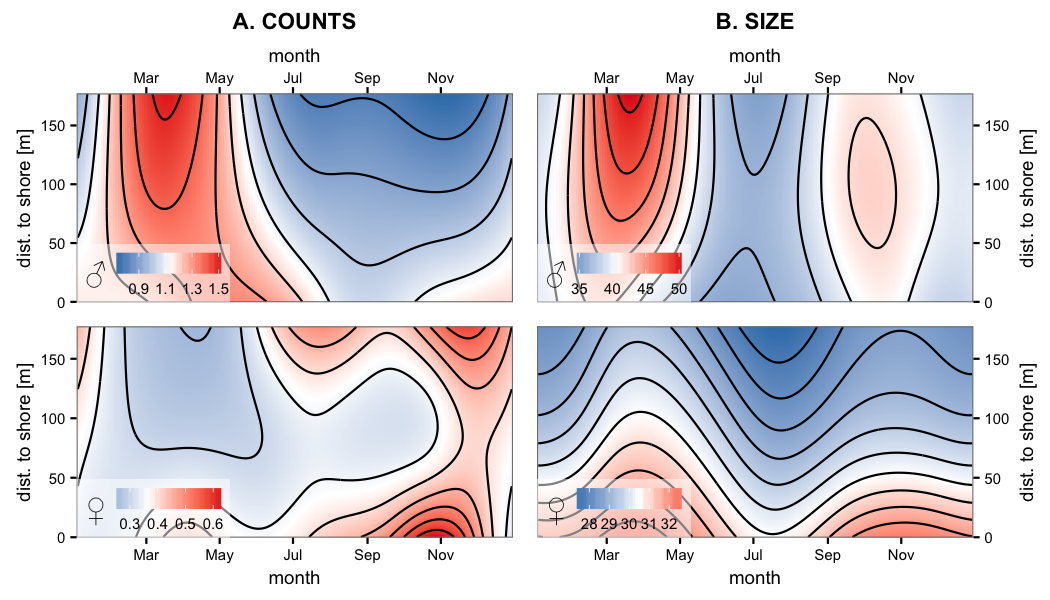
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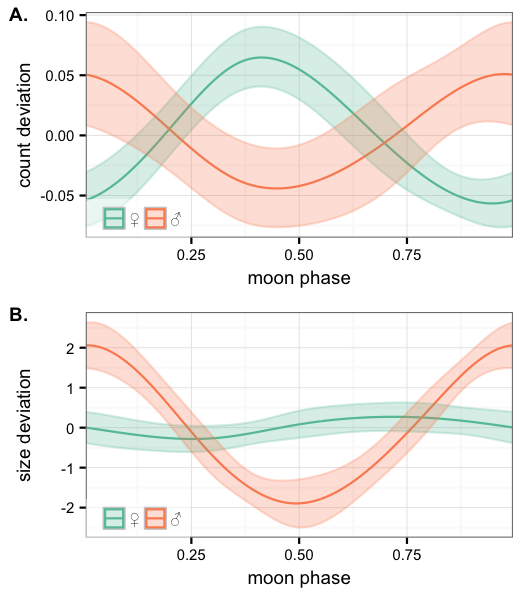
FIGURES

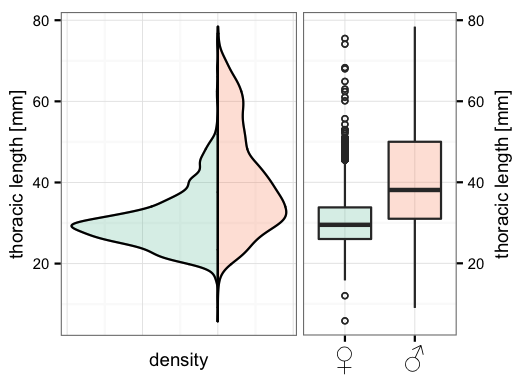
**Figure 1.** Aldabra Atoll and monitoring transects for *Birgus latro*.

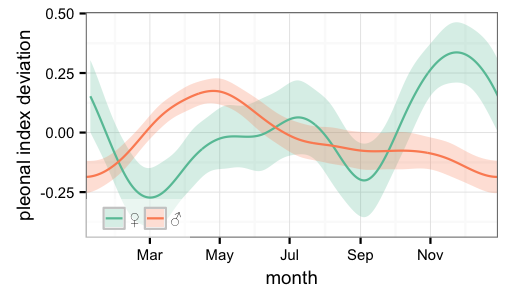
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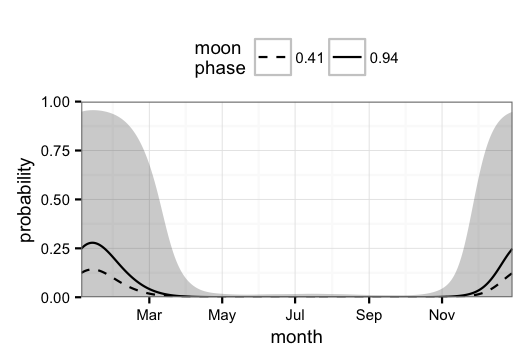
**Figure 2.** *Birgus latro* density on Aldabra Atoll (A) over the years 2007–2016; and (B) over the yearly cycle. The solid lines show the values predicted by the Generalised Additive Model, while grey ribbons depict the standard error. The dashed lines indicate the mean *B. latro* density.

**Figure 3.** Contour plots of the effect of time of the year and distance from shore on (A) the counts and (B) the size. Top panels represent male *Birgus latro* and bottom panels represent female *B. latro*. In all panels, shades of red and blue indicate values larger and smaller than the average respectively.

**Figure 4.** Association between the phase of the moon and (A) the count and (B) the size of encountered female (green) and male (orange) *Birgus latro* on Aldabra*.* Y-axes show the effect on the mean counts (0.36 females; 1.13 males) and the mean sizes (thoracic length: 30.5mm for females; 40.6mm for males) per transect section respectively. The solid lines show the values predicted by the Generalised Additive Model, while ribbons represent the standard error. The phase of the moon is defined as 0 and 1 for new moon, 0.25 for first quarter, 0.5 for full moon, and 0.75 for last quarter (Meeus 1982).

**Figure 5**: Size distribution of female (green) and male (orange) *Birgus latro* encountered on Aldabra.

**Figure 6**: Association between time of the year and the mean pleon size for *Birgus latro* females (green) and males (orange) on Aldabra. Pleon size was estimated using an index between 1 and 4 (see text for category descriptions).

**Figure 7:** Probability of encountering an ovigerous *B. latro* female during a survey on Aldabra from 2007–2016. The solid and dashed lines correspond to the maximum and minimum encounter probability during the moon cycle, respectively. A moon phase of 0.41 corresponds to about three days before full moon and 0.94 to around two days before new moon (Meeus 1982). Grey ribbon indicates confidence interval of the mean probability across the year.

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