



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

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ABSTRACT: *Birgus latro*, the largest terrestrial arthropod in the world, has undergone a substantial decline globally over the last decades, with only a few healthy populations remaining where they are actively protected. We aimed to quantify demographic and spatio-temporal dynamics of a protected population of *B. latro* on Aldabra Atoll (Seychelles). Based on results along 2 transects on the atoll from 2007 to 2016, we calculated an average (\pm SE) density of 23.7 ± 1.1 ind. ha⁻¹. This suggests a population of around 5000 *B. latro* in the coastal area of Picard Island, which is likely to be an underestimate due to the cryptic nature of the species. The average density within the study area was stable over the study period, and over the yearly cycle, the population exhibited high spatial and temporal variability in count, size and sex ratio and in association with the lunar cycle. Aldabra's *B. latro* population is male-biased (3:1 male:female) and sexually dimorphic, with males being larger than females. Males and females moult at different times of the year, and the breeding season overlaps with the region's wet season (December–March) and was in synchrony with the lunar phase. *B. latro* on Aldabra present colour polymorphism in a 4:1:1 ratio of orange:blue:intermediate (mixture of orange and blue). Results confirm that Aldabra is an important refuge for *B. latro* and potentially a natural source population for other areas in the region. Similar long-term studies on *B. latro* are encouraged to improve knowledge on the species and to support conservation actions to halt the species' decline.

KEY WORDS: Arthropod conservation · Population size · Spatio-temporal variability · Seasonal dynamics · Moulting · Reproductive season · Indian Ocean

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1. INTRODUCTION

The global decline of wildlife populations is now well described (WWF 2020). These alarming declines are a result of anthropogenic disturbance to ecosystems. While the loss of populations is well documented for vertebrates, the picture is less clear for

invertebrates (Collen et al. 2012), yet invertebrates dominate many ecosystems in terms of biomass and play a critical role in ecosystem functioning (Wilson 1987, Baillie et al. 2010). Furthermore, the spatial and temporal dynamics of invertebrate taxa of conservation concern are poorly understood (Collen et al. 2012), because continuous studies over multiple

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years on invertebrates are limited. Defining invertebrate population status and trends is therefore essential to understand the extent and magnitude of the current extinction crisis. In the face of this decline, effectively managed protected areas serve as refuges where species populations still thrive, and communities are larger and more diverse (Barnes et al. 2016, Gray et al. 2016, Sala & Giakoumi 2018). Such populations can act as a key reference for species monitoring and as indicators for conservation management.

The largest terrestrial arthropod, the coconut crab *Birgus latro*, faces major conservation threats globally and has been recently re-classified on the IUCN Red List from Data Deficient to Vulnerable (Cumberlidge 2020). Over the last few decades, the range of this species across the tropical Indo-Pacific region, as well as the size and distribution of populations, has substantially decreased in human-inhabited areas (Schiller 1992). This decline is mostly attributed to loss of habitat, predation on juvenile stages by invasive species such as rats and unmanaged harvesting for human consumption (Laidre 2018a).

B. latro populations persist in locations where they are being actively protected. In the Indian Ocean, the distribution of *B. latro* is now largely confined to Aldabra Atoll (Seychelles), the Chagos Archipelago (British Indian Ocean Territory), Christmas Island (Australia) and Chumbe Island (Tanzania) (Cumberlidge 2020). *B. latro* is locally extinct in Mauritius and is believed to no longer occur on Mayotte and the Comoros Islands, although a few individuals have recently been re-discovered on Glorieuses Islands 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 the Seychelles in low incidence, and the species has been occasionally recorded on some of the outer Seychelles islands (Poupin et al. 2013).

Where they occur, coconut crabs play an important ecological role in island ecosystems (Paulay & Starmer 2011, Laidre 2017). The omnivorous crabs feed on a variety of plants and animals, and actively scavenge (Krieger et al. 2016); as scavengers, they remove rotting material and help to decompose leaf litter, and their consumption of seeds and seedlings controls plant numbers (Alexander 1979). As the species breeds by means of marine larvae, it contributes to the transfer of energy and material between land and sea (Hamasaki et al. 2011). *B. latro* also actively hunts (Krieger et al. 2016, Laidre 2017), suggesting that it may function as a top predator in island eco-

systems (Laidre 2018a). Furthermore, *B. latro* contributes to soil aeration and erosion through burrowing activities (Laidre 2018b), and its juveniles are a food source for birds (Alexander 1979).

On Aldabra, *B. latro* has benefited from complete protection since the designation of the atoll as a Special Reserve in 1981. The reserve is strictly used for conservation and research, with no permanent human habitation, and is regularly patrolled for unauthorized boats and illegal poaching. *B. latro* is abundant and widely distributed across the atoll, inhabiting rock crevices and holes, vegetation and sandy areas (Grubb 1971). The species is an important scavenger of dead Aldabra giant tortoises *Aldabrachelys gigantea* and preys on marine turtle eggs and hatchlings (Haig 1984). Although it is one of the few remaining viable populations in the Indian Ocean, the status and ecological characteristics of Aldabra's *B. latro* population have never been documented. Furthermore, as a protected atoll with minimal human disturbance, Aldabra provides an opportunity to understand if population changes are caused by ecological or climatic drivers, as opposed to anthropogenic influences.

Here, we investigated population characteristics, dynamics and behavioural patterns of *B. latro* on Aldabra over a 9 yr period between 2007 and 2016, in which fortnightly counts and biometric data were collected. We aimed to: (1) estimate population density and temporal patterns in population numbers; (2) identify habitat preferences and activity patterns; (3) assess sex ratio and population size distribution; (4) determine moult cycles (i.e. whether there is synchronous seasonal moulting) and timing of breeding and whether this is related to the lunar phase; and (5) assess colour morph ratio of the population. We provide baseline information on the life history and population dynamics of one of the few remaining relatively pristine populations of *B. latro* relevant to future monitoring and conservation strategies for this species.

2. MATERIALS AND METHODS

2.1. 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. The atoll has been protected since 1968 and was inscribed as a UNESCO World Heritage Site in 1982. It is ca. 1100 km south-west of Mahé, the main island of the Seychelles, and ca.

400 km north of Madagascar (Fig. 1). Aldabra is composed of a characteristic highly pitted and eroded coral limestone formation called ‘champignon’ (Stoddart & Wright 1970). 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 defined by 2 distinct seasons: the wet season caused by the north-west monsoon lasts from November to April (Stoddart & Mole 1977), while the dry season lasts from May to October, dominated by south-east trade winds.

2.2. Survey design and sampling

The distribution of *Birgus latro* is structured by distance from the coastline (Schiller 1992). Population surveys of *B. latro* were conducted along 2 transects established on existing paths at different distances from the shore (Fig. 1) on Picard, one of Aldabra’s 4 islands. Both transects were divided into 50 m sections. The ‘shore’ transect was 1.4 km long and 1–26 m from the shore (high water mark). The ‘inland’ transect was 1.8 km long and 38–177 m from the shore. Each transect was surveyed (2 people walking

the transects, taking an average of 90 min) after sunset (19:00–22:00 h), every 2 wk 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: (1) distance to the mid-transect line (estimated to nearest metre); (2) sex (female *B. latro* possess 2 large, feathery pleopods on the ventral surface of their abdomen to support their egg-masses; Fletcher 1993), and whether they were carrying eggs; (3) thoracic length (linear distance between anterior and posterior borders of the thoracic groove, measured with Vernier callipers to the nearest mm; see Fig. 2 in Drew et al. 2010); (4) moult, indicated from the degree of pleonal expansion (*B. latro* abdomens swell considerably prior to moulting and the proximity of the next moult can be gauged by the degree of pleonal expansion; Amesbury 1980, Fletcher et al. 1990, Drew et al. 2010) using a 4-level categorical scale (where 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; category 2: pleon slightly swollen and fleshy abdomen visible between first

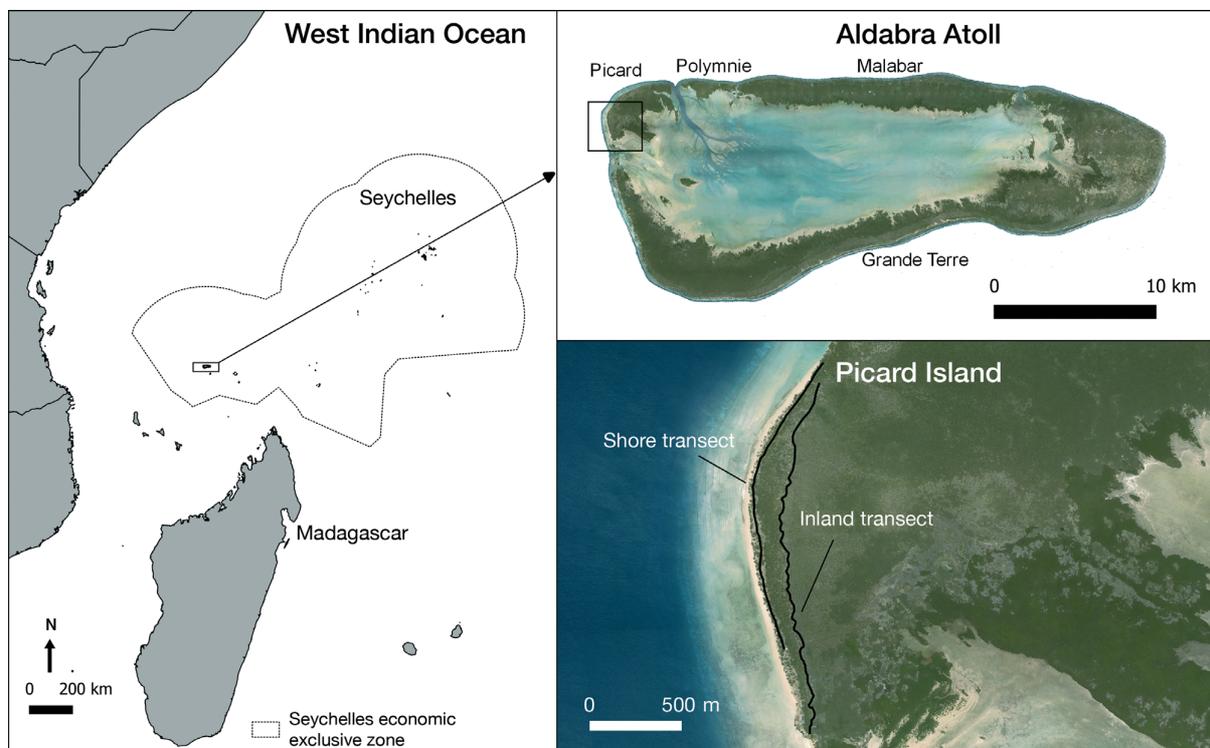


Fig. 1. Aldabra Atoll, Seychelles, and location of monitoring transects for *Birgus latro*

and second plates, and somewhat visible between second and third plates; category 3: pleon swollen and fleshy abdomen clearly visible between first, second and third plates, and somewhat visible between third and fourth plates; and category 4: strongly swollen pleon with fleshy abdomen visible between all tergal plates; see Figs. S1–S5 in the Supplement at www.int-res.com/articles/suppl/m665/p103_supp.pdf); and (5) colour morph (*B. latro* occurs in different colour variants across its range but is commonly distinguished into a red and blue morph; Nokelainen et al. 2018), judged by the colour of the dorsal carapace and underside of the front claws. In our study we used 3 categories: 'orange' when the individual had an orange carapace and white claws, 'blue' when the individual had a blue carapace with blue and white claws or 'intermediate' when the carapace and claws were a mixture of orange and blue (Figs. S2–S6).

2.3. Habitat classification

To control for potential habitat effects, we visually assessed the dominant habitat category in each 50 m transect section. This was classified into 8 habitat categories; open mixed scrub, exposed surface, *Casuarina equisetifolia* and coconut, grasses, sand, dense *Pemphis acidula* bush, mangrove and cham-pignon (for more details about the different categories, see Walton et al. 2019).

2.4. Data analysis

2.4.1. Density and abundance

We estimated the density of *B. latro* in R 3.5.2 (R Core Team 2018) using the hierarchical distance sampling model of Royle et al. (2004) implemented in the package 'unmarked' (Fiske & Chandler 2011). We used the numbers of individuals within 5 distance categories (0–1, 1–2, 2–3, 3–4 and 4–5 m) from the mid-transect line to estimate the overall density and evaluated the association between habitat with both the detectability and density of *B. latro*.

Due to the large number of surveys (see Section 3), we used an approximate form of model selection to ascertain the overall importance of habitat. Specifically, we fitted 4 models for each survey using a half-normal detection function. In the first, we assumed that habitat influences both detectability and density. In the second and third models, we assumed that

habitat only influences detectability or density, respectively. In the fourth model, we assumed that both detectability and density are independent from the habitat. For each survey, we compared these 4 models using Akaike's information criterion (AIC) and determined the difference between each model's AIC and the smallest AIC (Δ AIC). Finally, we calculated the median Δ AIC for each model across all surveys to determine which of the 4 models performed better overall. These models suggested that habitat had a limited influence on detectability (see Section 3), and therefore *B. latro* counts in our study can provide an indication of their observable density.

Next, we used a generalised additive model (GAM) to determine whether *B. latro* counts varied significantly (1) over the years, (2) over the annual cycle and (3) 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, with models with the lowest AIC values presenting the most parsimonious (best fitting) models. 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 0 to 1, with both extremes corresponding to new moon, 0.25 to the first quarter, 0.5 to full moon, and 0.75 to the last quarter (Meeus 1982). To assess potential sex-specific differences at a finer spatial and temporal scale, we used a GAM for male and female individuals independently. It is also plausible that environmental factors interact with habitat requirements. Because Aldabra's weather is highly seasonal and environmental factors like rainfall, temperature and wind are highly correlated with the day of the year, an interaction between day of the year and distance from shore was included in the model (Wood 2006b). Competing models, from which we removed one explanatory variable at a time, were assessed using the AIC.

2.4.2. Sex ratio and size

We calculated overall 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. For males, individuals with a thoracic length ≥ 28 mm were considered adults (Fletcher et al. 1990, Drew et al. 2010). For females, the thoracic length threshold was 23.5 mm, which is based on the minimum size of ovigerous females we observed. We used thoracic length to determine

whether the Aldabra population exhibits sexual size dimorphism. We evaluated the difference by visually examining the size distribution for both sexes and performing Mann–Whitney tests on the thoracic length measurements. Similar to the counts, we used a set of GAMs to infer the effects that time of year, distance from shore and lunar phase may have on the sizes of individuals encountered.

2.4.3. Moulting and reproduction

We constructed 2 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 and 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 predictors.

2.4.4. Colour morph ratio

We assessed colour morph ratio of the overall sampled population and of females and males separately using individual counts. We tested for association between gender and colouration, and transect and colouration using Pearson's chi-squared tests.

3. RESULTS

3.1. Density changes over time and population estimate

Overall, 265 surveys were completed with 8607 *Birgus latro* sighted on the 2 transects over the study period. Overall, the most parsimonious distance sampling models were those that assumed no influence of habitat on either detectability or density. Specifically, the median ΔAIC of models in which we assumed that both detectability and density are independent from the habitat was 0.35 (min. 0, max. 71.5), while that of the models in which we assumed that habitat influenced both was 8.35 (min. 0, max. 22.2). The median ΔAIC of models in which habitat influences only detectability or density was 3.25 (min. 0, max. 45.2) and 4.35 (min. 0, max. 38.7) respectively, which indicates that the models that ignored habitat effect are between 4 and 55 times

more likely than the other 3 model types (based on the Akaike weights of competing models; Wagenmakers & Farrell 2004, Fig. S7). The high variability in ΔAIC values within each model type suggests that, for some surveys, habitat differences help explain the variability in detectability and/or density. Indeed, the median Nagelkerke (1991) R-squared index of all models compared to the null was 0.19 (min. 0, max. 0.69; Fig. S8). However, the differences across model types indicate that overall *B. latro* densities and abundances can be calculated without accounting for habitat effects (see 'Model outputs' in the Supplement).

The results from the chosen distance sampling models indicate that observed *B. latro* density in the study area was 2.95–105.36 ind. ha⁻¹, averaging 23.7 ± 1.1 ind. ha⁻¹ (mean \pm SE) across both transects. The density varied between years, but with no apparent long-term trend (Fig. 2A). The overall mean detectability of *B. latro* was 0.48, which corresponds to an effective strip half-width of 2.4 m. We calculated 2 estimates of the population size of *B. latro* on

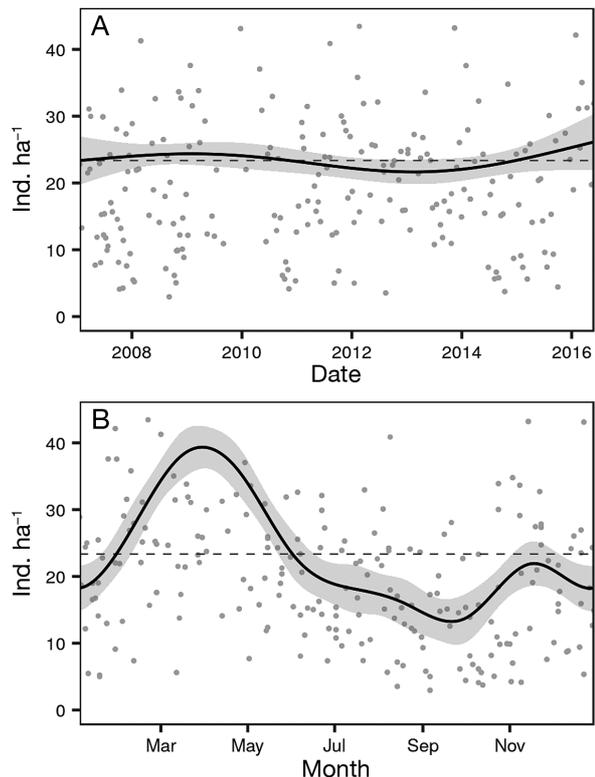


Fig. 2. *Birgus latro* densities (A) between 2007 and 2016 and (B) over the yearly cycle. Dots: *B. latro* densities; solid lines: density predicted by the generalised additive model; grey ribbons: standard error of the prediction; horizontal dashed lines: mean *B. latro* density

Picard: (1) by extrapolating the density to the approximate area of the habitat type surveyed close to the Picard coastline (208 ha, Fig. S9) and (2) since our results revealed that habitat type did not affect *B. latro* density in the study area, we extrapolated the density to the total surface area of the island (875 ha; Walton et al. 2019). The first method estimated ca. 5000 individuals, while the second produced a conservative estimate of ca. 20 000 individuals on Picard.

3.2. Effect of season, habitat and lunar phase

All 3 explanatory variables were associated with the number of crabs encountered (see ‘Model outputs’ in the Supplement). The number of *B. latro* encountered was above average (>23.7 ind. ha⁻¹) between February and June, with a clear peak in April, and below average between July and December (Fig. 2B). The number of *B. latro* males and females was strongly influenced by the time of year and the distance from shore. In general, more males were encountered in January–June than in 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 counts were higher on both shore and inland transect areas, particularly between October and November (Fig. 3A).

There were significant and distinct effects of lunar phase on males and females separately (Fig. 4A). Females were most likely to be encountered during periods of full moon, and males during new moon.

3.3. Sex ratio and size

The overall *B. latro* sex ratio of observed individuals was approximately 3:1 (76% male; $n = 6536$), and was similar for sexually mature individuals (3:1, 76% male; $n = 5682$). This ratio shows temporal and spatial variation, ranging from 57% of individuals encountered being male during November along the shore transect, to 86% during March along the inland transect.

Marked sexual size dimorphism was observed (Fig. 5), with males being larger (mean \pm SE thoracic length: 40.6 ± 0.16 mm; range: 9–78 mm; $n = 6536$) than females (30.5 ± 0.16 mm; range: 6–76 mm; $n = 2071$). Although the overall size probability distribution of males and females did not differ ($n_{\text{males}} =$

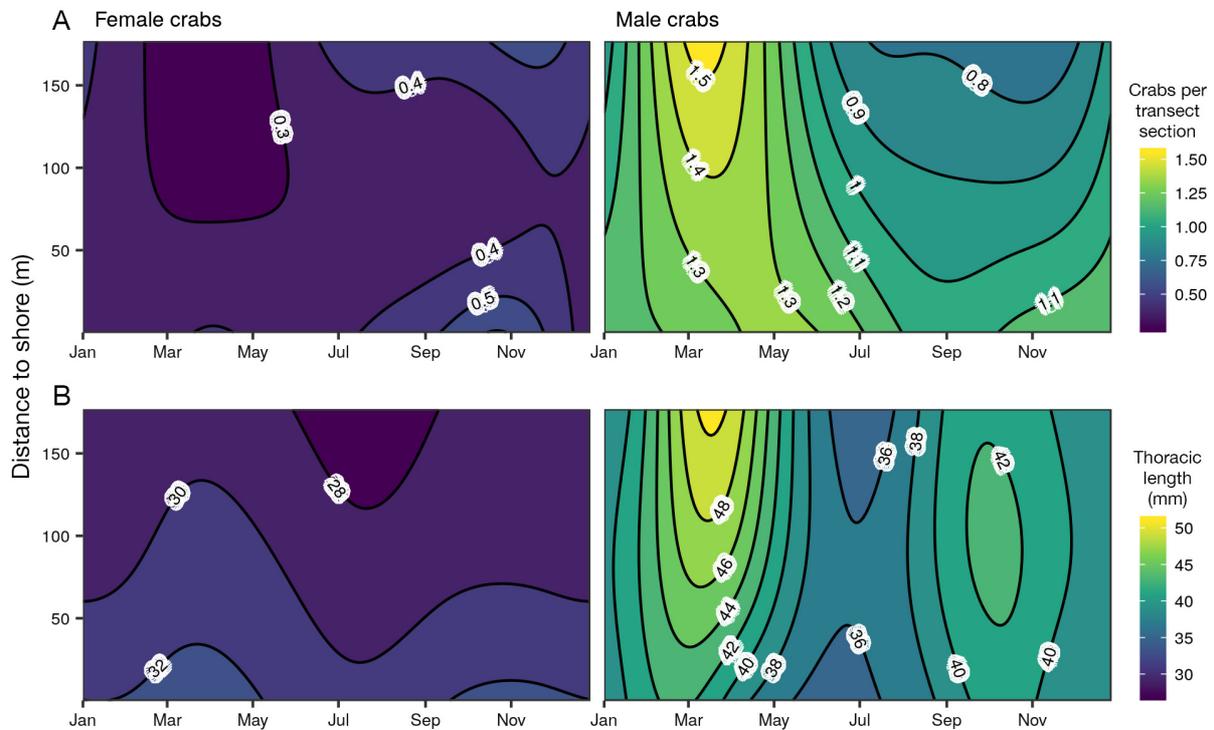


Fig. 3. Contour plots of the effect of time of the year and distance from shore on (A) counts and (B) mean size of male and female *Birgus latro*

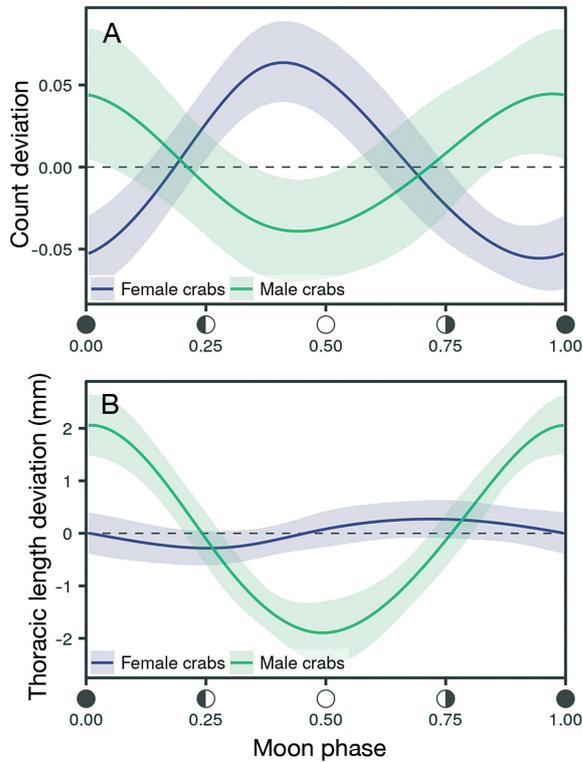


Fig. 4. Association between lunar phase and (A) count and (B) size of *Birgus latro* on Aldabra. Y-axes show the marginal effect on mean counts (0.36 females; 1.13 males) and mean sizes (thoracic length; females: 30.5 mm, males: 40.6 mm) per transect section, respectively. Solid lines: values predicted by the GAM; ribbons: standard error. Observed data are depicted in Fig. S10

6182, $n_{\text{females}} = 1994$; 2 sample Kolmogorov-Smirnov test, $p = 0.725$), males had more individuals of larger sizes than females. Specifically, the size of male individuals in the upper decile was significantly larger than that of females (Mann-Whitney of upper decile, $n_{\text{males}} = 666$, $n_{\text{females}} = 197$; $p < 0.001$). The mean size of both males and females encountered showed 2 distinct and synchronous peaks during the year, one between October and December, and another more pronounced peak between March and May (Fig. 3B).

All 3 explanatory variables included in our models had an important effect on the size of *B. latro* encountered (see 'Model outputs' in the Supplement). 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 size of males encountered, however, is inconspicuous in December and January and

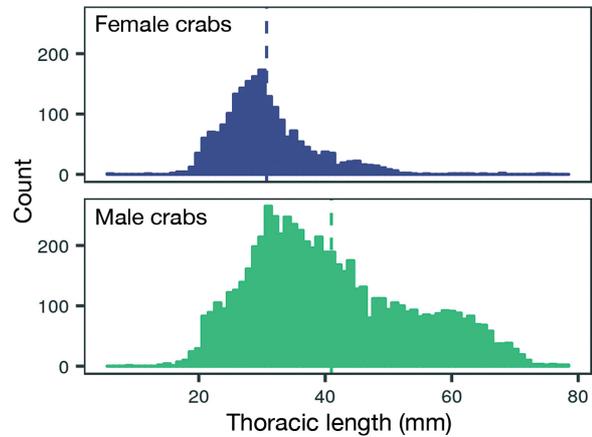


Fig. 5. Size distribution of female and male *Birgus latro* encountered on Aldabra. Dashed lines: mean values for each distribution

from June to August (Fig. 3B). Furthermore, males encountered close to new moon were larger than those encountered close to full moon, while females showed no size variation over the lunar cycle (Fig. 4B).

3.4. Moulting and reproduction

Males with a thoracic length >30 mm exhibited an annual cycle in pleon size, with a peak in April–May (Fig. 6), while female pleons were largest in November, with a less conspicuous peak of pleon expansion in June–July (Fig. 6). Throughout the monitoring period, only 14 *B. latro* females (of 2071 individuals

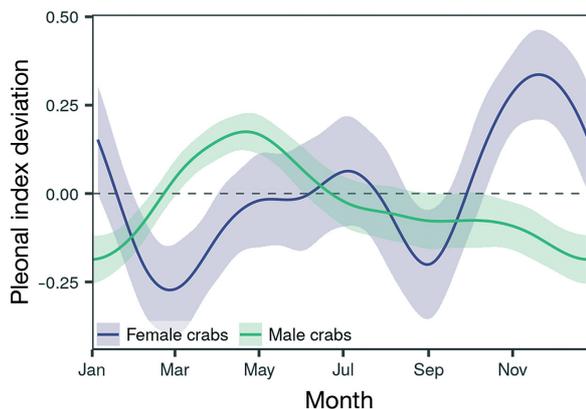


Fig. 6. Association between time of the year and the mean pleon size for *Birgus latro* females and males on Aldabra. Pleon size was estimated using an index between 1 and 4 (see Section 2.2 for category descriptions). Observed data are depicted in Fig. S11

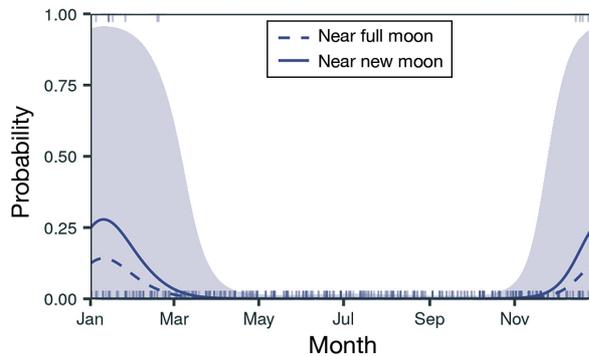


Fig. 7. Probability of encountering an ovigerous *Birgus latro* female during a survey on Aldabra during 2007–2016. Solid and dashed lines: maximum and minimum encounter probability during the moon cycle, respectively; grey ribbon: confidence interval of the mean probability across the year; vertical lines on the top and bottom of the panel: observations. The size distribution of ovigerous female *B. latro* encountered is given in Fig. S12

in 12 of 484 transects) were ovigerous, with the timing of encounters indicating a reproductive season between December and March and some evidence suggesting an increased encounter probability just before the new moon (Fig. 7).

3.5. Colour morph ratio

The overall colour morph ratio of observed individuals was approximately 4:1:1 (67% orange, 17% blue, 16% intermediate). This ratio was similar for males and females (male: 67% orange, 17% blue, 16% intermediate; female: 68% orange, 15% blue, 16% intermediate), and colouration was not associated with sex ($\chi^2 = 1.913$, $df = 1$, $p = 0.167$) or transect ($\chi^2 = 0.743$, $df = 1$, $p = 0.38$).

4. DISCUSSION

Our study presents results from the longest continuous monitoring programme of *Birgus latro* to date and confirms that Aldabra hosts a substantial *B. latro* population in the Indian Ocean (with ca. 5000 individuals along Picard's coastline, which is only the third largest island of Aldabra; Fig. 1). Aldabra appears to have a lower density estimate of *B. latro* compared to other unharvested populations (i.e. Aldabra: 23.7 ind. ha⁻¹; Ikuren Islet, Enewetak Atoll, Marshall Islands: 147 ind. ha⁻¹; Taiaro, French Polynesia: 190 ind. ha⁻¹, Chauvet & Kadiri-Jan 1999; Chagos Archipelago: 300 ind. ha⁻¹, Vogt & Guzman 2013; Christ-

mas Island: 67–160 ind. ha⁻¹, with partial protection, Drew et al. 2010); however, comparisons should be made with caution, as the methods and lengths of the studies differ. Chumbe Island (Tanzania) and Palmyra Atoll also host unharvested populations of *B. latro* (Cumberlidge 2020). The stable population on Picard suggests that *B. latro* is not declining on Aldabra. Moreover, Aldabra's other islands, including 2 that are much larger than Picard, are uninhabited and even less disturbed, and *B. latro* populations are unlikely to be declining on any of them. This suggests that declines elsewhere in the Western Indian Ocean are due to anthropogenic causes.

Our total population estimate of Picard (ca. 20 000 *B. latro*) would be improved by expanding the monitoring to other parts of Picard and Aldabra. The study location was chosen due to logistical feasibility and accessibility. Moreover, the resolution at which habitat influence on abundance was measured in our study is well below the home range of individual *B. latro* (Krieger et al. 2012), and habitat type may therefore play an important role in *B. latro* distribution at the landscape scale. Furthermore, burrow searches were not included in our survey. Burrow searches account for non-foraging individuals in the study area (Laidre 2018b), suggesting the population could be much larger than estimated on Picard.

We found substantial spatial and temporal heterogeneity in *B. latro* numbers, size and sex. Adult *B. latro* are not sessile but are constantly moving locally and can undertake long-distance (up to 4.2 km) movements (Krieger et al. 2012). This movement pattern is linked to their complex life cycle associated with reproductive migrations, moulting requirements, availability of resources and behavioural variations associated with the environmental conditions of the site (Drew & Hansson 2014). The peak in the number of crabs observed from February to June is largely due to an increase in the number of active males in the study area. During this period, large males favoured inland areas, presumably richer in resources and burrows, while females and smaller males were mostly encountered in near-shore habitats. Drew & Hansson (2014) noted that large males often actively drive out females and smaller males from preferential feeding areas. Later in the year, from July to December, the overall number of *B. latro* encounters drops, again particularly for large males, likely due to moulting during the drier months of the year (Fletcher et al. 1991). *B. latro* undergo moulting in shallow burrows to minimize vulnerability to predation and desiccation (Drew et al. 2010). Contrastingly, female counts increased later in the year,

potentially exploiting the available resources in preferred feeding areas after these have been vacated by large males (Drew & Hansson 2014). Female counts peaked between September and December near-shore, which coincided with a period in which mature males are commonly encountered. This suggests a breeding migration of female *B. latro* to the shore to release larvae into the ocean (Schiller et al. 1991). Studies have shown that male *B. latro* also move closer to shore for reproduction for a shorter period (Krieger et al. 2012, Sato & Yoseda 2013). Sexual maturity of males in our study was based on a thoracic length of >28 mm, but smaller males can also be sexually active although unsuccessful in mating until they grow larger (Sato 2012).

The sex ratio appears to be biased towards males, which may be a consequence of the sampling design. Transect studies typically report male-biased ratios, compared to grid sampling, and are sensitive to variations in habitat use between sexes (Drew et al. 2012). Female *B. latro* have an affinity to denser vegetation and are less likely to be encountered on transects along existing paths (Drew et al. 2012). Furthermore, James (2008) suggested that female *B. latro* are more sedentary outside the breeding season compared to males, increasing the chances of encountering male *B. latro* in surveys along paths. Behavioural sex differences should therefore be considered when designing *B. latro* population surveys.

All studied populations of *B. latro* to date show sexual dimorphism, with males being consistently larger than females (Drew et al. 2010, Anagnostou & Schubart 2014). This is also the case on Aldabra, where the maximum thoracic length of both male and female *B. latro* recorded on Picard is larger than other studied populations (male/female thoracic length [mm]): Aldabra: 78/76, present study; Igurin, Marshall Islands: 74/52, Guam, Mariana Islands: 76/47, Niue: 53/36, Lifou, New Caledonia: 76/46.5, Vauvilliers, New Caledonia: 76.5/57.5, Taiaro, French Polynesia: 66.5/60, Chauvet & Kadiri-Jan 1999, Drew et al. 2010; Christmas Island: 72.5/50.3, Anagnostou & Schubart 2014). The larger sizes of male and female *B. latro* on Aldabra may be attributed to the non-harvesting of the population, since larger individuals are usually targeted during harvesting (Sato 2012).

Based on encounters of ovigerous females, the reproductive season of *B. latro* on Aldabra presumably occurs between December and March, during the rainy season. This corresponds with the period of highest peak of female pleonal expansion in November to December, which is related to gonad development (Fletcher et al. 1991, Sato & Yoseda 2009), and

also coincides with the reproductive seasons in other *B. latro* populations in the southern hemisphere (e.g. Christmas Island, New Caledonia; Drew et al. 2010). Moreover, signs of synchrony with the lunar phase were found; most ovigerous females were encountered during surveys close to new moon. This synchrony is likely related to the timing of spawning or egg extrusion (Sato & Yoseda 2009). The few studies detailing *B. latro* mating behaviour indicate that courtship and copulation are brief (e.g. Schiller et al. 1991). The time between mating and egg extrusion is unknown, but as females have no seminal receptacle, it is thought that egg extrusion occurs shortly after mating (Sato & Yoseda 2009, Drew et al. 2010). Egg maturation, from egg extrusion to hatching, is 25–45 d, with most eggs maturing 27–29 d after extrusion (Schiller et al. 1991, Sato & Yoseda 2009). Thus if egg extrusion occurs around the new moon phase, most larvae will hatch with the next new moon phase (Sato & Yoseda 2009). An important conservation implication from this finding is that protection of *B. latro* is likely to be most effective if beaches within its range are protected from exploitation particularly during new moon. This would curb harvesting of the species at a time when its occurrence is predictable, and many reproductively mature females are highly vulnerable.

Based on our colour categories, *B. latro* on Aldabra is polymorphic, present in orange, blue and intermediate colour variants in the ratio of 4:1:1, respectively. This contradicts reports stating the species is present only in orange/red colour on Aldabra (Altevogt & Davies 1975, Caro & Morgan 2018). The higher proportion of orange *B. latro* on Aldabra is similar to observations on many other islands where *B. latro* occurs in a 3:1 red:blue ratio (Caro & Morgan 2018). Our intermediate colour category (a mixture between orange and blue) is also prevalent on Christmas Island, where *B. latro* occurs in a 1:2:1 ratio between the red dorsum/white ventrum, red dorsum/blue ventrum and blue dorsum/blue ventrum (Caro & Morgan 2018). Although colour assessment and terminologies vary among studies, colour polymorphism in *B. latro* is not associated with sex, size, chelal pinch-force, behavioural disposition or background habitat matching, and its functional significance remains unclear (Caro et al. 2019).

B. latro has faced a dramatic decline globally over the last decades, which is expected to continue (Cumberlidge 2020). Our study confirms that healthy populations of *B. latro* can persist where there is active protection against harvesting and protection of the species' habitat, and we highly recommend this conservation action to halt the species' decline.

Furthermore, protected locations like Aldabra, which hosts a relatively large and stable *B. latro* population on Picard, may be an important natural source population for other areas within its known historic range (Poupin et al. 2013). The *B. latro* population on Aldabra exhibits high spatial and temporal variability, mainly due to life history traits and resource availability, therefore long-term studies are encouraged to understand behavioural patterns and ecological requirements of this species. Similar studies are recommended for other *B. latro* populations to improve the knowledge base and support conservation actions for this invertebrate species.

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