Troubled giants: The updated conservation status of the coconut crab 
(Birgus latro)

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Abstract. The coconut crab, Birgus latro (Linnaeus, 1767), the largest land arthropod in the world, is widely distributed on islands and atolls across the Indian and Pacific Oceans, but there is strong evidence that populations are declining in the face of anthropogenic threats. Here we review the data on population trends, habitat availability, distribution, and threats worldwide used by the IUCN Red List of Threatened Species to reassess the global conservation status of B. latro. The results indicate that crab populations are suffering declines in many parts of their range associated with urbanisation and coastal habitat fragmentation driven by increasing human populations and overexploitation. Immediate threats to B. latro include habitat loss, overharvesting, introduced predators, and road kills, while future threats potentially include sea level rises and ocean acidification. These widespread threats, coupled with the lack of protective conservation measures in most areas, together justify the elevated global extinction risk assessment change from Data Deficient to Vulnerable A2cd+4cd (IUCN version 3.1).

Key words. conservation, exploitation, extinction threat, land-use change, terrestrial hermit crab

INTRODUCTION

The coconut crab or robber crab, Birgus latro (Linnaeus, 1767), is a terrestrial hermit crab (Anomura: Coenobitidae) and the largest land arthropod in the world, weighing over 4 kg, with a 1-metre leg span. This charismatic invertebrate is found over a vast area of the Indian and Pacific Oceans, where it now lives on small, scattered island chains (archipelagos) and coral atolls that offer a wide range of topography and habitat types (Fig. 1). Here we collate the data now available on B. latro’s ecology, distribution, threats, population trends, and protection levels (Kadiri-Jan & Chauvet, 1998; Chauvet & Kadiri-Jan, 1999; Sato & Yoseda, 2008; Drew et al., 2010; Orchard, 2012; Patankar & D’Souza, 2012; Poupin et al., 2013; Drew & Hansson, 2014; Helagi et al., 2015; Caro et al., 2020). These studies, which were used for the most recent conservation assessment of B. latro, present a growing body of evidence that these crabs are declining or even extirpated in many parts of their range, due primarily to the widespread destruction of their coastal habitat and the overharvesting of adults. In July 2020, the International Union for the Conservation of Nature Red List of Threatened Species (hereafter referred to as the Red List) elevated the extinction risk status of B. latro from Data Deficient (DD) (Eldredge, 1996) to Vulnerable (Cumberlidge, 2020). In this work, we review the conservation implications of this change for this now globally threatened species. The listing of B. latro as threatened with extinction now warrants additional prioritisation for conservation action because it is an evolutionarily distinct and globally endangered species (EDGE) (Isaac et al., 2007) in an endangered monotypic genus (Birgus), and is the only living representative of a unique phylogenetic lineage (Wolfe et al., 2019).

METHODS

The updated extinction risk assessment of Vulnerable A2cd+4cd for B. latro (Cumberlidge, 2020) is based on the IUCN (2012) Red List Categories and Criteria (version 3.1). The Red List protocols aim to evaluate a species’ extinction risk according to five criteria depending on the data available: (A) population size reductions, (B) geographic range changes, (C) small population sizes that are declining, (D) very small
or restricted populations, and (E) quantitative analyses of
extinction risk. A wealth of assessment data available for
*B. latro* includes information on distribution, habitats, and
threats (criterion B, the geographic range, either B1 [Extent
of Occurrence, EOO] or B2 [Area of Occupancy, AOO], or
both), and population size and trends (criteria A, C, and D).
Geographical, ecological, and threat data were compiled from
literature, museum records, and specialist knowledge. The
EOOs and AOOs were estimated from point locality data
through the open source Geospatial Conservation Assessment
Tool (GeoCAT) (Bachman et al., 2011).

**GEOGRAPHIC RANGE**

*Birgus latro* is widely distributed throughout much of the
Indian and Pacific Oceans, occurring either on oceanic
islands or small offshore islands, but very rarely on larger
inhabited continental landmasses (Figs. 1–3; Tables 1, 2).
Adults and juveniles of *B. latro* are strictly terrestrial, and
locality records indicate a distributional range that stretches
from the east coast of Africa to Indonesia, Micronesia,
Melanesia, and Polynesia, and as far east as Pitcairn Island
in the Pacific Ocean. The range of *B. latro* is so large that
it includes four Biogeographic Realms (Afrotropic, Indo-
Malayan, Australasian, and Oceanic) (Fig. 1). The northern
limits of *B. latro* reach beyond the Tropic of Cancer in the
Pacific Ocean, as far north as the Ryukyu Islands (Kagoshima
Prefecture) in Japan (26°N) (Yamaguchi & Holthuis, 2001),
while the southern limits extend to the Gambier Islands in
French Polynesia (23°S), close to the Tropic of Capricorn
(Fig. 4). This species is not known to be native to Hawaii
despite reports of its presence in Honolulu (which proved to
be a rare case of human introduction of *B. latro* that failed
to become established). Interestingly, the range of *B. latro*
in the Indian Ocean is much narrower, reaching only 11.5°N
(North Sentinel Islands in the Andaman and Nicobar Islands
in the Eastern Indian Ocean) and 12.6°S (Quisiva Island off
the coast of Mozambique). It is noteworthy that *B. latro* is not
found north of the equator anywhere in the Western Indian
Ocean, and its southernmost locality in this region today
is off the coast of Mozambique (13°S) (Fig. 4). Historical
records, however, show that *B. latro* used to range as far
south as the Tropic of Capricorn on Juan de Nova Island
in the Mozambique Channel and the Mascarenes (between
21 and 23°S) (Fig. 4) (Darwin, 1909; Poupin et al., 2013).

The wide distributional range of *B. latro* has been achieved
by the long-range dispersal capabilities of its planktonic
larvae, which can be carried over great distances by ocean
currents. The pelagic larvae develop at sea for four to six
weeks depending on temperature, during which time the
larvae are distributed widely. The first three weeks or so
are spent as zoeae drifting in the plankton, after which
they metamorphose into actively swimming glaucothoe (or
megalopae) that migrate landwards to shallow seas, where
they sink to the benthos, acquire mollusc shells, and move
onto land (Hamasaki et al., 2009, 2011, 2013a, b, 2015).
The interaction of larval dispersal ability and oceanographic
currents contributes significantly to both their vertical and
horizontal distribution in ocean waters. Onshore recruitment
of young crabs back to their parents’ location depends on
favourable oceanic current patterns that bring the glaucothoe
back to shore. In contrast, dispersal by the terrestrial juveniles
and adults is quite modest, and amounts to only a few
kilometres from the coast at best, because these crabs need
to migrate back to the sea to spawn.

Conservation assessments using the IUCN Red List protocols
under criterion B require the quantification of three items: the
geographic range (EOO), the proportion of the range actually
occupied by this species (AOO), and the number of locations
where this species is known to occur. Cumberlidge (2020)
estimated the EOO as the minimum convex polygon using
Fig. 2. Updated distribution of *Birgus latro* (Linnaeus, 1767) in the Indian Ocean region.

Fig. 3. Updated distribution of *Birgus latro* (Linnaeus, 1767) in the Pacific Ocean region.
Table 1. Islands and the countries to which they belong in the Indian Ocean region, where *Birgus latro* has been reported to occur.

<table>
<thead>
<tr>
<th>Country</th>
<th>Locations</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian Territory</td>
<td>Christmas Island, Cocos (Keeling) Islands (including West Island)</td>
<td>Reyne, 1939; Gibson-Hill, 1947; Rumpff, 1986; Hicks et al., 1990; Drew et al., 2010; Orchard, 2012; Drew &amp; Hansson, 2014; Helagi et al., 2015</td>
</tr>
<tr>
<td>British Indian Ocean Territory</td>
<td>Diego Garcia Atoll, Salomon, Peros Banhos Atoll, Egmont Islands, Chagos Archipelago</td>
<td>Reyne, 1939; Laidre, 2018, 2019</td>
</tr>
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<td>Comoros Islands</td>
<td>Anjouan, Moheli, Grand Comore</td>
<td>Bouchard et al., 2013; Poupin et al., 2013</td>
</tr>
<tr>
<td>India, Andaman Islands</td>
<td>North and South Sentinel, and Little Andaman Islands</td>
<td>Patankar &amp; D’Souza, 2012</td>
</tr>
<tr>
<td>India, Nicobar Islands</td>
<td>Little Nicobar, Great Nicobar (Campbell Bay), Camorta, Menchal, Cabra Islands, Tillanchong</td>
<td>Patankar &amp; D’Souza, 2012</td>
</tr>
<tr>
<td>Mascarene Islands</td>
<td>North Agalega Islands</td>
<td>Reyne, 1939; Poupin et al., 2013</td>
</tr>
<tr>
<td>Mozambique Islands</td>
<td>Ibo and Rolas Islands, Quirimbas Archipelago</td>
<td>Poupin et al., 2013</td>
</tr>
<tr>
<td>Seychelles</td>
<td>Aldabra, Silhouette, Ile Alphonse, Astove, Assumption Island, Cosmoledo Island, Cousine, Aride, Amirantes islands (D’Arros, Desroches), Bijoutier, Coetivy, Assumption, Cosmoledo, Astove, Farquhar, Providence, St. Francois islands</td>
<td>Bowler, 1999; Duhec, 2011; Jupiter et al., 2013; Poupin et al., 2013</td>
</tr>
<tr>
<td>Tanzania, United Republic of</td>
<td>Outlying islands off Pemba and Unguja, the two main islands in the Zanzibari archipelago. These include Chumbe, Mnemba, Fundo, and Kisiwa Panza. Islands in the Dar es Salaam Marine Reserve system including Bongoyo and Mbudy. Remnant populations off Kilwa including Mafia, Songo Songo, Fanjove Islands.</td>
<td>Nordlund &amp; Walther, 2010; Nokelainen et al., 2018; Caro et al., 2020</td>
</tr>
</tbody>
</table>

Table 2. Islands and the countries to which they belong in the Pacific Ocean region, where *Birgus latro* has been reported to occur. Some of this information may be out of date given the age of some references.

<table>
<thead>
<tr>
<th>Country</th>
<th>Locality</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Samoa</td>
<td>Samoa, Swains Island</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Bismarck Archipelago</td>
<td>New Ireland</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Cook Islands</td>
<td>Pukapuka, Nassau, Palmerston Island, Suwarrow Atoll, Rakahanga, Manihiki, Aitutaki, Rarotonga, Takutea Island, Atiu, Mangaia, Penrhyn [= Tongareva], Ma’uke</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Fiji</td>
<td>Aiwa Islands, Yandua</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>French Polynesia</td>
<td>Bora Bora, Tetiaroa, Tuamotu Archipelago (Makatea), Gambier Islands, Society Islands</td>
<td>Reyne, 1939; Chauvet &amp; Kadiri-Jan, 1999; Kingsley, 2021</td>
</tr>
<tr>
<td>USA</td>
<td>Guam</td>
<td>Reyne, 1939; Amesbury, 1980</td>
</tr>
<tr>
<td>Indonesia</td>
<td>East Kalimantan (Indonesian Borneo): Maratua Island; North Sulawesi: Salibabu Island; Central Sulawesi: Pasoso Island, Togean Island, Malenge Island, Batudaka Island, Bokan Island, Labobo Island, Bangkurring Island, Menui Islands; South Sulawesi: Pasi Island; East Java: Masalembu Island; Southwest Sulawesi: Lentea Island, Kadatua Island, Kabaena Island, Siompu Island, Liwutongkid Island; North Maluku: Morotai Island, Ternate Island, Gebe Island, Utu Island, Yoi Island, Liwo Island, Kayoa Island; Maluku: Marsegui Island, Yamdena Island; West Papua: Sain Island, Fam Island, coast of Manokwari, Wairundu Island; Papua: Auki Island, Owi Island, Pai Island, Pakreki Island, Biak Island</td>
<td>Reyne, 1939; Rondo &amp; Limbong, 1990; Ramli, 1997; Monk et al., 2000; Rafiani, 2005; Abubakar, 2009; Jahidin, 2010; Supyan et al., 2013; Pandiangan et al., 2015; Widiyanti et al., 2015; Supyan &amp; Abubakar, 2016; Heryanto &amp; Wowor, 2017; Minawati, 2017; Rahman et al., 2017; Heryanto et al., 2018; Serosero et al., 2019; Sri Hartini (pers. comm.); Fazlur R. Tadeko (pers. comm.); Ricardo F. Tapilatu (pers. comm.)</td>
</tr>
<tr>
<td>Japan</td>
<td>Ryukyu and Ogasawara Islands</td>
<td>Reyne, 1939; Yamaguchi &amp; Holthuis, 2001; Fujita, 2017</td>
</tr>
<tr>
<td>Country</td>
<td>Locality</td>
<td>Citation</td>
</tr>
<tr>
<td>----------------------------------------</td>
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<tr>
<td>Kiribati</td>
<td>Nikumaroro Island, Kiritimati, Vostok Island, Flint Island, Teraina</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Marshall Islands</td>
<td>Ralik Chain, I Gurin (Enewetak Atoll), Ikuren (Enewetak Atoll), Rongelap Atoll, Kwajelin Atoll, Jaluit Atoll</td>
<td>Reyne, 1939; Drew et al., 2010</td>
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<tr>
<td>Federated States of Micronesia</td>
<td>Sorel Atoll, Yap (Caroline Islands)</td>
<td>Reyne, 1939; Buden, 2012</td>
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<tr>
<td>Republic of Nauru</td>
<td>Nauru</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Niue, Republic of Belau</td>
<td>Niue (Lifou Island) in the Marshall Islands</td>
<td>Reyne, 1939; Schiller, 1992; Helagi et al., 2015</td>
</tr>
<tr>
<td>Northern Mariana Islands</td>
<td>Ascuncion, Saipan, Pagan, Northern Islands, Guguan</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Republic of Palau</td>
<td>Kayangel Island (Caroline Islands)</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Papua New Guinea</td>
<td>Wuvulu Island, Purdy Islands</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Philippines</td>
<td>Aparri (Luzon), Balabac, Bantayan, Batanes, Bohol, Bongao, Calayan, Cagayan (Luzon), Cagayanillo, Cebu, Camotes, Dalupiri, Fuga, Laguna (Luzon), Mactan, Marinduque, Mindoro, Olango Island, Polillo, Quezon, Romblon Island, Samar, Santa Cruz, Tawi-Tawi</td>
<td>Reyne, 1939; Perrucho et al., 2018; Subang et al., 2020</td>
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<td>Pitcairn Islands</td>
<td>Pitcairn Island</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>Solomon Islands</td>
<td>Malaita Province, Malaupaina, San Cristobal, Shortland Islands</td>
<td>Reyne, 1939</td>
</tr>
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<td>Taiwan, Province of China</td>
<td>Green Island, Orchid Island</td>
<td>Reyne, 1939; Chen et al., 2004, 2006</td>
</tr>
<tr>
<td>Tokelau Chain</td>
<td>Ataful, Nukunonu, Fakaofo</td>
<td>Helagi et al., 2015</td>
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<td>Tonga</td>
<td>Tongatapu</td>
<td>Reyne, 1939</td>
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<td>Tuvalu</td>
<td>Tuvalu, Ellice Group, Funafuti Atoll</td>
<td>Reyne, 1939</td>
</tr>
<tr>
<td>United States Minor Outlying Islands</td>
<td>Palmyra Atoll</td>
<td>Handler et al., 2007; T. White (pers. obs.) (Not extinct, as reported by Reyne, 1939; Drew et al., 2013)</td>
</tr>
<tr>
<td>Vanuatu</td>
<td>Espiritu Santo, Hiu (Hiw), Loh, Port Vila, Tegua, Toga</td>
<td>Reyne, 1939; Brown &amp; Fielder, 1991; Fletcher et al., 1991; Schiller et al., 1991</td>
</tr>
</tbody>
</table>

GeoCAT (Bachman et al., 2011), based on the more than 200 terrestrial point localities available. This produced an impressive distributional range for this species of 81,056,813 km², one of the largest areas for any species on Earth. However, this massive EOO obscures the importance of terrestrial habitat to this species, because clearly the ocean area (> 81 million km²) within this range dwarfs the land mass area (around 500,000 km²) by a factor of 162 times.

Cumberlidge (2020) estimated the AOO of *B. latro* using two different approaches to better understand how much of the range actually supports crab populations. The first used GeoCAT with the assumption that each of the terrestrial point localities occupies a grid cell measuring 4 km², which gave an AOO of 546 km² based on the summed area of all cells (Bachman et al., 2011). This relatively small AOO value, however, is likely to be an underestimate given the large number of localities that remain unsampled within the overall range. The second approach to estimate the AOO took into account the restriction of this species to the coastal areas of islands where suitable habitats are found. This value was calculated by estimating the total length of the coastline of every land mass where the species is known to occur, then multiplying this value by 3 km (the assumed average distance that this species lives inland), given that it ventures as far as 5–6 km from the shore on Christmas Island and Nuie (Gibson-Hill, 1947; Helagi et al., 2015). This method produced an estimated total land area potentially occupied by *B. latro* of about 75,000 km² (about a fifth of the total coastal land mass within the range). Even so, this is likely to be a huge overestimate. We are aware that *B. latro* may not occupy all of the coastal region of islands and atolls because not all of this area actually constitutes their preferred habitat (coastal land with inaccessible rocky shorelines and cliffs,
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Fig. 4. Updated localities where Birgus latro (Linnaeus, 1767) is either extirpated (red, darkest circles) or its continued existence is uncertain (yellow, lightest circles). Note that the scale of the map may imply a wider area of extirpation than is actually known, so reference to the text and Table 3 is recommended to see the exact localities where extirpation is suspected.

with undisturbed humid rain forest close enough to the sea to allow short distance spawning migrations). The AOO of B. latro was estimated to lie between these two figures: 546 km² (vulnerable, VU) and 75,000 km² (not threatened, LC). The EOO and AOO estimates for B. latro should be viewed in the context of the fact that there are still large areas of unsampled suitable habitat within the vast distributional range of this species.

The third metric, the number of locations (as opposed to localities) used by Red List protocols under criterion B, groups together localities that are close enough to each other that they would be equally affected by the same threat. When this is the case, groups of adjacent localities are counted as a single location, and the number of locations is factored in when assigning a species to a category. Birgus latro is known to occur in a minimum of up to 200 localities, and these represent 135 locations, which (in the absence of other data) would place it in a threatened category for this measure (Cumberlidge, 2020). It should be noted that Red List assessments do not rely on distributional data alone, and that the final recommendation is ideally based on other data sets, particularly population trends and threats (IUCN, 2012; Cumberlidge, 2020).

There is good reason to believe that the absence of B. latro at some localities within its range that have been sampled frequently actually represents extirpation (Poupin et al., 2013). For example, the historical range of B. latro included the coastal waters of East and southern Africa, Madagascar, Mauritius, the Indian subcontinent, mainland Asia, large islands in Indonesia (Borneo, Sumatra, Java, Sulawesi, and Indonesian Papua [recently, West (Barat) Papua and Papua Provinces]), and mainland Australia (Reyne, 1939), but the species is no longer found in any of these places today (Fig. 3; Table 3). The absence of B. latro from suitable habitats on the continental coastlines and larger adjacent islands is likely due to greater predation pressures there from humans and non-humans, compared to typically lower predation pressures on small remote offshore islands. In other instances, the absence of B. latro may be the result of changes in land-use patterns due to growing human populations, with the result that these crabs are now extirpated in some areas that were once part of their range.

When considering the vast geographic range of B. latro, it is also necessary to take into account oceanic and terrestrial phases of its life cycle, because the aquatic larval stages disperse in the ocean currents for between four to six weeks. In contrast, the terrestrial phase of the life cycle begins along shorelines, where shell-carrying glaucothoe and juvenile crabs live, and continues inland with adults that are true land crabs—returning to the seashore seasonally but never again entering the ocean. Although both marine and terrestrial phases are equally necessary for the successful completion of the B. latro life cycle, only a few weeks are spent in the ocean waters, whereas the majority of their 60-year life span is spent on land, where they are typically restricted to relatively small land masses. When assessing the extinction risk status of B. latro, however, most conservation metrics (distribution, habitat, population trends, harvesting, and threats) relate to the terrestrial phase in which this species spends a fair part of its life, while relatively little is known of the status of the oceanic larval stages of this species.

HABITAT AND ECOLOGY

Birgus latro is a widespread, well-adapted terrestrial crab that has to breathe air and will drown if immersed in seawater for even a short time. Juvenile B. latro protect their soft abdomen inside an empty gastropod shell (Fig. 5A, B), but adult crabs have an enlarged abdomen protected by a hard, waterproof exoskeleton (Fig. 6C). Adult B. latro feed primarily on fallen
Table 3. Areas and islands in the Indian and Pacific Ocean and the countries to which they belong, where *Birgus latro* is extirpated (locally extinct).

<table>
<thead>
<tr>
<th>Country</th>
<th>Locations</th>
<th>Presence</th>
<th>Citation</th>
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<tbody>
<tr>
<td>French Indian Ocean Overseas Department</td>
<td>Mayotte</td>
<td>Extirpated (locally extinct)</td>
<td>Bouchard et al., 2013; Poupin et al., 2013</td>
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<tr>
<td>French Indian Ocean Territory islands</td>
<td>Glorioso Islands, Grande Glorieuse, Ile du Lys</td>
<td>Extirpated (locally extinct)</td>
<td>Coppinger, 1884; Miers, 1884; Poupin et al., 2013</td>
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<td>French Polynesia</td>
<td>Marquesas</td>
<td>Extirpated (locally extinct)</td>
<td>Adamson, 1935; Reyne, 1939; Poupin, 1996</td>
</tr>
<tr>
<td>India, Nicobar Islands</td>
<td>Car Nicobar, Katchal, Trinket</td>
<td>Extirpated (locally extinct)</td>
<td>Patankar &amp; D’Souza, 2012</td>
</tr>
<tr>
<td>Madagascar</td>
<td>Northern coastline</td>
<td>Extirpated (locally extinct)</td>
<td>Reyne, 1939</td>
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<tr>
<td>Mascarene Islands</td>
<td>Cargados Carajos Shoals, Mauritius, Réunion, Rodrigues</td>
<td>Extirpated (locally extinct)</td>
<td>Reyne, 1939; Drew et al., 2013; Poupin et al., 2013</td>
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<tr>
<td>Mozambique</td>
<td>Coastal region</td>
<td>Extirpated (locally extinct)</td>
<td>Reay &amp; Haig, 1990; Nordlund &amp; Walther, 2010; Poupin et al., 2013</td>
</tr>
<tr>
<td>Mozambique Channel</td>
<td>Juan de Nova Island, Europa Island</td>
<td>Extirpated (locally extinct)</td>
<td>Poupin et al., 2013</td>
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<tr>
<td>Seychelles</td>
<td>Desneuf, Mahe, Marie Louise, Remire</td>
<td>Extirpated (locally extinct)</td>
<td>Bowler, 1999; Poupin et al., 2013</td>
</tr>
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<td>Tanzania</td>
<td>Mainland coastline</td>
<td>Extirpated (locally extinct)</td>
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<td>Mozambique</td>
<td>Mainland coastline</td>
<td>Extirpated (locally extinct)</td>
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<td>Northeast coast</td>
<td>Extirpated (locally extinct)</td>
<td>Reyne, 1939</td>
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<td>Chile</td>
<td>Easter Island</td>
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<td>Reyne, 1939</td>
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<td>Kiribati</td>
<td>Tabuaeran (Fanning) Island</td>
<td>Extirpated (locally extinct)</td>
<td>Brown &amp; Fielder, 1991</td>
</tr>
</tbody>
</table>

fruits, seeds, and nuts (including coconuts), and occasionally take plant and animal remains. The preferred habitat of *B. latro* is the shaded floors of humid subtropical and tropical lowland forests near the coast that offer abundant rock crevices and soil deep enough for burrowing. *Birgus latro* can be active during the day (except in areas where they are harvested by humans, where crabs are nocturnal), but crabs avoid extreme temperatures by spending time in cool, humid burrows, where water loss is minimised.

The exact habitat of adult *B. latro* varies between islands and depends on topography. For example, on Christmas Island (Indian Ocean, Australia), most adult *B. latro* live as far as 3–5 km inland in dense, humid tropical rain forest up to 300 m above sea level, and there are fewer crabs in the extensive stands of *Pandanus* and isolated coconut tree groves around the coastline on the lower and drier shore terraces. On Lifou Atoll (New Caledonia), *B. latro* is found in rain forest, sparsely vegetated woodlands, and coastal rubble, where it is frequently associated with the piles of plant litter found under coconut trees. On Pemba Island (Tanzania) and Okinawa Island (Japan), *B. latro* is active only at night, and spends the day in holes and crevices in coral rag coastal forest. In Nuie in the Marshall Islands (Republic of Belau), *B. latro* is most abundant in the high-humidity, closed-canopy coastal forests, and hardly any crabs are found in open areas with no canopy, where the humidity is low and the vegetation either low scrub or secondary forest. On Christmas Island and Vanuatu, the glaucothoe and small juveniles of *B. latro* with mollusc shells (Fig. 5C) spend the day in the relatively humid interstitial spaces in coral rubble, emerging at dusk to feed on the surrounding land (Drew & Hansson, 2014).

The breeding season for *B. latro* between May and September is when crabs living inland migrate to the coastal supratidal zones, sometimes gathering in large numbers on sea cliffs in inaccessible caverns, caves, and crevices. Here, crabs mate, and the females later release their fertilised eggs by the hundreds of thousands into the incoming high tides. On contact with seawater, the eggs hatch into tiny aquatic larvae that develop for up to 42 days in the surface waters of the ocean, before metamorphosing into benthic juvenile crabs.
During their time in the surface waters, they live among floating logs, coconuts, or rafts of vegetation and disperse over a wide area. The fully developed planktonic larvae migrate to coastal waters on nocturnal flood tides (Hamasaki et al., 2015). The final larval metamorphosis results in benthic, shrimp-like glaucothoe, which use their pleopods to either swim or crawl on the seabed as they seek out empty gastropod shells to protect their soft pleon, before migrating to the shore (Reese & Kinzie, 1968). The glaucothoe move from the sea to land at night during full tides, then spend about four weeks on the shore, around the high-tide mark. Juveniles of *B. latro* up to 24 months old select a bigger mollusc shell each time they moult (Fig. 5C), and expand their territory to include cliff faces as well as the shore. Eventually, after about two years, juvenile crabs reach a size where their pleon hardens and they no longer need to inhabit a shell. It is at this stage that these crabs switch to full-time air breathing and move further inland.

*Birgus latro* is a long-lived species with a slow rate of development for an anomuran, reaching sexual maturity after six years for males and between seven to nine years
Fig. 6. *Birgus latro* (Linnaeus, 1767) in its natural habitat on Christmas Island in the Indian Ocean. A, two adults mating; B, gravid female carrying eggs; C, female releasing eggs into the sea. Photographs by Max Orchard.

for females, when they have a carapace thoracic length (TL) of 2.5 cm or greater (Fletcher et al., 1990; Fletcher, 1993; Sato & Yoseda, 2008; Sato et al., 2013). In general, breeding continues until crabs reach 30 years or so in age (although individuals can live for as long as 60 years) (Sato et al., 2013). Studies on the number of breeding females in populations of *B. latro* in Vanuatu (Fletcher et al., 1990, 1991; Fletcher, 1993) indicate that most are between nine and 30 years old, and that there are very few in the older age groups (largest size ranges). This would give an estimated generation length of between nine and 30 years, with an average of 20 years.

Terrestrial species with a planktonic dispersal phase such as *B. latro* depend on frequent episodes of successful recruitment of offspring back into the land-based population. The millions of *B. latro* larvae shed into the plankton are subject to predation throughout their development, and are relatively intolerant to changes in the pH and temperature of the sea water (Schiller et al., 1991). These factors
mean that recruitment of post-larval *B. latro* back into the terrestrial population is often irregular, and may not occur every year (Fletcher et al., 1991). The slow growth rate, late age of maturity, intermittent onshore recruitment of juvenile crabs, and complex life cycle involving both land and marine habitats mean that populations in decline due to the removal of large numbers of breeding adults do not rebound rapidly. In fact, it takes *B. latro* several years to replace heavy losses, and their populations can take years to recover, even if protected.

Many populations of *B. latro*, e.g., in the Indian Ocean (Zanzibar and Quirimbas Archipelagos, and Christmas and Cocos-Keeling Islands) and the West Pacific (Eastern Indonesia, Taiwan, and Japan), exhibit colour polymorphism where predominantly red/orange individuals coexist in the same population as predominantly blue individuals. On the other hand, some islands have only one colour morph: e.g., Aldabra (red), and Okinawa and New Guinea (blue) (Caro & Morgan, 2018; Nokelainen et al., 2018; Caro et al., 2019, 2020). Nokelainen et al. (2018) and Caro (2021) investigated the possible evolutionary basis of colour polymorphism in *B. latro* but were unable to reach a clear conclusion about its adaptive significance. Dramatic colour polymorphism in *B. latro* tends to be most obvious in adults, with small specimens typically either blue or brown. The genetic basis of this colour polymorphism has been the subject of several studies (Lavery et al., 1996; Anagnostou & Schubart, 2016; Yorisue et al., 2020; H.-T. Shih et al., pers. comm.), but is still not understood over the broad geographic range of this species.
Threats to the continued existence of *B. latro* in most of its range are all anthropogenic. One of the primary threats to this species is the widespread destruction and modification of its coastal habitat by farming and commercial development, made worse by the loss of terrestrial habitat due to rising sea levels (Fig. 3). Shrinking habitats are particularly threatening to *B. latro* because its long generation time means it has a limited capacity to adapt to rapidly changing environmental threats. Other threats to these crabs include overharvesting for food and trade (Fig. 4), with predation by introduced animals and road kills (Fig. 7) representing lesser, but still problematic, challenges. The combined impact of these threats is undoubtedly causing population declines in many parts of the range.

Harvesting of *B. latro* for food has been a constant practice wherever these crabs come into contact with human populations expanding to reach ever more remote and uninhabited parts of the Indian and Pacific Oceans. This is a significant factor affecting the survival of the species today (Fig. 2). These large, easy-to-catch, slow-moving land crabs are particularly vulnerable to capture because they can be caught by hand without any specialised equipment (only a flashlight). As *B. latro* habitats and numbers shrink, harvesters have focused their search on increasingly smaller areas. Pressure on *B. latro* populations remains high because these purportedly tasty crustaceans are a valuable cash commodity in local economies—for the table, as tourist trophies, and even as an aphrodisiac in some of the Pacific islands (Brown & Fielder, 1991).

On some islands and atolls, juvenile *B. latro* are vulnerable to introduced predators such as pigs (*Sus scrofa*) and rats (*Rattus* spp.), as well as natural predators such as monitor lizards (*Varanus indicus*) and seabirds (Buden, 2012; Laidre, 2017, 2018, 2019). On Christmas Island, *B. latro* has been attacked and killed by invasive, aggressive yellow crazy ants (*Anoplolepis gracilipes*), and on Palmyra Atoll in the Pacific Line Islands, crab populations have declined due to infestations of invasive scale insects (*Pulvinaria* sp., *Coccidae*) (Handler et al., 2007). In Vanuatu, *B. latro* are killed by coconut tree farmers who believe that crabs feed at night on coconut seedlings. In several places in its range, *B. latro* that must cross roads during their mass migrations to the sea are killed by vehicles (Chen et al., 2004, 2006; Orchard, 2012; Fig. 7). In Sorol and Yap Atolls in the Pacific, *B. latro* populations are depleted and have not rebounded despite the large amount of suitable habitat, probably because of overharvesting coupled with losses to introduced and natural predators that tend to target juvenile crabs (Kepler, 1994; Whitten et al., 2002; Buden, 2012).

In the Cocos-Keeling Islands in the Indian Ocean, *B. latro* used to be common on the inhabited West and Home Islands, but overharvesting for food over the last 50 years has virtually extirpated this species, except for occasional small specimens found in more isolated areas (P. K. L. Ng, pers. obs.). On the other hand, *B. latro* is common and unafraid of humans on the isolated and largely uninhabited North Keeling Island, a protected area (in the Pulau Keeling National Park) that lies 30 km from the inhabited islands to the south.

Rising sea levels are of great concern because this would flood the numerous, isolated, low-lying island archipelagos and coral atolls in the Indian and Pacific Oceans, which comprise a large (and relatively safe) part of the range of *B. latro*. Sea level increases driven by increasing global temperatures associated with the climate crisis are estimated to be rising at a rate of about 3 mm a year (WCRP Global Sea Level Budget Group, 2018). This is a long-term concern for the future survival of *B. latro*, because many of the low-lying islands and coral atolls where *B. latro* lives could be washed away in 10 to 20 years, wiping out vast areas of habitat on which these crabs depend for their existence. The loss of islands and atolls would also mean that the planktonic larvae of *B. latro* will have fewer places to return to when they mature into benthic juveniles ready to come ashore. In short, shrinking land habitat is an existential problem for the long-term survival of *B. latro*, because although their larval stages develop in the oceans, adult coconut crabs are obligate
Fig. 9. Threats to *Birgus latro* (Linnaeus, 1767) on Christmas Island (Indian Ocean) from aggressive, invasive yellow crazy ants (*Anoplolepis gracilipes*). A, ants attacking the arthrodial membranes between peg articles; B, ants attacking the eyestalks; C, ants swarming on the body of a coconut crab. Photographs by Max Orchard. These images were kindly provided by Atura Film GmbH / NDR Doclights, from the film “Realm of the Robber Crab”.

Air-breathing land animals that cannot survive immersion in seawater. Another concern associated with the climate crisis is the measurable decline in the pH of seawater caused by the increasing amount of atmospheric carbon dioxide (an acidic gas) that is dissolving in the world’s oceans. *B. latro* larvae are probably more vulnerable than adults to fluctuations in the pH, temperature, and oxygen levels of seawater, because ocean acidification has been linked to changes in the behaviour of pelagic brachyuran crab larvae (Gravinese et al., 2019). Lowered seawater pH may similarly impact the developing larval stages of *B. latro* and depress the onshore recruitment of juveniles.

The impact of commercial exploitation for human consumption on *B. latro* populations in eastern Indonesia has been studied extensively on Ju (Yoi) Island in the Central Halmahera Regency of North Maluku Province, and on Pasoso Island in Central Sulawesi (Sulistiono et al., 2008b, 2009). The relatively high market price of *B. latro* in many parts of this region (US$2–5 each on Ju Island) drives their collection for live export (in packages of up to 80 crabs) to other parts of Indonesia, such as Ternate in North Maluku and Manado in North Sulawesi (Sulistiono et al., 2009), where crabs fetch a high price in seafood restaurants (US$20 each). Moreover, the price of a large female *B. latro* can reach up to US$35 in some restaurants in Ternate (Serosero et al., 2019). Inevitably, the unsustainable exploitation of *B. latro* populations on Ju and other islands in Indonesia has resulted in a sharp decline in large (> 1 kg) specimens despite local protection. In Japan, the commercial exploitation of *B. latro* not only means that large coconut crabs are used for food, it also means that juvenile crabs are sold locally for the local and international pet trade as well as auctioned via the internet. For example, dealers in Singapore sell the crabs to enthusiasts for US$150–300 each, depending on size. Of concern is that various zoological gardens and public aquariums also obtain *B. latro* through these channels for display.
POPULATION LEVELS AND TRENDS

Precise global population levels of *B. latro* are difficult to gauge. On the one hand there are large populations of *B. latro* living on protected uninhabited islands and coral atolls. Some of the wealthiest populations of *B. latro* are on Aldabra Atoll (155.4 km²) in the Seychelles, on Chumbe Island (0.33 km²) in Tanzania, on the Chagos Archipelago (60 km²) in the Indian Ocean, and on Palmyra Atoll (11.9 km²) in the Pacific Ocean. On all of these islands and coral atolls there is either a low human population or they are uninhabited, and crabs receive active protection. Monitoring of *B. latro* on the protected islands of Chumbe, Bongoyo, and Mbudya off the Tanzanian coastline indicates that these places host healthy populations of coconut crabs. This is likely to be the case for seven other remote islands in the Dar es Salaam Marine Reserve system (Caro et al., 2020). In general, areas that best support *B. latro* populations are relatively undisturbed places that are uninhabited and where no one stays overnight. The islands where *B. latro* are thriving under active protection in the western Indian Ocean are crucial reservoirs and recruitment sources for repopulating or replenishing other suitable islands. In the Pacific Ocean, *B. latro* on the remote Palmyra Atoll (12 km²) in the Northern Line Islands has a favourable conservation status because crab populations number in the thousands to tens of thousands of individuals. This atoll is managed as a United States National Wildlife Refuge and Marine National Monument, and is largely uninhabited, so crabs are mostly undisturbed and receive active protection in a place where threat levels are low (T. White, pers. obs.). The population of *B. latro* in Niue, Polynesia (261.5 km²), appears to be stable (based on five surveys since 1994; Helagi et al., 2015), thanks to government regulation of harvesting, despite the heavy exploitation of crabs for local consumption and export to New Zealand. The above positive outlook for some populations of *B. latro* is the exception rather than the rule. The wide historic range of *B. latro* is now much smaller (Figs. 1–4), and there are declines and losses of crab populations on previously uninhabited islands across the Indo-Pacific. These changes have coincided with the arrival of humans, who have altered habitats, harvested crabs, and introduced predatory species. In fact, declines of *B. latro* populations have been reported from most areas where there is a significant human population, and this species has been extirpated from mainland localities in Australia and Madagascar and inhabited larger islands (Table 3). In Vanuatu, *B. latro* is listed as an endangered species by the National Biodiversity Strategy and Action Plan Review Project, mainly due to falls in crab populations linked to overharvesting for the restaurant trade (Fletcher et al., 1991).

In general, there is a continuing fall in the number of breeding individuals in the majority of areas where population assessments have been made. Demographic studies show continuing reductions of ~30% of mature individuals in many locations over the last 15–20 years, associated with increasing levels of exploitation linked to falls in the EOO, AOO, and quality of habitat (Amesbury, 1980; Wells et al., 1983; Schiller, 1992). Population demographic studies on *B. latro* have been carried out on Christmas Island (Rumpff, 1986; Hicks et al., 1990; Drew et al., 2012); Guam (Amesbury, 1980); Niue (Schiller, 1992); Lifou, Loyalty Islands, New Caledonia (Kadiri-Jan & Chauvet, 1998); Vauvilliers, Loyalty Islands, New Caledonia (Kadiri-Jan, 1995); Tairao, Tuamotu, French Polynesia (Chauvet & Kadiri-Jan, 1999); Hatoma, Japan (Sato & Yoseda, 2008; Oka et al., 2015); and several islands in Sulawesi and Moluccas, Indonesia (Jahidin, 2010; Heryanto & Wowor, 2017; Supyan & Idham, 2017; Serosero et al., 2021). High population densities of *B. latro* have been reported on uninhabited islands such as Tairao in the Tuamotu Archipelago (190 crabs/ha), and Igunir in the Enewetok Atoll of the Marshall Islands (147 crabs/ha), but densities are much lower on inhabited islands such as Nuie (46 crabs/ha) and Lifou (27 crabs/ha) in New Caledonia (Drew et al., 2010). Recent surveys of *B. latro* populations on Palmyra Atoll in the Northern Line Islands (a US Territory which bans harvesting) found 20 crabs per survey, whereas on Teraina Island (in Kiribati, which allows harvesting), researchers found only two crabs per survey, which is consistent with reports of sharp declines over the last decade (T. White, pers. obs.). In general, the population size of *B. latro* on oceanic islands directly reflects levels of human activity, with crabs declining in Guam and Pemba where there are large human populations, and maintaining viable populations on uninhabited or sparsely populated islands and atolls.

*Birgus latro* remains abundant throughout the Australian territory of Christmas Island, where two thirds of the island is under the protection of the Christmas Island National Park (85 km²). *Birgus latro* is found all over the island, and despite the presence of humans, some estimates of crab populations report up to one million individuals, making it one of the strongholds of this species. These estimates, however, were made before the establishment of supercolonies of the invasive yellow crazy ant that have severely impacted land crab populations, including *B. latro*, across extensive areas of the island. Population studies since then have focused on areas relatively unaffected by the ants, but there can be no doubt that the total population of *B. latro* has been significantly reduced. The Christmas Island *B. latro* populations are not evenly distributed, with crabs most abundant (67–160 crabs/ha) in intact inland humid rainforest, and completely absent in places where the forest has been cleared for mining or human settlement. Although *B. latro* populations on Christmas Island are probably among the best protected anywhere in its range, they still only receive protection inside the National Park, and elsewhere crabs are still vulnerable to overharvesting by locals. High numbers of crabs are killed on the island’s roads, especially those used for haulage by the phosphate mining industry and for access to the Immigration Detention Centre.
**POPULATIONS OF BIRGUS LATRO AT RISK**

Although extensive, the actual geographic range of *Birgus latro* is rapidly diminishing. For example, *B. latro* populations are virtually extirpated along continental coastlines from Somalia to Mozambique (Fig. 4; Table 3). In addition, coconut crab populations are low on the coastal East African islands (Unguja and Pemba, Zanzibar) where human populations are high, and *B. latro* is now restricted to the outlying smaller islands off the coasts of these two larger islands. Crab populations are declining even on uninhabited Zanzibari islands that are visited by fishermen who camp overnight and eat crabs (Caro et al., 2020). *B. latro* populations found on the 115 islands and atolls of the granitic and coralline Seychelles Archipelago (459 km²) have suffered measurable recent and rapid declines of at least 80% over the past 15–20 years (Poupin et al., 2013). This is accompanied by declining EOOs, AOOs, and fragmented populations, linked to continuing threats from overharvesting and habitat destruction. The result is that in many of these places *B. latro* is found in only very low numbers, and may even be extirpated in others (Poupin et al., 2013). One bright spot is Aldabra Atoll (a protected UNESCO World Heritage Site) that supports an abundant *B. latro* population of more than one thousand terrestrial adults and juveniles. The recent surveys of most of the islands in the Seychelles Archipelago reported on by Poupin et al. (2013), however, indicate that *B. latro* is rare on Cousine, Aridé, the Amirantes islands of D’Arros and Desroches (Bowler, 1999; Jupiter et al., 2013), Alphonse (Duhec, 2011), Bijoutier, Coetivy, Assumption, Cosmoledo, Astove, and Farquhar. Although *B. latro* may still occur in small numbers on Providence and St. Francois islands, Poupin et al. (2013) were unable to confirm this. *Birgus latro* may even be extirpated on the islands of Desneuf, Mahe, Marie Louise, and Remire, because no crabs were found during recent surveys (Poupin et al., 2013).

Populations of *B. latro* on the four main Comoro Islands (2,236 km²) have suffered rapid population declines of at least 50% over the past 15–20 years, and are now found in only very low numbers on Grande Comore (Njazidja, 1,025 km²), Mohéli (Mwali, 211 km²), and Anjouan (Nzwani, 424 km²) (Poupin et al., 2013). This species may even be extirpated on Mayotte, where recent searches produced no evidence of its presence (Bouchard et al., 2013; Poupin et al., 2013). Other metrics include declining EOOs, AOOs, fragmented populations, and declining habitat quality.

*Birgus latro* populations on the five Glorioso Islands (5 km²) have suffered rapid reductions in population levels (of at least 80% over the past 15–20 years), and this species, if present at all, is found only in very low numbers (Poupin et al., 2013). These crabs have been subject to consistent threats from overharvesting and habitat destruction, and are vulnerable to local extirpation. While *B. latro* may still be present on Grande Glorieuse island, it is extremely rare, and may only persist because of the indirect protection from the military base there, which acts as a deterrent to illegal collecting. On the other hand, this species has been extirpated from Ile du Lys, where it is known only from a single record made in 1882 (Coppinger, 1884; Miers, 1884) and was not found during recent surveys (Poupin et al., 2013). Similarly, in two islands in the Mozambique Channel (32.4 km²), *B. latro* is extremely rare on Juan de Nova Island (4.4 km²) and probably extirpated on Europa Island (28 km²) (Poupin et al., 2013). *Birgus latro* is presumed to be extirpated in Madagascar and all four Mascarene Islands (4,536 km²) because exhaustive surveys of suitable habitat in these inhabited islands have failed to report a single individual. Specifically, *B. latro* has been extirpated from Mauritius (1,900 km²), where it was reported to be declining by Charles Darwin in 1836; the Agalega Islands (26 km²; Poupin et al., 2013); and the Cargados Carajos Shoals (Saint Brandon; 5 km²; Reyn, 1939). *Birgus latro* has also been extirpated from Reunion (2,500 km²) and Rodrigues (110 km²), though it is possible that they may never have been there in the first place.

Populations of *B. latro* in many of the 300 islands of the Andaman and Nicobar Islands (8,249 km²) are small, fragmented, and appear to be in serious decline. Threats include overharvesting, despite social taboos against harvesting and legal protection under the Indian Wildlife Protection Act; and habitat destruction for agriculture and by the 2004 tsunami. The result is that *B. latro* may now be extirpated on some islands (such as Katchal, Trinket, and Car Nicobar), because recent searches produced no evidence of its presence (Patankar & D’Souza, 2012). Elsewhere in this archipelago, *B. latro* is known from only a few locations, and in general there are reductions in both the area and quality of its habitat. The general lack of protective conservation measures for *B. latro* in the Andaman and Nicobar Islands, together with the continuing threats, indicate that the extinction threat for this species is high (Patankar & D’Souza, 2012).

Large numbers of terrestrial adult and juvenile *B. latro* are found on Christmas Island (135 km²), but their populations may not be stable due to continuing threats. Here the majority (> 70%) of *B. latro* live in a protected area and receive active conservation measures (Fig. 7D). They can be found throughout Christmas Island, both within the National Park as well as wandering outside in the unprotected parts of the island throughout the year. About 20 localities have been recorded according to published research studies, but the small size of Christmas Island means that the recorded localities are very close to each other, and are treated as only two distinct locations according to IUCN Red List protocols (see above). Despite the earlier positive figures for *B. latro* populations on Christmas Island, these crabs have nevertheless undergone measurable drops between 1979 and 2012 (Drew et al., 2010; Drew & Hansson, 2014) caused by habitat destruction, invasive species (including the yellow crazy ant), road kills, and harvesting by local residents. It is of concern that these population reductions are taking place despite active conservation protection both in the Christmas Island National Park and along its migration routes outside of the National Park. Without active protection, the extinction risk assessment of *B. latro* on Christmas Island would quickly
meet the threshold for a more threatened category, should new threats or population data demonstrate that the species is likely to decline further within five years.

A number of authors have reported that adult *B. latro* from Christmas Island in the Indian Ocean grow to a larger size than those from the West Pacific Ocean (McLaughlin et al., 2007; Oka et al., 2015; Anagnostou & Schubart, 2016; Seroso et al., 2019). It is possible, however, that the smaller size of *B. latro* in its West Pacific populations is due to the harvesting of large specimens (including ovigerous females) for human consumption, given the high market price of *B. latro* in parts of Indonesia such as the north Maluku Islands and Sulawesi (Sulistiono et al., 2009; Gurusu et al., 2017; Seroso et al., 2019, 2021). Studies show that unregulated harvesting in eastern Indonesia that selects by gender has measurably impacted the sex ratio of *B. latro* populations in some places. For example, although populations of *B. latro* on Halmahera Island and several other islands in central Sulawesi have similar numbers of males and females (male:female ratio 1.09:1.06), populations in a different part of Halmahera Island have many more females than males (male:female ratio 0.41:1.0) (Sulistiono et al., 2008a; Gurusu et al., 2017; Seroso et al., 2019), and on Siompu Island off southeast Sulawesi, males outnumber females 3:1 (Jahidin, 2010).

In the Philippines, *B. latro* has been reported from Zamboanga del Norte Province and from the islands of Bohol, Cebu, Sulu, Tawi-Tawi, and Basilan, and from Balabac and Cagayancillo Islands in Palawan Province (but not on the island of Palawan itself). Although the Bureau of Fisheries and Aquatic Resources of the Department of Agriculture of the Philippines listed *B. latro* as a threatened species and has legislated against its collection and sale since 2001, this Fisheries Administrative Order is often superseded, and the crab is still collected for food (Subang et al., 2020). In the Batanes Province of the Philippines, *B. latro* populations on the islands of Batan, Sabtang, and Itbayat are declining due to overharvesting and habitat destruction, with the result that these crabs are listed as locally endangered (Perrucho et al., 2018).

On Teraina atoll (10 km²) in Kiribati in the Northern Line islands in the Pacific Ocean, *B. latro* populations are vulnerable to local extirpation, and numbers are falling sharply (down at least 80% over the past 15–20 years) due to measurable habitat destruction and widespread harvesting (T. White, pers. obs.). Other metrics that support a high extinction threat in Teraina relate to the small size of the atoll: crab populations are found in a single location, with a declining EOO (10 km²), a low AOO (8 km²), and a lack of protective conservation measures.

*Birgus latro* populations in Taiwan are found in Kenting National Park on the island’s southern coast, and on offshore islands Lanyu and Lyudao (Green Island). Crabs are common on Lyudao (15.1 km²), but most individuals are small (less than a kilogram) and large specimens are very rare. Populations of these crabs have declined by at least 30% over the past 15–20 years due to consistent threats associated with increasing tourism, namely, overharvesting, road kills, habitat destruction from burning forests, and introduced predators. Other factors pointing to a high extinction threat relate to the small size of Lyudao: its populations are effectively a single location when considering the impact of threats, and *B. latro* has a small and declining range with less suitable habitat to support crab populations. As a result, *B. latro* has received protection under the Wildlife Conservation Law in Taiwan since 1995, and poachers can be jailed if convicted. A number of conservation studies of *B. latro* in Taiwan have focused on population genetics using microsatellites (Gan et al., 2008), larval development (Wang et al., 2007), and habitat conservation (Chen et al., 2004, 2006).

On the island of Guam (549 km²) in the Northern Mariana Islands in Micronesia, declines of at least 30% in *B. latro* populations over the past 15–20 years have been due to overharvesting, road kills, introduced predators, and widespread coastal habitat destruction along migration routes that deny crabs access to the ocean (Amesbury, 1980). In the mid-1990s *Birgus* was sold in markets on Guam for US$20–30 each, but local legislation restricted the sale of juveniles and ovigerous females as the number of crabs decreased. The underlying high extinction threats to the small and declining crab populations on Guam include harvesting coupled with a shrinking range, less suitable habitat, and the fact that the closely clustered populations on this small island effectively represent a single vulnerable location.

*Birgus latro* populations have only a limited capacity to support harvesting of large adults of both sexes, because this species can take up to nine years to reach sexual maturity and only reproduces once per annum, so replacement and recovery are slow. The selective harvesting of either males or females can skew the sex ratio from the expected ratio of 1:1 (i.e., 50% males:50% females). For example, the selective harvesting of large males (> 4 cm TL) in Japanese populations of *B. latro* in the Ryukyu Islands skews the sex ratio, resulting in more large females (which are larger) and fewer adult males (which are smaller) in the reproductive population (Yorisue et al., 2020). This gender and size imbalance may be one of the causes of long-term population decline in this species, because females mate less frequently and with less success if they cannot encounter males that are either equal-sized or larger than themselves (Sato et al., 2010; Sato & Suzuki, 2010; Sato & Yoseda, 2010). Even if a large female does mate with a smaller male, fertilisation is less likely because such matings provide females with lower quantities of sperm (Sato, 2011; Yorisue et al., 2020).

**CONSERVATION OF BIRGUS LATRO**

Although conservation management plans (to different degrees) are in place in Japan, Taiwan, the Philippines, Indonesia, Guam, Vanuatu, Tuvalu, Funafuti Atoll, Christmas Island, Aldabra, Niue, and the Tanzanian Islands, this species is nevertheless unprotected in the majority of its range. Most unprotected *B. latro* populations in the world are in
Table 4. Legal protection of *Birgus latro* in Japan (see Fig. 10, except for Ogasawara). See text for the details of local protection ordinances.

<table>
<thead>
<tr>
<th>Prefecture</th>
<th>Municipalities</th>
<th>Legal protection locally</th>
<th>Amount of fine</th>
</tr>
</thead>
<tbody>
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<td>Ogasawara</td>
<td>None</td>
<td></td>
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<tr>
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<td></td>
<td>Yonaguni Village</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tarama Village</td>
<td>Protection with fine</td>
<td>¥50,000</td>
</tr>
<tr>
<td></td>
<td>Miyakojima City</td>
<td>Protection with fine</td>
<td>¥100,000</td>
</tr>
<tr>
<td></td>
<td>Ishigaki City</td>
<td>Protection with fine</td>
<td>¥100,000</td>
</tr>
<tr>
<td></td>
<td>Taketomi Town</td>
<td>In preparation</td>
<td></td>
</tr>
</tbody>
</table>

long-term decline because crabs are captured frequently, and their numbers are slow to recover. That is, unregulated capture is not sustainable. Protection policies for *B. latro* should, therefore, take into account the slow recruitment and replacement rate of this slow-growing species. In addition, the successful conservation of *B. latro* populations needs to be a community-driven initiative that incorporates multiple stakeholders. Conservation measures aimed at sustainable harvesting include hunting bans, no-take areas, catch-size limits, minimum size limits, and a ban on the capture of egg-bearing females. Sustainably managing the populations of these charismatic crustaceans increases the opportunities for tourism, and will have a wider benefit for the whole of the local community.

Several municipalities in southern Japan enforce *B. latro* protection ordinances (Table 4). In Miyakojima City, there are four protected areas with year-round bans on *B. latro* collection that have been in force since April 2014 (Fig. 10). In other less-protected areas, the collection of ovigerous females (TL < 8 cm and > 12 cm) is banned, and there is a three-month ban (1 June to 31 August) on the collection of all *B. latro* (penalty ~ US$950, ¥100,000). In Tarama Village (Fig. 10), limits on the harvesting of *B. latro* have been in force since March 2010. There is a year-round ban on the collection of small crabs (TL < 4 cm) and of ovigerous females, and a two-month ban (from 1 July to 31 August) on the collection of crabs of any size (penalty ~ US$475, ¥50,000). In Ishigaki City (Fig. 10), there are three protected areas with year-round bans on *B. latro* collection that have been in force since June 2014. In other less-protected areas, there is a ban on the collection of small males (TL < 4 cm), large males (TL > 5.5 cm), and females of any size, and a nine-month ban (1 December to 31 August) on the collection of all *B. latro* (penalty ~ US$950, ¥100,000). In Kagoshima Prefecture, there is a year-round ban on the collection of crabs of any size (penalty ~ US$4,750, ¥500,000). On Naha, the availability of large *B. latro* (sold for US$30–40 each) has
declined since the 1990s (most crabs now weigh less than 1 kg), and the open sale of live *B. latro* in plastic boxes to tourists has now stopped.

In Lyudao, Taiwan, *B. latro* has been legally protected by the Wildlife Conservation Law since 1995. Conservation strategies in Taiwan consist of protecting these crabs in their inland forest habitat and during their annual migrations to and from the coast, when they are shedding eggs in the sea, and when juveniles return to land (Chen et al., 2004). Other conservation actions in Taiwan include captive breeding programmes and educating the community about the need to conserve these charismatic giant arthropods. On Guam, conservation measures aimed at protecting *B. latro* are enforced both in US military installations as well as in the other non-military parts of the island, and include limiting harvesting to crabs of a certain size and making it illegal to catch ovigerous females during the time of year when they are present in the population.

Christmas Island supports what is probably the world’s largest population of *B. latro*, most of which is carefully managed in the Christmas Island National Park (including The Dales and Hosnie’s Spring, which are both Wetlands of International Importance under the Ramsar Convention on Wetlands). Control measures on Christmas Island focus on the invasive yellow crazy ants that attack crabs, as well as measures aimed at the mitigation of road kills. In Nuie, large adult females (TL > 8 cm, around 14–15 years old) can be harvested, but small adult females (TL 2.5–3.5 cm) are protected because they make up 95% of the female population and produce 100,000–250,000 eggs when they spawn (Helfman, 1973; Helagi et al., 2015).

The Northern Mariana Islands allow licensed harvesting of *B. latro*, but the bag is restricted to five large (TL 7.6 cm), non-egg-bearing adults a day, and to 15 crabs over the three-month season from September to November. In Tuvalu, *B. latro* is protected in Funafuti Marine Conservation Area on Funafuti Atoll (33 km²). In Indonesia, *B. latro* is protected under a regulation issued by the Minister of Environment and Forestry of the Republic of Indonesia, No. P. 106/MENTHIK/SETJEN/KUM.1/12/2018. However, hunting of *B. latro* is allowed in North Maluku Province with special permits that limit size and catch number.

Other conservation tools include careful mapping of *B. latro* habitat using remotely sensed electronic tracking of individual crabs, and mapping of suitable habitat cover (Krieger et al., 2012; T. White, pers. obs.). On Palmyra Atoll, such tracking has already demonstrated a loss of the native forest habitat of *B. latro*, and has linked habitat loss to reductions in its population levels. Habitat monitoring could provide a better understanding of the population levels and conservation status of *B. latro* across its entire range if it were to be expanded to survey other parts of this range across the Indo-Pacific. Given that areas with perfectly suitable habitat may be devoid of crabs, the value of quantifying habitat may be more of a guide to how its availability has declined. If harvesting moratoriums are to be successful, there needs to be enough suitable, undisturbed habitat remaining for crabs to make a strong recovery.

**Conservation measures.** The following are possible conservation measures and recommendations for threatened populations of *B. latro* (not in order of priority):

- Establish community-based conservation initiatives aimed at protecting the species and its habitat.
- Establish sanctuaries to protect coastal and inland forest habitats with primarily native vegetation (as opposed to only Cocos palms).
- Close major *B. latro* migration routes and spawning areas to public access during the breeding season.
- Monitor and eradicate (or at least suppress) introduced species that impact *B. latro* populations.
- Monitor *B. latro* populations and carry out detailed research on crab ecology and genetics.
- In places where harvesting is legal, implement a closed harvesting season (together with a permit/licensing system), set very small bag limits, and ban the collection of egg-bearing females for at least part of the year.
- Where relevant, implement a ban on the export of *B. latro*.
- Introduce public awareness campaigns informing of the need to arrest declines in *B. latro* populations and habitat quality, and the need to restrict harvesting and regulate coastal land development.
- Recommend/propose adding *B. latro* to CITES Appendix III.

**CONCLUSIONS**

The availability of accurate data on population trends and habitat quality, together with EOO, AOO, and location metrics, has allowed *B. latro* to be assessed under IUCN Red List Criteria A and B. It is clear that this species has suffered rapid population declines of at least 30% over the past 15–20 years in more than a dozen locations where studies have been carried out. For example, in the Indian Ocean, population reductions of *B. latro* have been quantified by studies in seven locations: Comoro Islands, Glorioso Islands, Mozambique Channel Islands, Seychelles Archipelago, Mascarene Islands (Poupin et al., 2013), Andaman and Nicobar Islands (Patankar & D’Souza, 2012), and Christmas Island (Rumphf, 1986; Hicks et al., 1990; Drew et al., 2010).

Population reductions have also been recorded on Pemba Island, Tanzania, over a three-year period as part of a long-term monitoring programme (Caro et al., 2020). Similarly, falling population numbers have been reported from seven sites in the Pacific Ocean: Guam, Mariana Islands (Amesbury, 1980); Niue (Schiller, 1992); Lifou, Loyalty Islands, New Caledonia (Kadiri-Jan & Chauvet, 1998); Vauvilliers, Loyalty Islands, New Caledonia (Kadiri-Jan, 1995); Taiaro, Tuamotu, French Polynesia (Chauvet & Kadiri-Jan, 1999); and Hatoma, Japan (Sato & Yoseda, 2008).

The vast amount of biological information that has become available recently for this conspicuous and popular species...
has made it clear that the earlier IUCN Red List assessment of DD (Eldredge, 1996) was untenable. The change from DD to a threatened category (Vulnerable) is based on a large amount of better-quality data on distribution, habitat, population size and trends, and threats, especially in places where *B. latro*’s habitat is coming under increasing pressure from growing human populations. Although the global range of *B. latro* is extensive, and population densities in a few places are impressive, both the range and numbers are nevertheless declining (even in the global stronghold of this species on Christmas Island). In addition, this species has been completely extirpated along a number of continental coastlines in the Indian and Pacific Oceans, and is on the edge of local extinction in many other areas (Table 3). The reasons for these declines are common to most localities: unchecked habitat destruction and overharvesting, and to a lesser extent, exacerbated by introduced species, road kills, and possibly, the climate crisis. The shrinking populations, declining area and quality of habitat, continued immediate threats, and lack of protective conservation measures in many areas justify the elevated global IUCN Red List extinction risk assessment for *B. latro* of Vulnerable A2cd+4cd (Cumberlidge, 2020).

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

NOTE

One of the main authors of this paper, Max Orchard, unexpectedly passed away on the morning of 17 August 2021. In his many years as warden on Christmas Island, he was a champion for conservation on the island, especially of its crabs, with his friends aptly bequeathing him the title of Australia’s “Crab Hero”.

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