British Indian Ocean Territory Biodiversity Action Plan
COCONUT CRAB

By Mark E. Laidre

Figure 1. Coconut crab (*Birgus latro*) eating a freshly cracked open coconut within the Chagos Archipelago. Photo: Mark Laidre (from [1]).

SUMMARY

Taxonomy: Kingdom: Animalia, Phylum: Arthropoda, Subphylum: Crustacea, Class: Malacostraca, Order: Decapoda, Superfamily: Paguroidea, Family: Coenobitidae, Genus: *Birgus*, Species: *Birgus latro* (Linnaeus, 1767).

Distribution: Across the Indo-Pacific on remote coral atolls and tropical islands [1].

Evolution: Evolutionarily, coconut crabs are hermit crabs, belonging to the infraorder Anomura (Crustacea: Decapoda) [2]. Coconut crabs' closest evolutionary relatives are terrestrial hermit crabs (*Coenobita* spp.) [3], which are the only other genus in the family Coenobitidae. However, while coconut crabs share some similarities with terrestrial hermit crabs, especially early on in their life history, coconut crabs have evolved into an extraordinarily different creature, one with many unique biological traits [1,4,5].

Description: World's largest terrestrial invertebrate [1]. As adults, coconut crabs can reach over 1 meter in leg span and weigh up to 4 kg. Exhibit a distinctive body plan (Fig. 1), with two extremely powerful claws (left claw larger than right claw) and two prominent ambulatory legs on either side.

IUCN Red List status: Data Deficient [6]. Previously listed as 'Vulnerable' in 1981, but since 1996 has been listed as 'Data Deficient' (not due to recovery but simply lack of available data).

Local trend: Apparently stable, but population size in Chagos Archipelago, particularly across the northern atolls, is unknown.

Threats: A principal threat to coconut crabs worldwide is: (*i*) climate change-induced habitat destruction, together with rising sea levels which, if not halted, will ultimately drown the species. Another, equally significant worldwide threat to coconut crabs is: (*ii*) overharvesting by humans for

Citation: Laidre M. 2020. British Indian Ocean Territory Biodiversity Action Plan: Coconut Crab. Prepared by Bangor University for the BIOT Administration, FCO, King Charles Street, London.

food consumption (Darwin himself declared: "These crabs are very good to eat" [7]). Within the Chagos Archipelago, the coconut crab population is protected by British law, so no legal harvest takes place. Yet, poaching and illegal harvest by humans remains a serious threat within BIOT. Other major threats to this species within BIOT include: (*iii*) being driven over by vehicles on Diego Garcia while crossing roads; (*iv*) hazardous plastic containers, which wash onto the beach from the ocean and in which juveniles can become trapped and die; (*v*) invasive rat predation on early life stages; and (*vi*) a limited availability of empty shells, both in the intertidal and on land. In particular, with few empty shells there is likely a bottleneck in recruitment, both from sea to land and from juvenile to adult stages. More generally, (*vii*) an incomplete knowledge of fundamental aspects of this species' behavior and ecology currently hinders conservation management within BIOT and worldwide [8]. More research on this species, especially its life history transitions from oceanic larval stages to juvenile shell-wearing stages to fully adult stages, is vital to its successful conservation.

DISTRIBUTION

Global: Coconut crabs are distributed across the Indian and Pacific Oceans on remote coral atolls and tropical islands (Fig. 2). Their east-west range extends from islands off the east coast of Africa (near Zanzibar) to the Gambier Islands in the east Pacific. Their north-south range is largely limited by the borders of the tropical zone (latitudes: 23.41 N and 23.41 S); though a few populations do occur in the subtropics (e.g., in Taiwan and the Ryukyu Islands of Japan). In addition to the Chagos Archipelago, coconut crabs can be found in the following locations: Seychelles' Aldabra Atoll, Christmas Island, Palmyra Atoll, Cocos (Keeling) Islands, Indonesia, the Philippines, Malaysia, Kiribati, New Caledonia, Papua New Guinea, and Vanuatu. Across their vast distribution, spanning the Indian and Pacific Oceans, many populations of coconut crabs have now declined or gone locally extinct. For example, coconut crabs were once present on the island of Mauritius, but are no longer found there. Coconut crabs were also once present on some large land masses, including the northeastern coast of Australia (Queensland) and northern areas of Madagascar, but are no longer found in either of these areas. Many other locations where coconut crabs were abundant in the past have not been re-surveyed for decades, so it remains unclear if they are still present in these areas [4]. A systematic survey of population abundance, and genetic diversity [9], is now sorely needed across coconut crabs' entire range, so that this species' status can be updated and appropriate conservation measures taken.

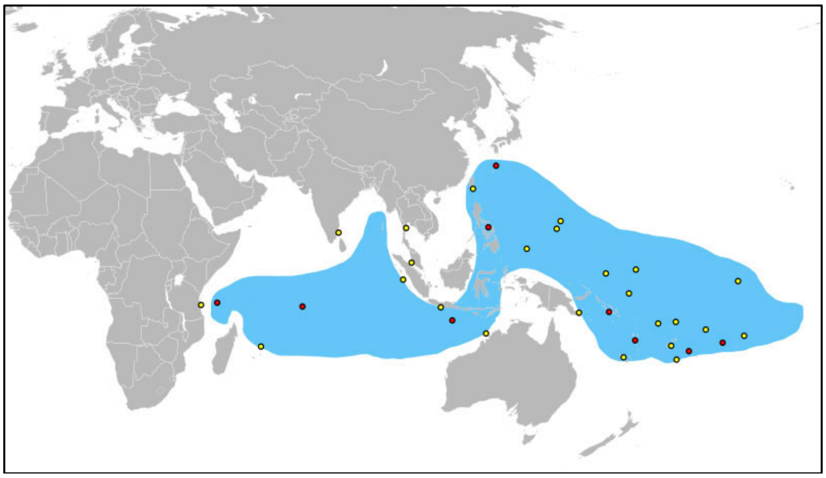

Figure 2. Worldwide distribution of coconut crabs (*Birgus latro*) (Figure extracted from [4]).

Local: In the Chagos Archipelago [10,11], coconut crabs are present on every major island cluster (Fig. 3), including Diego Garcia atoll and all five of the northern atolls (Egmont Islands, Western

Great Chagos Bank Islands, Peros Banhos, Solomon Islands, and Nelson's Island). The only known island where coconut crabs have not been observed (Carr, personal communication 6 February 2020) is North Brother Island, which is part of the Great Chagos Bank Atoll. Also, on Nelson's Island, few coconut crabs have been seen, potentially due to this island's isolation, which may limit recruitment via ocean currents.

Coconut crabs appear to be present on islands in the Chagos Archipelago regardless of the presence or absence of invasive rats. However, the relative abundance of coconut crabs on islands with versus without rats is currently unknown. Diego Garcia has a strong rat presence. In contrast, some of the northern atolls (e.g., Peros Banhos; Fig. 4) have islands both with and without rats, and coconut crabs are present on them all.

Aside from a 2015 survey on a subset of the northern atolls, which still requires analysis, most systematic surveys of coconut crabs in the Chagos Archipelago have been conducted on Diego Garcia (Fig. 5). On Diego Garcia, coconut crabs are present across the entire island, though are found in the greatest abundance on the undeveloped eastern end of this island, within the plantation, which is a conservation area. More systematic surveys of coconut crabs are sorely needed across all islands comprising the northern atolls.

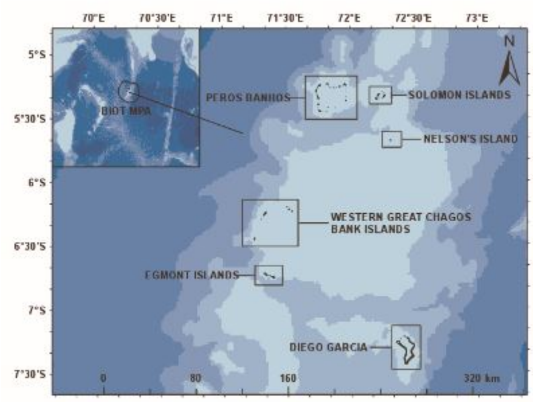

Figure 3. The Chagos Archipelago (British Indian Ocean Territory - BIOT) showing its position in the central Indian Ocean and its atolls, including Diego Garcia and the northern atolls (Egmont Islands, Western Great Chagos Bank Islands, Peros Banhos, Solomon Islands, and Nelson's Island). MPA = Marine Protected Area. (Figure extracted from Carr's BAP on Sooty Terns).

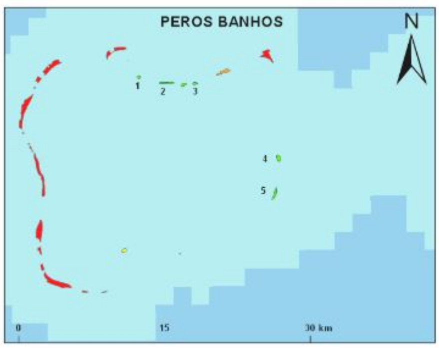

Figure 4. Islands comprising one of the northern atolls (Peros Banhos) in the Chagos Archipelago. Across Peros Banhos, coconut crabs are present on every island, including islands where rats are present (red), islands where rats are absent (green), island where rats have been eradicated (yellow), and islands where rat presence/absence is uncertain (orange). Coconut crabs' relative abundance across these different islands is presently unknown.

STATUS

Status – population estimate: In the Chagos Archipelago, systematic surveys of coconut crabs have mostly concentrated on Diego Garcia (Fig. 5). On Diego Garcia, densities of coconut crabs appear to be among the highest recorded for this species anywhere in the world. In particular, Vogt and Guzman [12], using the DISTANCE transect methodology [13], found coconut crab densities on the east side of the island, in the Minni Minni conservation area, were on average approximately 300 crabs per hectare (and two of their transects in this area revealed density estimates of 467 and 489 crabs per hectare). These remarkably high densities are almost certainly linked to the abundance of coconut within the coconut plantations, which were planted centuries ago [14]. The high density of coconut crabs in the Minni Minni conservation area contrasted with lower densities of coconut crabs in areas of Diego Garcia that are not conservation areas: there approximately 150 crabs per hectare at the southern tip of Diego Garcia and approximately 50 crabs per hectare on the west side of Diego Garcia, the developed part of the island (Fig. 6). These density estimates are not without substantial error. However, a crude extrapolation of these estimates across the 2,719 hectares of Diego Garcia equates to a population size on Diego Garcia of several hundred thousand coconut crabs. No repeat surveys using the same methodology have been made on Diego Garcia since Vogt and Guzman's study. Hence, the current population of coconut crabs on Diego Garcia may have changed. Continued yearly data is needed to track the trend of these population dynamics across time.

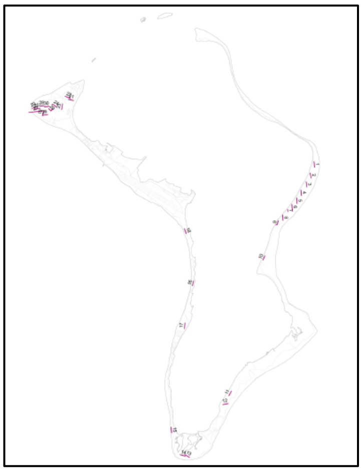

Figure 5. Diego Garcia. Red lines denote systematic transect surveys of coconut crabs (Figure extracted from [12]).

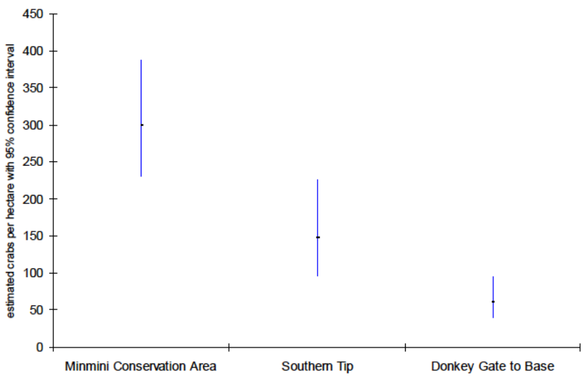

Figure 6. Estimates of coconut crab population density (crabs per hectare) across three locations on Diego Garcia (Figure extracted from [12]).

Status – population demographics: Even as sexually mature adults, coconut crabs can vary markedly in size (Fig. 7). To provide insight into the population demographics of coconut crabs, the same survey [12] on Diego Garcia, which compared the population density of coconut crabs across different locations, also examined the sizes of individuals across these different locations. Notably, coconut crabs found at the Minni Minni conservation area were significantly larger in size compared to those found at the baseside non-conservation areas (Fig. 8). These results suggest that conservation areas not only facilitate higher densities of coconut crabs, but also facilitate the growth of bigger individuals.

Figure 7. Extreme variation in body size of coconut crabs in Chagos Archipelago: both individuals are sexually mature adults. Photo: Mark Laidre (from [1]).

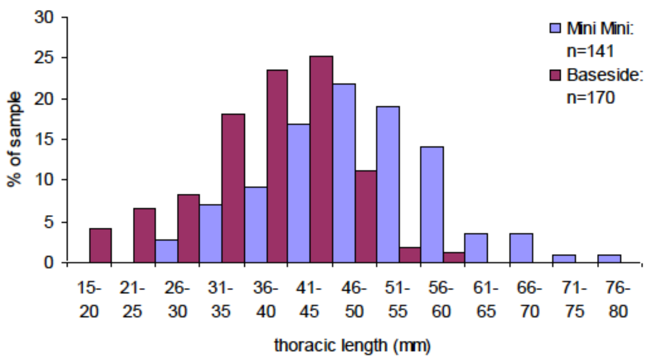

Figure 8. Size of coconut crabs (thoracic length in mm) at two locations on Diego Garcia: the Minni Minni conservation area (in blue) versus the baseside non-conservation areas (in purple). (Figure extracted from [12]).

ECOLOGY

Ecology – life history and shell-wearing stage: Over their lifetime, coconut crabs transition from being microscopic larvae in the ocean to shell-wearing juveniles on land to, eventually, massive shell-less adults [1]. Initially, female coconut crabs carry their fertilized eggs on their abdomen, then release them into the ocean as larvae. These larval coconut crabs disperse through the ocean planktonically. After approximately a month at sea, the larva then transition to a fully terrestrial existence [15], and thereafter cannot remain submerged underwater without drowning, thus being restricted to whatever island they land upon. To transition from sea to land [15], individuals must first move into an unoccupied gastropod shell in the intertidal [16], so the availability of small empty shells in this area is essential. Once on land, the juvenile stage of coconut crabs [17] is spent transitioning to larger shells, which can involve complex social dynamics [3, 18-27] similar to that of the terrestrial hermit crabs from which coconut crabs evolved. Again, the availability of empty shells, in this case on land, is essential for coconut crabs to progress through their juvenile stage.

Despite intense searching for juvenile coconut crabs within the Chagos Archipelago, the author did not find a single one among several thousand occupied shells on land (Laidre unpublished). Notably, the occupants of all these shells were other sympatric species of terrestrial hermit crab (see below), suggesting that the availability of empty shells, both in the ocean and on land, may be a critical bottleneck for juvenile recruitment to adult life stages. Once coconut crabs do grow to adulthood, they re-calcify their otherwise soft abdomens and cease using externally-derived shells—for none would be large enough to accommodate the extreme size which they ultimately attain in adulthood.

Ecology – habitat, underground burrows, and mating: While coconut crabs must occupy the same shell 'housing market' [3, 18-27] as hermit crabs when they are juveniles, as adults they are no longer reliant on shells and instead carve out expansive underground burrows [23]. These burrows, often located beneath the roots of coconut trees and lined extensively with the husk of coconuts, provide a humidity- and temperature-controlled micro-environment, which the crabs occupy during the heat of the day (Fig. 9). Not all individuals occupy burrows though. In Chagos Archipelago, most burrow owners are large males, while smaller males and females are typically free-wandering (Laidre, unpublished). Burrows are defended vigorously against conspecifics, suggesting they are valuable resources.

Figure 9. Burrow of a coconut crab (*Birgus latro*) carved into the ground beneath the roots of a coconut tree (*Cocos nucifera*) in the Chagos Archipelago. Burrow owner at entrance, with substantial coconut husk located at mouth of burrow in front of owner. Photo: Mark Laidre (from [23]).

It has been hypothesized [23] that the large quantities of remnant coconut husk placed outside the mouth of coconut crab burrows (Fig. 9) may act as a signal, both to receptive females and to intruding males: the accumulated husk could effectively advertise the burrow owner's strength, based on the number of coconuts the owner recently husked. Interestingly, coconut crabs have a miniscule penis size, one of the smallest relative to their body size among all closely-related species [26]. Their small male sexual structure may be a consequence of putting extreme investment into non-sexual bodily structures, like claws, which enable them to defend burrows. Of the few observations of mating in coconut crabs in the wild [4], nearly all have taken place inside or immediately around burrows, indicating that these underground dwellings may be central to the reproductive biology and mate choice of the species [23]. Further research on burrows, especially detailed monitoring around burrows using camera traps, is likely to reveal fundamentals of reproductive and territorial behavior, which must be understood to conserve this species.

Ecology – foraging, diet, and predation: Usually at dusk, individuals emerge from their burrows and then throughout the night can be found actively wandering in coconut groves, in other forested areas, and in open areas along the beach, foraging for food. Nighttime is thus the ideal time for surveying individuals as they move and forage out in the open. A core aspect of coconut crabs' foraging behavior focuses on the objects for which they are named: coconuts. Using their powerful claws, coconut crabs are able to break open coconuts and then consume the inner flesh [1]. In the Chagos Archipelago, coconut shells leftover by the coconut crabs are sometimes subsequently occupied as homes by sympatric species of terrestrial hermit crab [27] (Fig. 10).

Figure 10. A sympatric species of terrestrial hermit crab (*Coenobita brevimanus*) living inside an empty coconut shell, leftover after foraging by coconut crabs (*Birgus latro*) in the Chagos Archipelago. Photo: Mark Laidre (from [27]).

While coconut crabs frequently forage on coconuts, the exact proportion of their diet constituted by coconuts is highly variable and individuals do not subsist exclusively on this one resource. In fact, studies of their diet [1, 4, 5] have indicated coconut crabs are highly omnivorous, and like their terrestrial hermit crab relatives [28], eat a wide range of plant and animal matter. This diverse diet, encompassing various fruits and nuts, vegetation, and carrion, makes evolutionary sense: the relative isolation of these crabs on far-flung islands means the predictability of any singular food resource—coconut or otherwise—would be uncertain at best.

In addition to consuming various dead animals, coconut crabs have also been observed to engage in active predation, hunting prey items both small and large. For instance, coconut crabs have been observed attacking and consuming invertebrates, like the red crab (*Gecarcoidea natalis*) on Christmas Island [29], as well as vertebrates, like the Polynesian rat (*Rattus exulans*) [30]. In the Chagos Archipelago, coconut crabs have been observed predating adults of the red-footed booby (*Sula sula*) [31]. Coconut crabs are thus one of the few invertebrates with a capacity to kill both mammalian and avian prey, including large adults. Coconut crabs may therefore act as 'ruler of the atoll', functioning as apex predators, playing a dominant role in their island ecosystems, and potentially strongly shaping community dynamics [31]. Indeed, comparisons of small islands with and without coconut crabs suggests that the presence of coconut crabs may have strong impacts on nesting birds [31] (Fig. 10). Further research on this topic offers an intriguing avenue for fully elucidating this species' ecological role.

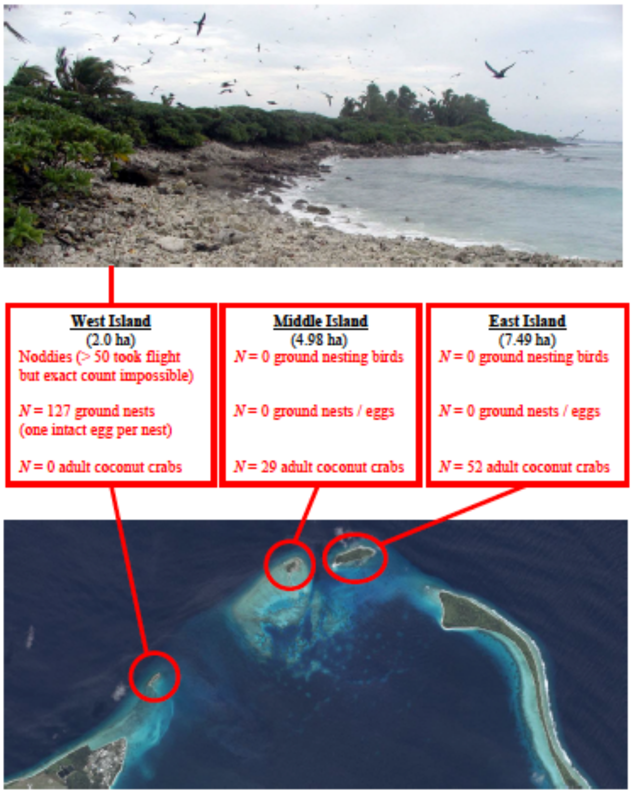

Figure 11. Pattern of abundance of coconut crabs (*Birgus latro*) and ground-nesting birds and eggs across three small islands in the mouth of the Diego Garcia atoll (Figure extracted from [31]).

Ecology – coconut plantations: In the Chagos Archipelago, coconut is a naturally occurring tree [32]. However, historically, native habitat was cleared throughout the entire archipelago to make way for coconut plantations [14]. Presently, >75% of island cover is dominated by coconut trees [33]. And although these coconut plantations have not been managed for over 50 years [14], the resulting habitat holds minimal natural biodiversity [34]. It is probable that the development of such vast coconut plantations has artificially increased the density of coconut crabs beyond what is 'normal', effectively providing unusually concentrated food resources. If these former coconut plantations are felled in the future, and native habitat is rehabilitated to help conserve breeding seabirds [11, 35, 36], then it's possible the density of coconut crabs may partially decrease as a consequence. Nevertheless, given the omnivorous tendencies of coconut crabs, many individuals should still survive and be capable of flexibly exploiting alternative foods in the face of reduced coconut availability.

Ecology – brains and olfactory sensing: Coconut crabs have a surprisingly complex brain, a large portion of which is devoted to olfactory sensing [37]. Unlike most crustaceans, coconut crabs must employ their olfactory sense on land, where relevant chemicals are typically hydrophobic molecules in the gaseous phase rather than hydrophilic molecules in aqueous solution. Their sea-to-land evolutionary transition thus presented a special challenge for olfactory sensing. Interestingly, detailed studies of brain structure, as well as electroantennogram responses, have revealed that coconut crabs converged on similar neural solutions and olfactory specializations to those of insects [28], such as the fruitfly (*Drosophila melanogaster*). Coconut crabs' extreme sensitivity to airborne chemicals on land and their ability to orient to these chemicals thus appears to be a product of convergent evolution to a terrestrial environment. More research is needed to understand the extent to which coconut crab brains are specialized for additional modalities, including visual and acoustic sensing, which may complement their acute chemical sense.

Figure 12. Coconut crab (*Birgus latro*) in the Chagos Archipelago stealing calipers from the author. This regular sort of theft has led to the crabs' other moniker: 'robber crabs'. Photo: Mark Laidre.

Ecology – neophilia and 'robbing': Coconut crabs are also referred to as 'robber crabs' [1]. This moniker appears to originate from these crabs stealing various items from humans (e.g., watches, cooking pots, and shoes). Such theft does not appear to be merely anecdotal. Rather, it has been consistently experienced by a number of biologists, including the author of this BAP (Fig. 12). In peer-reviewed journals, biologist have reported quite similar interactions with coconut crabs while based on remote atolls [39]. For example, one biologist commented [40]: "I have seen sandals, cooking-tins and even knives and forks stolen from jungle camps, and I once found a pair of crabs fighting over a silver wrist-watch, taken from a pile of clothes fifteen yards away". Another biologist [41] echoed that coconut crabs "carried off cutlery and other items from the camps, a habit well known locally". And yet another [42] noted that "Nothing could be left out at camps in safety; cooking utensils, cutlery, machetes; all were taken, and on one occasion a Primus stove was dragged off into the bush. On another occasion a *Birgus* was observed on the coastal strand line towing a whiskey bottle behind it."

Controlled experiments are needed to disentangle how and why coconut crabs engage in such theft. However, some of the key mechanistic and evolutionary aspects contributing to this robbing behavior are clear [1]. At a mechanistic level, the exceptional olfactory sensitivity of coconut crabs enables them to sense any objects that have even minute food-associated or human-associated odors [37, 38], and it is this scent that lures the crabs in. At an evolutionary level, coconut crab evolved in remote locations, where food was often limiting and where their extreme adult size meant they faced little or no danger from any heterospecific [1, 31]. Natural selection therefore likely favored high levels of exploratory behavior in coconut crabs, perhaps even neophilia, since this enables individuals to exploit the smell of rare but valuable food resources, which would otherwise be left unexploited. Ultimately, a deeper understanding of their fascinating robbing behavior may prove essential in conservation efforts to mitigate human-wildlife conflict involving coconut crabs. Indeed, given that poaching by humans represents one of the greatest threats to this species worldwide, future studies of the crabs' attraction to human-associated odors, as well as experimental tests of how to reduce this attraction, would be valuable.

Ecology – molting and longevity: To attain the extreme size that coconut crabs reach as adults requires individuals molt and grow incrementally across their lives. Molting is a particularly dangerous life history event [43], for it means a crustacean is without a protective exoskeleton and is therefore vulnerable, both to abiotic hazards (e.g., desiccation) as well as biotic dangers (e.g., being eaten by conspecifics or heterospecifics). Little is known about coconut crab molting behavior in the wild, though it is likely that molting, given how dangerous it is, occurs exclusively inside protected burrows [23]. Perhaps not surprisingly, mark-recapture studies have revealed that growth is a very slow process in coconut crabs, with individuals commonly experiencing conditions that result in zero or even negative growth [44]. Negative growth can occur when individuals are injured or lose a limb (e.g., a claw or walking leg is torn off during a fight), which then requires the individual to channel resources into regenerating the limb, resources which would otherwise have gone into growth and maintenance of body size. Integrating measurements of growth rates across coconut crabs' lives has produced conservative estimates of longevity. Remarkably, these estimates suggest that large individuals may be well over 100 yrs in age, and that, in general, individuals do not reach full adult sizes for at least several decades [44, 45]. These findings have important conservation implications: even minimal harvesting of a coconut crab population can mean that population will take decades to recover. More research is needed on molting, growth, and longevity in coconut crabs, especially long-term studies that track the same individuals across their lifetime.

Ecology – color morphs of coconut crabs: In the Chagos Archipelago, two color morphs of coconut crab exist: red and purple (Fig. 13). The purple color morph is much rarer than the red color morph, and neither color morph is not strongly linked to a particular sex or size (Laidre, unpublished). It remains unclear what, if any, function these colors have; what factors (e.g., diet or genetics) give rise to the different colors; and whether the two color morphs interbreed. More research is needed on this topic.

Figure 13. In the Chagos Archipelago, two color morphs of coconut crab exist: red (left) and purple (right). Here, the two compete over a dead rat, held by the purple crab.

Ecology – sympatric species of terrestrial hermit crab: Coconut crabs' closest evolutionary relatives are terrestrial hermit crabs (*Coenobita* spp.) [2]. At most locations across coconut crabs' extensive range, they overlap with one or more sympatric species of terrestrial hermit crab. In the Chagos Archipelago, three (native) sympatric species of terrestrial hermit crab co-exist on the same islands as coconut crabs. Each of these three sympatric species has unique morphological characteristics, with color providing an imperfect but still useful 'rule of thumb' guide: *Coenobita brevimanus* is typically purple in color; *Coenobita rugosus* is typically gray in color; and *Coenobita perlatus* is typically red in color (Fig. 14). All three of these species are highly abundant in the Chagos Archipelago, potentially saturating the shell 'housing market' [22]. Of several thousand shells the author sampled on Diego Garcia (Laidre, unpublished), all of these shells were occupied by one of the sympatric terrestrial hermit crab species, and none of the shells were occupied by juvenile coconut crabs (which have distinctive morphology that is independent of surface-level color differences). The availability of empty shells may therefore be a bottleneck for coconut crab recruitment from juvenile to adult life stages. Future experimental studies could help shed light on the importance of the shell housing market for conservation management by introducing surplus empty shells onto select islands in the Chagos Archipelago.

Figure 14. In the Chagos Archipelago, three sympatric species of terrestrial hermit crab co-exist with coconut crabs: *Coenobita brevimanus* (left in purple); *Coenobita rugosus* (middle in gray), and *Coenobita perlatus* (right in red). Photo: Mark Laidre.

THREATS

Figure 15. Coconut crab (*Birgus latro*) run over by a vehicle at the edge of a road within the Diego Garcia plantations. To the right of this 'roadkill' coconut crab is another, live coconut crab, which was attracted to the site by the scent of death. Photo: Mark Laidre.

Terrestrial – vehicles and road crossing: Over the course of two months, the author observed dozens of instances in which coconut crabs were run over by vehicles along the roads of Diego Garcia (Fig. 15). Many of these 'roadkill' coconut crabs were of a substantial adult size, thus being at least several decades old, if not older [44, 45]. Preventing vehicles from killing coconut crabs would be an important first conservation step on Diego Garcia; and the solution might be as simple as installing signs (to advertise the crabs' presence), along with specific requirements (for drivers to slow down, to avoid hitting coconut crabs along the road, or else be penalized). It also might be possible to install an above or belowground bridge system across certain roadways, which could help corral crabs to locations that were safe to cross, thereby avoiding unnecessary casualties. Such a bridge system for 'crab crossings' has been successfully installed on Christmas Island and is highly effective in avoiding deaths, especially during the annual red crab migration [4]. **Impact – High**.

Marine and Terrestrial – shell availability: Limited shell availability, both in the ocean and on land, may present a critical bottleneck, since shells are necessary for coconut crabs to initially transition from sea to land [15, 16] and to subsequently transition from juvenile to adulthood [17]. In the Chagos Archipelago, three other sympatric species of terrestrial hermit crab permanently occupy the shell 'housing market', so competition for shells is quite high. To ameliorate this shell competition, either (i) empty shells could be added or (ii) individuals of some of the sympatric terrestrial hermit crab species (which are extremely abundant and not at conservation risk) could be selectively removed from their shells, thereby freeing up shell resources for juvenile coconut crabs. Future studies should track the impact of experimentally altering shell availability on select islands, since only through such experimental studies can we quantify the importance of the shell 'housing market' for conservation management of coconut crabs. **Impact – High**.

Terrestrial - invasive rats: Black (ship) rats (*Rattus rattus*) were introduced to the Chagos Archipelago about 230 years ago [14] and are still present on 26 of the 55 islands that make up 94% of the archipelago's terrestrial landmass [46]. While these invasive rats have well-documented negative impacts upon seabirds, catastrophically affecting the birds' breeding populations [11, 35, 36], their impact on coconut crabs is unclear at present. This relationship may be complex, due to variability in the direction and magnitude of rats' impact on different life stages of coconut crabs.

Figure 16. Coconut crab (*Birgus latro*) in the Chagos Archipelago dragging dead rat (*Rattus rattus*) up tree. The crab ate the rat, yet it is unclear if it originally killed it or found it dead. Photo: Mark Laidre.

Plausibly, rats may prey upon juvenile coconut crabs or even upon small-sized adult coconut crabs. Rats have been directly observed preying upon other native crab species within the Chagos Archipelago, such as rock crabs *Graspus* spp. (Carr, personal communication 6 February 2020); but currently no direct observations exist of rats preying upon coconut crabs, regardless of size. Even if rats do negatively impact juvenile coconut crabs, their impact on adult coconut crabs is likely to be more multifaceted. Adult coconut crabs frequently compete directly with rats over coconuts and other food resources. In some cases, rats will open a coconut and then a coconut crab will steal this coconut (and sometimes vice versa); but with no consistent 'winner' emerging in these inter-species contests (Laidre unpublished). Furthermore, adult coconut crabs on Diego Garcia can regularly be found feeding on dead rats (Fig. 16), with rat carcasses likely providing a major source of protein.

Indeed, the unusually high densities of coconut crabs on Chagos might be linked not just to the abundant coconuts in the plantations but also the abundant rats, which together provide a diet rich in fat and protein, fueling individual and population growth. It is important to note that cases of coconut crabs feeding on rats on Diego Garcia do not necessarily imply active predation, since the rats on Diego Garcia are often killed with poison, which the coconut crabs subsequently consume to no ill affect.

At present, it remains unclear if rats act as predators, competitors, prey, or all of the above to coconut crabs. Also, whether rats negatively or positively impact coconut crabs may depend strongly on the life stage. More research is thus necessary to disentangle this complex relationship, including (i) studies of rats' foraging behavior and fecal contents; (ii) systematic comparisons of coconut crab density across islands with versus without rats; and (ii) before-to-after measures of coconut crab population density and behavior on islands that have targeted experimental eradication of rats. **Impact – Unknown**.

Marine and Terrestrial – hazardous plastic: Plastic waste from the ocean frequently washes onto the beach. Such plastic is known to pose a major hazard to hermit crabs [47] and, by extrapolation, to juvenile coconut crabs. Individuals climb into these plastic containers, where they become trapped and die [47]. The residual scent of foods and drinks on these plastic containers also make them even more attractive, particularly given coconut crabs' keen olfactory sense [37, 38] and novelty-seeking [39-42]. Exacerbating this problem further, once one individual dies within a plastic container, the scent of its death can heighten the attractiveness of the container to even more individuals [48], generating positive feedback of death after death. In the Chagos Archipelago, large quantities of plastic containers have accumulated at many locations along the beaches (Fig. 17). To ensure this plastic does not endanger coconut crabs, it is essential that regular beach clean-ups be undertaken on Diego Garcia and the northern atolls. **Impact – High**.

Figure 17. Plastic materials that have washed from the ocean onto the beaches of the Chagos Archipelago can pose a threat to juvenile coconut crabs. Photo: Mark Laidre.

Terrestrial – poaching and illegal harvest by humans: The Chagos Archipelago Marine Protected Area (MPA) was declared in 2010 as a Class 1 strict no-take MPA, where harvesting of resources is illegal. Despite this designation, illegal harvesting of coconut crabs still occurs, both on Diego Garcia, and on the outer atolls where passing yachts frequently dock. The extent and impact of this harvesting in the Chagos Archipelago is unknown. However, it is clear that in other locations where coconut crabs have been harvested illegally for human consumption, populations have suffered as a consequence [4]. Some means of combatting illegal harvest would be: (i) better educating those on Diego Garcia, including emphasizing that coconut crabs on DG consume poisoned rats, which can make them poisonous to humans. The scientific literature also includes well-documented cases in which consumption of coconut crabs led to human death due to the presence of lethal plant toxins [49], which coconut crabs can consume to no ill effect but which are poisonous to humans. Additional measures that could be taken to combat illegal harvest include: (ii) installing a camera trap network on Diego Garcia and across the northern atolls, thereby monitor coconut crab and human activity, with subsequent penalties to those who engage in illegal harvest. Finally, it would be especially worthwhile to (iii) uniquely tag individual coconut crabs (each with an RFID tag injected into their abdomen), since then these individuals could be permanently tracked across their lives. **Impact – High**.

Marine and Terrestrial – sea level rise: If placed in the ocean, adult coconut crabs will sink and then ultimately drown if submerged for too long. All islands in the Chagos Archipelago are those of typical atolls, with a low elevation of generally < 2m [10]. Projected global mean sea level rise for 1.5°C of global warming has an indicative range of 0.26 – 0.77m, relative to 1986–2005 [50]. Also, a short series of sea level data from the Chagos indicates a rise currently of 5.5 mm per year [51]. Based upon the above figures, with an even rise in global temperature of 1.5°C, most of the archipelago would be submerged in *c*. 360 years, effectively killing all its coconut crabs. Many models of global warming predict higher temperature rises in shorter timeframes, which would bring forward the date the archipelago would disappear underwater. **Impact – High**.

General – lack of fundamental knowledge required for conservation management of coconut crabs in the Chagos Archipelago: Despite coconut crabs being one of the most abundant and charismatic inhabitants of the Chagos Archipelago, there remain many critical gaps in knowledge for making sound conservation management decisions about this species [8]. Primary among these gaps is our limited knowledge about life history transitions. A major priority for research on Chagos coconut crabs should therefore be elucidating what factors, like shell availability, influence recruitment from juveniles to adults; locating and safeguarding nursery areas, where individuals can transition from sea to land; and sampling larval stages in the ocean to quantify factors influencing dispersal between islands. Furthermore, during adulthood, burrows appear to be critical to mate choice and reproduction in coconut crabs, yet little is known about these fundamental aspects of coconut crab biology. By installing a network of camera traps, each strategically positioned just outside a burrow, it will help reveal how the availability and distribution of these critical underground resources ultimately structures the population, shaping mating and territorial interactions. By also uniquely tagging many individuals across the population, it will then be possible to track these individuals across their lives, better establishing the key determinants of growth and reproductive success. In addition to conducting transect surveys on all islands, information on population genetic diversity on these islands would be highly valuable, both for comparison within the Chagos Archipelago itself and for comparison with other locations outside of the Archipelago. Finally, given coconut crabs' diverse diet and predatory tendencies, more research should be devoted to understanding their microbiome, including what, if any, diseases may exist in their populations and how these may be transmitted between individuals. **Impact – High**.

RELEVANT POLICIES AND LEGISLATION

International: While many populations of coconut crabs have now declined or gone locally extinct across the species' distribution, the current IUCN Red List status of 'Data Deficient' means that coconut crabs do not presently have any broader protections outside of local laws. A systematic survey across the species' entire distribution is sorely needed to better establish the current conservation needs of coconut crabs.

Local: In BIOT Law, coconut crabs are fully protected by The Protection and Preservation of Wildlife Ordinance 1970 and they also fall under The Strict Nature Reserve Regulations 1998.

MANAGEMENT NOTES

Global threats (such as rising sea levels, illegal harvesting, and hazardous plastics) cannot be solved without international cooperation. Every effort should therefore be made by the BIOT Administration and organizations working in the Chagos Archipelago to support research into and solutions to these critical worldwide threats. Other threats to coconut crabs, including all those deemed "High Impact", can be resolved with BIOTA support and funding. Ultimately, by supporting fundamental research on coconut crabs in the Chagos Archipelago, the knowledge that will be generated can enhance the natural biodiversity of the entire archipelago and lead to worldwide solutions for conserving this unique species.

SPECIES ACTION PLAN

PROPOSED ACTION	OUTCOME(S)	TIMEFRAME	PROPOSED START	PRIORITY	LEAD
POLICY & LEGISLATION					
Produce conservation management plans for all islands of the Chagos Archipelago, prioritizing the management action required and establishing associated costs and logistic requirements.	Conservation management plans for all islands of the Chagos Archipelago, excluding Diego Garcia atoll.	1 year	June 2020	High	BIOTA with assistance from relevant experts from Bertarelli Programme of Marine Science, Royal Botanical Gardens Kew, Chagos Conservation Trust, Dartmouth, and associated experts
Enforce driving requirements (and associated penalties) to ensure that vehicles avoid running over coconut crabs as they are crossing roads on Diego Garcia.	Fewer roadkill deaths of coconut crabs on Diego Garcia.	To continue indefinitely	June 2020	High	BIOT Administration Environmental Officer (BIOTA EO)
MANAGEMENT					
Remove hazardous plastic containers along edge of beach via systematic 'beach clean-ups' that involve local servicemen on Diego Garcia	Fewer deaths of juvenile coconut crabs from being trapped in plastic containers.	3 years	January 2021	High	BIOT Administration Environmental Officer (BIOTA EO)
Install camera trap network to document and reduce poaching and illegal harvest of coconut crabs on Diego Garcia and northern atolls	Fewer illegally harvested adult coconut crabs.	3 years	January 2021	High	Dartmouth, Bertarelli Programme of Marine Science, and Chagos Conservation Trust (CCT)

Prioritise, fund and implement effective control measures to deny Illegal, unregulated and unreported harvesting of marine resources in the Chagos Marine Protected Area.	Prevent IUU harvesting of marine resources in the Chagos Archipelago	25 years	August 2019	High	BIOTA
Using aerial baiting assisted by ground teams on islands where necessary, eradicate invasive rats from all islands of the Chagos Archipelago (except Diego Garcia) thereby assisting island ecological restoration and breeding birds; ensure that before-to-after measures are also collected of coconut crab population density and behavior to understand rats' complex impacts on crabs	All rats eradicated from rat-infested islands in the Chagos Archipelago; this strategy is critical for breeding seabird conservation, even if it may have somewhat unpredictable consequences on the coconut crab population	3 years	January 2021	High	Chagos Conservation Trust (CCT), Bertarelli Programme of Marine Science, Dartmouth, Chagos Seabird Ecology (BPMS ChaSE) team
As part of the same operation as the rat eradication programme, conduct vegetation management on islands (except Diego Garcia), which were ecologically altered for coconut farming or, where alien invasive species are impacting natural ecosystems, to assist island ecological restoration and breeding birds; ensure again that before-to-after measures are collected of coconut crab population density and behavior to understand impact of fewer available coconuts on crabs	Restore native habitat to areas of former coconut plantations; this will likely reduce the coconut crab population from what, at present, is probably an artificially high density	3 years	January 2021	High	CCT / BPMS ChaSE Royal Botanical Gardens (RBG) Kew, Dartmouth

RESEARCH & MONITORING					
Install network of > 100 camera traps around burrows to research the importance of burrows in structuring the population and shaping mating and territorial interactions among coconut crabs	Establish the role of burrows in influencing reproduction, mate choice, and territorial conflicts among coconut crabs	2 years	November 2020	High	Dartmouth
Individually tag > 10,000 coconut crabs across all size classes, injecting each with a unique RFID tag into their abdomen to permanently track them across their lives	Establish growth curves of individuals across their entire lives as well as longevity and population dynamics	30+ years	November 2020	High	Dartmouth, Chagos Conservation Trust (CCT)
Locate nurseries of juvenile coconut crabs in the Chagos Archipelago and conduct experimental research on the impact of empty shell availability on juvenile recruitment	Establish the degree to which shell availability acts as a bottleneck on transitions from sea to land and from juveniles to adults	3 years	November 2020	High	Dartmouth
Conduct systematic surveys of coconut crabs across all islands in the Chagos Archipelago, particularly the northern atolls	Estimate population size and abundance of coconut crabs across every island in the Chagos Archipelago	10 years	November 2020	High	Dartmouth, Bertarelli Programme of Marine Science, Chagos Conservation Trust (CCT)
Collect genetic samples (and microbiome samples) of coconut crabs across all islands in the Chagos Archipelago	Establish population genetic diversity within and between islands in the Chagos Archipelago and compare this to other sites around the world	10 years	November 2020	High	Dartmouth, Bertarelli Programme of Marine Science, Chagos Conservation Trust (CCT)
Conduct sampling of oceanic larval stages of coconut crabs and research factors influencing their dispersal between islands	Establish key factors influencing oceanic larval dispersal of coconut crabs and their successful recruitment from sea to land	3 years	November 2020	High	Dartmouth, Bertarelli Programme of Marine Science
Supplement above hypothesis-	This deeper knowledge can then ultimately	10 years	November 2020	Low	Dartmouth

driven research with exploratory observations, which deepen our knowledge of unknown yet fundamental aspects of coconut crabs' behavior, ecology, and natural history	be harnessed for future applications to conservation				
Monitor islands for rats biannually for 10 yrs after the eradication phase	To ensure success of eradication operation and provide a rapid response against any island that did not have rats eradicated	10 years	January 2024	High	BPMS ChaSE
As part of the biannual monitoring of rats, conduct concurrent control/eradication of pest plant species	To ensure control and eradication measures are successful or ongoing	10 years	January 2024	High	BPMS ChaSE
Research and model the possible timeframe and potential impact of rising sea levels in the Chagos Archipelago	Understanding the impact of sea level rise in destroying habitat for coconut crab and other species in the Chagos Archipelago	3 years	January 2021	Low	BPMS, Dartmouth, and associated experts

REFERENCES

1. Laidre, M.E. (2018). Coconut crabs. Current Biology 28: R58-R60.
2. Bracken-Grissom, H.D. et al. (2013). A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). BMC Evolutionary Biology 13: 128.
3. Laidre, M.E. (2014). The social lives of hermits. Natural History 122: 24-29.
4. Drew, M.M., S. Harzsch, M. Stensmyr, S. Erland, and Hansson, B.S. (2010). A review of the biology and ecology of the robber crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). Zoologischer Anzeiger 249: 45-67.
5. Greenaway, P. (2003). Terrestrial adaptations in the Anomura (Crustacea: Decapoda). Memoirs of Museum Victoria 60: 13-26.
6. Eldredge, L.G. (1996). *Birgus latro*. The IUCN Red List of Threatened Species 1996: e.T2811A9484078. https://dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T2811A9484078.en Downloaded on 06 February 2020.
7. Darwin, C. (1845 / 2001). The voyage of the Beagle. New York: Modern Library.
8. Laidre, M.E. (2017). Coconut crabs: from behaviour to conservation. Chagos News 51: 4-7.
9. Gan, C.-H. et al. (2008). Isolation and characteristics of 10 microsatellite markers from the endangered coconut crab (*Birgus latro*). Molecular Ecology Resources 8: 1448-1450.
10. Sheppard, C.R.C., Seaward, M.R.D., Klaus, R. and Topp, J.M.W. (1999). The Chagos Archipelago: an introduction. In: Sheppard, C.R.C. and Seaward, M.R.D (Eds.). Ecology of the Chagos Archipelago. Ecology of the Chagos Archipelago. The Linnean Society Occasional Publications, Westbury Academic and Scientific Publishing, Otley, pp.1-20.
11. Carr, P. (2011). A guide to the birds of the British Indian Ocean Territory. Oxford, UK: Pisces Publications for the Royal Society for the Protection of Birds.
12. Vogt, S. and Guzman, A.N. (2013). Population densities and demographics of the coconut crab, *Birgus latro*, on Diego Garcia, British Indian Ocean Territory. U.S. Navy Report.
13. Buckland, S. T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and L. Thomas. (2001). Introduction to distance sampling: estimating abundance of biological populations. New York: Oxford University Press.
14. Wenban-Smith, N. and Carter, M. (2017). Chagos: a history. London, UK: Chagos Conservation Trust.
15. Hamasaki, K., Sugizaki, M. Sugimoto, A., Murakami, Y., and Kitada, S. (2011). Emigration behaviour during sea-to-land transition of the coconut crab *Birgus latro*: effects of gastropod shells, substrata, shelters and humidity. Journal of Experimental Marine Biology and Ecology 403: 81-89.
16. Reese, E.S. (1968). Shell use: an adaptation for emigration from the sea by the coconut crab. Science 161: 385-386.
17. Kadiri-Jan T. and C. Chauvet. (1998). Distribution of the juvenile coconut crab, *Birgus latro* (L.), on the island of Lifou, New Caledonia. Ecoscience 5: 275-278.
18. Laidre, M.E. (2010). How rugged individualists enable one another to find food and shelter: field experiments with tropical hermit crabs. Proceedings of the Royal Society of London Series B, Biological Sciences 277: 1361-1369.
19. Laidre, M.E. (2011). Ecological relations between hermit crabs and their shell-supplying gastropods: constrained consumers. Journal of Experimental Marine Biology and Ecology 397: 65-70.
20. Laidre, M.E. (2012). Homes for hermits: temporal, spatial and structural dynamics as transportable homes are incorporated into a population. Journal of Zoology 288: 33-40.
21. Laidre, M.E. (2012). Niche construction drives social dependence in hermit crabs. Current Biology 22: R861-R863.
22. Laidre, M.E. & G.J. Vermeij. (2012). A biodiverse housing market in hermit crabs: proposal for a new biodiversity index. Cuadernos de Investigación UNED 4: 175-179.

23. Laidre ME. (2018). Evolutionary ecology of burrow construction and social life. Chapter 11 In: Life Histories (edited by Wellborn GA, Thiel M), pp 279-301. New York: Oxford University Press.
24. Laidre, M.E. (2018). Social cognition in the wild: from lab to field in hermit crabs. In: Field and Laboratory Methods in Animal Cognition: A Comparative Guide (edited by N. Bueno-Guerra and F. Amici), pp 237-239. New York: Cambridge University Press.
25. Laidre, M.E. (2019). Architectural modification of shells by terrestrial hermit crabs alters social dynamics in later generations. Ecology 100: e02767.
26. Laidre, M.E. (2019). Private parts for private property: evolution of penis size with more valuable, easily stolen shells. Royal Society Open Science 6: 181760.
27. Laidre, M.E. (2019). Life, in a nutshell. Frontiers in Ecology and the Environment 17: 202-202.
28. Laidre, M.E. (2013). Foraging across ecosystems: diet diversity and social foraging spanning aquatic and terrestrial ecosystems by an invertebrate. Marine Ecology 34: 80-89.
29. Krieger, J., Drew, M.M., Hansson, B.S., and Harzsch, S. (2016). Notes on the foraging strategies of the giant robber crab Birgus latro (Anomala) on Christmas Island: evidence for active predation on red crabs Gecarcoidea natalis (Brachyura). Zoological Studies 55: 6.
30. Kessler, C. (2005). Observation of a coconut crab, *Birgus latro* (Linnaeus, 1767) predation on a Polynesian rat, *Rattus exulans* (Peale, 1848). Crustaceana 78: 761-762.
31. Laidre, M.E. (2017). Ruler of the atoll: the world's largest land invertebrate. Frontiers in Ecology and the Environment 15: 527-528.
32. Topp, J.M.W. and Sheppard, C.R.C. (1999). Higher Plants of the Chagos Archipelago. In: Sheppard, C.R.C. & Seaward, M.R.D (Eds.). Ecology of the Chagos Archipelago. Linnean Society Occasional Publications 2, Westbury Publishing.
33. Carr, P. (2013). Factors influencing breeding island selection of red-footed booby *Sula sula* (Linn. 1766) in the Chagos archipelago, central Indian Ocean, and the implications for future island management plans. *MSc Thesis. Warwick University, UK*.
34. Carr P., Hillman J.C., Seaward M.R.D., Vogt S. and Sheppard C.R.C. (2013). Coral Islands of the British Indian Ocean Territory (Chagos Archipelago). Pages 271-282 in C.R.C. Sheppard (ed.). *Coral Reefs of the United Kingdom Overseas Territories, Coral Reefs of the World 4.* DOI 10.1007/978-94-007-5965-7_20, © Springer Science+Business Media, Dordrecht.
35. Carr, P., Votier, S.C., Koldewey, H., Godley, B., Wood, H. and Nicoll M.A.C. (2019). Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Submitted.
36. Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S. and MacNeil, M.A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559: 250-253.
37. Krieger, J., Sandeman, R.E., Sandeman, D.C., Hansson, B.S., and Harzsch, S. (2010). Brain architecture of the largest living land arthropod, the giant robber crab *Birgus latro* (Crustacea, Anomura, Coenobitidae): evidence for a prominent central olfactory pathway? Frontiers in Zoology 7:25.
38. Stensmyr, M.C., Erland, S., Hallberg, E., Wallén, R., Greenaway, P., and Hansson, B.S. (2005). Insect-like olfactory adaptations in the terrestrial giant robber crab. Current Biology 15: 116-121.
39. Burton, A. (2013). A Christmas crustacean. Frontiers in Ecology and the Environment 11: 572-572.
40. Gibson-Hill, C.A. (1947). Field notes on the terrestrial crabs. Bulletin of the Raffles Museum 18: 43-52.
41. Grubb, P. (1971). Ecology of terrestrial decapod crustaceans on Aldabra. Philosophical Transactions of the Royal Society of London B 260: 411-416.

42. Alexander, H.G.L. (1979). A preliminary assessment of the role of the terrestrial decapod crustaceans in the Aldabran ecosystem. Philosophical Transactions of the Royal Society of London B 286: 241-246.
43. Burggren, W.W. and McMahon, B.R. (editors). (1988). Biology of the land crabs. New York: Cambridge University Press.
44. Drew, M.M., M.J. Smith, and B.S. Hansson. (2013). Factors influencing growth of giant terrestrial robber crab *Birgus latro* (Anomura: Coenobitidae) on Christmas Island. Aquatic Biology 19: 129-141.
45. Fletcher, W.J., I.W. Brown, and D.R. Fielder. (1990). Growth of the coconut crab *Birgus latro* in Vanuatu. Journal of Experimental Marine Biology and Ecology 141: 63-78.
46. Harper G., Carr P. and Pitman, H. (2019). Eradicating black rats from the Chagos – working towards the whole archipelago. Pages 26–30 in C.R. Veitch, M.N. Clout, A.R. Martin, J.C. Russell and C.J. West. (Eds.). *Proceedings of the Island Invasives 2017 Conference*. Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.
47. Lavers, J.L., Sharp, P.B., Stuckenbrock, S., and Bond, A.L. (2020, in press). Entrapment in plastic debris endangers hermit crabs. Journal of Hazardous Materials
48. Valdes, L. and Laidre, M.E. (2019). Scent of death: evolution from sea to land of an extreme collective attraction to conspecific death. Ecology and Evolution 9: 2171-2179.
49. Maillaud C, Lefebvre S, Sebat C, Barguil Y, Cabalion P, Cheze M, Hnawia E, Nour M, Durand F. (2010). Double lethal coconut crab (*Birgus latro* L.) poisoning. Toxicon 55: 81-6.
50. Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K.L., Engelbrecht, F., Guiot, J., Hijioka, Y., Mehrotra, S., Payne, A., Seneviratne, S.I., Thomas, A., Warren, R. and Zhou, G. (2018). Impacts of 1.5ºC Global Warming on Natural and Human Systems. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I.Gomis, E. Lonnoy, T.Maycock, M.Tignor, and T. Waterfield (eds.)]. In Press.
51. Sheppard, C.R.C. (2002). Island elevations, reef condition and sea level rise in atolls of Chagos, British Indian Ocean Territory. *Cordio Report 2002*, pp.202-211.