

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)

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Jakob Krieger, Michelle M. Drew, Bill S. Hansson, and Steffen Harzsch (2016) Christmas Island, Indian Ocean, currently supports one of the largest populations of the giant terrestrial robber crab, *Birgus latro* (Crustacea, Anomala, Coenobitidae), the largest land living arthropod. Robber crabs are considered opportunistic omnivores feeding on a diversity of plants as well as animal derived foods. Previous reports indicate that the *B. latro* is primarily an omnivorous scavenger; however, there is some anecdotal evidence suggesting that the species may also hunt actively. Between 2010 and 2012 during three field trips to Christmas Island, we observed and documented active predatory behavior of *B. latro* on the endemic Christmas Island red crab, *Gecarcoidea natalis* (Brachyura, Gecarcinidae). Our observations suggest that *B. latro* does actively hunt, and exhibits at least two distinct predatory strategies. Large robber crabs are able to actively overwhelm and kill red crabs, while smaller individuals are likely to provoke red crabs to autotomize limbs on which to feed. These findings may indicate a much tighter predator-prey relationship between robber crabs and red crabs than considered before.

Key words: Food spectrum, Feeding strategy, Land crab, Predator-prey relationship.

BACKGROUND

The giant robber crab *Birgus latro* (Linnaeus, 1758) (Malacostraca, Anomala, Coenobitidae) is the world's largest extant land-living arthropod and the only terrestrial hermit crab that does not carry a mollusk shell as an adult. Individuals have been recorded to weigh up to 4 kg (review Drew et al. 2010) and recent studies suggest that they may live over 100 years (Drew et al. 2013). The species is widely distributed on remote tropical islands of the Indian and Pacific Oceans, with Christmas Island (Indian Ocean) arguably holding one of the largest and most undisturbed populations in the world (review Drew et al. 2010). Christmas Island is an

oceanic island located approximately 360 km south of Java, Indonesia, in the Indian Ocean that covers an area of ca. 135 km². Since 1978, the crab has been protected from hunting within the National Park and golf course of the island (Drew et al. 2010; 2012), constituting over 60 % of the island's area (Drew et al. 2010). Despite the species wide range, evidence would suggest that many of its other populations are declining, most likely due to human harvesting and habitat destruction, but as the species is poorly studied it is listed as data deficient (DD) under the IUCN Red List (Eldredge 1996).

Birgus latro are considered opportunistic omnivores (Harms 1937; Reyne 1939; Drew et al.

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2010), which on Christmas Island are commonly found feeding on the fruit of numerous plant species including *Ficus* spp., *Terminalia catappa* (Indian Almond), *Pandanus* spp., *Inocarpus edulis* (Tahitian chestnut), *Barringtonia racemosa*, *Ochrosia ackeringae* and *Artocarpus integrifolia* and *Arenga listeri* (Lister's palm) (Andrews 1900; Gibson-Hill 1947; Rumpff 1986; O'Dowd and Lake 1987; Wilde et al. 2004). The crabs strongly favor the pith of fallen arenga palm (*A. listeri*; Figs. 1J, K) and will often congregate in large numbers to access this resource (Drew and Hansson 2014). They are also capable of opening coconuts. The process is; however, often lengthy and involves many individuals before access to the coconut flesh is acquired (Fig. 1H; Alexander 1979; Rumpff 1986; Vogel and Kent 1971). *Birgus latro* will also actively scavenge and has been observed to eat various carrion including the Christmas Island endemic red crabs *Gecarcoidea natalis* (Figs. 1A, B; Hicks et al. 1990; Rumpff 1986), flying foxes (Fig. 1D, E; Harms 1937), turtle hatchlings (Alexander 1979), and birds (Harms 1937; Wilde et al. 2004; Hennicke 2012).

Christmas Island supports a high diversity of terrestrial crustaceans (review Hicks et al. 1990; Orchard 2012) including representatives of both Anomala and Brachyura. Harms (1932; 1937) observed that a population of *B. latro* on Christmas Island actively hunted the claws (chelipeds) of the blue crab, *Discoplax celeste*. Hicks (1985) and Wilde et al. (2004) reported that *B. latro* actively killed Christmas Island red crabs, *Gecarcoidea natalis* (Pocock, 1888). Orchard (2012) noted that *B. latro* will actively dig for *G. natalis* sheltering in burrows, killing them before consuming them. Rumpff (1986), also reported similar behavior but stated that it was most likely opportunistic behavior and was the exception rather than the rule (review Orchard 2012).

With a population estimate of 44 million, the endemic *Gecarcoidea natalis* is among the most prominent of species of terrestrial crabs on Christmas Island and well known for its annual spawning migrations (Adamczewska and Morris 2001). On Christmas Island, densities of red crabs range from 0.09 to 0.57 crabs per square meter (Adamczewska and Morris 2001) presenting an abundant food resource for potential predators. Here, we report observations made between 2010 and 2012, of *Birgus latro* actively preying on *G. natalis*, indicating two body size-dependent hunting strategies in this species.

MATERIALS AND METHODS

Crabs were observed near Aldrich Hill near the southern coast of the Island and within the Christmas Island National Park (10°30'22"S, 105°36'60"E). Photographs and videos were made using a Sony® DCR TRV-320E featuring night-shot optics, a Sony® DCR SR-47, and an Olympus® μ TOUGH-8010. Digital images were modified for image enhancement only, using the software packages Adobe® Illustrator CS4 and Photoshop CS4. All video processing was conducted using MAGIX® Video deluxe 2013 plus. All observations were conducted with permission from Christmas Island National Parks, Parks Australia North (permit numbers: AU-COM2008043, AU-COM2010090, AU-COM2011106, and CINP_2012_6).

RESULTS

In December 5-31, 2010; in July 7-August 4, 2011; and in October 13-November 6, 2012, we conducted field studies focusing on the migratory behavior of robber crabs, *Birgus latro*, in the rainforest of Christmas Island (Indian Ocean, Australia; Krieger et al. 2012) but also studied feeding and foraging behavior of the robber crabs. During these periods, we observed the animals to actively feed on a dead specimen of black-eared flying fox, *Pteropus melanotus natalis* (Figs. 1D, E); yellow locusts *Valanga irregularis*, (Figs. 1F, G); dead Christmas Island red crabs *Gecarcoidea natalis*, (Figs. 1B, C); coconuts *Cocos nucifera* (Fig. 1H); and fruits as well as the wood of arenga palm *Arenga listeri* (Figs. 1J, K). These observations are in line with previously reported food items for this species and support its nature of being a semi-nomadic foraging scavenger that only occasionally captures prey (Harms 1937; Kessler 2005; Hennicke 2012).

However, during our observations, we also noticed that many parts of the forest were characterized by the presence of accumulations of red crab carcasses. These leftovers frequently included cheliped shells of red crabs, and they were frequently discovered in and around potential and actual hiding places for robber crabs, such as niches of tree roots or crab burrows (Figs. 2A-D). Because robber crabs prefer to feed in locations of relative safety when the food item is manageable (Figs. 1B, D, 3H), the large piles of red crab shells near suitable and actual hiding locations might



Fig. 1. Various natural food sources for *Birgus latro* on Christmas Island. A selection of various natural food sources is given as examples from A to K. (A) Photograph of a female robber crab lurking motionlessly above a red crab burrow in the rain forest. Photographs of specimens of robber crabs feeding on: (B) a freshly killed red crab *Gecarcoidea natalis*; (C) a red crab roadkill; (D) and (E) wing of a black-eared flying fox *Pteropus melanotus natalis*; (F) a carcass of the Yellow locust *Valanga irregularis* in a garden of the settlement (living animal is shown in (G)); (H) the husk of an opened rotten coconut *Cocos nucifera*; (J) the fallen fruits of the Lister's palm *Arenga listeri* (white asterisk); (K) and the wood (black asterisk) of a freshly cut Lister's palm.

indicate that feeding on red crabs is more frequent than previously observed. We therefore attempted to investigate this behavior further.

On two occasions, we were able to document two robber crabs feeding on or killing living specimens of red crabs indicating an active predation. On October 16, 2012, a relatively small *B. latro* was filmed (Fig. 3) interacting with a red crab in the national park in the vicinity of Aldrich Hill (10°30'06"S, 105°36'04"E). This robber crab used its chelipeds to hold on to the red crab's chelipeds, and both animals were observed wrestling in this grip for approximately three minutes before the red crab autotomized its right cheliped enabling it to escape. The victorious *B. latro* then retreated with the autotomized red crab cheliped to feed on it (Fig. 3H). In this instance, the observed behavior was similar to that reported by Harms (1932; 1937) who reported robber crabs actively hunting for claws (chelipeds) of the blue crab, *Discoplax celeste*.

On a second occasion on the December 14,

2010, we discovered an alive red crab in the grip of a large male specimen of *B. latro* (Fig. 4) in the rain forest 200 m away from the coastline at (10°30'32"S, 105°35'50"E). The initial capture act was not observed but we filmed the robber crab shifting its weight to its pleon and the fourth pair of pereopods and then using its first to third pair of pereopods to form a cage to prevent the red crab from escaping. The robber crab then proceeded and consecutively removed one of the fourth, and both fifth pereopods of the red crab using its chelipeds. Finally, after searching for a favorable pinching point with its left cheliped (crushing or master claw), the robber crab killed the red crab by penetrating its carapace approximately 4 cm posterior to the eyestalk (see time series in Fig. 4 and Additional movie 1). A similar behavior was observed in the brachyuran crabs, *Daldorfia horrida* and *Scylla serrata* when processing their prey such as bivalves, gastropods, small brachyuran crabs or hermit crabs (Zipser and Vermeij 1978; Hill 1979).



Fig. 2. Red crab remains. The photographs (combined A to D) show numerous leftovers (red arrowheads) of red crabs in niches of tree roots (A and B) and in the vicinity of ground holes (C and D).

DISCUSSION

Our findings support the idea that red crabs or other available land crabs may play a greater role as prey of *Birgus latro* than considered before. Two putative primary strategies can be inferred from the two crabs observed. While larger robber crabs are able to capture and kill red crabs, smaller individuals will more likely capture and then wrestle with their putative prey crabs forcing them to autotomize walking legs or claws before releasing them.

From this limited data set, robber crabs appear to be sit and wait predators either positioning themselves over or in front of red

crab holes or in tree root niches and capture prey when red crabs come close or emerge from their holes (red arrow in Fig. 1A). This apparent ambush tactic might be a favored strategy with regard to an optimal energetic benefit - energetic cost ratio. Smaller but more agile animals might harvest red crab legs, while truncated red crabs are presumably an easy prey for less agile adult robber crabs. Exercised red crabs feature walking speeds from 0.14 to 0.48 km h⁻¹ (Adamczewska and Morris 1994) which is comparable to the average walking speed of one specimen of *B. latro* of 0.15 km h⁻¹ (Krieger et al. 2012). However, for short distances, robber crabs are able to move faster (estimated walking speed of 0.54 km h⁻¹



Fig. 3. Snapshot series of a video-taped female robber crab wrestling with a red crab. The snapshot series shows the female robber crab in an attempt to overwhelm a red crab of half of their own size (from A to G). Finally the red crab autotomized its larger right cheliped that was subsequently eaten by the robber crab (H).



Fig. 4. Snapshot series of a video-taped male robber crab catching and killing a red crab. The photograph (combined panorama based on three single pictures) illustrates the place of catch (arrow) near the shore terrace, the senior author, and the loose vegetation of screw pines *Pandanus* spp. The snapshot series (from B to J) shows a male robber crab handling (B to D) and killing (E to J) of a freshly caught red crab. The complete movie file shows this in more detail [see Additional movie 1].

based on unpublished video footages of competing and escaping robber crabs) when disturbed (Greenaway et al. 1988).

On a physiological level, robber crabs have a higher demand for storage polysaccharides, fats and proteins than sympatric species of land crabs on Christmas Island (Wilde et al. 2004). Terrestrial crustaceans often have limited access to minerals such as sodium, magnesium, calcium, or potassium, compared to marine environments where dissolved minerals are available almost *ad libitum*. Thus, terrestrial crustaceans must access their mineral demands either through food or salt water intake (Greenaway 1988). As red crabs occur at enormous densities (114 g·m⁻²) on Christmas Island (Green et al. 1999) and are available all year round (Greenaway 2001; Wilde et al. 2004) it is likely that robber crabs use them more frequently as food source than has been previously suggested.

CONCLUSIONS

Our field observations of encounters between robber crabs and red crabs on Christmas Island suggest that *Birgus latro* is not just an opportunistic scavenger but is an active predator as well. Although further investigation is needed, we propose that there is a much tighter predator-prey relationship between *B. latro* and *Gecarcoidea natalis* than considered before. Large *B. latro* individuals appear to actively overwhelm and kill red crabs, while smaller robber crabs which may not be able to use this strategy, may force their prey to autotomize limbs. The presence of red crab remains, composed of red crab shells in close proximity or within putative and actual refugia of robber crabs supports this hypothesis. The vegetation on Christmas Island is generally poor in mineral content (i.e. sodium and calcium), and our data may provide a suitable explanation as to how robber crabs meet their physiological demands for essential minerals. *Birgus latro* has been reported to be a slow-moving crustacean over long distances that however, is capable of rapid locomotion over short distances when disturbed (Greenaway et al. 1988). Therefore, robber crabs can be likely considered as ambush predators. However, as we only observed encounters between robber crabs and red crabs directly after the moment of prey capture in the field, the question how robber crabs exactly hunt and capture their prey remains unanswered and

needs further investigation.

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REFERENCES

- Adamczewska AM, Morris S. 1994. Exercise in the terrestrial Christmas Island Red Crab *Gecarcoidea natalis* - II. Energetics of Locomotion. *The Journal of Experimental Biology* **188**:257-274.
- Adamczewska AM, Morris S. 2001. Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breeding migration. *Biol Bull* **200**:305.
- Alexander HGL. 1979. A Preliminary Assessment of the Rôle of the Terrestrial Decapod Crustaceans in the Aldabran Ecosystem. *Phil Trans R Soc B* **286**:241-246.
- Andrews CW. 1900. A monograph of Christmas Island (Indian Ocean): physical features and geology. Kessinger Publishing.
- Drew MM, Hansson BS. 2014. The population structure of *Birgus latro* (Crustacea: Decapoda: Anomura: Coenobitidae) on Christmas Island with incidental notes on behaviour.
- Drew MM, Hartnoll RG, Hansson BS. 2012. An improved mark-recapture method using passive integrated transponder (PIT) tags in *Birgus latro* (Linnaeus, 1767)(Decapoda, Anomura). *Crustaceana* **85**:89-102.
- Drew MM, Harzsch S, Erland S, Hansson BS. 2010. A review of the biology and ecology of the Robber Crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). *Zool Anz* **249**:45-67.
- Drew MM, Smith MJ, Hansson BS. 2013. Factors influencing growth of giant terrestrial robber crab *Birgus latro* (Anomura: Coenobitidae) on Christmas Island. *Aquat Biol* **19**:129-141. doi:10.3354/ab00523.
- Eldredge LG. 1996. *Birgus latro*. In: The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Accessed 8 December 2014.
- Gibson-Hill CA. 1947. Field notes on the terrestrial crabs. *Bull Raffles Mus* **18**:43-52.
- Greenaway P. 1988. Ion and water balance. In: Burggren WW, McMahon BR (eds) *Biology of the Land Crabs*. Cambridge

- University Press, Cambridge, pp. 211-248.
- Greenaway P. 2001. Sodium and water balance in free-ranging robber crabs, *Birgus latro* (Anomura: Coenobitidae). *J Crustacean Biol* **21**:317-327.
- Greenaway P, Morris S, McMahon B. 1988. Adaptations to a Terrestrial Existence by the Robber Crab *Birgus latro*: II. *In Vivo* Respiratory Gas Exchange and Transport. *J Exp Biol* **140**:493-509.
- Green PT, Lake PS, O'Dowd DJ. 1999. Monopolization of litter processing by a dominant land crab on a tropical oceanic island. *Oecologia* **119**:435-444. doi:10.1007/s004420050805.
- Harms JW. 1937. Lebensablauf und Stammesgeschichte des *Birgus latro* L. von der Weihnachtsinsel. *Jenaische Zeitschrift für Naturwissenschaft* **75**:1-34.
- Harms JW. 1932. Die Realisation von Genen und die konsekutive Adaptation. II. *Birgus latro* (L.) Als Landkreb und seine Beziehungen zu den Coenobiten. *Z Wiss Zool Abt A* **140**:168-290.
- Hennicke JC. 2012. Christmas Island Goshawk predation on Abbott's Booby chick and competition with a Robber Crab. *Australian Field Ornithology* **29**:196.
- Hicks JW. 1985. The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). *Aust J Zool* **33**:127-142.
- Hicks JW, Rumpff H, Yorkston H. 1990. Christmas crabs. Christmas Island Natural History Association (2nd ed.)
- Hill BJ. 1979. Aspects of the feeding strategy of the predatory crab *Scylla serrata*. *Mar Biol* **55**:209-214. doi:10.1007/BF00396820.
- 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.
- Krieger J, Grandy R, Drew MM, Erland S, Stensmyr MC, Harzsch S, Hansson BS. 2012. Giant Robber Crabs Monitored from Space: GPS-Based Telemetric Studies on Christmas Island (Indian Ocean). *PLoS ONE* **7**:e49809. doi:10.1371/journal.pone.0049809.
- O'Dowd DJ, Lake PS. 1987. The Role of Terrestrial Crabs in the Dynamics of Rainforest on Christmas Island. Departments of Zoology and Botany, Monash University.
- Orchard M. 2012. Crabs of Christmas Island, 1st edn. Christmas Island Natural History Association, Christmas Island, Indian Ocean.
- Reyne A. 1939. On the food habits of the coconut crab (*Birgus latro* L.), with notes on its distribution. *Archives Neerlandaises de Zoologie* **3**:283-320.
- Rumpff H. 1986. Freilanduntersuchungen zur Ethologie, Ökologie und Populationsbiologie des Palmendiebes, *Birgus latro* L. (Paguridea, Crustacea, Decapoda), auf Christmas Island (Indischer Ozean). Dissertation, Westfälische Wilhelms-Universität.
- Vogel HH, Kent JR. 1971. A curious case: The coconut crab. *Fauna (Oslo)* **2**:4-11.
- Wilde JE, Linton SM, Greenaway P. 2004. Dietary assimilation and the digestive strategy of the omnivorous anomuran land crab *Birgus latro* (Coenobitidae). *J Comp Physiol B* **174**:299-308. doi:10.1007/s00360-004-0415-7.
- Zipser E, Vermeij GJ. 1978. Crushing behavior of tropical and temperate crabs. *J Exp Mar Biol Ecol* **31**:155-172. doi:10.1016/0022-0981(78)90127-2.

Additional files:

Additional movie 1.mp4 – Video recording of a male robber crab processing a red crab as shown in Fig. 4. Please click "here" to download.