PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Ecology of Terrestrial Decapod Crustaceans on Aldabra

P. Grubb

Phil. Trans. R. Soc. Lond. B 1971 **260**, 411-416
doi: 10.1098/rstb.1971.0020

Phil. Trans. Roy. Soc. Lond. B. **260**, 411–416 (1971) [411]
Printed in Great Britain

Ecology of terrestrial decapod crustaceans on Aldabra

By P. Grubb
Department of Zoology, University of Ghana, Legon, Accra, Ghana

Contents

The ecology of the following pagurid and brachyuran decapods on Aldabra is described briefly: *Coenobita rugosus*, *C. perlatus*, *C. clypeatus*, *Birgus latro*, *Geograpsus stormi*, *G. grayi*, *Grapsus tenuicrustatus*, *Cardisoma carnifex*, *C. frontalis*, *Ocypode cordimana*, *O. ceratopthalma*.

Cardisoma carnifex and *Birgus latro* are the only species which range far from the shore. *C. carnifex* occurs in very large numbers, especially around freshwater pools. It is largely a detritus feeder. *Birgus latro* is also common and, though partly predaceous, is often associated with *Pandanus*, the fruit of which it eats. *Coenobita rugosus* feeds on the faeces of giant tortoises on the dunes.

1. Introduction

The following notes are intended to supplement the account of tortoise biology so as to present an introduction to the natural history of the larger ground-living animals on Aldabra. Land crabs—especially *Cardisoma carnifex*—are so abundant that their role as scavengers and detritus feeders must be of considerable significance in the Aldabra ecosystem. It may be hoped that adequate studies of their ecology will be conducted in the near future.

2. *Coenobita*

Hermit crabs of the genus *Coenobita* are abundant on Aldabra. They are remarkable for the modification of the left chela and second pereiopod, which together form an operculum blocking the aperture of the gastropod shell in which the animal lives. The two larger species stridulate, using the chelae, to produce a loud rasping noise (see Borradaile 1903).

Coenobita rugosus

This, the commonest species, is variable in colour, but usually pearly buff with a dark grey or brown patch on the left chela. Some individuals have reddish marks on the pereiopods and these may belong to a different species.

C. rugosus occurs mostly among dune vegetation but it ranges up to 300 m from the shore on South Island, and was found in dense scrub at the edges of cliffs on the north coast of Middle Island. Crabs of this species normally inhabit the shells of *Nerita* or *Thais*. During the day, they

shelter under beach debris or leaf litter and detritus, and in the night they descend the beach to feed on decaying algae. At Anse Mais, showers brought the crabs out during the day from their shelter among rotting palm fronds.

Along the south coast, there is a conspicuous association between the tortoises and these hermit crabs. Both resort to the same shelters under *Guettarda* and other bushes, the crabs hiding in the debris of broken branches, sand and dried tortoise faeces—200 or more could be found under each bush. When a tortoise defaecates, the crabs emerge and gather to feed on the faeces. They also feed on dead tortoises and their decaying stomach contents.

Coenobita perlatus

C. perlatus is twice as large as *C. rugosus* and is pale orange-red in colour. It lives in the shells of such gastropods as *Turbo* or *Bursa* and never occurs far from the shore or adjacent dunes having been found also in tidal caves on Middle Island where *C. rugosus* is absent. *C. perlatus* is much the scarcer of the two species.

Coenobita clypeatus

C. clypeatus is often larger than *C. perlatus*, with the larger chela up to 4 cm long. It is dull purple all over, with white teeth to the chelae, and the eye stalks are cylindrical rather than flattened as in the other two members of the genus. *C. clypeatus* was found on coastal champignon at Cinq Cases, among sisal plantations at the Settlement and on the beach at the Middle Island camp, but it is nowhere numerous. It nearly always inhabits the shells of *Turbo marmoratus* but also utilizes those of *Semifusus*.

3. *Birgus*

The immense coconut or robber crab (*Birgus latro*)—the largest terrestrial arthropod—does not utilize a gastropod shell when adult, though it is closely related to *Coenobita* species. It occurs in two colour phases—a blue and a red—and in a small sample there were 36 reddish animals to 12 blue ones. The sex ratio in this sample was 30 males to 18 females, so it is perhaps not representative of the population, but for the moment it can be assumed that there is a simple mode of colour inheritance, red being dominant to blue.

The robber crab is the second most abundant terrestrial decapod on Aldabra and, with *Cardisoma carnifex*, the only species distributed widely throughout the atoll. It is not associated with the large solution pans, nor was it observed in *Pemphis* scrub, but it is abundant in the sandy coconut grove at Anse Mais and in damp *Pandanus* thickets on South Island. *Birgus* was also found in the barren coastal champignon where *Cardisoma* is absent, as well as throughout the platin. Tracks were sometimes seen on the dunes and the upper shore, but no evidence was found of the crabs contacting the sea.

The robber crab can dig—an animal confined under a packing case dug itself out over night—and those at Anse Mais make burrows in the sand. These burrows are also inhabited by *Geograpsus grayi* and the cockroach *Periplaneta americana*. Normally, however, *Birgus* inhabits a rock crevice, often at the bottom of a deep pothole or in the shelter of *Acrostichum* or other vegetation. At Takamaka, robber crabs occur with *Cardisoma* under the shelves of rock overhanging the large pool.

Birgus moves very slowly when not alarmed and emits a continuous ticking sound. When approached, it backs clumsily and stamps sharply with one or both of the long second pereiopods. It cannot normally be induced to extend the chelipeds. The chelae are extremely powerful,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

their broad dentate crushing surface being lined with bunches of tactile bristles which when touched result in immediate closure of the chela. With the chelae the animals can puncture tins and presumably are capable of feeding on young tortoises. Both the chelae are always present and only one out of nearly 50 animals showed any evidence of regenerating one of the limbs.

Birgus uses its long pereiopods with their curved dactyls for climbing. On narrow branches it commonly slips over, so that it continues climbing upside down in the manner of a sloth, which has claws modified in much the same way as the dactyls of *Birgus*. Though they were never observed in coco palms, the crabs will rapidly climb a coco bole when placed on one, and they were seen in *Pandanus* and *Ficus nautarum* trees, though not above 2 m from the ground.

Pandanus appears to be an important source of food for the robber crab, and up to ten of the large decapods were seen attempting to feed from a single fruit. In one case, it was monopolized by the largest individual. When others approached, it rushed at them with the chelipeds fully extended and raised. This threat display could develop into a brief pushing contest, and activity of this type was seen following casual encounters.

Feeding on *Pandanus* is conducted by stripping fibres off with the smaller chela, and transfering them to the fourth maxillipeds which reach out and seize them. The larger chela holds the fruit in position. Two robber crabs were once seen attempting to reach a strongly scented *Pandanus* fruit by creeping under or round the group of tortoises feeding on it. Robber crabs commonly take the segments of *Pandanus* fruit away with them, carrying each with the large chela only, or with both the chelipeds as well as the chelate fourth pereiopods, the body being held very high off the ground to make this possible. Not all the fruit is eaten, for dry undamaged segments can be found about the resting places of the crabs. These also carried off cutlery and other items from the camps, a habit well known locally and reflected in the name 'robber crab' itself.

Feeding on *Fimbristylis cymosa* and on the remains of dead tortoises was recorded and once a large *Birgus* was seen dragging off the carcass of a *Cardisoma carnifex* from which the carapace had been removed.

Drinking is done by immersing the chelae in rain pools and transfering the water droplets to the fourth maxillipeds.

4. Grapsidae

Crabs of the genus *Geograpsus* are not as widely distributed on Aldabra as is *Cardisoma carnifex*, and they are solitary. They do not dig and never occur in association with mud, but like *C. carnifex*, they have a threat display in which the chelipeds are extended above the head. This display is absent in the littoral *Grapsus tenuicrustatus* and is one of several features presumably reflecting the adoption of a terrestrial existence by *Geograpsus*. *Geograpsus* also differs from *Grapsus* in the development of large and presumably tactile bristles on the pereiopods and in having relatively large and powerful chelae, without spoon shaped tips. All individuals observed retained both chelae intact.

Geograpsus stormi

This species is referred to as *G. crinipes* by Borradaile (1903). It is a bright orange to buff crab, about 8 cm across the carapace. It was not recorded more than 300 m from the shore. Females

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

in berry were observed on 30 December 1967 and on 8 March 1968, and on the first occasion, a female was seen lying prone in a wave-washed pool, presumably facilitating hatching of the larvae. On the same day female *C. carnifex* in berry were active. Dry corpses of crabs which had attempted to reach the sea to breed were found along the south-coast beaches but were much fewer than those of *C. carnifex*. A *G. stormi* was seen making off with a *Cardisoma* that had been killed in camp but no other record of feeding was made.

Geograpsus grayi

This is a commoner species on Aldabra than *G. stormi*. It is very pale buff and a variable amount of dark maroon may extend over the whole carapace or form a large spot anteriorly. In size it is about 5 cm across the carapace.

One individual was seen over 1 km from the shore in open platin, but the crabs are most abundant in champignon near the coast. On West Island they occur in the champignon near the coast immediately behind the sandy ground of Settlement, and they live in similar places at Cinq Cases and Middle Island. They are found less regularly on the shore than is *G. stormi*.

G. grayi is able to climb, for individuals were observed on the roof of a house and in the joists of a shack. The crabs make their abode in champignon crevices but were also seen about 1 m off the ground in a tree hole and in the abandoned holes of *Ocypode* or *Birgus*. A crab in the process of moulting was secured from a *Birgus* burrow. Feeding on moths and the bug *Dysdercus fasciatus* was recorded and in turn one crab was observed being seized by a rail, *Dryolimnas cuvieri*.

Grapsus tenuicrustatus

Other grapsids are not terrestrial, but *Grapsus tenuicrustatus* was seen running among *Casuarina* needles in the cèdre woods on Middle Island, near blow holes in the cliff overhang.

5. *Cardisoma*

Cardisoma carnifex

The large land crab *C. carnifex* is up to 12 cm across the carapace. It is reddish brown, the red colour brightest on the bristly pereiopods, with yellowish chelae. There is a conspicuous sexual dimorphism, the males being largest with one of the chelae grotesquely developed so as to rival the cephalothorax in size in the biggest specimens.

Cardisoma normally walks sideways with a slow high-stepping gait, the cephalothorax raised well off the ground and the chelipeds folded and held horizontally, the tips meeting across the buccal frame. When approached, it rears back and spreads the chelipeds, with the chelae open. This threat is not carried through and in the largest males, the propodus and dactyl of each chela meet only at the tips and cannot produce an effective bite. There is no clapping display, in which the chelae are brought smartly together, as in the marine portunids, *Thalamita* and *Scylla*. The land crabs threaten occasionally by raising the chellipeds and approaching each other, but most of the time they appear to ignore each other.

C. carnifex is the commonest terrestrial decapod on Aldabra. Many of these land crabs may be seen together feeding or resting, and they seem tolerant of crowding. They occur in a great variety of habitats, though always in the neighbourhood of fresh or saline water or wet mud.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The crabs are most abundant around the large solution pans in the platin, but they are found throughout the platin woodland in small numbers. They also occur in the saline tidal pools amid *Pemphis* scrub on South Island where they are scarce and generally below average size. Individuals found in potholes in the platin, as at Takamaka, also tend to be small and young, and about 7 cm across the carapace. Larger individuals are more common in tidal pools on West Island where the abundance of mud makes the habitat more suitable. Land crabs are completely absent from the coastal strip of open champignon on South Island as well as the associated dunes and *Sporobolus* swards and the open mud flats landward of the *Avicennia* forest.

The crabs dig out their own burrows, transporting the mud with the chelipeds. The development of burrows is commonly inhibited by the impregnability of the champignon and many crabs simply resort to crevices in the coral rock from which mud has been removed. Around solution pans or on tidal mud flats, where they can dig freely, they produce crater-like piles of mud up to 20 cm high, with the burrow entrance in the centre. These mud piles at a distance resemble flamingo nests, and may account for rumours of breeding by those birds on Aldabra.

Land crabs feed largely on mud, but they also take fallen leaves and will seize fresh leaves when these are offered. In the evening they gather in hundreds at the edges of solution pans to feed. They pull down the leaves of *Lumnitzera* bushes and even half climb up the branches to take the leaves but are unable to climb properly. Towards evening, they also walk onto the open platin to feed on the sedges *Fimbristylis ferruginea* and *F. cymosa* and the regular clicking of their jaws as they graze can be heard throughout the night.

Land crabs may account for the low browse line on *Lumnitzera* trees but they appear to exert no marked effect on *Fimbristylis* swards. The crabs do not compete with the giant tortoises for food, for they were never observed feeding on 'tortoise turf' and *Fimbristylis* was rarely consumed by the reptiles.

The crabs often lie up with tortoises under *Ficus nautarum* and other shade trees. They will feed on the faeces of the tortoises but never appear to be dependent on them in the same way as is *Coenobita rugosus*.

Deposition of eggs in the sea by female *Cardisoma carnifex* was observed at Settlement on West Island, and at Cinq Cases, South Island. The crabs were seen to march down to the sea in the evenings and submerge at least the lower half of the body. After the megalopa larvae hatched the crabs returned to land.

On West Island they were diverted by the lights at Settlement, and it was clear that the activity was related to the full moon, the crabs being more active during six lunar cycles, the dates on which they were first observed being 2 and 30 December 1967, 18 and 30 January 1968, and mid-February. None were noted from 25 to 30 March. At Cinq Cases, the crabs came down to the shore while it was still light. During the day they sheltered under beach debris on the dunes or in caves and crevices at high-water mark. Many crabs were killed by prolonged exposure to the sun and their bleached remains from an earlier breeding season were noted in August 1967. Other mortality factors were significant, for the dismembered carcasses were found floating in the sea at low water, with no indication of how death was caused.

There was little further indication of the nature of predation on *C. carnifex*. Many crabs lack one of the pereiopods or chelipeds, or have it regenerating. A few crabs have lost both chelae and it is not clear how they can feed. A tortoise was once observed to bite repeatedly at a *C. carnifex*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

but its jaws slipped on the shell. Remains of *C. frontalis* were observed in tortoise faeces at Dune d'Messe and tortoises would eagerly consume crabs which had been killed. *Birgus latro* may be an important predator and crabs behaved very warily in proximity of the species. One of these huge pagurids was observed carrying off the carcass of a land crab in its chelae.

Cardisoma frontalis

This is a smaller and much darker species than *C. carnifex*, with redder chelae and spicules on the front of the carapace. It was observed at Anse Var, West Island, at Middle Island near the camp, and at Cinq Cases on open coastal champignon. None were seen approaching the sea to deposit eggs and it was thought at first that the species was rare. At Dune d'Messe, however, it appeared to replace *C. carnifex* in the mixed scrub. The specimen found at Middle Island was a female in berry secured on 16 March 1968, outside the breeding season of *C. carnifex*.

6. *Ocypode*

Ocypode cordimana

O. cordimana lacks 'horns' on the eyes and in colour is steely grey-blue to pale buff with reddish outer edges to the chelae. It makes a burrow with a straight exit that only just takes the crab. Sand is carted out of the burrow and scattered just outside to form a triangle of debris. Only males were found in the burrows on the shore during a search made in March 1968. These burrows occur in a line along the top 3 m of the sandy beach. The other species of *Ocypode*, *O. ceratophthalmus*, burrows below this zone, which is nevertheless washed by high springs.

The normal call of the male *O. cordimana* is a trisyllabic 'errr-er-er' (with a rhythm of 'dash, dot, dot') but it can break into a more complex series of the same long and short notes. The species has no stridulatory organ but the chela vibrates rapidly during calling and clearly the sound is made in much the same way as in *O. ceratophthalmus*—by friction between the propodus and ischium of the larger chelipid.

Females were found as far inland as the houses of Settlement, about 100 m from the high-tide mark, and there were some males here also.

Ocypode ceratopthalma

This species, with its spiral burrow, its habit of depositing sand in a pile some distance from the burrow and its prominent 'horns' or ocular peduncles, is a well-known crab (for references see Hughes 1966). The call of the male is bird-like, resembling that of a pigeon or dove, and consisting of a series of long drawn out notes, each rising in pitch. *O. ceratophthalmus* wanders inland on West Island but not as far as does *O. cordimana*. Batches of interconnecting burrows built very close together were found on the beach in the spring of 1968, both in January and March, and were inhabited by *O. ceratophthalmus*.

I am grateful to Dr W. Macnae and Dr J. D. Taylor for identifying some of the species mentioned in this account.

References (Grubb)

Borradaile, L. A. 1903 Land crustaceans. Pp. 64–100 in *The fauna and geography of the Maldive and Laccadive Archipelagoes*, ed. J. S. Gardiner. Cambridge University Press.

Hughes, D. A. 1966 Behavioural and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae). *J. Zool., Lond.* **150**, 129–143.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES