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A preliminary assessment of the rôle of the terrestrial decapod crustaceans in the Aldabran ecosystem

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Land crabs are the largest terrestrial invertebrates on Aldabra. The 12 species occupy most trophic levels, and some crabs are responsible for the transfer of energy from land to sea and vice versa. Some species may be responsible for preventing, or severely reducing colonization of Aldabra by exotic plant species. Other species are important in hastening leaf litter breakdown by digestion, while scavenging forms reduce the number of carrion-breeding flies. Burrowing forms may aerate the soil, and the littoral crab, *Grapsus tenuicrustatus*, by feeding on surface encrusting alga may speed erosion and aid soil formation. The hermit crabs form an important part of the diet of the flightless rail, and by depositing gastropod shells on land may provide drinking and breeding places for other animals.

Introduction

A working definition of terrestrial decapod crustaceans may be given as those crabs which habitually spend the greater part of their lives above water level. Thus defined, Aldabra is inhabited by 12 species of land crab, ranging from the littoral *Grapsus tenuicrustatus* through to well adapted terrestrial species like *Birgus latro*. Intermediate degrees of adaptation are shown by the other species: *Cardisoma carnifex*, *C. rotunda*, *Coenobita brevimana*, *C. cavipes*, *C. perlata*, *C. rugosa*, *Geograpsus crinipes*, *G. grayi*, *Ocypoda ceratophthalma* and *O. cordimana*.

The terrestrial decapod crustacea are an interesting group of animals owing to their secondary adaptation to life on land. Since all possess marine larvae it seems likely that initial colonization of Aldabra was achieved by larvae being brought from other regions of the Indian Ocean, presumably by the South Equatorial current. Nevertheless there exists the possibility that adult animals may have reached Aldabra on driftwood or similar flotsam, perhaps from the Malagasy region.

Hedley (1896) and Hesse, Allee & Schmidt (1937) have pointed out that coral atoll islands provide particularly suitable habitats for land crustaceans; thus it is not surprising that they should feature prominently in the Aldabran fauna. The land crabs are the largest invertebrates on Aldabra and occupy most trophic levels; consequently they are deeply involved in the energetics of the ecosystem.

Energy transfer

Material of terrestrial origin may be transferred to the sea in a number of ways.

(1) Since all of the terrestrial decapods breed by means of marine larvae, the mortality of these larvae at sea represents a considerable energy loss to the terrestrial ecosystem. Some idea of the number of larvae lost may be gained from examining mean egg counts from two common and widely distributed species: *Birgus latro* 90 730 and *Cardisoma carnifex* 458 188. These very

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large figures suggest considerable larval mortality. However, it should be noted that the surviving larvae will feed at sea and on metamorphosis will return to land thus helping to offset the deficit.

(2) When shedding eggs the ovigerous female crabs are occasionally washed away. This is particularly the case with *Cardisoma carnifex*, whose exoskeletons were seen washed up on the beaches. Mortality among egg shedding females is not thought to be high but the observed incidences of *C. carnifex* carcases was proportionately higher during the breeding season than otherwise. It is not clear what feeds on the soft parts of the crabs but even if only bacteria are responsible it would still be a contribution to the marine budget.

(3) Marine predators also take land crabs. The most common example is predation on *Grapsus tenuicrustatus* by moray eels (*Muraena* spp.). The crabs showed a marked reluctance to enter pools and if they crossed water going from one rock to another the movement was so frantic that they 'ran' over the surface of the water. Sometimes the crabs sank which resulted in their seizure by any moray eel in the vicinity. However, *Grapsus tenuicrustatus* feeds principally on encrusting marine algae so the net energy loss is considerably reduced.

On one occasion the stomach contents of a larger grouper (*Epinephelus* sp.) was found to contain the remains of three adult *Cardisoma carnifex*. These animals may have been swept away during egg shedding, but since one was a male it is not clear how this prey was obtained.

Although no observations were made it appears likely that *Ocypoda ceratophthalma* would be taken by predatory fish since these crabs are frequently engulfed by waves when feeding at the water's edge. The same may also be true of coenobites.

So far consideration has been given to material which has been transferred from land into sea, but crabs are also responsible for the transfer of material of marine origin onto land. The rôle of returning metamorphosed larvae has been mentioned above. Unfortunately, no figures are available for percentage return but I believe it to be small. Crabs of the genus *Ocypoda* are important predators on turtle hatchlings and turtle eggs, thus preventing the return of material of marine origin to the sea. Details of this will be discussed later.

Although primarily predatory, ocypodes are also scavengers. They were frequently observed with *Coenobita perlata* and *C. rugosa*, feeding along the beach strand line. Much stranded organic material is eaten by these crabs and faeces deposited inland will not only contribute towards the terrestrial budget but hasten the breakdown of materials and the release of nutrients to plants. *Birgus latro* was also observed feeding on beaches at night but this is not thought to be a major feature of their feeding behaviour.

The terrestrial hermit crabs (*Coenobita* spp.) are responsible for dragging marine gastropod mollusc shells onto land. Out of a sample of 11976 adopted gastropod shells examined, only five were terrestrial forms and the rest marine. Although energy contribution is minimal, the abandoned shells sometimes fill with rainwater, thus providing drinking facilities for some animals and breeding grounds for others. Rails (*Dryolimnas cuvieri aldabranus*) were seen to drink from water-filled upturned shells, as were coenobites and *Birgus latro*. Mosquito larvae were seen in shells in places where no other standing fresh water was to be found.

Coenobita perlata were seen feeding on the bodies of a stranded turtle, various species of marine crabs and fish remains.

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Scavenging

Several examples of scavenging by crabs have been cited above. It is necessary to emphasize this rôle, not only because of the energy turnover involved but the effect scavenging might have on population numbers of some other groups. Fosberg (1956) suggested that the scavenging effects of coenobites might explain the comparative scarcity of carrion-breeding flies on the Marshall Islands. No comparative figures are available at present, but subjectively, relatively few of these insects are found on Aldabra, presumably for the same reason. It would be interesting to observe the results of excluding crabs from an area where corpses of a variety of animals, e.g. tortoises, crabs, rats, washed-up fish and perhaps goats were present. This might be achieved experimentally by introducing a fixed quantity of carrion into two experimental plots; one on the main land mass, the other on an islet where the crab population is nil; and comparing insect larval numbers.

Cardisoma carnifex feeds extensively on fallen leaves and detritus. It undoubtedly plays an important part in the speeding up of leaf litter breakdown. This was especially noticeable in high-density *Cardisoma* areas where few leaves rested on the ground; in places where no or very few *Cardisoma* occur, such as the islets in west channels, the leaf litter was up to 10 cm deep.

Some experimental work was conducted to gain some idea of the turnover of food materials and energy uptake in *Cardisoma carnifex*. Two of the materials given were common foodstuffs; fallen leaves of *Casuarina equisetifolia* and tufts of the sedge *Fimbristylis cymosa*. Dry weight food consumption figures varied considerably, but values for energy assimilation for both groups of foods were similar, being 9.06 J g^{-1} d^{-1} for *Casuarina* and 12.06 J g^{-1} d^{-1} for *Fimbristylis*.

Population estimates based on burrow distribution in high-density *Cardisoma carnifex* areas gave a figure of 3683 crabs per ha. From data accumulated on *Cardisoma* populations, the mean mass of crabs was 322 g. Thus it may be calculated that the energy assimilation in high-density *Cardisoma* areas is in the order of 10.5–14.6 MJ ha^{-1} d^{-1}. These figures do, of course, apply to only one set of circumstances, but may be taken to indicate the scale of energy turnover by crabs.

Tortoise faeces were eagerly consumed by coenobites and hundreds of these crabs were to be found under bushes on the south coast which sheltered tortoises. Tortoise faeces 'sown' on beds of sterile soil often produced seedlings, demonstrating that seeds may pass through the digestive tract unharmed (D. Wood, personal communication). If this is a method of seed dispersal in the plants concerned, the coprophagous habits of the coenobites would prevent this, since the mouthpart and gastric mill mastication in these crabs is so efficient that no seeds were observed to have remained intact upon microscopic examination of the faeces.

Several crab species feed on decaying vegetation. It is likely that they lack a digestive cellulase and rely on bacteria and fungi to initiate the breakdown process. Some species of fish have been shown to have faster growth rates if fed on predigested food (J. R. H. Western, personal communication) and it may be that in these crabs a parallel situation exists.

Herbivory

Both *Cardisoma carnifex* and *C. rotunda* are herbivores, and plants known to be prominent in the diet of *Birgus latro*, *Coenobita perlata* and *C. rugosa*. Other crabs may be, but this was not observed. The most obvious effect is the consumption of seeds and seedlings thus exercising

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control over plant numbers. Many records were made of the consumption of ground level vegetation by *Cardisoma carnifex*. Especially favoured food plants were young *Colubrina asiatica*, *Euphorbia prostrata* and *Fimbristylis cymosa*, in addition to various grasses and sedges.

Coenobites often feed along the strand line on beaches and they may prevent the establishment or development of exotic plant species by consuming seeds and seedlings of plants washed up on the shore. The high degree of endemism among Aldabran plant species (Renvoize 1971) suggests restricted competition from more vigorous exogenous forms. It may well be that coenobites and perhaps other herbivorous crabs are responsible for this reduced competition. Newly arrived species of plant introduced as seeds in the faeces of migrant birds may suffer the same fate from the more 'inland' species of crab, such as *Cardisoma*, which have been observed eating bird faeces.

Coenobita rugosa eagerly consumes the terminal shoots of the alien *Catharanthus roseus* thereby substantially altering its growth form from an erect, rather spindly plant to a very bushy one. Since flowers are borne on the shoot tips the 'pruning' activities of the crab may increase the reproductive capacity of this plant considerably.

Another introduced plant, the coconut (*Cocos nucifera*) has a decided effect on the size and growth form of *Birgus latro*. Studies undertaken at six sites revealed that the mean mass of *Birgus* from coconut-dense areas was almost twice that of crabs from coconut-free areas. Details of this will be published elsewhere.

Carnivory

There are many examples of the capture and subsequent consumption of prey, in addition to the instances of carrion scavenging mentioned above.

The habitual carnivorous crabs are the genera *Geograpsus* and *Ocypoda*, although other species are known to take animal food occasionally. In tortoise nesting areas *Birgus* is said to be an important predator of hatchlings (I. R. Swingland, personal communication) but this was not observed by me, probably because the *Birgus* study areas were remote from tortoise breeding sites.

Ocypodes are important predators of turtle hatchlings and eggs and were seen digging into turtle nests for food, confirming the observations of Wiens (1962). There can be little doubt that this was deliberate, since burrows were dug in the middle of turtle nest depressions which were some distance from the crab's normal burrow sites. The Seychellois consider this habit commonplace and say that turtle eggs and hatchlings are brought to the surface for consumption. Yolk and other remnants are scavenged by coenobites. Large *Coenobita rugosa* have also been seen to dig down after turtle eggs, presumably attracted by scent (J. A. Stevenson, personal communication). On one occasion ocypodes accounted for 50% mortality of hatchling turtles out of observed emergences at Dune Jean Louis.

Geograpsus crinipes, together with *Ocypoda cordimana*, prey heavily on small coenobites, particularly *Coenobita rugosa*. Other, smaller, land crabs are taken from time to time, as are insects. Hughes (1966) considered that *Ocypoda ceratophthalma* is cannabalistic, but this was only rarely observed on Aldabra. However, many small *O. ceratophthalma* are consumed by *Geograpsus crinipes*, these two species exhibiting a considerable degree of habitat synchrony. Curiously, *Ocypoda ceratophthalma* was not observed eating small geograpsids.

On one occasion *Birgus latro* was seen consuming the coccid *Icerya seychellarum*. If this habit

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were a regular occurrence, it might provide the means for biological control of *Icerya*, whose presence has been associated with destruction of trees on the island. However, I believe this was an isolated case where the insect had fallen to the ground from a tree.

Predation

In addition to examples given of carnivory among crabs themselves, the crabs are preyed upon by several other groups.

Crabs were taken by several bird species. On the shore-line turnstones (*Arenaria interpres*) and crab plovers (*Dromas ardeola*) were seen to feed on *Ocypoda ceratophthalma*. Further inland pied crows (*Corvus alba*) were seen to feed on *Ocypoda cordimana*.

Small coenobites would appear to be important item of the flightless rail's diet and were seen to be consumed in quantity at Middle Camp. Rails would often run and grab the legs of coenobites, shaking them vigorously in order to snap them off. This prevents the hermit crab from forming the legs into the characteristic 'operculum' which blocks the entrance to the adopted shell. If the crabs were located when the limbs were withdrawn, then the rail would deliver a number of heavy blows with the beak in order to smash the 'operculum'. The soft abdomen was usually consumed first, followed by the rest of the body. Parent rails were seen to catch and break up coenobites to feed their young.

Records of stomach contents of feral cats shot on Aldabra showed *Grapsus tenuicrustatus* to be an important feature of the diet (J. A. Stevenson, personal communication). It is possible that feral cats and perhaps dogs might have died out from starvation but for the fact they were sustained by crabs.

Mosquitoes are known to feed on the heads and necks of tortoises, and although it was never observed it is possible that mosquitoes also feed on the fleshy abdomens of *Birgus latro*, particularly in areas such as Ile Michel where both *Birgus* and mosquitoes are abundant and tortoises almost non-existent. Furthermore, it is possible that the crabs may provide blood meals for other insect groups, notably members of the Ceratopogonidae.

Edaphic factors

Although soil drainage is good, the activities of burrowing crabs further increase drainage and aeration. The 'tilling' activities are important in soil turnover, especially in view of the lack of earthworms which traditionally fill this rôle.

Tortoises often shelter under trees and shrubs and defecate there. Coenobites gather to feed on the faeces and also burrow down into the soil for shelter. The burrowing activities tend to dig in the tortoise faeces thus enriching the soil with humus and nutrients. Tortoise faeces not dug in tend to dry out and disintegrate, and are dispersed by the wind.

Macnae (1971) pointed out that *Grapsus tenuicrustatus* is important in the ecology of Aldabra since it eats blue-green algae growing on the surface of the limestone rock. The algae etch the outer few millimetres of the rock surface and this layer is removed during the crab's feeding activities. Thus *G. tenuicrustatus* is not only responsible for erosion of the limestone, but the resultant powder helps to form soil.

Erosion is hastened by the burrowing activities of crabs such as *Cardisoma carnifex* which make burrows in champignon crevices in solution pans.

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Additional factors

Coenobites are good climbers and were found in a variety of bushes, with *Pemphis acidula* being the most commonly climbed. Bushes were sometimes literally festooned with them. It is not clear why they climb, perhaps to obtain food, perhaps to avoid predators; possibly both. In their wanderings, coenobites might be responsible for pollination of some of the plants they climb by transfer of pollen adhering to their appendages.

Birgus often drag coconuts back to their burrows for fibre stripping and subsequent consumption of the nut. Sometimes the nuts are abandoned before consumption and later germinate. *Birgus* may therefore be responsible for a wider distribution of this plant around the periphery of coconut plantations.

Although the crabs do not appear to compete directly with other groups, sympatric species of hermit crabs do compete for available shells (H. G. L. Alexander, unpublished data). However, one observation on Iles Moustique showed three *Coenobita cavipes* stealing fish regurgitated by a caspian tern (*Hydroprogne caspia*) for its chick.

One man-made hazard affecting crab populations on Aldabra is crude oil. During the period of the northwest monsoon (January–March), considerable quantities were washed up on beaches and many crabs which visit beaches were affected. Coenobites were particularly badly affected, the majority being contaminated with oil on their bodies and/or their adopted shells. This contamination was most noticeable on north coast pocket beaches where a number of dead oil-covered coenobites were found.

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