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Local Ecological Knowledge and Biology of the Land Crab *Cardisoma hirtipes* (Decapoda: Gecarcinidae) at West Nggela, Solomon Islands[1]

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ABSTRACT: A rich body of local knowledge on the behavior and reproductive biology of the land crab *Cardisoma hirtipes* (called *Kakau Tina* in the Nggela language) is reported here from West Nggela, Solomon Islands. Aspects of West Nggela local knowledge about *C. hirtipes* were verified by observation, reports, and studies of the reproductive condition of crabs during the 1995–1996 wet season at West Nggela. Local ecological knowledge appeared to inform harvesting strategies and was congruent with scientific knowledge about the crabs. A behavior known as "dipping," displayed by *C. hirtipes* before mating and ovulation, is well known to the Nggela people, but has not been reported in the biological literature for this species. Nggela people harvest *C. hirtipes* in large numbers when the crabs are dipping and can accurately predict the diel, lunar, and seasonal timing of this event. *Cardisoma carnifex* (*Tubala* in Nggela), which occurs in smaller numbers at West Nggela, plays a relatively minor role in the subsistence economy, and comparatively little local knowledge on its behavior and breeding biology was found.

THE ABUNDANT LAND CRAB *Cardisoma hirtipes* appears to form an important component of the subsistence economy at West Nggela (alias Florida), Solomon Islands (Figures 1 and 2), during the few months of each year when it migrates from the forest to the shore as part of its reproductive cycle. In this article I shall detail some of the West Nggela people's extensive body of ecological knowledge of this crab, which informs their harvesting strategies and is congruent with, and indeed sometimes extends, biological knowledge of the species. The related crab *Cardisoma carnifex* is not nearly as abundant as *C. hirtipes,* is only of minor importance to subsistence, and at West Nggela its breeding biology is apparently not as well understood by local people.

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Biology of Cardisoma *Species*

Cardiosoma hirtipes is found in the Indo-Pacific Region from the Bay of Bengal to Hawai'i, including the southern islands of Japan and Christmas Island in the Indian Ocean (Turkay 1974, Turkay and Sakai 1976). *Cardiosoma hirtipes* digs burrows down to the water table in heavy soils and, although it is most abundant around creeks and swampy areas, it ranges extensively across coastal lowlands in some parts of the Solomon Islands. Many are run over by cars each wet season when crossing coastal roads near Honiara, the capital city, on Guadalcanal. *Cardiosoma hirtipes* appears to spawn on a lunar cycle over at least 3 months between October and February. Aspects of the breeding biology of *C. hirtipes* have been described by Shokita (1971; Ryukyu Islands), Johannes (1981; Palau), and Hicks et al. (1990; Christmas Island).

Cardiosoma carnifex occurs from the Red Sea and the east coast of Africa to the Tuamotus (Turkay 1973, 1974), including the southern islands of Japan and the northern

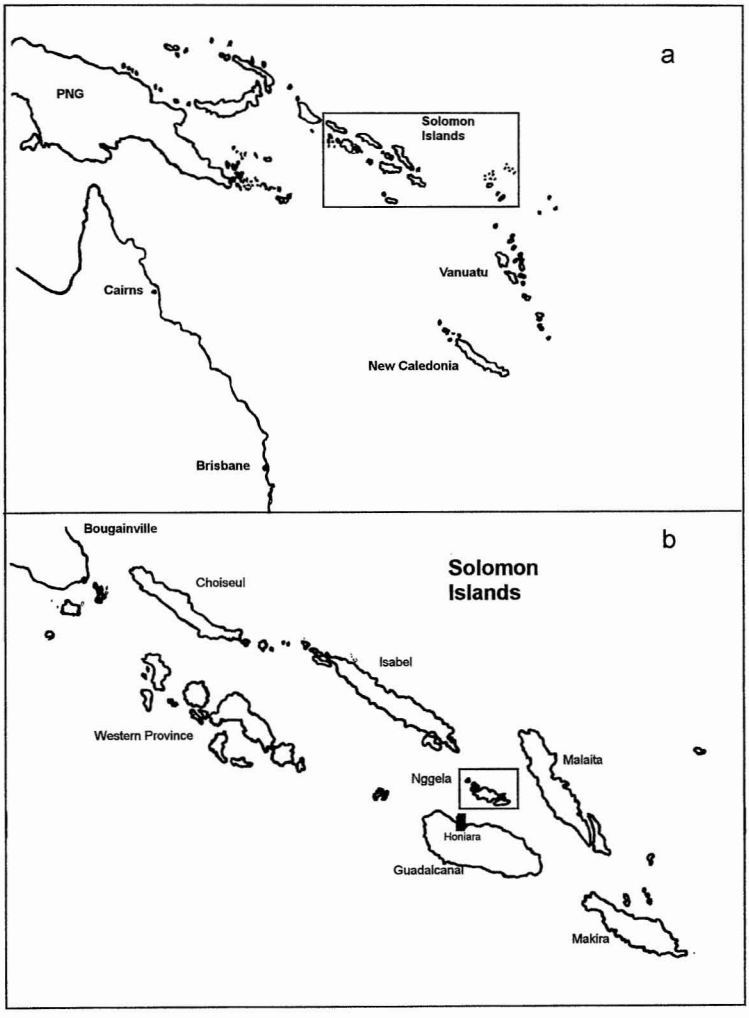

FIGURE 1. (*a*) Map of eastern Australia and the Southwest Pacific showing position of the Solomon Islands. (*b*) Map of the Solomon Islands showing the Nggela group of islands (boxed).

Great Barrier Reef (Turkay 1974, Turkay and Sakai 1976, Quinn et al. 1991). It inhabits mainly sandy soils, where it burrows down to the water table. At West Nggela it occurs in a few small patches of low-lying coastal land.

Reproduction in these species, as in most gecarcinid crabs, does not actually involve the shedding of eggs, but rather the release of zoea larvae (from the egg mass carried under the tail of berried females), which hatch immediately on contact with the sea (but see Bliss et al. [1978] and Hicks [1985] for exceptions). This takes place when the crabs migrate (sometimes en masse) down the beach, typically after dusk at a certain lunar phase, such as full moon or new moon. Fertilization and ovulation (extrusion of the eggs onto the egg-bearing pleopods on the crab's abdomen) usually occur shortly after copulation (though sperm can be stored for many days in some species [Klaassen 1975, Bliss

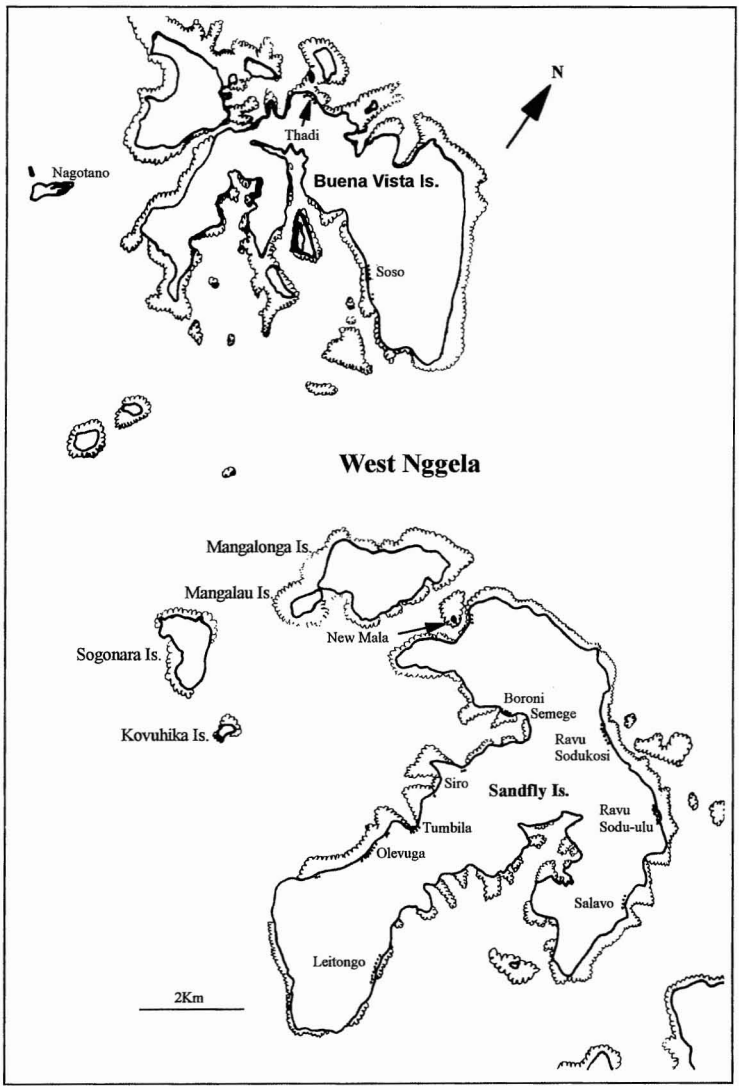

FIGURE 2. Map of West Nggela, showing positions of villages, including Semege substation.

et al. 1978, Adiyodi 1988]), after which time females usually hide in a temporary burrow near the shore until the eggs are ready to hatch.

Both species are active by day and night (ranging farther from their burrows after dark). They forage mostly on fallen leaves and fruits, and occasionally on small animals and carrion (Alexander 1977, Johannes 1981, Wood and Boutelier 1985, Hicks et al. 1990).

MATERIALS AND METHODS

Local knowledge on the natural history and subsistence harvesting of the two species at West Nggela was collected by structured

and unstructured interview, and by participant observation. Information was accepted only if it was agreed upon by at least five informants, in separate interviews. Men and women were asked questions of an abstract nature pertaining to the seasonal, lunar, and diel timing of reproductive conditions and behaviors of both *Cardisoma* species. This category of information was treated as ecological knowledge. They were also asked about the sex ratio of crabs at particular times, methods for cooking the crabs, and preferred condition of the crabs for consumption. Answers to questions pertaining to nonabstract subjects, such as the number or sex ratio of crabs in a recent harvest, were treated as reports, rather than ecological knowledge. These were used in conjunction with my own observations and investigations to confirm or deny items of ecological knowledge. Interviews were usually conducted at people's homes (mostly in the evenings) or when searching for crabs. Most questions were asked (and answered) in the Nggela language, with some recourse to Solomon Pijin.

Crabs were collected at regular intervals in early 1996 (and once in late 1995), from around Semege substation and Boroni village on Sandfly Island (Figure 2), either by walking at night with lights or by digging them up from their burrows (usually by day). After collection they were carried in a bucket to Semege substation (covered with foliage, to reduce aggression and minimize dehydration) and measured and weighed. Because weight varies exponentially with size, a regression of maximum carapace width ("length") against log wet weight was then calculated, and log weight per unit length was then used to compare samples. This standardized weight measure was averaged for each sex, for each date of collection. Mean standardized weight was compared for a number of different sampling dates from December 1995 to March 1996 using one-way analysis of variance (ANOVA) and planned comparisons (Day and Quinn 1989), using Systat for Windows (Systat Inc. 1992). The crabs were also dissected to determine reproductive state and to check for parasite infestations.

RESULTS

Ecological Knowledge and Subsistence Practices

According to the West Nggela people, female *C. hirtipes* (*Kakau Tina*) migrate to the edge of the sea to "wash their eggs" (*sau lami*: *sau* = wash; *lami* = the eggs carried on the pleopods of a female crab in the berried condition [Figure 3*a*]) during the 3 or 4 days before, and sometimes including, the full moon. This, they say, occurs for at least 3 months every wet season, commencing as early as October and peaking in December (the Nggela name for the month of December is *Kakau*, which is also the generic name for crabs). Larval release mostly takes place shortly after dusk, but has been reported in the early morning (just before dawn) as well. The people prefer not to eat berried female crabs, because they have little internal fat (*koni*), and the meat tends to be lean and wrinkled (*nggonggova*).

Many informants also reported occasionally seeing berried females whose egg masses appeared to be rotten and wormy (*lami mabulu*: *mabulu* = stinking, rotten). The eggs of these females are believed to be inviable, and the condition is said to be more common late in the season.

The West Nggela people describe another type of migration to the sea that occurs approximately 3 weeks before *sau lami* and is known as *sapa toga* (*sapa* = go seaward; *toga* = one thousand, or "thousands"). This is when large numbers of crabs (of both sexes) migrate to the beach and immerse themselves in shallow seawater, before the females disappear into shallow burrows near the shore. West Nggela people say that in these burrows the females come into berry (i.e., extrude a mass of fertilized eggs onto egg-bearing pleopods on the tail—the process scientists refer to as ovulation). Analogous behavior (i.e., immersion in shallow seawater before ovulation) in other gecarcinid species is referred to (by scientists) as "dipping" (Hicks et al. 1990, Greenaway 1994). West Nggela people say that, like *sau lami*, *sapa toga* also takes place on a lunar cycle, usually

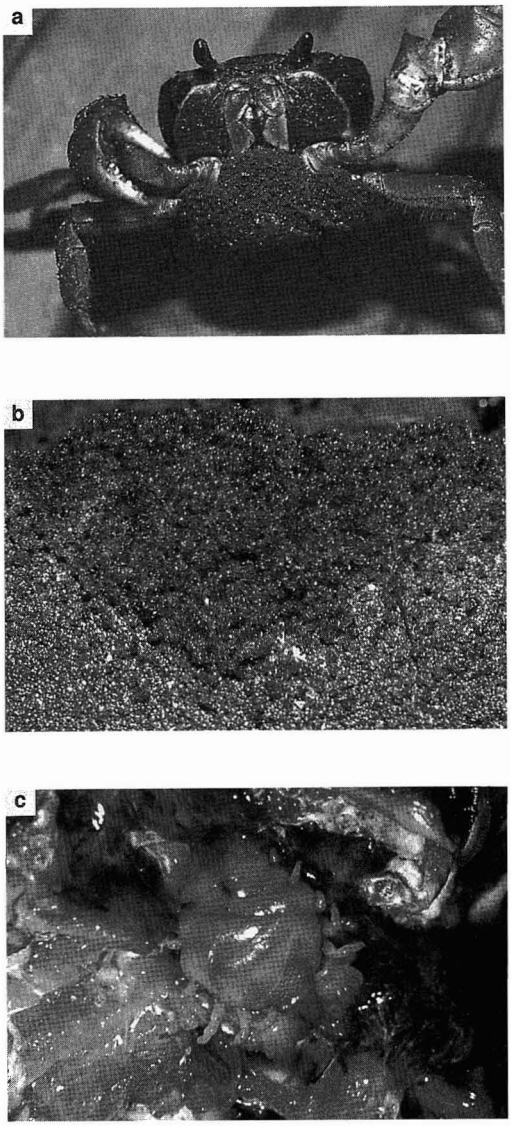

FIGURE 3. (*a*) Female *Cardisoma hirtipes* in the berried condition. Eggs change color from reddish brown to gray when close to hatching. (*b*) *Gasagave* (ostensibly megalopae of *Cardisoma hirtipes*) aggregating on a cement brick that was exposed to freshwater runoff from a building site at Semege substation, Sandfly Island, West Nggela (20 February 1996). (*c*) *Pouporu*, the (undescribed) isopod parasite common in the gill cavities of *Cardisoma hirtipes* in some parts of Sandfly Island, West Nggela.

during the week following a full moon. At that time the crabs are collected by the light of coconut-leaf torches. Females typically have full (yellow/orange) ovaries and are referred to as having, or "being" *koni* (*koni* = yellow/orange in color, or "the orange 'fat' of female crabs"). Crabs in this condition are regarded as a delicacy by most Nggela people and are typically roasted on an open fire. None of the West Nggela people interviewed for this study claimed to have seen copulation in *C. hirtipes*, and it is likely that it occurs in the shallow burrows where the females brood their egg mass, presumably soon after dipping.

Although *koni* females can be collected easily on or near the beach during a *sapa toga* event, this is said to be possible only relatively early in the breeding season. Late-season *koni* females are described as *koni raugia*, the latter term meaning to dig while at the same time feeling around (for a crab). This implies that gravid females can still be found late in the season, but do not dip (conspicuously at least) at that time.

There is reported to be some separation of sexes between nights during a *sapa toga* event, as described by the terms *samu ni mane* and *samu ni vaivine* (*samu* = unmarried; *mane* = man; *vaivine* = girl). *Samu ni mane* is generally believed to precede *samu ni vaivine.* The term *samu* connotes the fact that the crabs have not yet mated when they first arrive at the shore during the *sapa toga* migration.

Males are still harvested during *sapa toga* and although not *koni,* because this is exclusively a characteristic of females, are said to be *mona* (greasy, fatty). The Nggela expression *polo tuturu* (*polo* = to hide, *tuturu* = knees or elbows) describes the habit of male crabs sitting near the entrance to temporary shallow burrows near the shore, with their knees showing, around 3 days after the commencement of a *sapa toga*. It is likely that this term describes males that are guarding the entrance to burrows before (and perhaps also after) courting and copulation with a female.

West Nggela people say that dipping first occurs after the major emergence of Palolo

worms (*Eunice viridis*, or *Odu* in the Nggela language), which at West Nggela takes place one or two nights after full moon in October or November (see also Caspers [1984]). The main *Odu* emergence in 1995 occurred on 9 November at Ravu Sodukosi (see Figure 2) (pers. obs.).

Crab larvae that emerge from the sea at the completion of their final planktonic phase (the megalopa stage) are known to the Nggela people as *gasagave* (Figure 3*b*). West Nggela people said that the *gasagave* usually came ashore in or near the mouths of creeks or freshwater drains, but made no attempt to predict the exact timing of this event, other than saying that it occurred one or more times during the wet season. Some informants reported that in some seasons swarms of *gasagave* sometimes completely carpeted the beach. Most people believed that *gasagave* were baby land crabs. The likelihood that *gasagave* are the megalopae of *C. hirtipes* is discussed below.

Isopod parasites occasionally found in the gill chambers of *C. hirtipes* (Figure 3*c*) collected near Semege are called *Pouporu* by the Nggela people. *Pouporu* is also the name given to the Pacific Mole Crab, *Hippa pacifica*. Nothing is known about the parasite, which appears to be an undescribed species (Armand Kuris, University of California at Santa Barbara, pers. comm.). According to the West Nggela people, the parasite is common only in certain locations, the top of the bay near Semege being one of these.

Most West Nggela informants asserted that *C. carnifex* (*Tubala*) did not exhibit the spectacular synchronized dipping and spawning migrations of *C. hirtipes*, and added that in the former species spawning was haphazard and impossible to predict. Data gathered between December 1995 and March 1996 supported this assertion. Berried females were found on 8 February 1996 (full moon + 3 days), 15 February 1996 (new moon − 4 days), 27 February 1996 (first quarter), 4 March 1996 (full moon − 1 day), and 9 March 1996 (full moon + 4 days). The March record was a single female migrating to the beach shortly after dark, presumably to spawn. In the other cases (except 8 February), one or two berried females were collected together with large numbers of nonberried females (none of which was gravid).

The Nggela people have a traditional folk song, *Na Lingena Kakau*, about land crabs. A version of this song, as told by the paramount chief of West Nggela, Mr Christian Sale, is presented in the Appendix. The song contains information on the natural history and behavior of *C. hirtipes*, and cultural references (last stanza) to its subsistence use. The second stanza probably refers to the larval release migrations, because these are more synchronized than the earlier, predipping movement from inland, nonbreeding habitat. This is corroborated by the third and fourth lines of the third stanza, which describe the behavior of the female crabs (chelae held skyward [see Hicks et al. 1990:58]) when they are releasing larvae in the water. After the larvae are released they return their chelae to the normal "folded" position and return shoreward. *Cardiosoma hirtipes* also features (along with many other species, including *C. carnifex*) in folk songs from the Yaeyama Islands of southern Japan (Takeda and Ohyama 1994).

Observations

A calendar of reproduction-related behaviors for *C. hirtipes*, derived from West Nggela ecological knowledge, along with actual events reported by informants and/or observed by me, is presented in Figure 4. Fieldwork started in mid-December 1995, when women were observed collecting crabs from the beach near Semege. Subsequent observations and collections were made as opportunities allowed. It is thought that reproductive activity started in October or November 1995. Reports and personal observations confirmed that dipping and egg release usually took place at the expected times and lunar phases (see Figure 4), though in 1996 reproductive activity ceased earlier than many Nggela people expected. For the *sapa toga* event of January 1996, reports confirmed that males dominated numbers early in the event, but females were more

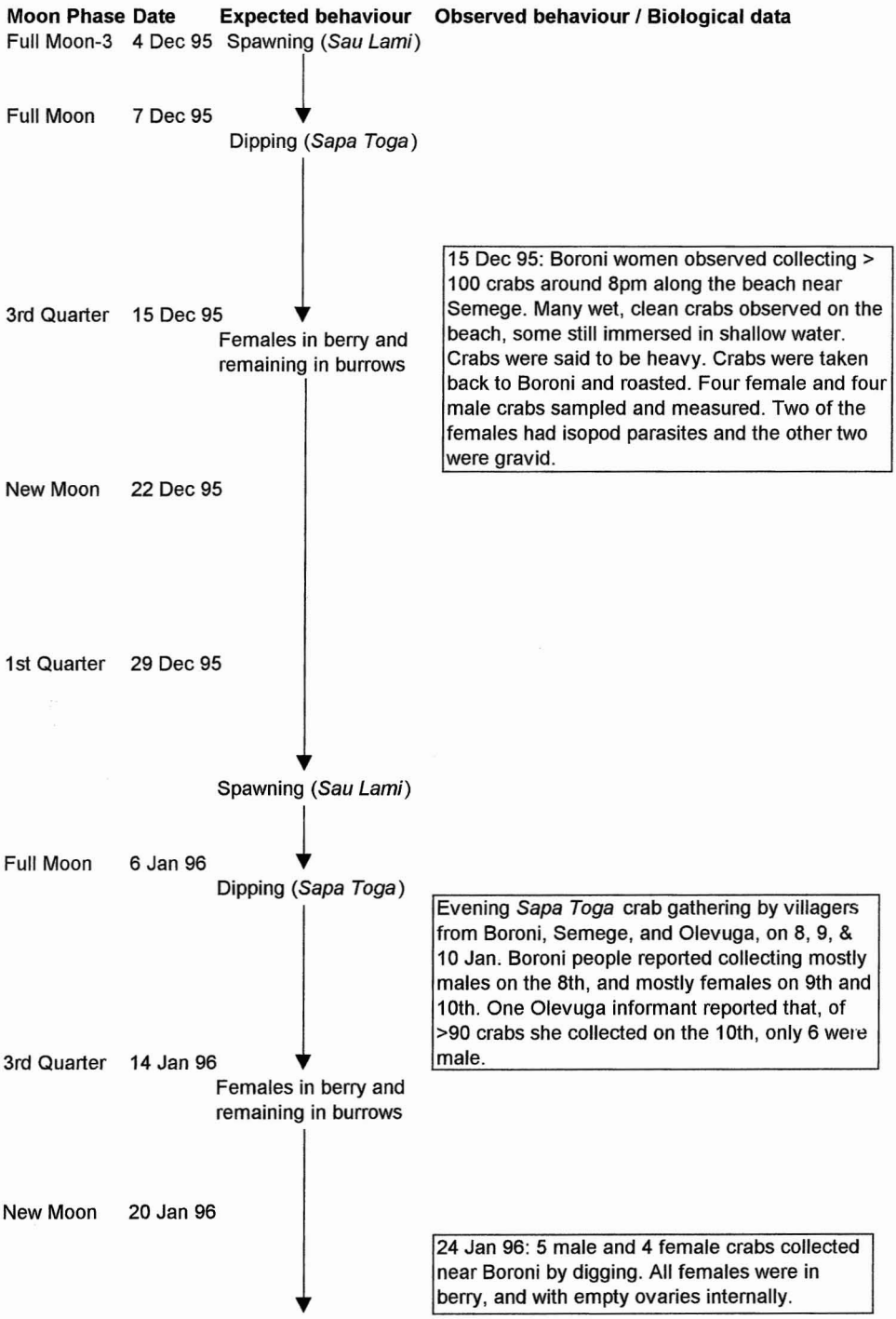

FIGURE 4. *Cardisoma hirtipes* (*Kakau Tina*): reproductive behavior, Sandfly Island.

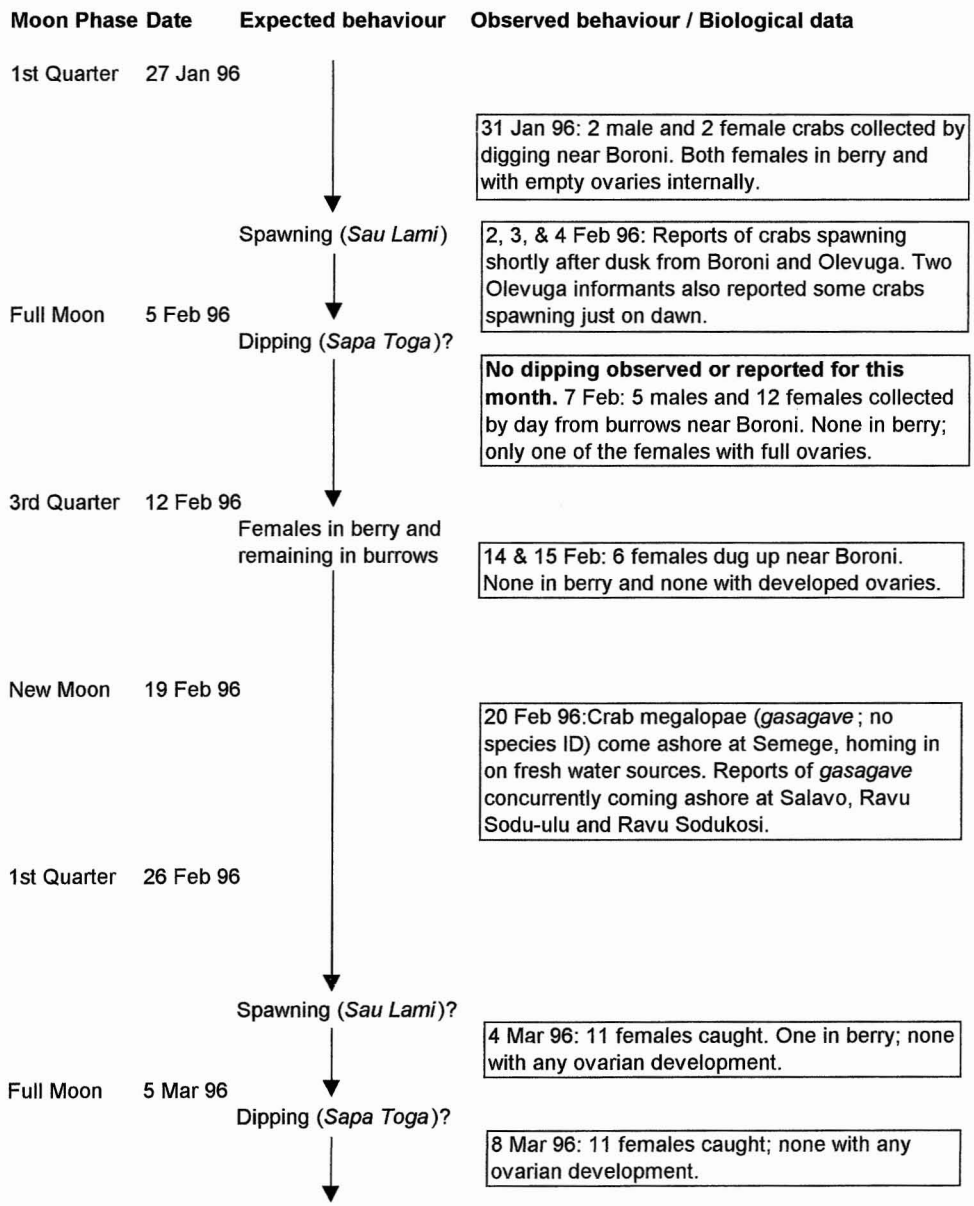

FIGURE 4. (continued)

abundant on subsequent nights, as expected. I observed what I assume to be megalopae on 20 February 1996 (Figures 3*b*, 4), when they aggregated on the beach around freshwater runoff from a building site at Semege and on the banks of a small creek. *Gasagave* were also reported to come ashore at Ravu Sodukosi, Ravu Sodu-ulu, and Salavo, on the east coast of Sandfly Island, around that time (Figure 2).

It was assumed that the average weight of female crabs would be higher at those times

of the lunar month when they were expected, according to West Nggela ecological knowledge, to have full ovaries (i.e., *koni*) or be in berry (i.e., *lami*), compared with other times of the month (e.g., when "spent"). The following information details the results of crab size and weight data for different dates in the 1995–1996 breeding season.

For male crabs measured and weighed on a specific date, weight (w, in grams) varied with maximum carapace width (L, in mm) according to the following regression:

$$w = 8.1006e^{0.0412L} \quad (r = 0.9749) \qquad (1)$$

So weights (w) were standardized to calculate a log weight per unit width ("standardized weight" or sw) by rearranging equation 1 to give:

$$sw = ln(w/8.1006)/0.0412 \qquad (2)$$

For the purposes of lunar phase comparisons, some samples were pooled if they fell within the same reproductive period (e.g., "dipping," "in berry," "spent" [females collected in the second quarter that released larvae in the previous quarter] [Figure 4]). Parasitized females (see Figure 4) were not included in the "dipping" sample used here. A one-way ANOVA showed no significant difference in mean standardized weight between any of the periods for which male crabs were sampled ($F = 1.123$; $df = 3, 19$; $P = 0.365$; Figure 5*a*).

An ANOVA of the data on the females, however, showed a significant difference between the pooled groups ($F = 5.777$; $df = 5, 45$; $P < 0.001$). Planned comparisons showed that females were significantly heavier when in berry than when spent ($P = 0.004$). Dipping females appeared to be slightly heavier than berried ones (Figure 5*b*) though the difference is not significant ($P = 0.196$). All females collected late in the season (i.e., after 7 February 1996), regardless of lunar phase, were significantly lighter than both the dipping and berried females ($P < 0.001$ for both). These data, and the fact that no berried females were found after 7 February 1996 (except for one berried female found on 4 March 1996 [Figure 4]) indicate that all

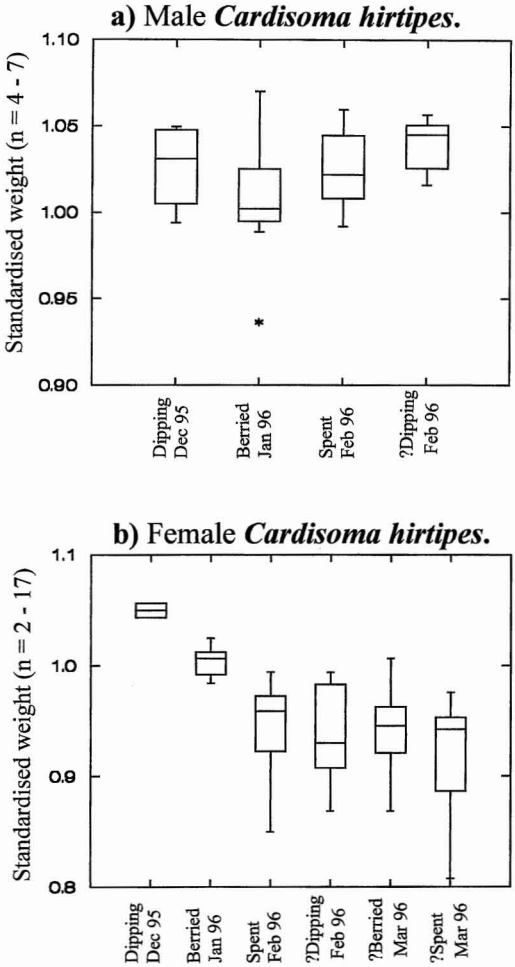

FIGURE 5. Box plots of standardized weights (see text) of male and female *Cardisoma hirtipes* sampled at various phases of the reproductive cycle for the latter two-thirds of the 1995–1996 breeding season at West Nggela. Note that *x*-axis labels describing reproductive phases of female crabs are also used for males, because males were also collected on the same dates. Note also that "?" refers to expected but not observed.

reproductive activity had ceased after that date. It should be noted that dipping may also have occurred in November 1995.

The standardized weight of two parasitized females sampled on 18 December 1995 was significantly lower than that of the healthy females (i.e., those in the "dipping" category) collected on the same date ($P = 0.033$).

DISCUSSION

West Nggela ecological knowledge concerning lunar and diel timing of the various reproductive phases for *C. hirtipes* appears to be validated by the observations presented here. Larval release by *C. hirtipes* starts just before the full moon at Yaeyama Island in the Ryukyus (Shokita 1971) and in Palau (Johannes 1981:37) but immediately precedes the new moon at Christmas Island, with minor events also occurring before the full moon (Hicks et al. 1990). The incubation time (i.e., from ovulation to hatching/release) must have been somewhere around 16–17 days, because large numbers of dipping (and presumably unmated) females were collected as late as 7 days after full moon and larval release usually commenced around 4 days before the next full moon (Figure 4). Earlier matings, with delayed fertilization and ovulation, are also possible if females are capable of storing sperm. Sperm storage by females is common in other land crab species (Klaassen 1975, Bliss et al. 1978, Adiyodi 1988). This coincides well with published incubation periods for other gecarcinid species: *Gecarcinus lateralis*, 15–16 days (Klaassen 1975, Bliss et al. 1978); *Cardisoma guanhumi*, 16 days (Henning 1975); *Gecarcoidea natalis*, >12–13 days (Hicks 1985).

Although the West Nggela people believe that the first occurrence of dipping usually follows the major emergence of Palolo worms (which was in November in 1995 at West Nggela), it should be noted that the onset of reproduction in land crabs is more likely to be related to the beginning of the rainy season (Gibson-Hill 1947, Hicks 1985, Wolcott 1988). The perceived coincidence of crab dipping with Palolo swarming at West Nggela may therefore be due to the proximity of the two events within the lunar cycle (just after full moon). It is quite possible for the rains to start in some years much later or earlier than the Palolo swarms (which are always in October or November [Caspers 1984]).

Ecological knowledge, confirmed by some reports, indicated that males were typically more abundant on the first night(s) of a dipping week (*samu ni mane*), with females predominating later (*samu ni vaivine*). On Christmas Island (Indian Ocean) *C. hirtipes* breeding migrations usually start with males arriving at the shore first, where they build temporary burrows for the purposes of mating, which they then defend against other males. The females arrive later and are courted by males before copulation and ovulation, after which they remain in the burrows until their developing larvae are ready to be released (Hicks et al. 1990; Hugh Yorkston, Great Barrier Reef Marine Park Authority, pers. comm.). This burrow-defending behavior of the males is described by the Nggela expression *polo tuturu*, mentioned above.

Dipping behavior has been observed in *C. hirtipes* on Christmas Island (Hugh Yorkston, Great Barrier Reef Marine Park Authority, pers. comm.), but no data on its timing or relationship to ovulation or other aspects of the reproductive cycle have been published. The function of dipping in *C. hirtipes* also remains a mystery. However, dipping in the Christmas Island red crab, *Gecarcoidea natalis*, has been the subject of some physiological investigations. Like *C. hirtipes*, males and females of *G. natalis* dip in the sea before courtship and mating (Hicks 1985, Hicks et al. 1990, Greenaway 1994). Greenaway (1994) found that hemolymph osmolality in *G. natalis* drops significantly as a result of their long migration from dry-season inland habitat to the sea at the start of the breeding season, but dipping in the sea returned hemolymph osmolality to normal levels. Whether or not the same processes occur in *C. hirtipes*, and for the same reasons, requires further work and can only be a subject of speculation here.

The weight change data gathered for this study indicate that females are heavier when gravid (*koni*, i.e., at the time of dipping), and when berried, than when spent (i.e., having just released their eggs). The question of whether or not individual females are capable of iteroparous spawning over consecutive lunar months cannot, however, be answered conclusively from the data presented here. The lack of any substantial gonad develop-

ment in berried females collected in late January 1996 (which would be necessary if they were to mate and ovulate in time for another spawning before the next full moon) may be because January was the last month in the breeding season for that year. At Christmas Island, tagging of female crabs showed that some individual *C. hirtipes* in fact spawned over three consecutive lunar months (Hugh Yorkston, Great Barrier Reef Marine Park Authority, unpubl. data). Similarly, 11% of tagged female *C. carnifex* spawned twice in one season at Lizard Island (Karen Diele, Queensland Museum, unpubl. data). Further data are needed to confirm this for the West Nggela populations. No *koni raugia* females were found in this study, and it appears that the latest dipping occurred in January 1996 and that most reproductive activity had ceased after 7 February 1996.

The presence of large numbers of *gasagave* in the tidal creek at Semege and at a freshwater runoff point (Figure 3*b*) suggests that they are the megalopae of *C. hirtipes*, because this is the only land crab species at Nggela that spawns en masse and whose larvae are known to home in on freshwater sources (Hicks et al. 1990; Hugh Yorkston, Great Barrier Reef Marine Park Authority, pers. comm.). If it is assumed that the *gasagave* seen on 20 February 1996 are from the previous spawning event, then the larvae were at sea for 16–18 days. This is around the minimum duration for the planktonic stage reported for Christmas Island *C. hirtipes* (Hicks et al. 1990; Hugh Yorkston, Great Barrier Reef Marine Park Authority, pers. comm.).

The condition known on Nggela as *lami mabulu* (where the egg masses of berried females are rotten or wormy) may derive either from eggs that have hatched prematurely or from eggs that have failed to hatch on a spawning run. The first condition has been observed for *G. lateralis*, whose ripe eggs hatch on exposure to water of a wide range of salinities (including fresh and hypersaline water, both of which are unsuitable for larval survival and development [Wolcott and Wolcott 1982]), thus hatching prematurely if drenched by rain before spawning (Klaassen 1975). Hicks (1985) reported that ripe eggs of *G. natalis* commenced hatching within 5 sec of immersion in seawater. He also observed that females ready to spawn carefully avoided standing water bodies such as tide pools. The second condition has been described by Karen Diele (Queensland Museum; pers. comm.), who observed incomplete shedding (hatching?) of eggs of *C. carnifex* at Lizard Island, despite repeated attempts by the females to shed them. On inspection many of the embryos in those clutches were underdeveloped and about 50% had died. No explanation for this phenomenon has been arrived at as yet.

The ecological knowledge and data presented here, suggesting that *C. carnifex* (*Tubala*) exhibits unpredictable spawning patterns, are not supported by published accounts of this species' breeding behavior elsewhere. In most other cases, *C. carnifex* displays highly synchronous lunar periodicity in its larval release runs (though no descriptions of dipping have been made in the literature). *Cardiosoma carnifex* females released larvae en masse 3 days before the full moon in December at Lizard Island (Quinn et al. 1991; Karen Diele, Queensland Museum, pers. comm.), and large larval release migrations peaking 2 days after new moon (just after dark) from January to March were observed at Aldabra (Grubb 1971, Alexander 1977). Because *C. carnifex* habitat is restricted to areas near the coast (usually sandy soil around mangrove swamps), it does not undergo any sort of extensive breeding migration, and this may preclude any need for dipping in the sea before mating and ovulation. It may be that *C. carnifex* spawned synchronously at other times of the year (e.g., October to December) at West Nggela, and more data are required to test this. I expect, however, that the West Nggela folk would have observed such behavior if indeed it occurs there.

The data presented here show that the West Nggela people possess a rich body of ecological knowledge about *C. hirtipes*, which informs their strategies for subsistence har-

vesting of the crab. Their ecological knowledge accords with, and extends, scientific knowledge about the species. Concentrated harvesting of *C. hirtipes* before ovulation (i.e., when dipping) betrays a level of local knowledge of its biology beyond that reported for any other subsistence economies. This information also points to avenues for further research into the biology of this fascinating and mysterious animal. Tagging studies could show whether individual females are iteroparous within a breeding season and, if so, the magnitude of the time interval between larval releases. Because dipping has not been reported previously in this species and its function is yet to be determined, further work is likely to reveal much about the animal's physiology, behavior, and ecology. Because of the limited scope of the study presented here, more research on the ecological knowledge of the West Nggela people is certain to reveal many more details of the crab's biology and ecology. Last, estimates of the abundance of *C. hirtipes*, in conjunction with local exploitation rates, will reveal important information on its current management status at West Nggela. Because of the broad and detailed observational database the West Nggela people have with respect to this species, much useful population-level information can no doubt be gathered through consultation with local experts, particularly elderly women.

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LITERATURE CITED

ADIYODI, R. G. 1988. Reproduction and development. Pages 139–185 *in* W. W. Burggren and B. R. McMahon, eds. Biology of the land crabs. Cambridge University Press, Cambridge.

ALEXANDER, H. G. L. 1977. An ecological study of the terrestrial decapod crustaceans of Aldabra. Ph.D. diss., University of London, London.

BLISS, D. E. J., J. VAN MONTFRANS, M. VAN MONTFRANS, and J. R. BOYER. 1978. Behaviour and growth of the land crab *Gecarcinus lateralis* (Freminville) in southern Florida. Bull. Am. Mus. Nat. Hist. 160:113–151.

CASPERS, H. 1984. Spawning periodicity and habitat of the Palolo worm, *Eunice viridis* (Polychaeta: Eunicidae) in the Samoan Islands. Mar. Biol. (Berl.) 79:229–236.

DAY, R. W., and G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59:433–463.

GIBSON-HILL, C. A. 1947. Field notes on the terrestrial crabs. Bull. Raffles Mus. 18:43–52.

GREENAWAY, P. 1994. Salt and water balance in field populations of the terrestrial crab *Gecarcoidea natalis*. J. Crustacean Biol. 14:438–453.

GRUBB, P. 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Philos. Trans. R. Soc. Lond. B Biol. Sci. 260: 411–416.

HENNING, H. G. 1975. Kampf-, fortpflanzungs- und hautungsverhaltenwachstum und geschlechtsreife von *Cardisoma guanhumi* Latreille (Crustacea, Brachyura). Forma Functio 8:463–510.

HICKS, J. W. 1985. The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). Aust. J. Zool. 33:127–142.

HICKS, J. W., H. RUMPFF, and H. YORKSTON.

1990. Christmas crabs. Christmas Island Natural History Association, Christmas Island, Indian Ocean.

JOHANNES, R. E. 1981. Words of the lagoon: Fishing and marine lore in the Palau District of Micronesia. University of California Press, Berkeley.

KLAASSEN, F. 1975. Okologische und ethologische untersuchungen zur fortpflanzungsbiologie von *Gecarcinus lateralis* (Decapoda: Brachyura). Forma Functio 8: 101–174.

QUINN, N. J., B. L. KOJIS, K. DIELE, and U. MEISCHNER. 1991. Reproductive behaviour of *Cardisoma carnifex* (Herbst, 1794) (Brachyura: Gecarcinidae) at Lizard Island, Great Barrier Reef. Mem. Queensl. Mus. 31:399.

SHOKITA, S. 1971. On the spawning habits of the land crab *Cardisoma hirtipes* Dana from Ishigaki Island, in the Ryukyu Islands. Biol. Mag. Okinawa 7:27–32.

SYSTAT INC. 1992. Systat for Windows, Version 5 ed. Systat Inc., Evanston, Illinois.

TAKEDA, J., and S. OHYAMA. 1994. Man and crabs in Yaeyama folk song: Crab-species identification and the folkzoological background. Humans and Nature 4:99–124.

TURKAY, M. 1973. Die Gecarcinidae Afrikas. Senckenb. Biol. 54:81–103.

———. 1974. Die Gecarcinidae Asiens und Ozeaniens. Senckenb. Biol. 55:223–259.

TURKAY, M., and K. SAKAI. 1976. Die Gecarcinidae von Japan (Crustacea, Decapoda). Res. Crustacea 7:11–22.

WOLCOTT, T. G. 1988. Ecology. Pages 55–96 *in* W. W. Burggren and B. R. McMahon, eds. Biology of the land crabs. Cambridge University Press, Cambridge.

WOLCOTT, T. G., and D. L. WOLCOTT. 1982. Larval loss and spawning behaviour in the land crab *Gecarcinus lateralis* (Freminville). J. Crustacean Biol. 2:477–485.

WOOD, C. M., and R. G. BOUTELIER. 1985. Osmoregulation, ionic exchange, blood chemistry, and nitrogenous waste excretion in the land crab *Cardisoma carnifex*: A field and laboratory study. Biol. Bull. (Woods Hole) 169:267–290.

APPENDIX

Na Lingena Kakau

TRADITIONAL NGGELA SONG ABOUT LAND CRABS (*Kakau Tina*)

Na Lingena Kakau	The Song of the Crab
Enigau lei vure soko	All you people
Tana lei sopa komu	In each village
Kau rongovia mai	Come all of you and hear
Na lingena kakau	The song of the crab
Te butu tana leao	It comes from the (primary) rain forest
Me sugi tana nananggu	And goes down at the overgrown garden
Me taoni hugu hugu	And follows the creeks in the mangroves
Me soga sapa i sagalea	And jumps seaward at the beach
Te sapa tana ihu	It goes seaward at the point
Me longa tana longgu	And comes shoreward in the bay
Me sapa ni sangara	And goes seaward with claws held out
Me longa ni polunggu	And comes shoreward with claws folded
Ra nggoti ateete	They break, making a cracking sound[a]
Ra bihu ka va ra nggoha	They split off [chelae], breaking off at the base[b]
Me poiposi si lake	And hiss on the fire
Me agoago i bingiti	And turn yellow/red in the oven

[a] This line refers to the way the women break all of the legs on one side together, and the sound this makes.

[b] This line alludes to the fact that when crabs are being collected, the chelae are usually broken off carefully, at the joint, which allows the crabs to survive if people need to keep them fresh for some time before consumption. However, if the chelae are broken off carelessly, at their bases (as in the song, before cooking on the fire), the meat from inside the insertion point on the crab's body comes out, and the crab soon dies (and rots, if it is not cooked immediately).