Red crabs in rain forest on Christmas Island, Indian Ocean: activity patterns, density and biomass

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ABSTRACT. The red crab *Gecarcoidea natalis* is the most abundant land crab on Christmas Island, Indian Ocean, and is found wherever native rain forest is still intact. The largest crabs grow to > 120 mm carapace width and reach > 500 g in mass. Red crabs are diurnally active, and moisture appears to be the most important factor governing surface activity – activity was nil below 77% RH, relatively low at 87% RH, and high above 95% RH. The crabs retreat to the interior of their burrows during dry periods, but emerge rapidly in response to rain. Because of their dependence on moisture for surface activity, red crabs show greater levels of activity during the wet season. Annual breeding migrations and moulting activity decreased the density of surface-active crabs at the main study sites for several weeks at the start of the wet season, and fruit and leaf fall caused dramatic local increases in the density of active red crabs. Density and biomass at the main study sites averaged 1.3 crabs m^{-2} and 1454 kg ha^{-1}, respectively, and 1.2 crabs m^{-2} and 1137 kg ha^{-1} at a total of five sites across the island. Rough calculations suggest that the island-wide population is at least 100 million individuals. Red crabs are the dominant consumer on the forest floor, and consume seeds, seedlings and leaf litter. Because they are both abundant and widespread, these animals have the potential to be the most important determinant of pattern and process in rain forest on Christmas Island.

KEY WORDS: land crabs, *Gecarcoidea*, Christmas Island, rain forest, biomass, crab activity.

INTRODUCTION

Oceanic islands are famed for supporting species that display unusual characteristics. Flightlessness, fearlessness and gigantism are arguably the best known of these, but some islands also support species with remarkable population densities. Land crabs occur on many islands throughout the tropics, where their density often exceeds 1 crab m^{-2} (Burggren & McMahon 1988). They are generally omnivorous, and could play a role in the dynamics of plant communities by acting as local seed dispersers or seed and seedling predators (English

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1913, Garcia-Franco *et al.* 1991, Green 1993; Howard 1950; Lee 1985, 1988, Louda & Zedler 1985, Niering 1963; O'Dowd & Lake 1990, 1991; Ridley 1930).

On Christmas Island, Indian Ocean, the red crab *Gecarcoidea natalis* Pocock (Brachyura, Gecarcinidae) is the most abundant of twenty terrestrial crab species (*sensu* Hartnoll 1988). Red crabs inhabit shallow burrows, and are found wherever the native rain forest is still intact. The genus is widespread throughout the Indo-Pacific region, occurring from the Red Sea to Rakata Krakatau, Taiwan, and the Marshall and Fiji Islands (Holthuis 1977, Morgan 1988, Türkay 1974). *G. natalis* is restricted to Christmas Island and the Cocos (Keeling) Islands, where it occurs on North Keeling and on some islands of the main atoll (Bunce 1988, Gibson-Hill 1948, Hicks *et al.* 1990).

Natural history accounts of *G. natalis* have noted the abundance of the crabs, but have focused almost entirely on their mass breeding migrations (e.g. Andrews 1900, Gibson-Hill 1947, Hicks 1985, Hicks *et al.* 1990). However, red crabs consume leaf litter, carrion, seeds and seedlings in a broad diet, and through differential seed and seedling predation, probably have a large negative impact on seedling recruitment for most species in rain forest on Christmas Island (Green 1993; O'Dowd & Lake 1990, 1991). They are the primary determinant of seedling density and diversity on the forest floor (Green 1993), so it is likely that seedling recruitment dynamics are closely linked with spatial and temporal variation in the density and activity of red crabs. Here, I describe diel and seasonal activity patterns, and quantify variation in the density and biomass of red crabs at several sites across Christmas Island, Indian Ocean.

METHODS

Christmas Island (105°40'E, 10°30'S) is an Australian Territory, lying approximately 360 km south of Java in the north-eastern Indian Ocean. It is an elevated, oceanic limestone island, with an area of 134 km². The island rises in a series of inland cliffs and terraces, and the highest point is Murray Hill (361 m), in the western part of the island. Most of the island is covered by rain forest where the native vegetation has not been cleared for phosphate mining, and about 70% of the original forest cover is still intact. There are distinct wet (November–May) and dry (June–October) seasons, and mean annual precipitation is about 2000 mm (Falkland 1986, Stoddart 1971).

Study sites

Most of the surveys and observations reported here were carried out at two sites on a north-facing hillside in the western area of the island (Figure 1). These were the Upper Site (US, mean elevation 280 m ASL), and the Lower Site (LS, mean elevation 250 m ASL). The sites lie immediately to the north of Murray Hill, and hereafter, US and LS are collectively referred to as the Murray Hill study sites. Both sites lie in 'plateau' rain forest, one of several
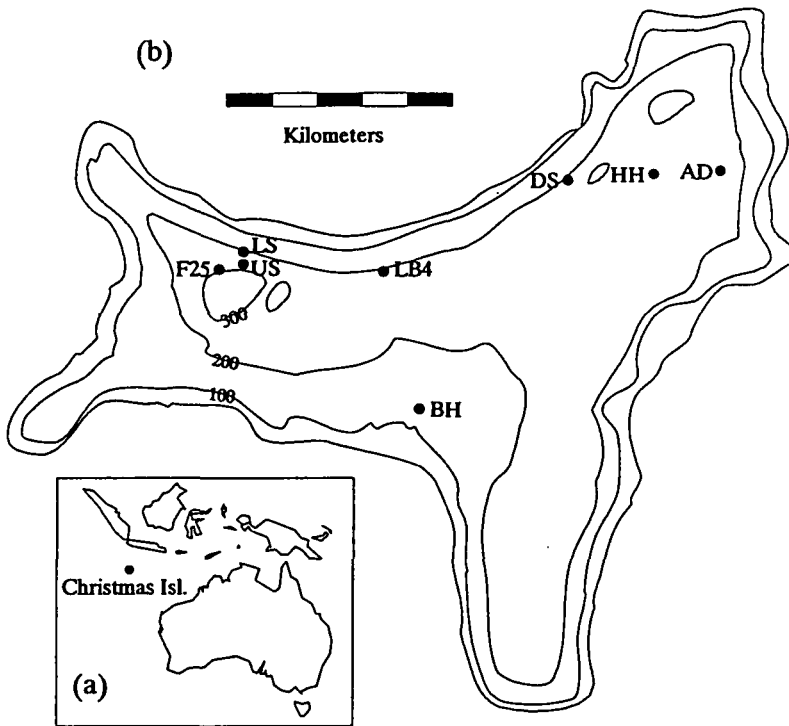
Figure 1. (a) Christmas Island, in relation to Australia, Indonesia and New Guinea, and (b) the location of sites on the island used in this study. Site codes are US – Upper Site, LS – Lower Site, F25 – Field 25 Section 4, BH – Blow Holes, LB4 – Loading Bridge 4, DS – Drumsite, HH – Hanitch Hill, AD – Aerodrome. Contours are marked at 100 m intervals.

major forest types on the island (Andrews 1900, Du Puy 1993, Mitchell 1975). Tracey (1991) likened this forest type to Webb's (1968) complex mesophyll vine forest, but noted its simple floristic composition. The soils of the Murray Hill area are unconsolidated, brown phosphatic soils, with materials typical of weathered volcanics, plus limestone scree (Phosphate Mining Company of Christmas Island Geological Map 1984).

Seasonal activity of red crabs

The density of surface-active red crabs was estimated by quadrat counts at LS and US on a total of 316 occasions over 34 mo, from 25 August 1988 to 20 May 1991 (an average of 2.2 counts per week). At each site, ten 5 m × 5 m quadrats were chosen randomly from a 7 × 7 grid of 49 quadrats. Each quadrat in the grid was separated by 3 m walkways to minimize disturbance. Quadrats were checked in the field and rejected if they contained very large trees or limestone boulders, because these objects would have obstructed a clear view of the quadrat and resulted in an underestimate of the density of active crabs. All species of crabs were counted at least twice each week between 0730 h and 0830 h, by counting the number of surface-active crabs in each of the ten

quadrats. A crab was considered to be active (foraging) if it was more than half-way out of the mouth of its burrow. The toss of a coin was used to determine which site was counted first.

The temperature range at each site was recorded by a maximum-minimum thermometer fixed to a tree at breast height near the centre of the plot. Each reading of maximum and minimum temperature spanned a three or four day period between crab counts. Relative humidity (RH) was recorded with wet and dry bulb thermometers. One estimation of RH was made at each site for each census, approximately 15 cm above the soil surface near the centre of each plot.

Daily rainfall records were obtained from the Christmas Island aerodrome (247 m, hereafter AD), 12.5 km from the Murray Hill sites (Figure 1). Although rainfall on Christmas Island is patchy, these records are sufficient to identify major rain events and characterize seasonal rainfall patterns that result in high humidity. Partial records (457 d between 7 October 1988 and 9 March 1990) from a weather station less than 1 km from the sites (Field 25 Section 4, hereafter F25) showed that although fewer rain days occurred at F25 (157) than at AD (240), total rainfall was higher at F25 (4529 mm) than at AD (3333 mm). Rain fell on the same day at F25 on 81% of rain days at AD, and on 29% of rainless days at AD. Discounting days were rainfall at F25 was ≤ 0.2 mm, rain was recorded at F25 on only 13% of rainless days at AD. Beyond a few millimetres, crab activity was related more to the *incidence* of rain than quantity (see Results), so the lesser total rainfall at AD is probably not significant in this context.

Diel activity of red crabs

The density of surface active crabs was estimated every 3 h for 30 h, from 0500 h on 7 June to 1100 h on 8 June 1992. At each count, the number of active crabs in 10 quadrats at US and LS were recorded. Temperature and humidity readings were also made during each count.

Red crab density and biomass

The density of red crabs was estimated at five sites, by counting the number of burrow entrances in replicated 5 m × 5 m quadrats. Burrows were counted on 10 quadrats at US and LS (the same quadrats used for activity counts), and on eight haphazardly positioned quadrats at each of three other sites; near Loading Bridge 4 (hereafter LB4, 225 m; Figure 1), Drumsite (DS, 200 m) and Hanitch Hill (HH, 270 m). Density was estimated at US and LS in August 1989, and at the other sites in June 1992. The difference is unlikely to have contributed significantly to differences in density (or biomass) between the two groups of sites, because burrow density on other plots at Murray Hill remained virtually unchanged between 1989 and 1992 (Green 1993).

Biomass was estimated indirectly. First, the entrance widths of all burrows on the crab density quadrats were measured at each site. Regression equations estimating carapace width from entrance width, and body mass from carapace width, were then used to estimate the mass of the crab occupying each burrow on the quadrats. The relationship between entrance width and carapace width was established by measuring red crabs excavated from burrows at LS, US and HH (entrance width was measured prior to excavation). This sample (n=70) included almost the entire size range of adult *G. natalis*. Red crabs were measured in the field at four different forest locations around the island (LS, HH, DS and near the Blow Holes; Figure 1) to establish a relationship between carapace width and live mass. Approximately equal numbers of males and females from a range of size classes were weighed and measured, and only crabs with similarly sized left and right chelae and intact legs were considered. Crab mass may have depended on the time of year that crabs were weighed. Lutz & Austin (1983) found that *Cardisoma guanhumi* rapidly gained weight during the first weeks of active foraging in the rainy season. In this study, *G. natalis* were weighed during June–July 1989 in relatively wet conditions, and crabs may have weighed in the upper range of what is normal. Regression equations were calculated for the relationship between entrance width and carapace width, and between carapace width and body mass, using SYSTAT™ 5.03 (Wilkinson 1990). Constants were calculated for both models, and sex was not considered in the calculation of the relationships. These equations were used to estimate the mass of the crab occupying each burrow, and the total mass of crabs in each 25 m² quadrat was then calculated. Some burrow entrances were sealed with a plug of soil, making the measurement of burrow entrance width impossible. The proportion of burrows with plugged entrances was determined for each quadrat, and the total biomass estimate for each quadrat was increased by this proportion to include plugged burrows in the estimation of biomass. Biomass was then calculated as the mean of either eight or 10 quadrats at each site. The error associated with this final estimate has at least two sources: cumulative error associated with both steps in the eventual calculation of individual crab mass, and error associated with between-quadrat variation. The calculation of the former is complex, but because the regression coefficients for the relationships between EW and CW, and between CW and M are high (see Results), most of the total error is probably due to between-quadrat variance (M. Thomas, *pers. comm.*). Between-quadrat errors for each site were calculated, but these are underestimates of the true variation in red crab biomass.

Red crabs have a heavily calcified exoskeleton which probably accounts for a significant proportion of total body mass. To estimate the proportion of total body mass contributed by the exoskeleton, the intact carcasses of 10 heat-stressed red crabs were collected during the annual migration in November 1991. The mass of each exoskeleton was weighed after the soft tissues had rotted away, and the live mass of each crab was estimated with the regression equation

relating carapace width and mass (above). Exoskeletal mass was expressed as a percentage of this live mass.

The method used here to estimate density and biomass involved a number of assumptions. These were (1) that each burrow had only one entrance, (2) that only one crab occupied each burrow, and (3) that all burrows were active, that is, there were no spare burrows which were not continuously occupied. Observations made during this and previous studies support these assumptions. All of the burrows excavated in this study had a single entrance, which terminated in a single chamber (n > 70). Of those that were occupied, no more than one crab was ever found in a burrow. O'Dowd & Lake (1989) found similar results when they excavated 22 burrows in plateau forest. Red crabs are solitary and do not tolerate intruders in their burrows (except during the breeding season), and on many occasions intruders were chased out of burrows by the resident crabs (*pers. obs.*). The assumption that there are not more burrows than there are crabs is problematic. There are no data about the fidelity of individual crabs to their burrows; however, indirect evidence indicates that individual crabs do occupy specific burrows for long periods of time. Given this, crabs are unlikely to excavate new burrows on a regular basis. This assumption is further supported by long-term data on rates of burrow turnover (Green 1993), and so the number of burrow entrances is probably an accurate indication of the actual number of resident crabs. It may even be a slight under estimation. During the diel activity study, many crabs were seen to shelter in and under limestone boulders at night, apparently without a permanent burrow. These homeless crabs would not have been included in the estimation of density and biomass. Small crabs (< 30 mm CW) are commonly found beneath large limestone rocks and fallen logs (*pers. obs.*), and very small crabs (< 10 mm CW) may inhabit the burrows of much larger crabs (H. Yorkston, *pers. comm.*). These crabs would also have been omitted from density and biomass estimates.

RESULTS

Relative abundance of land crab species at the sites

Four crab species were recorded at the Murray Hill sites during the study. These were the red crab (*Gecarcoidea natalis* (Pocock); Brachyura, Gecarcinidae), the robber crab (*Birgus latro* (L.); Anomura, Coenobitidae), the little nipper (*Geograpsus grayi* (H. Milne Edwards); Brachyura, Grapsidae) and the purple hermit crab (*Coenobita brevimanus* Dana; Anomura, Coenobitidae). Of these, *G. natalis* was by far the most abundant at both sites. Summed over all 316 counts, active red crabs were 89 times more common than robber crabs at US (8.9 vs 0.1 crabs 25 m^{-2}), and 35 times more common at LS (10.4 vs 0.3 crabs 25 m^{-2}). Active red crabs were almost equally abundant at both sites, but active robber crabs were recorded three times more frequently at LS. Little nippers were rarely seen on the plots during the morning counts, and only 15 and 13 crabs

were recorded at US and LS, respectively, over the entire study period. A single purple hermit crab was seen near US in December 1989.

Seasonal activity

The surface activity of red crabs varied markedly during the study, and showed pronounced seasonal rhythms. Over 34 mo, mean red crab activity ranged between nil surface-active crabs 25 m^{-2} (0 m^{-2}) to 25–30 crabs 25 m^{-2} (1.0 to 1.2 crabs m^{-2}) at both sites (Figure 2a; only monthly means are presented, and n $\geqslant$ 8 crab counts, RH or temperature readings for each month). In general, red crabs were active during the wet season and early dry season, and relatively inactive during the second half of the dry season (Figure 2a). Extended periods of high crab activity coincided with periods of almost daily rainfall, for example from December 1988 to July 1989 (Figure 2a). Prolonged periods of low to very low crab activity corresponded to times when relative humidity, ambient temperature and rainfall were relatively low (Figures 2b–d), and on some mornings mean crab activity was nil. During these periods RH was generally between 80 and 85% (Figure 2b), and reached extreme minimum values between 75 and 79%. Crab activity was noticeably higher in 1989 than 1990 (Figure 2a), coincident with higher annual rainfall in 1989 (2933 mm) than 1990 (1551 mm). The density of surface active crabs was also coupled to rainfall and humidity over much shorter periods. Bursts of surface activity ($\geqslant$ 10 crabs 25 m^{-2}) coincided with brief showers and sharp increases in RH (from *c.* 85 to 98%) during September and October 1988, November 1989 and November 1990 (Figure 3a, b and c respectively), some of the driest periods during the study. At both sites, red crab activity was nil at 77% RH, and very low (mostly < 5 crabs 25 m^{-2}) at 87% RH. Maximum surface activity occurred at 95% RH or greater (Figure 4).

The density of surface-active red crabs at the sites was also influenced by at least two other variables: annual breeding migrations and moulting activity. Red crabs migrated through the study plots at the start of the wet season in all years of the study, causing minor peaks in the density of active crabs on the plots. For example, the two major peaks of activity at 20 October and 3 November 1988 (> 25 crabs 25 m^{-2}) coincided with breeding migrations (Figure 5). The October peak was a 'false start', induced by heavy but intermittent rainfall. Not all active crabs were migrating; many were foraging without any obvious seaward movement. Migration-induced densities of *c.* 25 crabs 25 m^{-2} (1 crab m^{-2}) were also recorded on both sites on 12 and 13 December 1989. Red crab activity declined at the plateau sites for a short period after the migration. For example, mass egg-release occurred at the coast on the mornings of 3–4 December 1988. Crab activity on the study plots was relatively low prior to this, despite rainy periods and high humidity (Figure 5). Activity then returned to pre-migration levels once the crabs had made their way back up the inland cliffs and terraces to the plateau sites, some two weeks later.
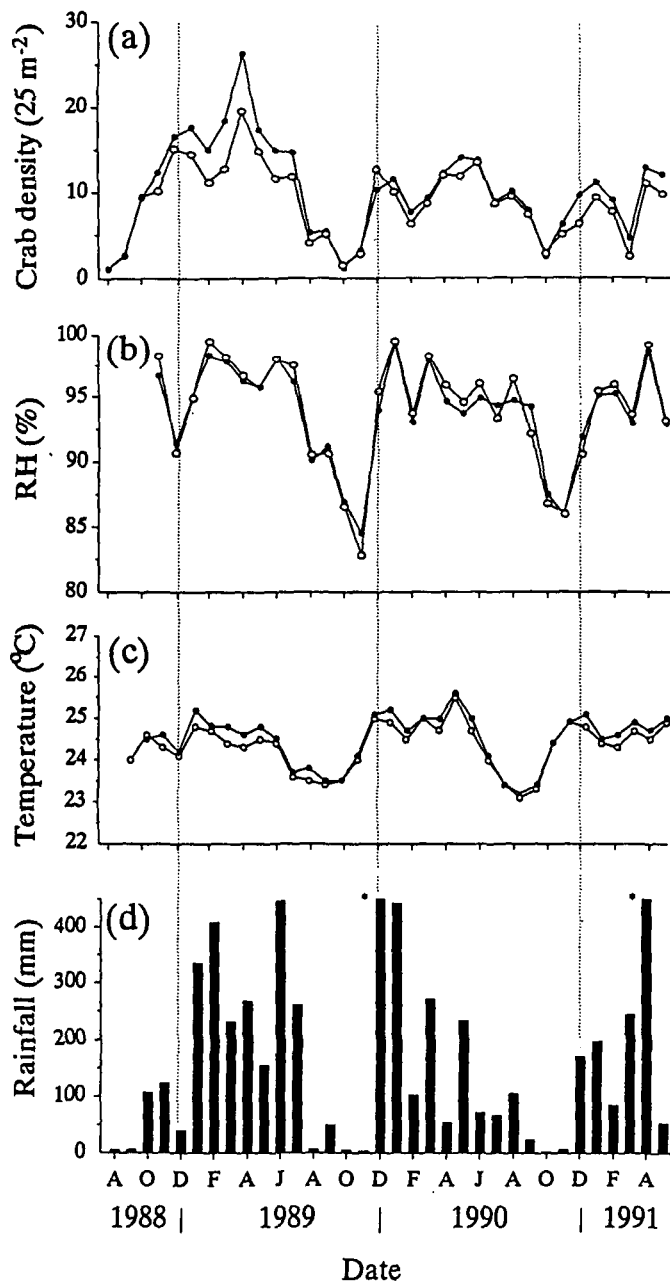
Figure 2. The seasonal pattern of (a) mean crab activity, (b) relative humidity, (c) ambient temperature and (d) rainfall over 34 mo from August 1988 to May 1991 at the Lower (●) and Upper (○) Sites, Christmas Island. *Rainfall was 759 mm in December 1989, and 565 mm in April 1991.

Moulting activity also lowered the density of active red crabs at the sites. A gradual decline in the density of active red crabs (from about 20 to 10 crabs 25 m^{-2}) occurred at both sites during January–February 1989 after the crabs had returned from breeding activities, even though rainfall and humidity were
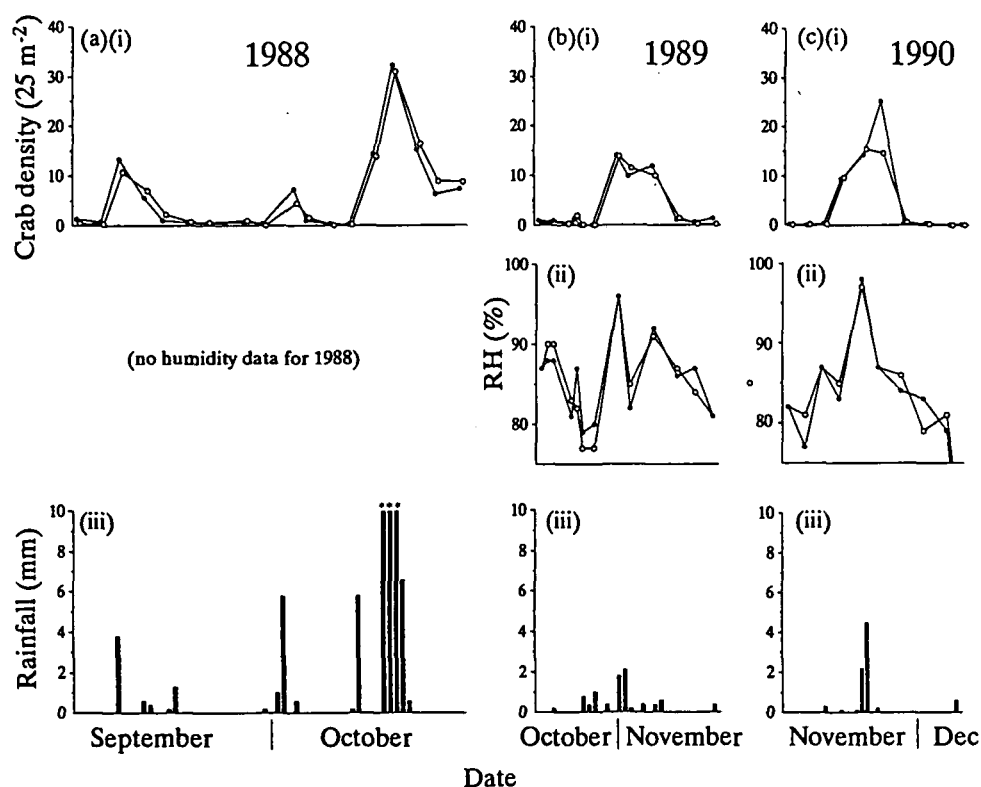
Figure 3. The influence of occasional rainfall on the density of active crabs and ground-level RH during dry periods on Christmas Island. Examples from (a) 1988 (1 September – 31 October), (b) 1989 (18 October – 16 November) and (c) 1990 (6 November – 6 December), at the Lower (●) and Upper (○) Sites. In each example (i) is the density of active crabs at 2 or 3 d intervals, (ii) is the ground-level RH (single reading for each date at each site), and (iii) is the daily rainfall. *Rainfall was 36.9, 34.4, and 15.4 mm on 19, 20 and 21 October 1988, respectively.

high (Figure 6). Similar declines occurred in February–March 1990, and in February–March 1991. These periods coincided with peak moulting activity in the crab population at the study sites, when up to 50% of red crabs at the study sites sealed themselves inside their burrows to complete the final phases of the premoult cycle and ecdysis (Green 1993).

Diel activity

Red crabs were active during daylight hours, and mostly inactive at night (Figure 7). The pattern of diel activity was similar at both sites. On the first day, activity was nil at 0500 h but then peaked at 0800 h, two hours after dawn (Figure 7a). Thereafter, activity fell until 1400 h, and peaked at 1700 h during heavy rain. Activity decreased to almost nil again at dusk (around 1830 h), and peaked again after dawn on the second day. Minimum activity around midday
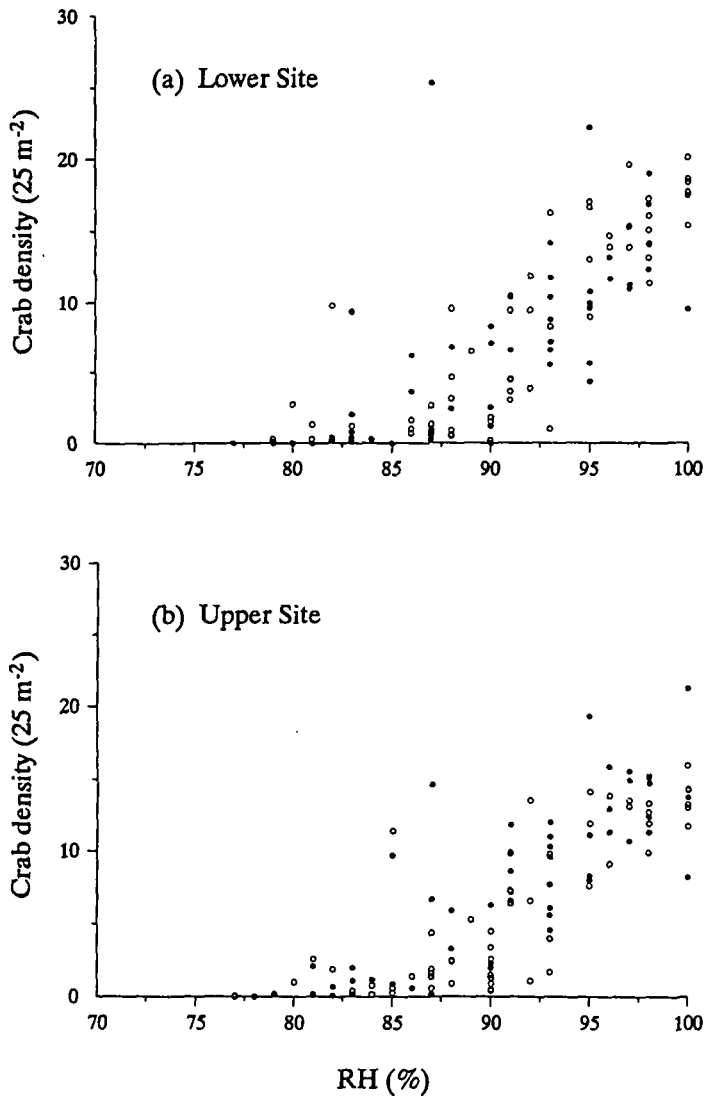
Figure 4. The relationship between the density of active red crabs and ground-level RH at (a) the Lower Site and (b) the Upper Site, excluding periods affected by breeding migrations and moulting activity. O = June–November 1989, ● = June–November 1990 N=113 for both sites.

coincided with relatively low RH (85–90%; Figure 7b) and high ambient temperature (27°C; Figure 7c). Crabs were virtually inactive at night despite higher RH and cooler temperatures.

Red crab density and biomass

The density of red crab burrows varied widely both within and between sites (Table 1). The highest and lowest densities for any quadrats were 3.16 burrows m^{-2} at DS and 0.08 burrows m^{-2} at LB4, respectively. DS sites also
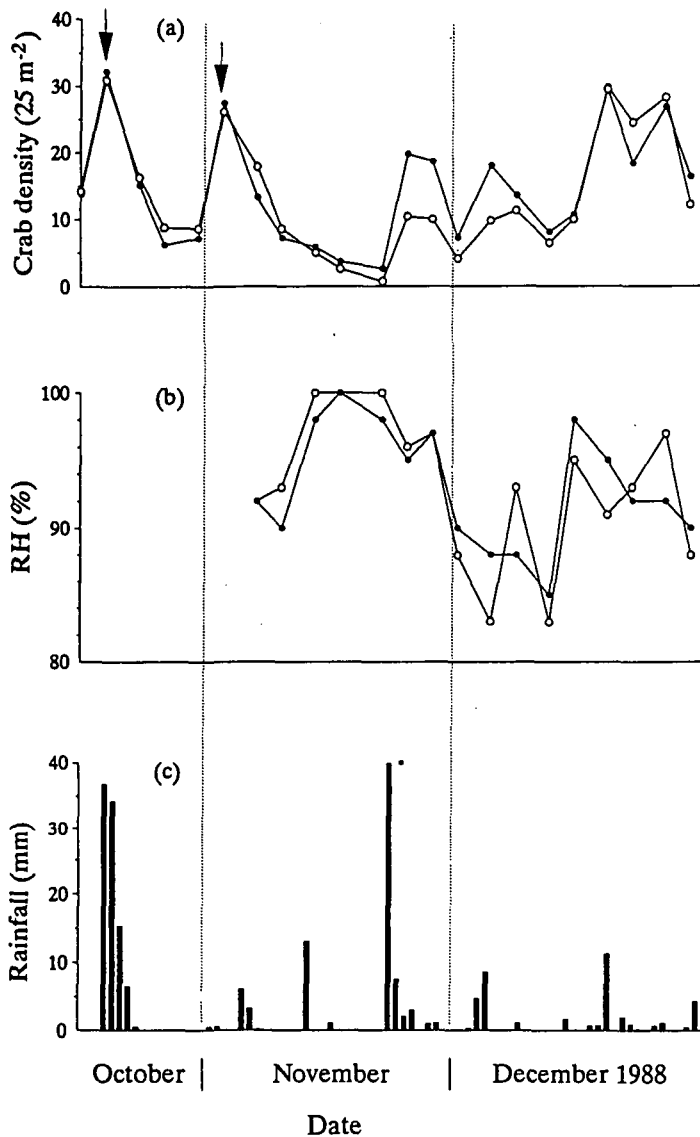
Figure 5. Patterns in (a) the density of active crabs, (b) RH and (c) daily rainfall during the 1988 breeding season (17 October to 31 December) at the Lower (●) and Upper (○) Sites, Christmas Island. *Rainfall on 23 November was 82.6 mm. Arrows in (a) indicate peaks associated with breeding migrations.

had the highest average burrow density (1.82 ± 0.70 burrows m^{-2}; of the five sites, Table 1), while the lowest average burrow density occurred at HH (0.42 ± 0.15 m^{-2}). Mean burrow density at LS, US and LB4 was similar at 1.30, 1.25 and 1.35 burrows m^{-2}, respectively.

Burrow entrance width (EW) was significantly correlated with the carapace width (CW) of the occupant (Pearson's $r = 0.92$, $n = 70$, $P < 0.001$; $EW = 1.12CW - 4.01$). CW and mass (M) were also significantly correlated (Pearson's $r = 0.99$
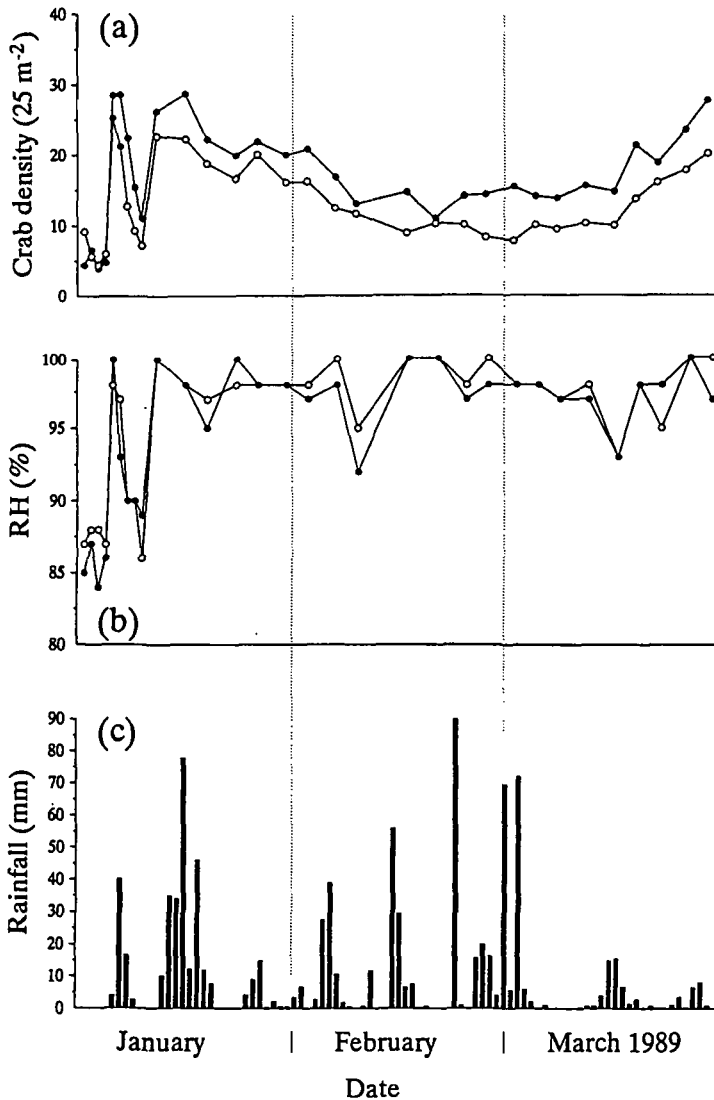
Figure 6. The influence of moulting activity on the density of active crabs between 1 January and 28 March 1989 at the Lower (●) and Upper (○) Sites, Christmas Island. (a) Density of active crabs, (b) RH and (c) rainfall.

on log-transformed data, n=274, P < 0.001; M=0.00064CW$^{2.85}$). The mean proportion of burrows at each site where EW could not be measured varied from 0.06 at HH, to 0.25 at DS (Table 1). Using these regressions for each burrow entrance, the highest red crab biomasses were calculated for the main study sites at Murray Hill. At LS and US, the mean biomass of red crabs was 1519 ± 285 and 1389 ± 655 kg ha^{-1}, respectively (mean ± SD; Table 1). Mean biomass was similar at DS and HH (995 ± 358 and 1022 ± 371 kg ha^{-1},
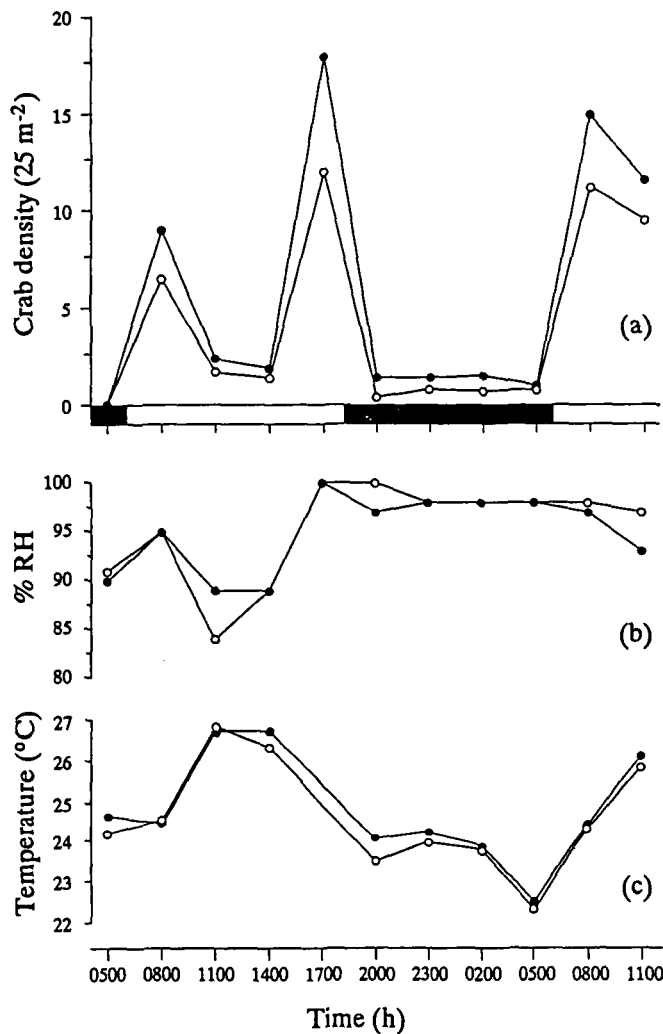
Figure 7. Changes in (a) diel activity of red crabs, (b) RH and (c) ambient temperature over 30 h from 0500h on 7 June to 1100h on 8 June 1992, at the Lower (●) and Upper (○) Sites, Christmas Island.

respectively), but much lower at LB4 (758 ± 253 kg ha⁻¹). The exoskeleton accounted for 27.9 ± 4.8% of total body mass.

There was no significant correlation between mean crab mass and burrow density within any of the five sites, but a significant correlation existed across sites (r=0.81, n=44, P < 0.001; Figure 8a). The total biomass of crabs in the 25 m² quadrats was significantly correlated with crab density at LS (r=0.81, n=10, P < 0.05), US (r=0.95, n=10, P < 0.001), LB4 (r=0.74, n=8, P < 0.05) and HH (r=0.94, n=8, P < 0.001; Figure 8b), but not at DS. Total biomass and burrow density were significantly correlated across all sites (r= 0.43, n=44, P < 0.05).

Table 1. Burrow density, proportion of burrows plugged, and estimated biomass of *Gecarcoidea natalis* at five sites in rain forest on Christmas Island, Indian Ocean. Density and biomass were estimated at LS and US in August 1989, and at DS, LB4 and HH in June 1992. n=10 for LS and US, n=8 for DS, LB4 and HH. Mean proportions were calculated on arcsine-transformed data. Biomass was calculated using the width of a burrow entrance as a predictor of the mass of the resident crab (see text). See Figure 1 for site names.

| | Murray Hill | | | | |
Site	LS	US	DS	LB4	HH
Burrow Density (m^{-2})					
Mean ± SD	1.30 ± 0.30	1.25 ± 0.57	1.82 ± 0.70	1.35 ± 0.47	0.42 ± 0.15
Range	0.72 − 1.64	0.64 − 2.28	1.12 − 3.16	0.08 − 2.24	0.24 − 0.60
Proportion Plugged	0.23	0.24	0.25	0.16	0.06
Biomass (kg ha^{-1})					
Mean ± SD	1519 ± 285	1389 ± 655	995 ± 358	758 ± 253	1022 ± 371

DISCUSSION

Activity

Rain forest on Christmas Island supports an abundant population of burrow-dwelling land crabs, whose surface activity varies predictably at all temporal scales ranging from diel to seasonal. The results from this study suggest that moisture is important in determining surface activity on both a seasonal and daily basis; high levels of activity were only sustained by regular rainy periods during the wet season, and crab activity was generally low during the dry season. Further, sharp increases in surface activity were frequently coincident with intermittent wet periods during otherwise dry conditions, and large numbers of crabs were frequently seen to emerge from their burrows within minutes of a heavy shower. Moisture is important because despite heavy calcification, the exoskeleton of terrestrial crabs is relatively permeable to water (Herreid 1969a, b), making them susceptible to desiccation. The humidity data further suggest that red crabs risk desiccation even at high relative humidities; activity was low when the ground-level relative humidity dropped below about 88%, and was nil at 77%. Similar limits were recorded by Hicks (1985). Red crabs retreated to a more favourable microclimate inside their burrows under these conditions. Most crabs plugged the burrow entrance with a loose wad of leaves in particularly dry conditions, such as the end of the dry season after months of little rain. The plug probably assists in the maintenance of a high relative humidity inside the burrow; although the relative humidity of the burrow chamber was not monitored in this study, it is maintained year-round at ≥ 93% in the burrow chamber of *Gecarcinus lateralis*, an ecological analogue of *G. natalis* (Bliss 1979).

The actual density of foraging crabs is influenced on a seasonal basis by activities associated with growth and reproduction. Red crabs annually return *en masse* to the sea to breed, and the breeding migration(s) usually coincides with the first rains of the wet season. The actual timing of movement to the coast is determined by the phase of the moon and adequate rainfall (Hicks
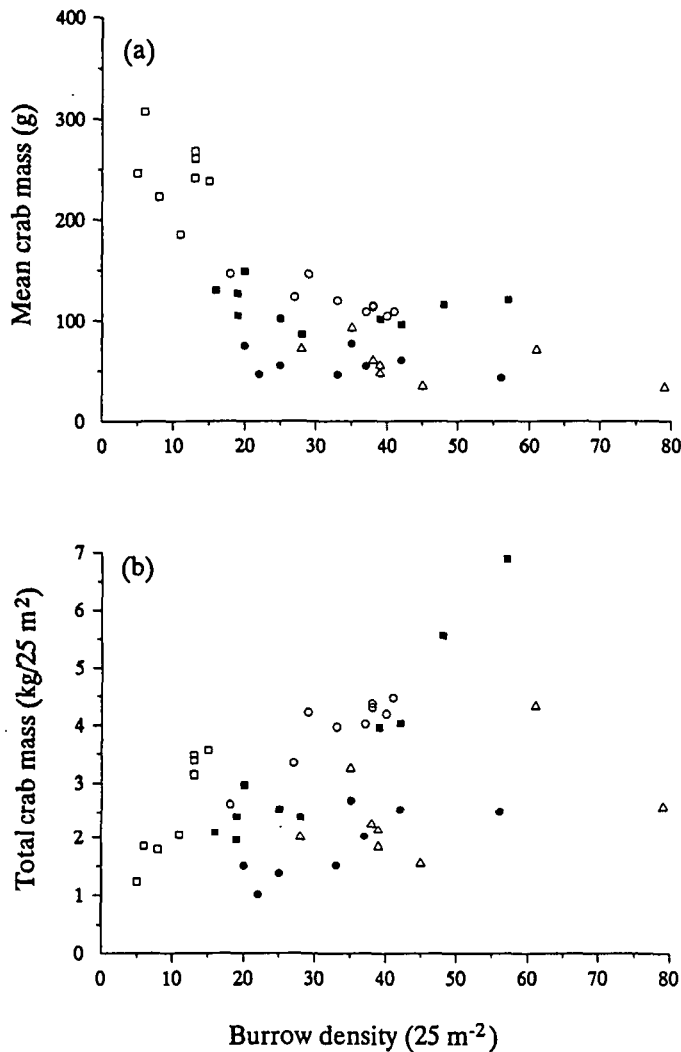
Figure 8. The relationship between burrow density and (a) mean crab mass and (b) total crab mass on Christmas Island. Each point represents a single 25m² quadrat. N = 44. Hanitch Hill (□, n = 8), Drumsite (△, n = 8), Lower Site (○, n = 10), Loading Bridge 4 (●, n = 8), Upper Site (■, n = 10). Mean crab mass was derived from entrance width data using the regression equations described in the text.

1985, Hicks *et al.* 1990, H. Yorkston unpubl. data). Migrations caused a decline in the number of active crabs at the Murray Hill study sites for some weeks each year, but at the same time caused a dramatic increase in the number of crabs in forest nearer the coast (*pers. obs.*, and see O'Dowd & Lake 1989). A comparison of pre- and post-migration activity data from this study suggest that perhaps half of the adult crabs participate each year. Hicks (1985) also estimated crab activity at a plateau site during the height of breeding activity at the coast to be around 50% of activity at the same site soon after the breeding

season finished. Once they have returned, the majority of breeders seal themselves in burrows to moult (Green 1993), causing another period of relatively low crab activity.

The density of active red crabs can be influenced further by more localized events, such as fruit and leaf fall. Very high densities were recorded from quadrats where crabs were browsing on the foliage of fallen branches, but throughout the study, the highest densities were recorded from quadrats above which canopy trees were dropping fruits. These densities reached 70 and 63 crabs 25 m^{-2} at LS and US respectively, where red crabs were foraging on the fruits and leaves of *Syzygium nervosum* and *Ficus microcarpa* syncarps. Red crabs were recorded feeding on the fruits of most of the canopy species on the plots. Even when feeding at high densities, the crabs rarely displayed aggression.

Diel activity

Red crabs are diurnally active, and even under favourable conditions, show little inclination toward nocturnal activity. The few 'active' crabs seen at night in this study were never foraging, and were always closely associated with a burrow entrance. Hicks *et al.* (1990) also considered red crabs to be mainly diurnal, even during breeding migrations. Relatively high levels of activity have been observed on golf course fairways during a full moon (*pers. obs.*), but observations like these are exceptional. The pattern of diel activity described here is typical of fine days from the late wet season to mid-dry season; activity peaks during the first hours of daylight, when the humidity is highest, but gradually declines during the day as the humidity falls and ambient temperature increases. Hicks (1985) reported a smaller peak late in the afternoon, but this was never obvious at the Murray Hill sites. Rain will induce further activity during the day, as it did in this study late in the afternoon. Red crabs are commonly active all day at the height of the wet season, and were often inactive all day, even at dawn, in the dry season (*pers. obs.*).

Diel activity is an apparently plastic characteristic in gecarcinid land crabs, and both nocturnal and diurnal activity has been recorded for *Gecarcinus lateralis* (Bliss *et al.* 1978, Bliss 1979), *Gecarcinus planatus* (Jiménez *et al.* 1994), *Cardisoma guanhumi* (Gifford 1962), and *Gecarcoidea lalandii* (Audy 1950, Audy *et al.* 1950; *pers. obs.*). Diel activity patterns are probably the net result of many competing factors, including 'phylogenetic inertia', physiological considerations, the diel activity of significant predators, location of food, social interactions related to resource partitioning and reproduction, and circadian locomotory rhythms (Palmer 1971, Powers & Bliss 1983). Tradeoffs like these evidently occur to determine diel activity in *G. natalis* on Christmas Island; high nighttime RH and low temperatures would promote nocturnal activity, but the avoidance of nocturnal predators (Hicks *et al.* 1990) and visual detection of food would promote diurnal activity.

Red crab density and biomass

Although moisture is an important determinant of surface activity in *G. natalis*, it is not obviously limiting to the distribution of the species across the island; red crabs occur in abundance throughout rain forest on Christmas Island, even many kilometres from permanent water sources. Their density and biomass is remarkable. Rough calculations suggest that the island-wide adult population is at least 100 million individuals, and the biomass estimates reported here for a single species far exceed those of entire faunas from mainland tropical rain forests. Odum *et al.* (1970) estimated the total biomass of carnivores, herbivores and soil fauna in lower montane rain forest at El Verde in Puerto Rico at 115 kg ha^{-1}, and Fittkau & Klinge (1973) estimated a total biomass of 210 kg ha^{-1} in a lowland rain forest in the central Amazon. The average biomass of *G. natalis* at the five sites in this study was 1137 kg ha^{-1}, a remarkable estimate even after the contribution of the exoskeleton to total body mass (almost 28%) is considered.

The only other biomass estimate for *G. natalis* on Christmas Island was made by Hicks (1985), who estimated biomasses of 899 kg ha^{-1}, 670 kg ha^{-1} and 829 kg ha^{-1} in 'deep soil' plateau rain forest, 'shallow soil' plateau forest and terrace forest, respectively. These estimates were derived by multiplying the mean density by the mean mass of surface active crabs, and did not include crabs that were underground at the time of counting. When mean crab mass is multiplied by burrow density (Hicks 1985), then the biomass of red crabs at these sites was around 1550 kg ha^{-1}, similar to the estimates reported here for the Murray Hill study sites.

The density and biomass of the red crab population on Christmas Island is variable. Data from this study suggest that variation in crab size contributes to this variability, but only at broad spatial scales. For example, mean crab mass and burrow density were not correlated at a local (within site) spatial scale, but the same correlation accounted for 81% of total variation when all sites were analysed together. Admittedly, one site (HH) contributed significantly to the relationship, but mean crab mass and burrow density are still significantly correlated even when this site is excluded. The preferred seaward and return migration routes of adult crabs, and variation in the sites of mass emergence and patterns of dispersion by juvenile crabs would contribute to variation in the abundance of the adult population at broad spatial scales. Other factors, such as soil depth and the frequency of limestone outcrops, may be locally important.

Several factors have probably contributed to and maintain high population densities on Christmas Island. First, oceanic islands typically lack many potential competitors and predators that are common in comparable adjacent mainland areas (Simberloff 1974, Williamson 1981). This has been hypothesized to result in 'ecological release', or the expansion of realized niches in island species, in turn resulting in higher population densities on islands (Wright

1980). Second, the reproductive potential of most gecarcinid land crabs is impressive. For example, berried females of *Gecarcinus lateralis* carry between 19 000 and 109 000 eggs each (Klaassen 1975), and the reproductive potential of female *G. natalis* is probably very similar. However, the most important factor contributing to high red crab densities is probably a low metabolic rate, and the ability to survive largely on a poor quality food resource (leaf litter). Calculations with energy consumption data for air-breathing crabs (Adamczewska & Morris 1994) and assimilation efficiency data for *G. natalis* (Greenaway & Linton 1995) indicate that at rest, a 300 g red crab can meet its daily energy requirements by eating 0.7 g of *Ficus* leaf litter, the equivalent of just one average-sized leaf. Similarly, Herreid & Full (1988) estimated that a single *Cardisoma guanhumi* could meet its caloric requirements by eating the equivalent of one small leaf per day. Although active red crabs probably require several times this amount for activity and growth, the relative abundance of leaf litter would enable this resource to be spread among a large number of individuals. A similar argument has been used to explalin the high biomass of tortoises on Aldabra (Hamilton & Coe 1982).

The density and biomass of other gecarcinid species

The abundance of land crabs on Christmas Island is not unique. Gecarcinid land crabs are widely distributed throughout mainly tropical latitudes, where they occupy a diverse array of insular and mainland habitats (Burggren & McMahon 1988). There are many anecdotal accounts of the abundance of species in three gecarcinid genera (*Gecarcoidea*, *Gecarcinus* and *Cardisoma*), but only a few attempts have been made to quantify either the density or biomass of these animals (Table 2). On Palau Jarak, the closely related species *G. lalandii* has been described as 'numerous' (Wyatt-Smith 1953), and occurs in vegetation which is remarkably similar to that on Christmas Island. The highest reported density of any gecarcinid species is for *Gecarcinus planatus* on Clipperton Atoll (eastern Pacific Ocean), where it reaches densities of 6 crabs m^{-2} (Ehrhardt & Niaussat 1970). Biomass estimates are scarce, but are likely to be very high because most species grow to large size.

Land crabs from other brachyuran and anomuran families also reach high densities, particularly on islands. For example, McCann (1938) reported that Salsette Island (off the coast of Bombay, India) was 'infested' with *Paratelphusa* (*Holthuisana*) *guerini* (Parathelphusidae). Hermit crabs (*Coenobita* spp.) are very common on many coral atolls throughout the tropics (Page & Willason 1982), and have been described as 'abundant' (Hedley 1896), and 'countless' (Degener & Gillaspy 1955). On Christmas Island, hermit crabs are only locally abundant on the island's few beaches, and are also found on the shore terrace. They are rarely seen at higher elevations (this study, H. Yorkston *pers. comm.*).

Red crabs and rain forest dynamics

Red crabs are generalist consumers, and are known to be voracious predators of the seeds and/or seedlings of many rain forest species (O'Dowd & Lake 1990,

Table 2. The abundance and biomass of gecarcinid land crabs. Estimates of density have been converted to the number of crabs m^{-2} from some authors' original data. Where density was not estimated, the description of abundance used by the author is used. Where known, body mass for the largest specimen reported in the literature is given in parentheses for each species (data from Gilchrist (1988), except for *G. natalis* (*pers. obs.*).

Location	Density (m^{-2})	Biomass $(kg\ ha^{-1})$	Author(s)
Gecarcoidea natalis (540g)			
Christmas Island	1.2[1]	1137[1]	This study
	1.7	1528[2]	Hicks (1985)
Gecarcoidea lalandii			
Palau Jarak	'common'	—	Audy (1950)
	'numerous'	—	Wyatt-Smith (1953)
Palau Aor, P. Ular	'in abundance'	—	Johnson (1965)
Andaman Islands	'numerous'	—	Kloss (1903)[3]
Gecarcinus planatus			
Clipperton Atoll	6.0	—	Ehrhardt & Niaussat (1970)
Gecarcinus spp.[4]			
Diego Garcia	'common'	—	Bourne (1886)
Cardisoma guanhumi (400g)			
Southern Florida	1.8	2000	Gifford (1962)
			Herreid & Gifford (1963)
Venezuela	0.8	—	Taissoun (1974) in Lutz & Austin (1983)
Andros Island (Bahamas)	1.0	—	Lutz & Austin (1983)
Cardisoma carnifex (400g)			
Aldabra	0.4	1186	Alexander (1979)
Andaman Islands	'common'	—	Alcock (1900)
Ifaluk (Caroline Is.)	1.2	—	Bates & Abbott (1958)
Pulau Weh (Sumatra)	*c.* 1.0	—	*pers. obs.*
Mataiua Atoll	'plentiful'	—	Delesalle & Colleagues (1985)
Cocos (Keeling) Ils.	common[5]	—	*pers. obs.*
Cardisoma hirtipes (600g)			
Andaman Islands	'common'	—	Alcock (1900)
Christmas Island	abundant[6]	—	*pers. obs.*

[1] average of five sites
[2] average of adjusted results for deep and shallow soil sites (see text)
[3] Kloss did not identify the species, but it was probably *G. lalandii*
[4] probably *Gecarcoidea* or *Cardisoma*, or both
[5] restricted to the lagoon side of atolls
[6] restricted to freshwater seepage areas for most of the year

1991; Green 1993). Through differential predation, red crabs may influence the diversity and relative species abundance of trees, shrubs and vines in rain forest on the island. They are important processors of leaf litter (O'Dowd & Lake 1989, Green 1993), and, given that the majority of nutrient cycling in tropical rain forests occurs via the decomposition of litter (Vitousek & Sanford 1986), red crabs may also be primary determinants of the way in which nutrients are cycled on the island. Further, red crabs are significant predators of the introduced giant African landsnail (*Achatina fulica*), and may have prevented this destructive invader from establishing in undisturbed rain forest (Lake & O'Dowd 1991). *G. natalis* is both widespread and abundant throughout rain forest on Christmas Island, and is the dominant consumer on the forest floor.

As a result, they have the potential to be the primary determinant of many patterns and processes which create structure in rain forest on Christmas Island.

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