

Ecology and Behavior of *Gecarcoidea natalis*, the Christmas Island Red Crab, During the Annual Breeding Migration

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Abstract. The terrestrial crab *Gecarcoidea natalis* is endemic to the forests of Christmas Island but must migrate each year to the coast to breed. During 1993 and 1995, radio-tracking, mark and recapture, and counting methods were used to establish the routes, walking speeds, direction of travel, and destinations of migrating crabs, as well as crab numbers and distribution. The density of crabs ranged from 0.09 to 0.57 crabs per square meter, which gave a population estimate of 43.7 million adult crabs on the island. During the dry season the crabs were relatively inactive but on arrival of the wet season immediately began their migration. The crabs generally walked in straight lines, and most crabs from around the Island traveled toward the northwest shore instead of simply walking toward the nearest shore. The maximum recorded distance walked by a red crab in one day was 1460 m, but the mean was 680 m per day in 1993 and 330 m in 1995. Comparing the 1993 and 1995 study seasons, there was a 3-week difference in the timing of the start of the migration, but the spawning date was fixed by the lunar phase and took place 17 to 18 days after mating. In 1993, late rain prompted a “rushed” migration and crabs walked directly to their shore destinations; in contrast, in 1995 most crabs made stops of 1 to 7 days during the downward migration. By giving the crabs a chance to feed along the way and minimizing the time that the population was concentrated near the shore, these stops may be important in ensuring that the animals have enough food after the long dry season. Furthermore, this behavior

implies that the crabs are able to judge how far away they are from the shore during the migration.

Introduction

The red crab *Gecarcoidea natalis* is endemic to Christmas Island and is distributed throughout the entire island (Hicks, 1985; O’Dowd and Lake, 1989; Hicks *et al.*, 1990; Green, 1993). For most of the year the red crabs are found within primary and mature regrowth forest (Hicks *et al.*, 1990; Green, 1997; pers. obs.), but each year these crabs must migrate to the coast to breed. The migration of red crabs is a well-documented phenomenon described by anecdotal observations (Andrews, 1900; Gibson-Hill, 1947) but by only limited quantitative data, including some information on crab densities and walking speeds across cleared areas (Hicks, 1985; O’Dowd and Lake, 1989; Green, 1993, 1997). There are no data on migratory routes, destinations or distances, nor on walking speeds of red crabs within the rainforest.

The arrival of the monsoonal rains allows increased activity of red crabs and stimulates the annual migration (Hicks, 1985; Green, 1993). During this breeding migration red crabs, like other terrestrial gecarcinids, must abandon their home ranges and travel down to the coast to mate and spawn (Garth, 1948; Gifford, 1962; Bliss *et al.*, 1978; Lake and O’Dowd, 1991; Pinder and Smits, 1993; Green, 1997). The downward migration normally requires at least a week, and the crabs migrate mainly during the first few hours of the morning and in the late afternoon (Hicks, 1985; Green, 1993). The males excavate burrows, which they must defend from other males, on the lowest shore terraces; mating occurs in or near the burrows. Soon after mating the males

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start the journey back inland to the forest, while the females lay their eggs and remain in the burrows for 2 weeks (Hicks, 1985; Hicks *et al.*, 1990). At the end of the incubation period the females vacate their burrows and make their way to the coastal cliffs, which almost completely surround the island, to cast their eggs into the ocean. The females then return to the forest while the crab larvae spend 3–4 weeks at sea before returning to land as juvenile crabs (Gibson-Hill, 1947; Hicks, 1985; Hicks *et al.*, 1990).

Since gecarcinid crabs must migrate to the shore to spawn, they must have well-developed navigational mechanisms. The means of navigation during the migrations are unknown, but visual cues, polarized light, magneto-reception, and learning are thought to be involved (Daumer *et al.*, 1963; Herrnkind, 1968; DeWilde, 1973; Bliss *et al.*, 1978; Lohmann *et al.*, 1995; Vannini and Cannicci, 1995; Deutschlander *et al.*, 1999).

Some data are available on the activity levels of terrestrial crustaceans in the natural environment (*e.g.*, Wolcott and Wolcott, 1985; Gherardi *et al.*, 1988; Gherardi and Vannini, 1989; Micheli *et al.*, 1990; Weinstein, 1995), but data comparing the activity patterns of gecarcinid crabs during normal foraging activities and during the migration are sparse (see DeWilde, 1973). The ecology of red crabs is characterized by a period of very low activity during the dry season, followed immediately by a breeding migration (Hicks, 1985; Green, 1997) that may require crabs to travel more than 4 km in less than a week. Such abrupt changes in activity levels impose specific demands on the physiology and metabolism patterns of red crabs.

The availability of food and water changes on a seasonal basis. Particularly during the migration, this could be a major determinant of the strategy, performance, and diel capacity for exercise. Limitations in food have implications for the importance and use of stored fuel reserves, both during the dry season and during the migratory activities. Thus, determining the distances traveled and the duration of the migration as well as the routes and destinations of the crabs was crucial in appreciating the physiological demands.

The aim of this study was to examine activity levels of red crabs in the field during the migration compared to the non-migratory season. The emphasis was to characterize the migration of *G. natalis* in detail, by determining the direction, speed, and distance traveled during the migration, as well the relationship between the point of origin of crabs in the forest and their shore destinations, thus providing a context for the physiological demands during their annual migration.

Materials and Methods

Christmas Island was formed by a series of geological uplifts. Thus, the structure of the island is reminiscent of a

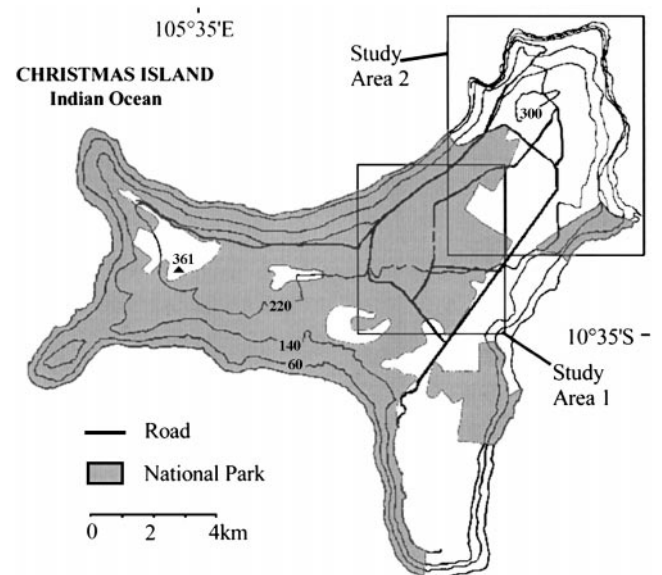


Figure 1. Christmas Island, Indian Ocean, showing areas of National Park and the location of the two study areas. Study Area 1 was located in the relatively undisturbed part of the island; Study Area 2 included the residential and industrial areas.

wedding cake, with a central plateau (>200 m above sea level) and a number of cliffs and terraces descending to a rugged shore line with few beaches (Fig. 1; Gray, 1995). Field studies on Christmas Island were carried out in two study areas. The primary study site (Study Area 1) was located on the central plateau, within the Christmas Island National Park (Fig. 1). This part of the Island is covered by primary rainforest and well-established secondary regrowth and has received minimum human disturbance over the past 20 years. Study Area 2, located in the northeast corner of the Island (Fig. 1), included the existing human settlement and airport, an area crisscrossed by many roads.

The annual activity cycle of red crabs was divided into a migratory and a non-migratory season. “The migratory season” (initiated by the arrival of the wet season, usually in November or December) is used in this study to collectively refer to the breeding behavior of the crabs, including the annual breeding migration, the related breeding activities, and the return journey from the shore terraces to the forest. The “non-migratory season” includes all other times of the year when the red crabs were not involved in breeding activities.

Non-migratory season

Population density. To obtain an index of density for red crabs, twelve stations (A to L) were selected; these included sites on the central plateau and on the upper terraces in both study areas (Fig. 2). All stations were located in primary or

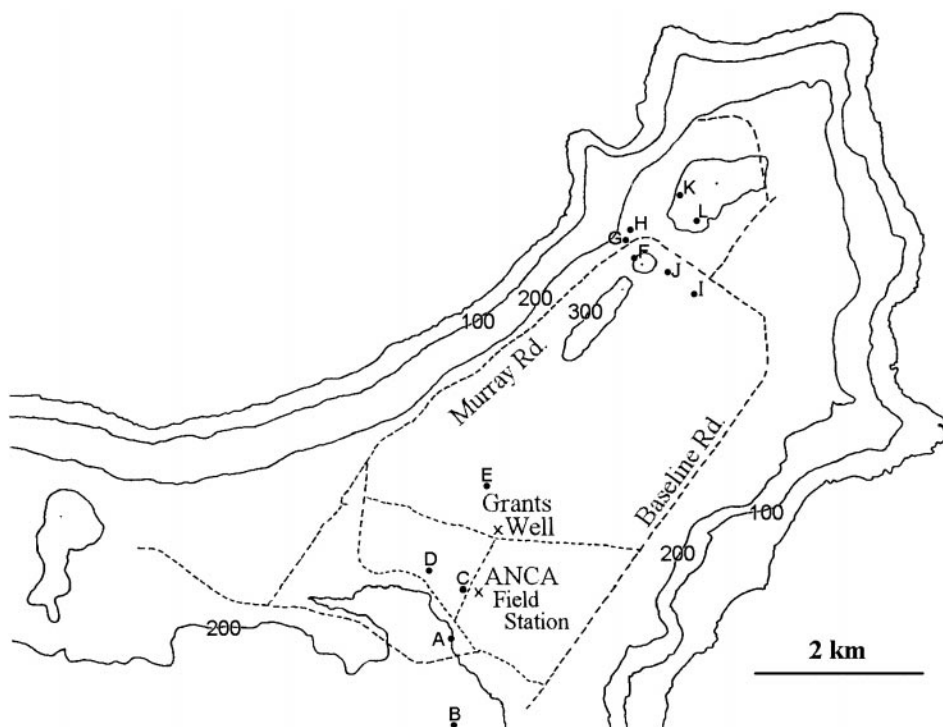


Figure 2. Locations of the sites for determining the density of red crabs during February and March 1995 (non-migratory season). Sites A-E were within Study area 1; sites F-L were in Study Area 2.

mature regrowth forest, but some were very close to cleared areas.

At each station the visible red crabs were counted in each of six grids (9×9 m). All counting was done either in the 2 hours after dawn, a period of foraging activity for red crabs, or during overcast conditions that normally stimulate a similar degree of activity (Hicks, 1985; Green, 1993, 1997). There is very little understory vegetation in the rainforest of Christmas Island, so foraging red crabs are easily visible and provide relatively accurate estimates of the crabs present in the area. Additionally, stations that were populated predominantly by large male crabs were discriminated from those with a more mixed population. These data were confirmed as having homogenous variance by using Bartlett's χ^2 test and were then analyzed by analysis of variance (ANOVA: Systat 5.03). *Post hoc* testing was by Tukey's HSD, and $P \leq 0.05$ was taken as significant in all cases.

Activity patterns. Two separate experiments were conducted to determine the activity patterns of red crabs during the non-migratory season (March 1993; wet season) at station B within Study Area 1 (for location, see Fig. 2). Firstly, crabs were selected at random and observed for a period of 2 min during their normal foraging activities. The distance that each crab walked during the 2 min was recorded ($n = 15$). During the second experiment, the actual walking speed of foraging crabs was recorded. A crab was

chosen at random and observed until it started walking; the crab was then timed for as long as it continued to walk, and the distance it traveled was recorded ($n = 14$). All crabs used in these two experiments were subsequently captured, sexed, and measured (carapace width). These observations were made when the red crabs are most active, *i.e.*, when the humidity was over 85% (Green, 1993).

Migratory activities

Three methods were used to obtain information about the migration of red crabs: radio tracking to obtain precise speeds, routes, and direction of travel; spray-painting large numbers of crabs to gain information on *en masse* direction of travel; and counting of crabs at designated stations to provide quantitative snapshots of the numbers of crabs present in various parts of the island.

In Study Area 1, crabs were studied during the migratory season (November/December) of 1993 and 1995, but in Study Area 2 crabs were studied during the 1995 migration season only. The behavior of migrating red crabs in a relatively undisturbed area (Study Area 1) was compared to that of crabs in the inhabited part of the island (Study Area 2). Since red crabs have rather small home ranges during most of the year (Lake and O'Dowd, 1991; Green, 1993; pers obs.), the areas within the rainforest selected for color

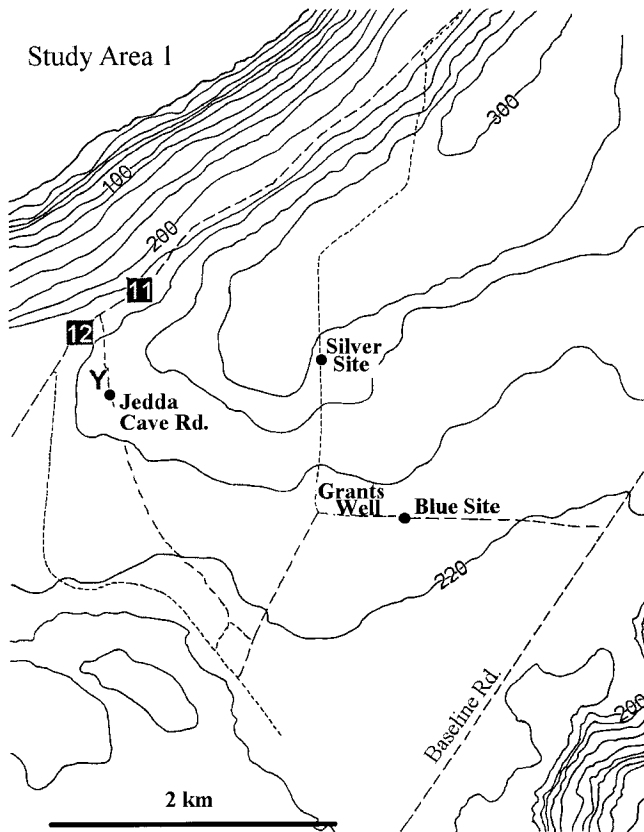


Figure 3. Study Area 1 showing locations of numbered grids (■) used for density counts during the migration and sites (●) of color coding crabs (where Y = yellow) and of radio-tracking "sites of origin" at Silver and Blue.

coding of the red crabs prior to the start of the migration were assumed to be the sites of origin for those crabs.

Radio-tracking of crabs. At the commencement of the migration in 1993, four large male red crabs (mass 400-503 g) were captured at each of two chosen study sites (Blue and Silver sites; for locations see Fig. 3) and fitted with radio transmitters (see below). During the 1995 migration this radio-tracking experiment was repeated by fitting male crabs (mass 415-480 g) originating at those same sites with radio transmitters on 8 and 9 November. Additionally, in 1995, radio transmitters were attached to three large male crabs (mass 460-570 g) at each of two more sites of origin (Yellow and Orange sites; Fig. 4) within Study Area 2, on 9 and 10 November respectively.

To attach the radio transmitters to the crabs a plastic sawn-off 20-ml syringe was first glued with an epoxy glue to the top of the carapace of each crab and allowed to set for a minimum of 6 hours. The radio transmitters (Microlite transmitters, model GP1; Titley Electronic, Ballina, NSW, Australia) were then inserted into the syringes with the antennae trailing behind the animals. The transmitter and the plastic syringe housing weighed 20-30 g. The postero-

dorsal surface of each crab was spray-painted with acrylic paint corresponding to the color associated with its site of origin. Each crab was released exactly the same spot where it was collected.

The crabs were tracked daily with a collapsible, directional antenna (A. H. Systems, Chatsworth, CA) connected to a Regal 2000 telemetry receiver (Titley Electronics). Crabs were firstly located by triangulation and, where possible, the location of each crab was confirmed visually. The triangulation technique proved quite reliable, pinpointing the location to within 30 m. The position and time of location for each crab fitted with a radio transmitter was recorded on a topographical map every day.

Color-coding of crabs. The posteriodorsal part of the carapace of crabs was spray-painted with nontoxic acrylic spray-paint, avoiding the eyes and mouthparts. In Study Area 1, at the commencement of the migration in 1993 (on the 17 Nov.), 530 crabs (male and female) were spray-painted yellow and 285 crabs were spray-painted blue (for location of sites, see Fig. 3). During the 1995 migration, 684 crabs were spray-painted blue and 750 were spray-painted silver at their respective sites of origin within Study Area 1 (Fig. 3).

In Study Area 2 (1995), 5622 red crabs were spray-painted different colors at eight locations within primary and mature regrowth forest in the plateau area (see Fig. 4 and Table 1 for location and the number of crabs painted at

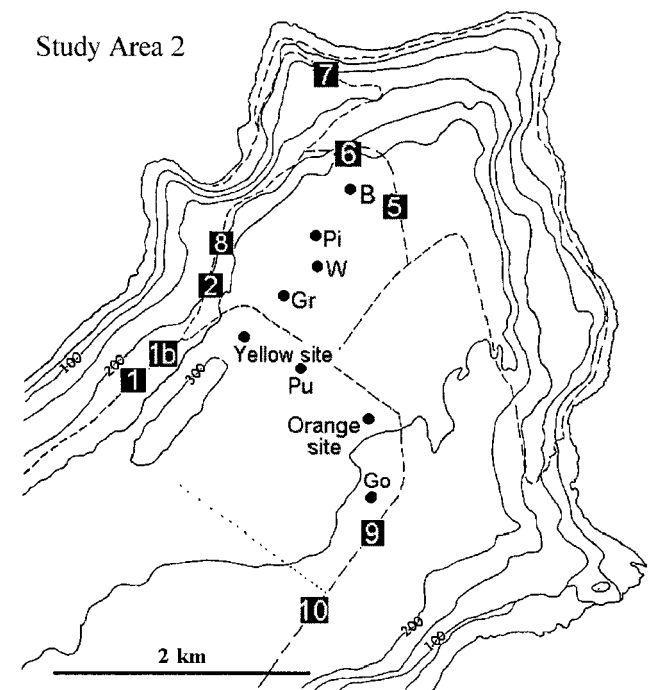


Figure 4. Study Area 2 showing locations of numbered grids (■) used for density counts during the migration and sites (●) of color coding crabs (where Pu = Purple, Gr = Green, W = White, Pi = Pink, B = Brown, Go = Gold) and of radio-tracking "sites of origin" at Orange and Yellow.

Table 1*Summary of 1995 color-coding experiment in Study Area 2*

Site code	Date painted*	Painted (no.)	Crabs	
			Sighted†	(%)
Purple (Pu)	5	556	70	13
Green (Gr)	5–8	999	310	31
Yellow (Y)	5–8	886	236	27
White (W)	5–8	701	269	38
Pink (Pi)	5–8	611	164	27
Brown (B)	7	169	15	9
Orange (O)	6–8	621	204	33
Gold (Go)	6–8	1079	70	6
TOTAL		5622	1338	23

* Day or range of days in November 1995.

† Between 8 November and 18 December 1995.

each site of origin). In Study Area 2, volunteers searched for painted crabs from 0630 to 1100 hours and from 1500 to 1730 between 8 November and 18 December 1995. To maximize sightings, the surveying took place mainly on and alongside roads and tracks, where color-coded crabs could be easily spotted as they crossed. All sightings reported by ANCA (Parks Australia) staff and local residents were also recorded.

Walking speed and density of crabs during the migration

Walking speeds of red crabs were measured for crabs crossing Murray Road (a limestone surface about 10 m wide; Fig. 2), during the downward and return male and female migrations. Observations on the migration patterns, mating activities, and spawning of the red crabs were recorded daily.

During the 1995 migration season, counting stations were set up on roads in Study Area 1 (2 stations; Fig. 3) and in Study Area 2 (9 stations; Fig. 4). At each counting station three counting grids (each 5 × 5 m) were spray-painted on the road. Counts were carried out at each station at 0800 and 1700 hours every day between 5 November and 18 December (a total of 87 counts at each station). The density of red crabs per square meter ± SEM was calculated from the mean of the three grids at each site. The data were analyzed by analysis of variance (ANOVA), using Systat for Windows version 5.03.

Results

Non-migratory season

Population density. The density of crabs ranged from 0.09 to 0.57/m². Sites located at the central plateau were occupied predominantly by large male crabs at a mean

density of 0.14 ± 0.03/m². This density was significantly lower than that of mixed populations located mostly at lower altitudes (Fig. 5). The exception was station K, which was on the plateau but inhabited by a mixed population. However, at that part of the plateau the island falls almost directly to the ocean, making it the first accessible habitat for the smaller and juvenile crabs in this part of the island. There was evidence of decreasing crab density with increasing elevation in both study areas (Fig. 5); the relationship could be described as follows: crab density (number/m²) = 1.047 - 0.003 (elevation in m); *r*² = 0.47, simple linear regression).

Activity patterns. In March 1993, red crabs had finished their migratory activities for the season but, with relative humidity over 90%, were still actively foraging above ground. Foraging red crabs walked intermittently, traversing an average distance of only 0.52 m in 2 min. During locomotion, the walking speeds ranged from 0.62 to 2.0 m · min⁻¹ (mean = 1.11 ± 0.50 m · min⁻¹). The average carapace width of these crabs was 8.25 cm (range 6.5 – 11.5 cm).

Migratory activities

The monsoonal rains arrived at different times in the two study seasons, resulting in very different migratory behavior of red crabs. In 1993, the rains were late, migration on the plateau was initiated by heavy local rainfall at noon on 17 November. Within an hour, large numbers of red crabs began accumulating on vehicle tracks and open areas within Study Area 1 and commenced their annual migration. The migration started 1 week after the optimal date predicted on the basis of the lunar cycle, and it lasted only about 6 days (Fig. 6).

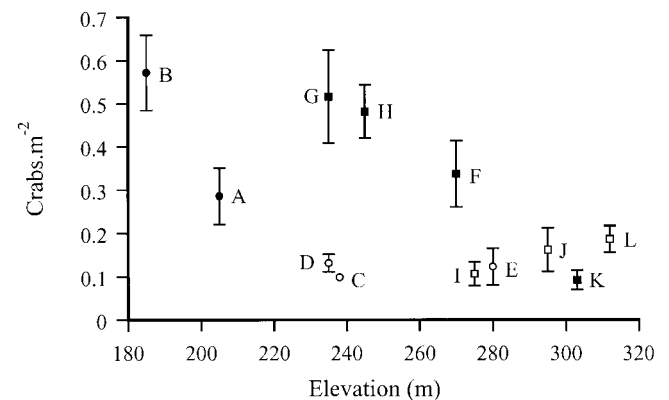


Figure 5. Density/elevation distribution of red crab population, mean number of crabs per m² ± SEM. Letters designate counting site (see Fig. 2 for location map). Closed symbols indicate a crab population of mixed sexes and different sizes. Open symbols indicate crab populations composed mostly of large male crabs. Sites from Study Area 1 are shown as circles (○, ●); sites from Study Area 2 are shown as squares (□, ■).

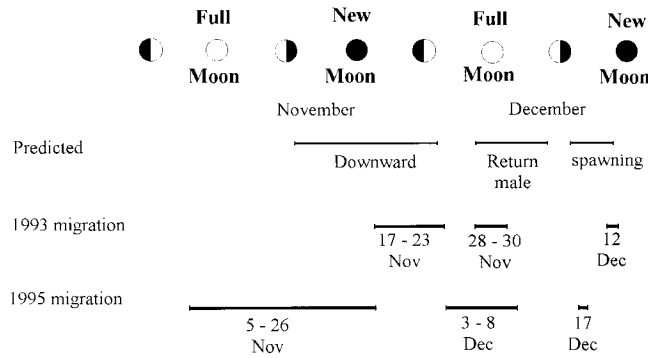


Figure 6. Graphical representation of the synchronization of breeding activities of *Gecarcoidea natalis* with the lunar phase. Predicted migratory activities were based on the descriptions presented by Hicks (1985) and Hicks *et al.* (1990). The actual timing of the downward migration, the return migration of male crabs, and the spawning recorded in 1993 and 1995 are also presented.

The migration of 1995 did not start abruptly on the plateau. A few light showers in October increased the humidity, and the red crabs became more active. A small percentage of red crabs were seen on their downward migration during the first week of November, before the main migration. The main migration on the plateau started 12 days before the date predicted by the lunar phase (Fig. 6), and consequently the red crabs were engaged in the downward migration for up to 3 weeks during the 1995 season.

Migration activity occurred almost exclusively during daylight. On rainy, overcast days the crabs were seen crossing roads throughout the day, although the numbers decreased during the middle of the day. However, on sunny days there was a distinct period of low activity during the middle of the day (1130–1500). During this time large numbers of red crabs accumulated in the bushes by the sides of the roads and resumed their migration later in the afternoon. A few individuals persisted in migrating for several hours after sunset on some days, but there was no migratory activity at night.

Migratory routes (Study Area 1)

Radio-tracking data showed that red crabs do not necessarily migrate to the nearest coast (Fig. 7a, b; Fig. 8a, b). All crabs with radio transmitters released in the Blue site in 1993 covered about 4.13 km to the northwestern shoreline within 6 days (Fig. 7), rather than walking only 1.8 km to the southeastern shore. Furthermore, the crabs did not need to follow contour lines to direct themselves towards the shoreline. Importantly, crabs radio-tracked from the same point of origin followed remarkably similar routes in both study seasons, and they traveled in surprisingly straight lines (Fig. 7a, b; Fig. 8a, b). The silver-coded crabs from the center of the Island also headed northwest, traveling approximately 2.4 km in as little as 3–4 days (Fig. 8a, b). The

Jedda Cave road, where 500 crabs were painted yellow in 1993 (Fig. 3), was used as a travel route by some individuals. Yellow-colored crabs were noted on the road up to 3 days after being painted (Fig. 9a). Other crabs simply crossed the road without taking advantage of easier routes along cleared areas. Sightings of color-coded red crabs (Fig. 9a–c) provided a larger data set confirming that crabs originating from a particular area on the island tend to migrate to similar areas on the shore to carry out their breeding activities.

The distances traveled by the red crabs with radio transmitters in Study Area 1 varied greatly, from 120 to 1460 m/day. During the “rushed” migration in 1993, seven of the radio-tracked crabs traveled more than 900 m/day, and the average distance traveled in a day was 680 m (Fig. 7a, b). During the 1995 migration, the longest distance traveled in a day was 1000 m, and the average daily distance was 330 m—less than half that recorded during the 1993 migration.

During the 1993 migration season, the crabs made progress towards their shore destinations each day (Fig. 7a, b). In contrast, during the 1995 season, 5 of the 7 radio-tracked crabs in Study Area 1 paused in their downward migration to the ocean and remained in one place (within ~ 20 m diameter) for 2 to 5 days before they resumed their journey to the coast (Fig. 8a, b).

Using the 1993 data and assuming that red crabs walk continuously for 12 h per day (*i.e.*, during the daylight hours), the calculated average walking speed during the migration of the crabs with radio transmitters was $1.1 \text{ m} \cdot \text{min}^{-1}$. This was considerably slower than the speed of $4.7 \pm 0.4 \text{ m} \cdot \text{min}^{-1}$ ($n = 17$) recorded for red crabs crossing Murray Road (10 m wide) during both of the study seasons. During the return migration, walking speeds for returning males ($5.1 \pm 0.3 \text{ m} \cdot \text{min}^{-1}$; $n = 13$) and returning females ($6.2 \pm 0.5 \text{ m} \cdot \text{min}^{-1}$; $n = 7$) crossing Murray Road were significantly faster than those of crabs on their downward migration ($P = 0.016$).

Migratory routes (Study Area 2)

In Study Area 2 the crabs also traveled predominantly northwest (Fig. 10a, b). Radio-tracking showed that crabs traveled along the sides of a road (thus becoming temporarily diverted from their course towards the shore) before eventually crossing the road to reach the terraces (Fig. 10a, b).

The crabs with radio transmitters from the Yellow site took between 10 and 13 days to travel 1.2 km to the shore terraces (Fig. 10b). The shore closest to the Orange site was 2.1 km due east, but most of the orange-coded crabs traveled more than 3.4 km in the northwest direction, walking for 17–21 days to reach the shore terraces at a point very close to the crabs from the Yellow site (Fig. 10a, b, Fig. 11).

Three crabs traveled over 1 km in a day, but the average

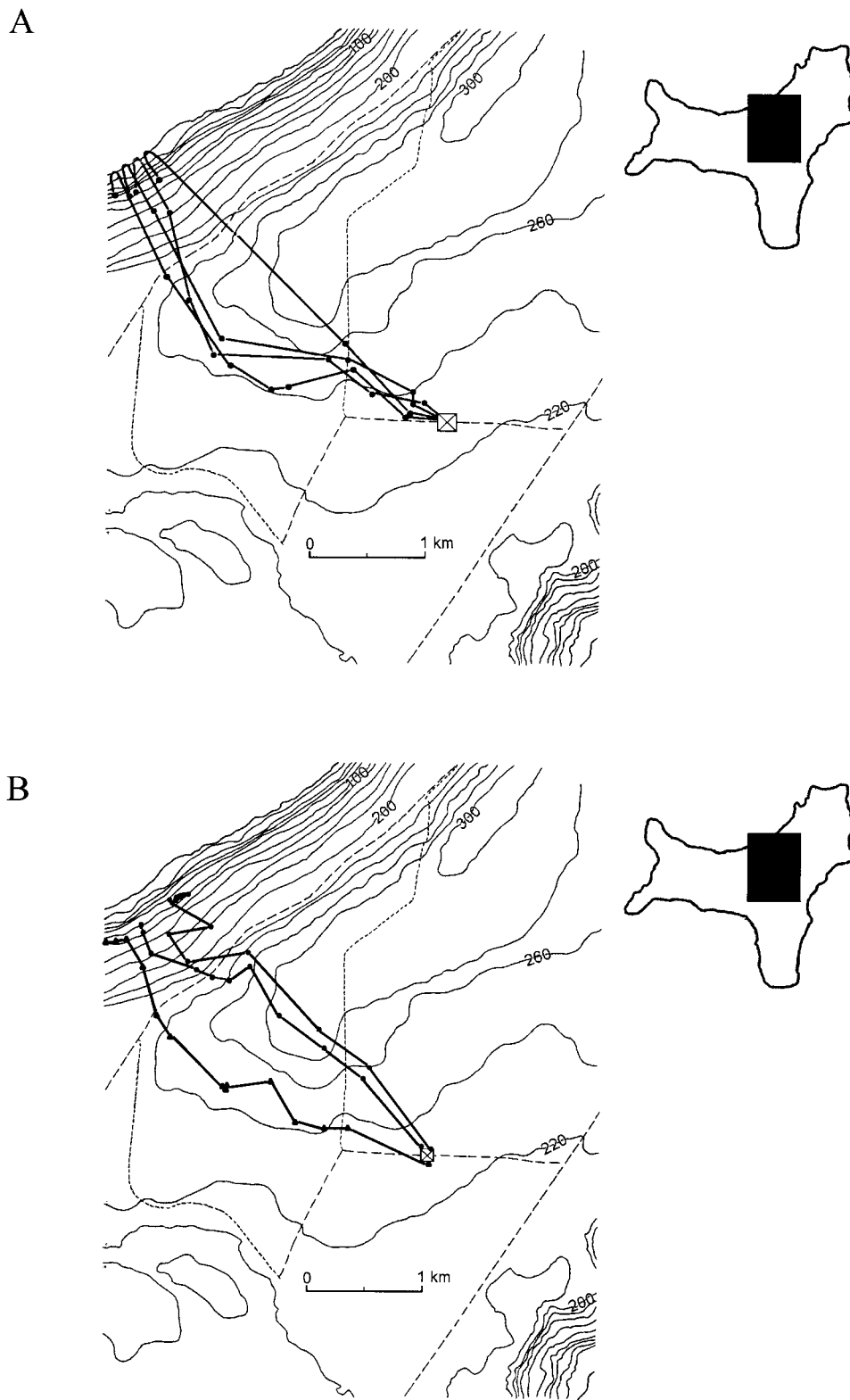


Figure 7. Migratory paths determined for radio-tracked crabs originating from the Blue site in Study Area 1 in 1993 (A) and in 1995 (B). The \boxtimes symbol shows site of origin. The location of the enlarged section is indicated by the black rectangle.

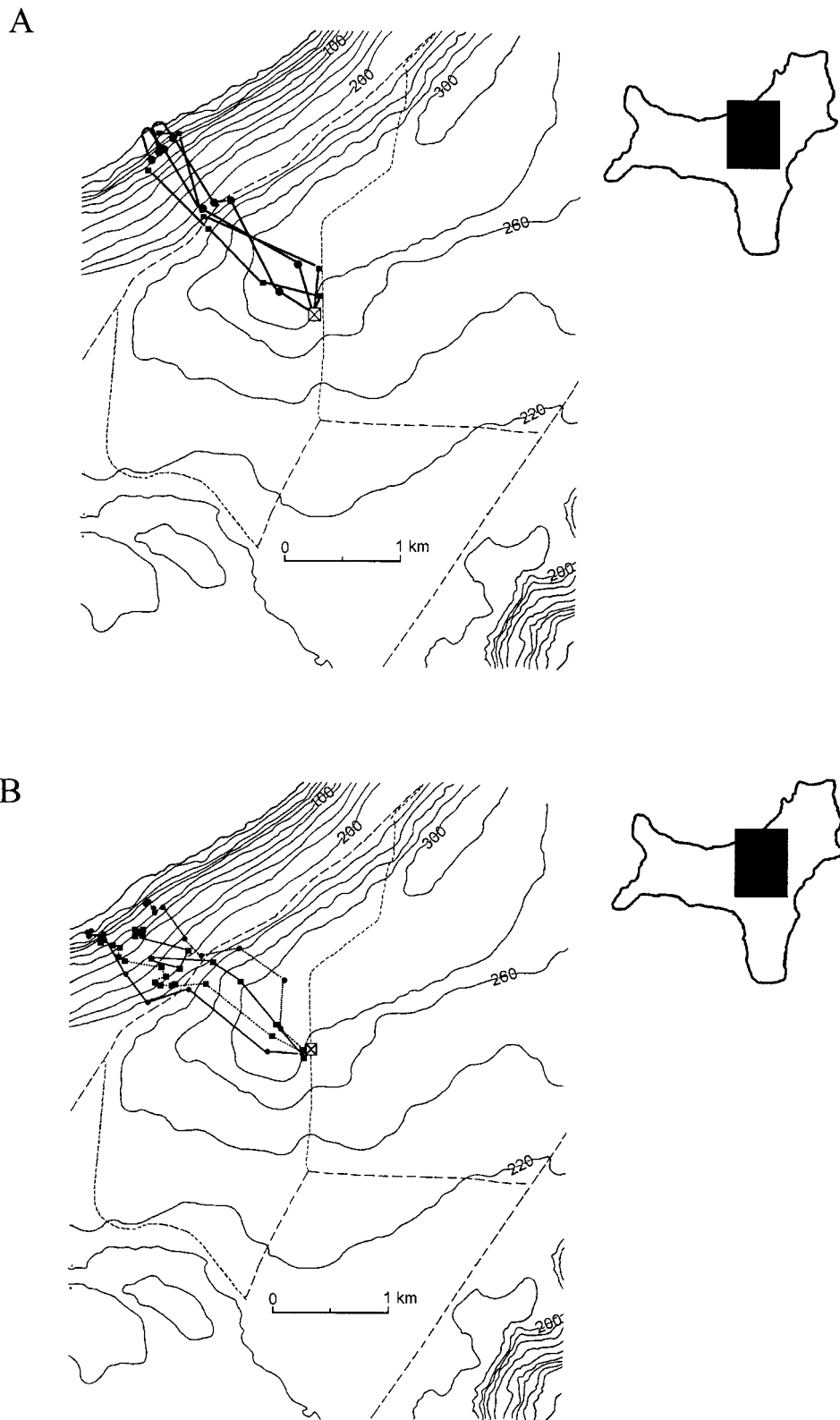


Figure 8. Migratory paths determined for radio-tracked crabs originating from the Silver site in Study Area 1 in 1993 (A) and in 1995 (B). The \boxtimes symbol shows site of origin. The location of the enlarged section is indicated by the black rectangle.

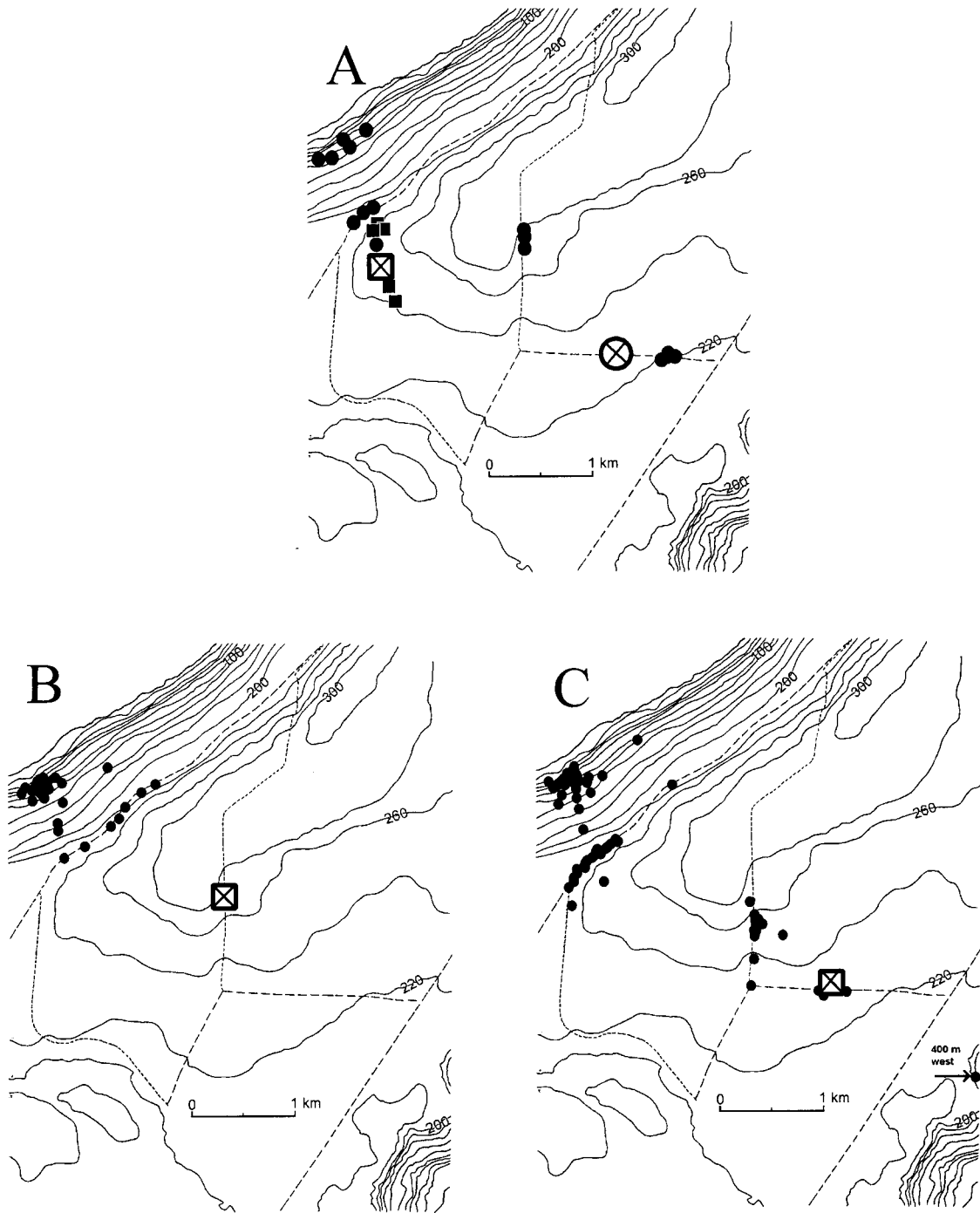


Figure 9. Locations of sightings of spray-painted crabs. (A) Yellow-painted crabs (■) and blue-painted crabs (●) during the 1993 migration. Yellow-coded crabs were seen for 3 days after painting on the Jeda Cave Road, and thus individual sightings are not shown. (B) Silver-painted crabs (●) during the 1995 migration. (C) Blue-painted crabs (●) during the 1995 migration. Open symbols show site of origin.

distance covered per day was only 200 m. In Study Area 2, 5 of the 6 radio-tracked crabs also made stops and remained within a small area (5-30 m diameter) for periods ranging from 1 to 7 days before continuing towards the coastal terraces (Fig. 10a, b).

Of the 5622 red crabs color-coded in eight sites within Study Area 2, 1338 sightings of color-coded crabs, on their downward or return migrations, were recorded. For every 100 color-coded crabs released, the subsequent sightings ranged from 38% for the white-coded crabs to only 6% for

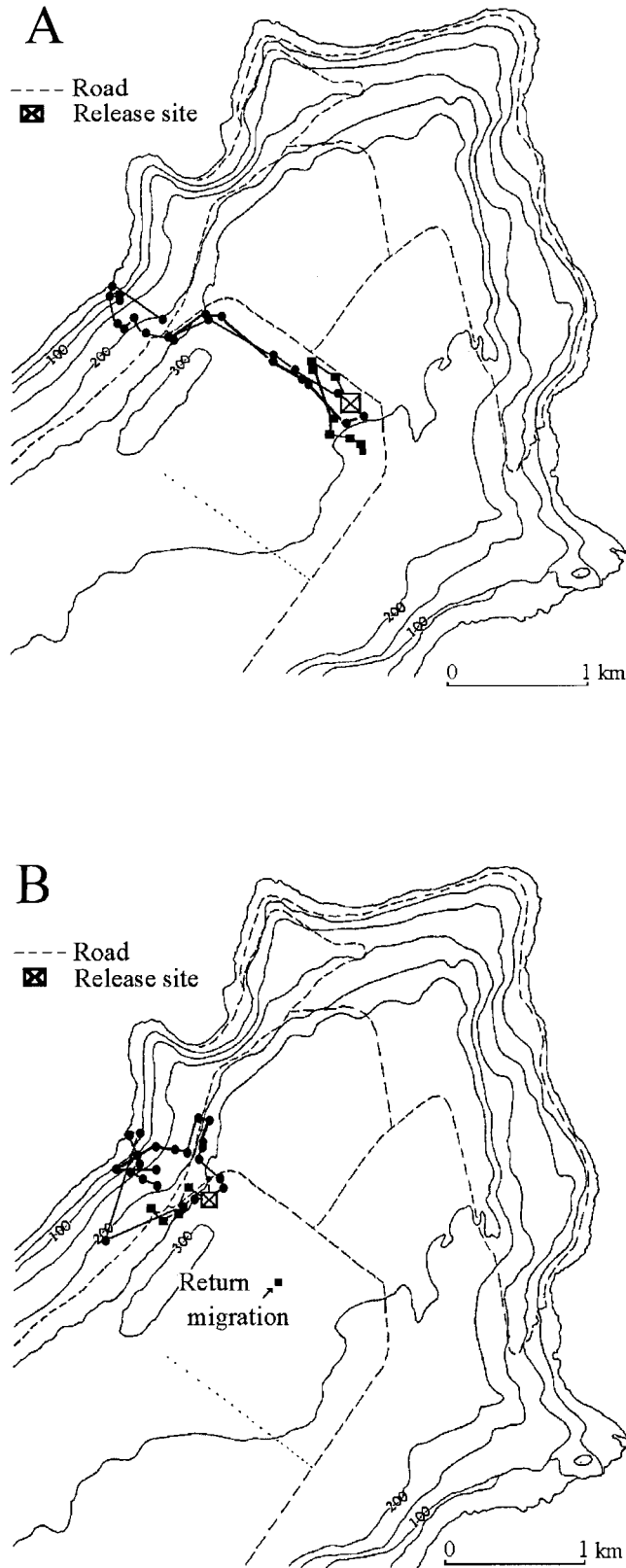


Figure 10. Migratory paths as determined by radio-tracking in Study Area 2 during the 1995 migration. (A) Three crabs from the Orange site. (B) Three crabs from the Yellow site. Open symbols show site of origin.

the gold-coded crabs (Table 1). The sightings indicated that painted crabs traveled predominantly towards the north-western coast regardless of their site of origin (Fig. 11). In 4 of the 8 color-coded groups the greatest number of sightings were on Murray Road between grid 1 and grid 8 (for location, see Fig. 4). Crabs originating from the Brown site were an exception as the majority of crabs from this site headed due north.

Terrace activities

At least half of the crabs fitted with radio transmitters descended to the lowest shore terrace, immediately above the ocean. Males on the shore terraces were engaged in digging burrows; in places, burrow density was $3/m^2$.

In the 1993 season, the first matings were sighted on 25 November, and the return migration of the males began on 28 November and lasted 3 days (Fig. 6). The female red crabs spawned pre-dawn (0300–0400 hours) on 12 and 13 December, and their return migration lasted only 2 days. During the return migration very small individuals (~ 2 cm carapace width) that had not been observed on the downward migration were seen traveling inland with the returning females.

In 1995, the first matings were sighted on 29 November, and the return migration of the males began in earnest on 3 December (Fig. 6). The main return migration of male crabs lasted 5 days, with a few late crabs still walking for 2 more days. The female red crabs spawned pre-dawn on 17 December, with two small-scale spawnings occurring in a few places on the Island on 16 and 18 December. The returning females reached Murray Road on 19 and 20 December in very large numbers.

Density of crabs during the migration

The downward migration (in 1995) lasted from 5 to 26 of November. Prior to 9 November, only a few crabs were seen crossing through the counting grids (see Fig. 4 for locations) and only in certain areas (Fig. 12). The main downward migration showed a wavelike increase and decrease in the number of crabs moving across roads on different days—for example, grid 1b (Fig. 12a), grid 6 (Fig. 12e), and grid 8 (Fig. 12d).

The density of crabs was greatest on Murray Road, in Study Area 2, between grids 1 and 8 (Fig. 12a-d). The maximum density of crabs recorded was $1.35/m^2$ on grid 2 during the downward migration (Fig. 12c), but in Study Area 1, the maximum densities reached only $0.4\text{--}0.5/m^2$ (Fig. 12i, j; see Fig. 3 for locations).

The lowest densities of crabs, $<0.2/m^2$, were recorded on Phosphate Hill (grids 5, 6, and 7; Fig. 12e, f) and on the Base Line Road (grids 9 and 10; Fig. 12g, h respectively). No crabs were ever recorded in grid 5 (Fig. 4). The number of days during which at least one crab was present in the

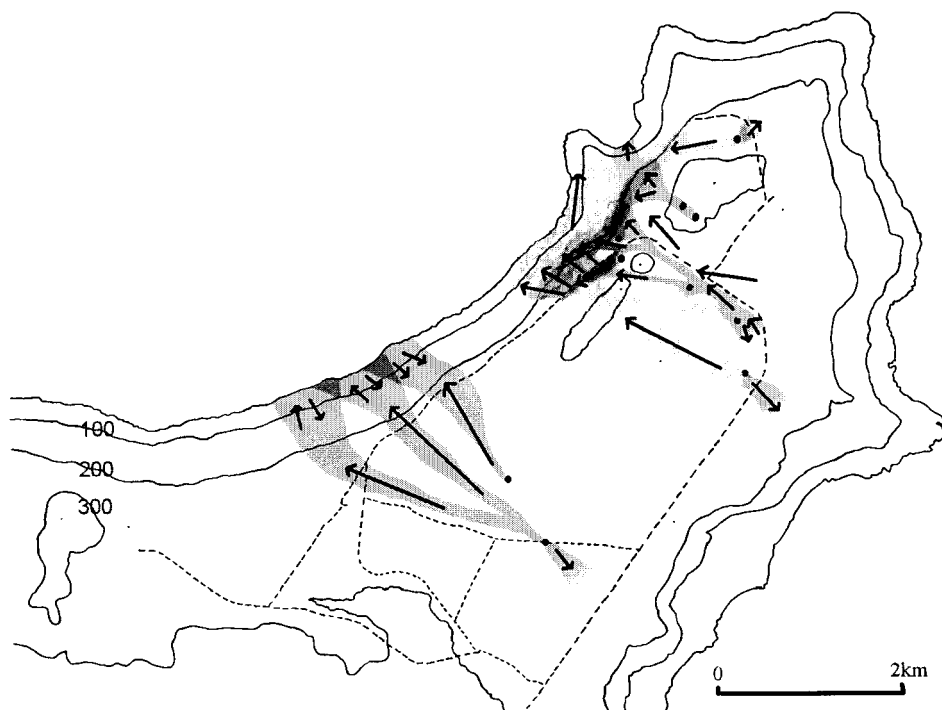


Figure 11. Composite showing general migration routes, directions, and destinations for the red crab migration. Derived from color-coding and radio-tracking data. Density of stipples indicates frequency of marked crab recaptures.

counting grids ranged from 2 at grid 7 to 11 at grid 6. In contrast, in the grids located on Murray Road, the crab migration lasted from 26 to 34 days.

Discussion

The distribution of *Gecarcoidea natalis* is not homogeneous throughout Christmas Island, and the activity levels and behavior of the crabs show extreme seasonal dichotomy. The largest male crabs live farthest from the coast; because they have the greatest distance to travel, they must start their migration before other crabs if they are to reach the shore together. Crabs from all locations walked in surprisingly straight lines to definite shore destinations to which they navigated together with their neighbors. Radio-tracking revealed that given adequate time to complete the migration, the male red crabs paused for several days *en route* to feed instead of crowding early into the limited terrace area adjacent to the shore. The migratory behavior, strategy, and potential stress (Adamczewska and Morris, 2001) are influenced by the distance an individual crab must travel. However, since the breeding migration is triggered by the arrival of the monsoonal rains and is synchronized with the lunar cycle (Hicks, 1985; Grey, 1995), the timing of the arrival of the seasonal rains will be fundamental in determining the speed of migration and the time spent walking each day.

The red crab population

The population of red crabs on Christmas Island was estimated by subdividing the area of the entire Island into three sections: (i) the terraces, with an area of 57.7 km² and an average density of 0.6 crabs per square meter; (ii) the plateau, with an area of 59.6 km² and a crab density of 0.15/m²; and (iii) mined or cleared areas, with an area of 16.7 km² and a density of 0.01/m² (Lake and O'Dowd, 1991). The estimated population of adult red crabs on Christmas Island was 43.7 million, substantially less than the 120–157 million crabs suggested previously (Hicks, 1985; Hicks *et al.*, 1990). Importantly, the density of red crabs was similar in the mature regrowth forest within Study Area 2 and the relatively undisturbed forest of the terraces in Study Area 1.

The densities of red crabs recorded in this study were very similar to the values of 0.04 to 0.4/m² obtained by Lake and O'Dowd (1991) in transects. The population density of red crabs is very high; although several studies report the densities of other terrestrial gecarcinids in the range of 0.4 to 6/m² (Green, 1993, and references therein), these are generally the maximum densities recorded. The densities of red crabs can reach up to 40/m² on the ocean cliffs and beaches during spawning (Hicks, 1985; pers. obs.). As a consequence of the high biomass, these crabs have a very

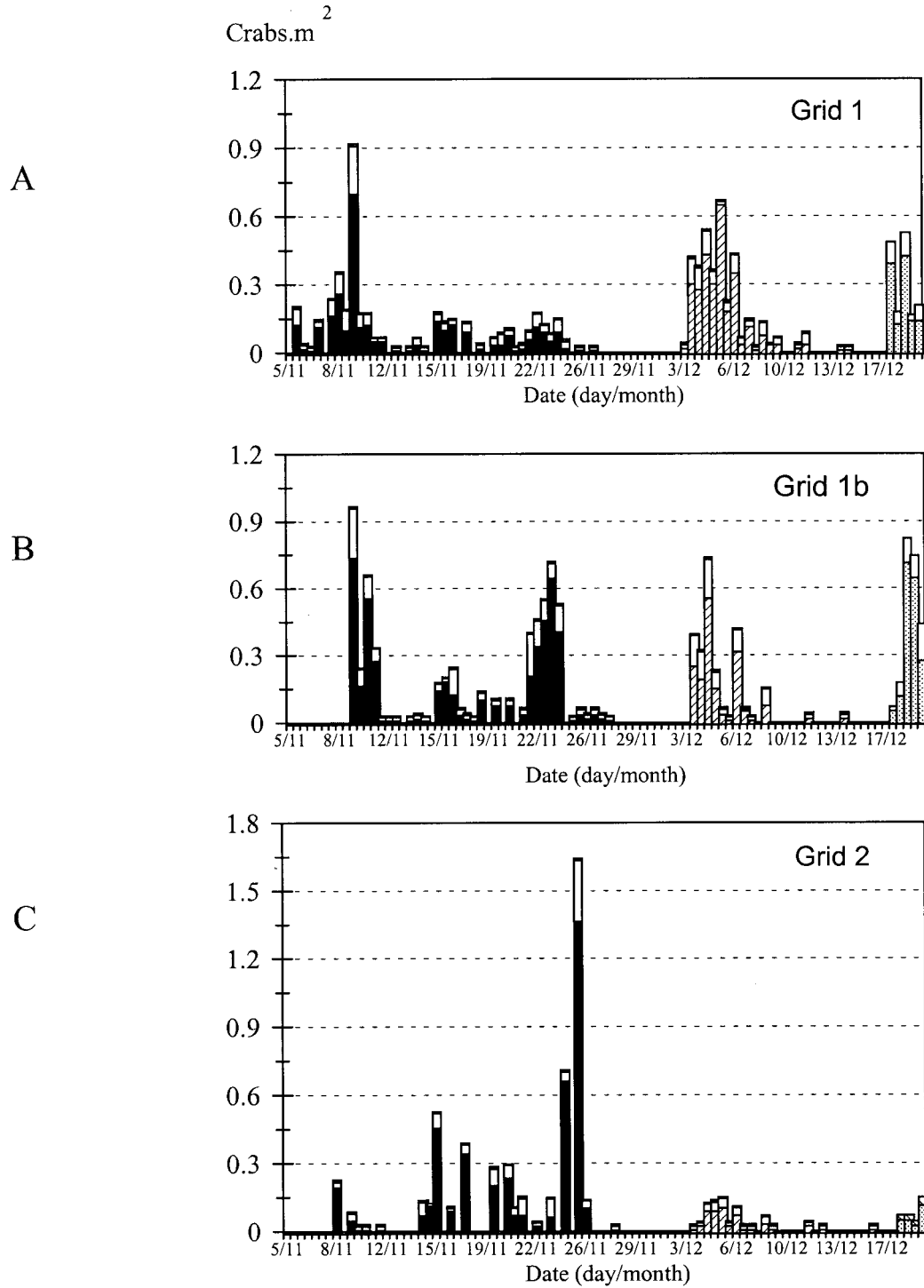


Figure 12. Density of crabs crossing roads during the downward migration (solid bars) and during the return migration of male crabs (bars with diagonal fill) and female crabs (bars with stippled fill) during the 1995 migratory season. Grids 1–10 were in Study Area 2; grids 11 and 12 were in Study Area 1. For location of grids, see Figures 3 and 4.

large impact on forest dynamics (Lake and O’Dowd, 1991; Green, 1993).

The density of red crabs on Christmas Island was

related to population structure and altitude. The top plateau is populated predominantly by large males and, progressing towards the shore, the coastal terraces are

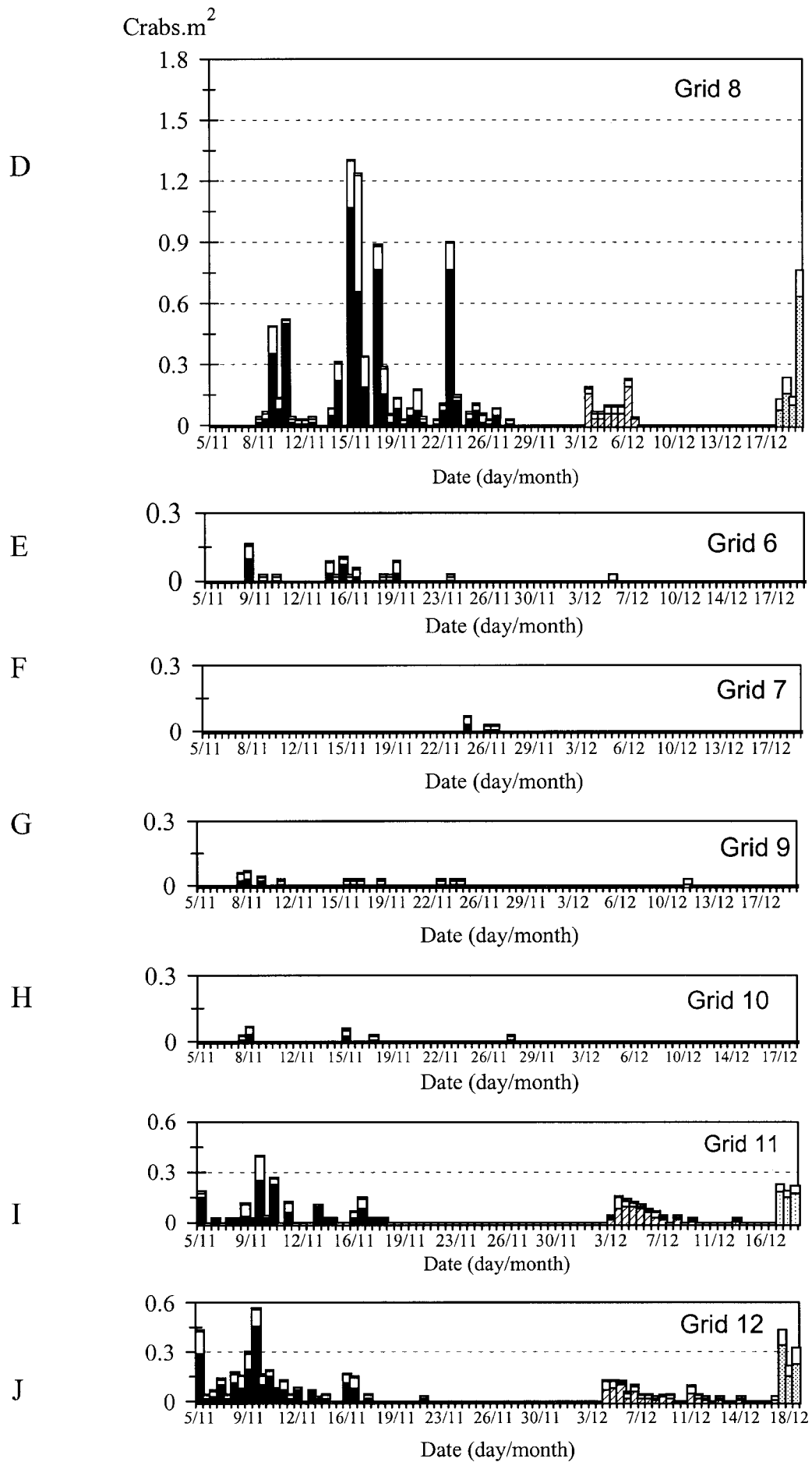


Figure 12. Continued.

populated by smaller individuals of both sexes (Fig. 5; Green, 1993, 1997). Crab densities decrease sharply in just 8–10 m when moving from the forest into cleared areas (Lake and O'Dowd, 1991). Walking speeds are slow, and the crabs seem quite sedentary during the non-migratory season; one marked crab was sighted within 15 m of where it was released 8 months earlier. Red crabs appear to be unaffected in their distribution and activities by conditions or events only a few meters removed (Lake and O'Dowd, 1991; pers. obs.), and they tend to have small foraging ranges during the non-migratory phase of the year.

Routes and destinations of migrating crabs

A combination of radio-tracking, color-coding, and counting stations located in various places around the island has revealed valuable information about the migratory patterns of red crabs. Three points have become apparent: firstly, crabs traveled predominantly towards the northwestern shore, which for some of the crabs was twice as far away as the southeastern shore; secondly, the crabs have specific shore destinations to which they apparently return each year; and thirdly, crabs originating from any one area on the plateau tend to travel in a similar direction and thereby reach the shore terraces in proximity to one another. The northwestern shore is much calmer, so the larvae probably have a better chance of landing ashore there after 3 weeks in the ocean. If the chances of recruitment on the northwestern shore are indeed substantially higher than elsewhere, then selective pressure would act in favor of the crabs that return to breed to the same shore where they emerged as larvae, as proposed by Gibson-Hill (1947) and DeWilde (1973).

The mode of navigation used by the red crabs during their migration remains speculative, but this study clearly shows that the crabs do not simply walk "down" toward the ocean as was suggested by Gibson-Hill (1947). Magnetic orientation could certainly account for straight paths taken by the red crabs (Vannini and Chelazzi, 1981; Lohmann *et al.*, 1995). Some gecarcinid crabs are thought to orient themselves towards the bright horizon (Klaassen, 1975; Bliss *et al.*, 1978; Wolcott and Wolcott, 1982); however, although red crabs in the jungle are unable to see the horizon, they do nonetheless avoid entering darkened areas.

If the young crabs can benefit from, or even need to, follow the older crabs to find their way to the shore to breed, then the idea of the "inexperienced" crabs following the "older, more experienced" crabs, proposed by DeWilde (1973), would certainly increase the breeding success of the young individuals. Additionally, traveling in groups would be advantageous in synchronizing the breeding activities.

Crabs originating from the Green site and from the Gold site had very similar degrees of dispersal at the coast despite having walked different distances (1.4 km and nearly 3 km respectively); such similarity could only be expected if they traveled as cohorts. Experiments to relocate crabs before and during the migration would provide useful information about the navigation mechanisms used by the red crabs.

A comparison of the two study seasons of 1993 and 1995 in Study Area 1 reveals a 3-week difference in the timing of the start of the downward migration in relation to the lunar phase. In contrast, the spawning date appeared to be very consistent and most predictable from the lunar phase (Fig. 6). The synchronization of the spawning activities of red crabs may be important in maximizing the chances of survival for the newly hatched larvae (Morgan and Christy, 1995). In 1995, the wavelike patterns in densities of crabs crossing through the density estimation grids may be partially attributed to the different distances that crabs may have to travel to reach any given point, but they were at least partially the result of different timing of the initial rainfall in the different parts of the Island (pers. obs.). The counting grids provide snapshot images of the numbers of crabs moving through various parts of the island and further support the conclusion, which was based on sightings of color-coded crabs, that red crabs preferentially migrate towards the northwestern shore.

The radio-tracking data revealed an important difference in the behavior of migrating crabs between the two study seasons. In 1993, the red crabs walked towards their shore destinations every day and walked relatively longer daily distances. In 1995, however, 10 out of 13 radio-tracked crabs made stops of 1 to 7 days duration at various locations before eventually arriving at the shore terraces. A consequence of this behavior is to minimize the duration of time that the entire island's red crab population is crowded on the shore terraces and the subsequent depletion of local food resources. Since the red crabs embark on their annual breeding migration immediately after the end of the dry season during which their feeding opportunities were greatly reduced (Green, 1993), early arrival of the monsoonal rains provides an opportunity for these animals to stop and feed during their downward migration. Furthermore, if the red crabs were "avoiding" reaching the terraces too early, this implies they "know" how long it will take to reach the shore and do not need to actually come in contact with the seawater to know when they have reached the coast (Hicks, 1985; Hicks *et al.*, 1990; Greenaway, 1994).

The red crabs quite clearly avoid open areas: most crabs would travel for some distance along the side of the road under the cover of vegetation before eventually crossing the road. This observation could explain the more erratic migratory routes of red crabs in the more disturbed part of the island (Fig. 10a, b). Although the red crabs do not have any

predators that might take advantage of their exposure in the open, desiccation and elevation in body temperature can reduce endurance and maximum speed of travel (Weinstein and Full, 1994; Weinstein *et al.*, 1994); this behavior minimizes exposure to lower humidity and higher temperatures in the clearings. The walking speed of red crabs crossing the road in this study was very similar to the $5.4 \text{ m} \cdot \text{min}^{-1}$ reported previously (Hicks, 1985), but was about 4 times faster than the overall migration speed estimated from the radio-tracking data.

After *G. natalis* completes its annual breeding activities, most crabs leave the lowest shore terraces and return to the upper terraces and the plateau. At least some crabs appear to follow a route similar to the one they took during their downward migration and to move farther inland than their place of origin (*e.g.*, Fig. 10b).

The environmental conditions restricting activity, coupled to the breeding biology of *G. natalis*, require the crabs to undertake a long migration after an extended period of relative inactivity. The breeding season, which can last from 3 to 6 weeks, represents the most active period of the year for the red crabs. Such varied activity levels impose quite different physiological demands on the animals. To assess the demands of the migration, we have also examined metabolic fuel stores, metabolic status, and capacity to maintain locomotion in red crabs during their migratory activities (Adamczewska and Morris, 2001).

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