

Movement of Coconut Crabs, *Birgus latro*, in a Rainforest Habitat in Vanuatu¹

W. J. FLETCHER^{2,3}, I. W. BROWN³, AND D. R. FIELDER⁴

ABSTRACT: Patterns of movement in the coconut crab, *Birgus latro* (L.), were studied using mark-recapture and radio-tracking techniques at a number of sites in the rainforest regions of eastern Santo, Republic of Vanuatu (South Pacific). Movement was assessed both for crabs caught and released in one place (indigenous) and for crabs caught and then released at a new location (introduced). Recapture rates in eastern Santo were very small (<1%), whereas on the small islet sites (area <2 ha) the rate approached 20%. There were no significant relationships between distance moved and either time at liberty or size of the individuals for introduced crabs. But for indigenous crabs, size of individual was negatively correlated with distance moved. Recapture rates of introduced and indigenous crabs were similar, but introduced crabs moved significantly further from their point of release. Almost all radio-tagged crabs moved from their point of release; smaller crabs tended to move further. On eastern Santo, only two of five radio-tagged crabs were located again; both had moved over 250-m away from their release point. On the islet sites, all radio-tagged crabs were found again at least once; some of these returned to a number of different sites, indicating that *B. latro* seems to be able to home to particular locations. Nonetheless, dispersal of animals from an area, at least after handling, is a common feature.

INFORMATION ABOUT THE MOVEMENT of individuals is vital in any study that attempts to delineate stocks and estimate their size. This is especially important when using mark-recapture techniques because specific analyses are required if a large proportion of individuals migrates during the period of study (Begon 1980). Handling and marking of individuals may have an effect on rates of migration. Many studies have found that such disturbances subsequently reduce the chances of recapturing an individual because of increased dispersal from the study area

(Chittleborough 1974) or by avoidance of the capture site (e.g. Mallet et al. 1987). Alternatively, the chance of recapturing tagged individuals of some species may actually become greater than for untagged ones (Morgan 1977). Such effects would bias any estimate of population density. Moreover, no estimate of density could be made if the effect is extreme, such that no or very few recaptures are obtained.

In the present study we investigated the motility of the coconut crab, *Birgus latro* (L.), at a number of sites in the Republic of Vanuatu (South Pacific). Coconut crabs are the largest terrestrial crustaceans that inhabit the coastal forest regions of many tropical Indo-Pacific islands (Reyne 1939). They are generally nocturnal, remaining completely hidden during the day under rocky ledges and in caves and emerging only on some nights to forage.

As a part of a study designed to estimate the density and population dynamics of this species, we carried out routine mark-recapture programs at several sites (subject to different

¹This study was funded by the Australian Centre for International Agricultural Research, research grant 8381. Manuscript accepted 9 February 1990.

²Current address: Western Australia Marine Research Laboratory, P.O. Box 20, North Beach, W.A., 6020, Australia.

³Southern Fisheries Research Centre, P.O. Box 76, Deception Bay, Qld., 4508, Australia.

⁴Zoology Department, University of Queensland, St Lucia, Qld., 4067, Australia.

histories of exploitation) with the intention of estimating the density of crabs in these different areas. Unfortunately, with the exception of one small island site, usually fewer than one or two recaptures were obtained per site, preventing any meaningful calculation of density. Such a poor result could be attributed to (1) the presence of an extremely large number of crabs; (2) a tendency for the crabs to move among areas regularly; or (3) increased mortality/emigration or reduced catchability as a result of capture, handling, and tagging. We attempted to distinguish between these hypotheses by the use of more detailed mark-recapture studies and by tracking the movements of individual crabs with small radio transmitters.

MATERIALS AND METHODS

Mark-Recapture

Individuals were caught on baited trails at a number of sites on the island of Santo (Republic of Vanuatu) over a 2-yr period, 1986–1987 (Figures 1 and 2). The baits (opened coconuts) were set at varying intervals (10–20 m, depending upon terrain) during the day and revisited at night; any crabs captured at or near the baits were measured and marked with a number scratched into their carapace. This unique number remained until the crab molted, and its presence apparently caused no ill effects in crabs maintained in enclosures (Fletcher et al. 1990). Molting generally occurs only once a year during the winter (May–September) dry season (Fletcher et al. 1990). Some individuals were also freeze-branded (see Fletcher et al. 1989 for details), which produced a visible mark after molting (when the scratch marks are lost), thereby extending the period of identification. Over 1000 crabs (1044) were marked at 15 sites and released at the point of capture.

At one small island site (Bier I.), in addition to 40 crabs that were caught and marked locally, we released 150 marked crabs that had been caught at other sites (all of these had been freeze/heat-branded). Because of the differences in the extent to which the two groups



FIGURE 1. Map of Vanuatu.

of animals were disturbed, these two sets of crabs were analyzed separately using nonparametric methods.

Radio-tracking

Movement of individual crabs was monitored using a Biotrack SR-1 system (Biotrack; Dorset, England). This comprised a receiver and a number of radio tags, each of which emitted a signal with a unique frequency between 10 and 600 KHz. Their lithium batteries maintained the signal for more than 6 months. Tags were attached to the dorsal surface of the carapace of each crab using nontoxic, quick-setting epoxy resin. Five crabs were marked at a mainland site (Hog Hbr) and released at their place of capture. Ten tagged crabs (four captured locally and six captured elsewhere

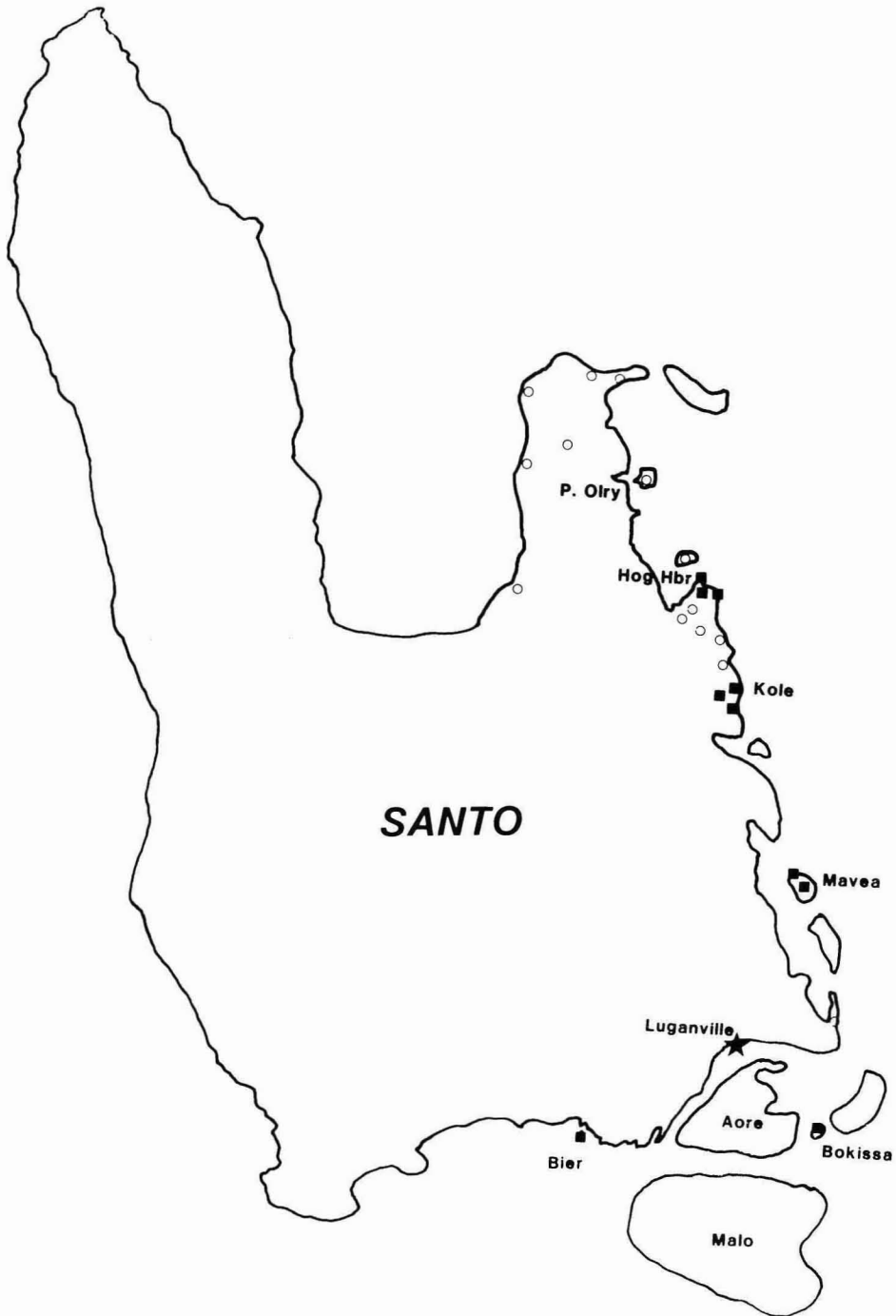


FIGURE 2. Map showing the major study areas on the island of Santo: ■, main sampling areas; ○, sites visited sporadically.

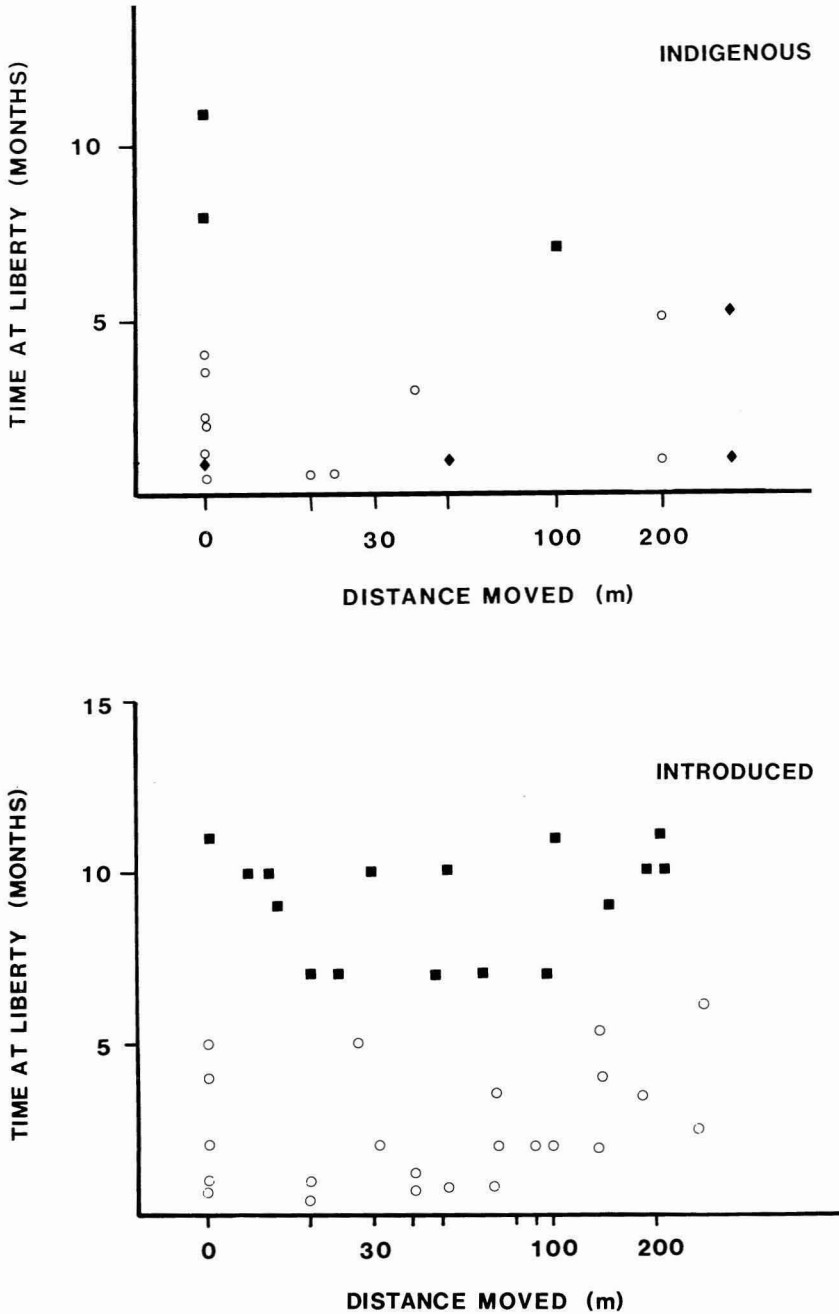


FIGURE 3. Distance between site of first capture and site where crab was recaptured in relation to time interval between marking and recapture. *Top*, indigenous crabs: those found and released at the one site. *Bottom*, introduced crabs: those crabs found in one area and transported to another location (generally to Bier I.). \circ , individuals that had not molted since release; \blacksquare , individuals that had molted; \blacklozenge , radio-tracked animals from the Hog Hbr site.

on eastern Santo) were released at random locations around Bier Island.

After release, day and night searches were made at 1–2-week intervals to locate the position of each radio-tagged crab. A crab (or the tag at least) was considered lost if it could not be found on three consecutive visits.

RESULTS

Mark-Recapture

INDIGENOUS CRABS: Only a small percentage (15%) of all the marked individuals were released on Bier I., yet this population accounted for 60% of the total recaptures. Furthermore, at the sites on Santo, nearly all the recaptures (six of eight) occurred less than 1 month after release. The frequency of recaptures having moved or not from their point of release did not differ significantly between the eastern Santo and islet sites ($P = 0.27$, Fisher's Exact Test). Approximately 50% of recaptures were found at the same location where they were released in both areas (Figure 3, *top*). There was no significant relationship between distance moved and time at liberty ($r = 0.03$, $P > 0.05$). Moreover, two crabs were recaptured at exactly the same place where they had been released, despite the fact that they had molted, which occurs in a different location from the rocky areas where the intermolt crabs are found (Amesbury 1980; Fletcher et al. 1990). There was, however, a significant tendency for larger crabs to move smaller distances than smaller individuals (Figure 4, *top*; $r_s = -0.66$, $P < 0.05$).

Distances covered by crabs that did move from their release site were all less than 300 m. This variable was, however, restricted because at the Bier I. site this distance is greater than the island's diameter, and at the mainland sites the maximum distance between baits was ca. 300 m.

INTRODUCED CRABS: Significantly more of these crabs moved from the point of release than was the case for locally captured crabs (Fisher's Exact Test, $P < 0.05$; Figure 3, *bottom*). There was no relationship between

time at liberty and distance moved for either molted or unmolted crabs, nor was there any relationship between size and distance moved ($r_s < 0.1$, $P \gg 0.05$).

Radio-tracking

Certain difficulties were encountered using radio-tracking techniques in the dense rain-forest environment. The signals from the tags could only be detected in the forest within a radius of 40 m, which was reduced to 20 m if the crab was secreted in a deep crevice. In many cases, therefore, tagged crabs may have been present in the search area but were not detected on every occasion; some individuals apparently disappeared completely after release despite extensive searching (Table 1). These crabs may have moved out of the search area, or the tag may have been removed and destroyed. Alternatively, if tags became detached from the crab while it was in a crevice (but continued to emit a signal that we could locate), we could falsely conclude that the crab was stationary. Particular care was needed, therefore, in the interpretation of the data to allow for these situations.

Nearly all of the radio-tagged crabs that were relocated had moved from their point of release (Table 1). The maximum distance from this release point was, however, related to the crabs' size: smaller crabs moved farther ($r_s = 0.67$, $P < 0.05$). At the Hog Hbr site, only two of the five tagged crabs were recaptured. One had moved to a crevice 50 m from its initial capture site, where it remained for 2 months before moving ca. 250 m to a position in the cliff behind the sampling area. The other crab moved to a similar position on that cliff only 1 week and had effectively disappeared after the third week. The remaining three crabs released at that site were never relocated, and it is probable that they had left the area.

At the Bier I. site, all the crabs released were found again at least once (Table 1). Two stayed at the same location, and they were even recaptured at baits in these same places after their tags were lost. The other crabs were found at a number of locations; these were sometimes on the opposite side of the island

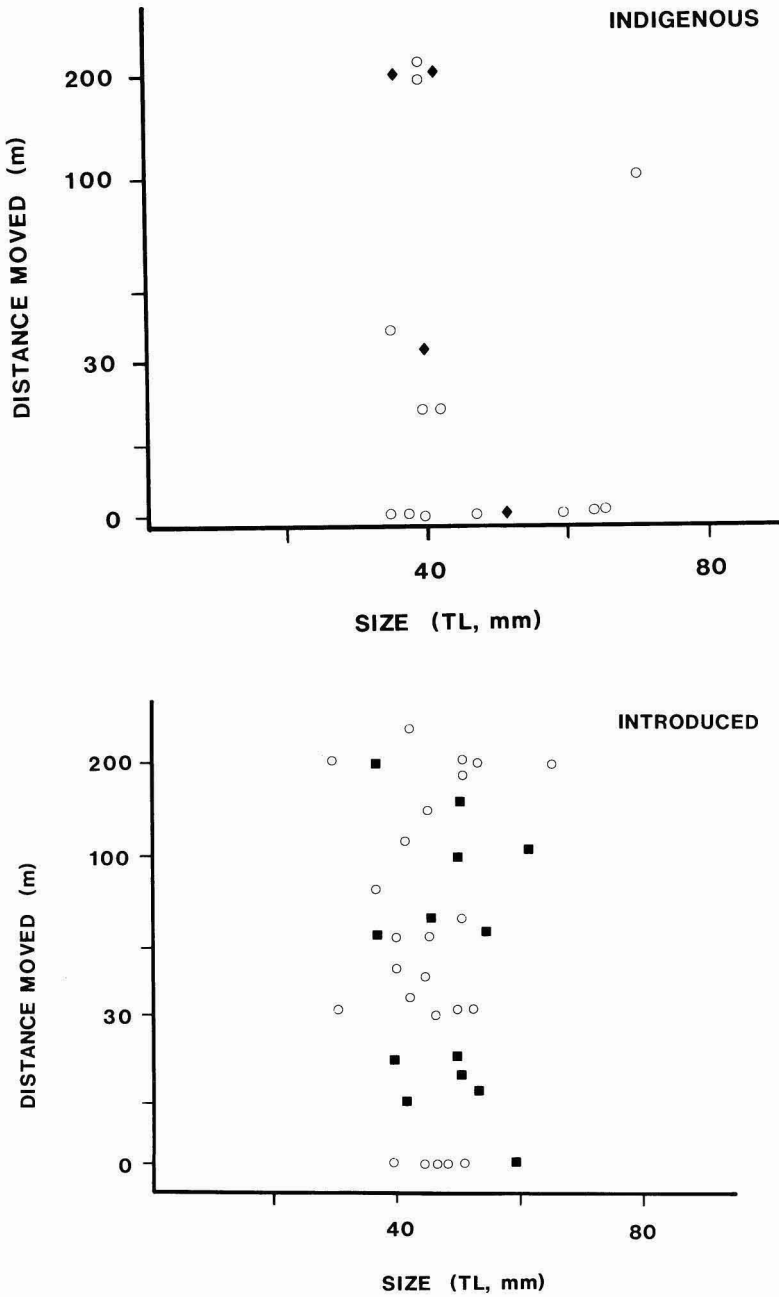


FIGURE 4. Distance moved between release and recapture in relation to size of crab for both indigenous (*top*) and introduced (*bottom*) crabs. TL, thoracic length (mm) of individuals. Symbols as in FIGURE 3.

TABLE I
SUMMARY OF MOVEMENT OF THE RADIO-TAGGED COCONUT CRABS (1987)

FREQ. DIST.	SITE	DATE RELEASED	DATE FOUND	DATE LOST	RECAPTURED WITHOUT TAG	MAX. DIST. MOVED (m)	TOTAL DIST. MOVED (m)
030	HH	13/5	*				
040	HH	13/5	*				
270	HH	16/7	22/7	10/12	—	200	250
290	HH	16/7	*				
100	HH	27/7	10/8	10/9	—	200	200
110	BI	1/5	8/5	#	—	20	20
595	BI	1/5	8/5	#	—	25	25
070	BI	1/5	8/5	9/7	—	35	40
300	BI	1/5	8/5	29/5	—	40	> 80
060	BI	15/5	21/5	5/10	—	200	1,000
280	BI	15/5	21/5	9/7	24/8	150	300
015	BI	25/6	9/7	5/10	—	20	20
160	BI	9/7	15/7	24/8	—	25	25
200	BI	14/7	14/7	5/8	2/9	10	20
050	BI	24/7	5/8	24/8	8/10	4	5
020	BI	24/7	5/8	24/8	—	35	35

NOTE: HH refers to Hog Hbr, BI refers to Bier I., * indicates individual was not found at all after release, # indicates tag probably was not attached to the crab.

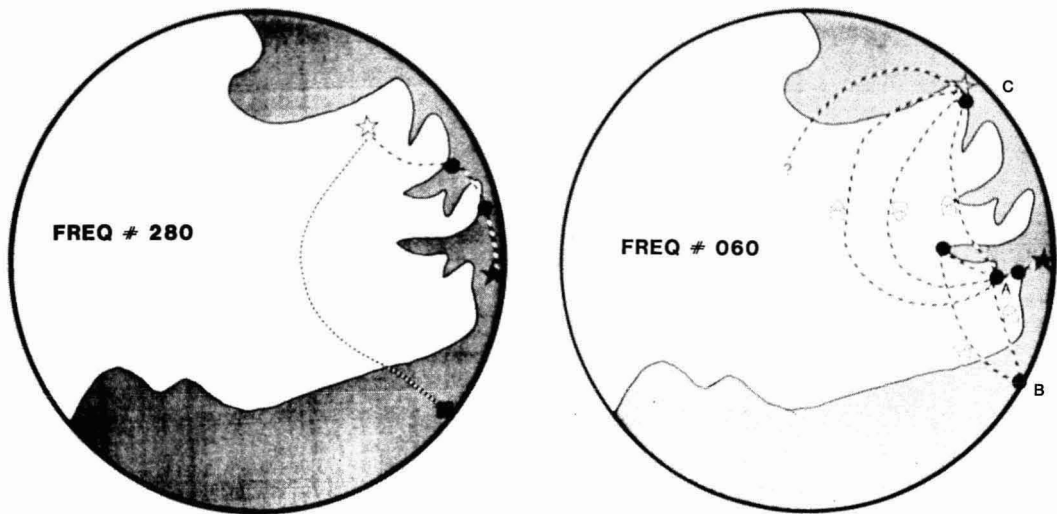


FIGURE 5. Path taken by two crabs with radio frequencies #280 (left) and #060 (right). ★, release point; ●, tracked position; ☆, where crab was last tracked; ■, where crab was found without the tag present. Shaded area indicates region where crevices were abundant.

from where they were located on the previous sampling visit (e.g., #280, Figure 5, left).

One crab (#060) moved to site A after its release, where it stayed for 3 weeks before moving to a crevice 15 m away (Figure 5,

right). It then moved to another location (B) for 10 days before moving back again to site A. It was then found to have moved across the island to a different sheltering site (C), where it remained for 2 weeks before it was

again located back in the original sheltering site (A). It remained there for 2 weeks before finally moving again to site C, where it stayed for 1 month before contact with it was lost. This crab was also found at coconut baits on two occasions during that period, but only at one location (site A).

Two crabs were tracked just 20 and 30 m from the places where they were released to ledges where they apparently remained until the end of the study (>6 months), suggesting that their tags had been dislodged.

Despite numerous searches at various times during the night, only two instances were recorded where crabs were out in the open away from the protection of crevices. On both occasions it was the one crab (#060) that was found less than 10 m from where it had been hiding earlier that day. All the other crabs were in their caves or crevices, suggesting that foraging occurs infrequently.

DISCUSSION

The results of this study show that coconut crabs are definitely able to return to a specific location. This was shown in particular by the movements of one crab that on a number of occasions made use of two specific shelter sites that were a considerable distance apart (>100 m) despite their being a large number of other suitable sites. Such homing ability has been demonstrated by other crustaceans (e.g., lobsters [Chittleborough 1974, Jernakoff 1987]). The fact that crabs were found at the same location even after they had molted (which takes 2–4 months in a different habitat [Fletcher, unpublished data]) indicates that these home bases may be maintained over long periods. Harms (1937) stated that females frequently returned to the same crevice after they had released their larvae even though this was some distance from the water. Helfman (1973), using a convex polygon index (see Jennrich and Turner 1969) and the median value of distances moved at recapture, calculated the radius of the home range for coconut crabs to be about 40 m. Furthermore, at high densities, coconut crabs have highly ritualistic displays when they encounter each

other, especially near food (Helfman 1978). Large crabs sometimes capture and eat smaller individuals. Therefore, being able to relocate the same unoccupied crevice could minimize the risks of cannibalism by reducing the possibility of encountering other crabs.

If coconut crabs are capable of maintaining some kind of home base, it is possible that they do not normally disperse from an area regularly. Many crabs were recaptured (those without radio-tagging) at the same location at which they were released. These results are not, however, too surprising because the proportion of the total area sampled at most sites was small; therefore, crabs that had not moved since release were the individuals most likely to be recaptured. Furthermore, most of the observations were made a relatively short time (<1 month) after release. Consequently, our recapture data are probably biased by coconut crabs that were nonmigratory (at least during that period). Similar results were obtained by Helfman (1973), who found that more than half the individuals recaptured in his study had moved less than 16 m.

In contrast to the recaptures, results from the radio-tagging indicated that most crabs did move away from their point of release, suggesting that dispersal is a common event. This technique also highlighted an additional bias in the recapture data, in that the crabs may regularly move between a number of different areas (in a home range) yet may only be captured at one place. For example, crab #060 was recaptured at baits at the same location, suggesting that the crab had remained at the one site, yet the radio-tracking showed that it had actually moved among a number of sheltering sites during that period.

Most crabs must move away from their crevices periodically to obtain seawater (to maintain osmolality [Gross 1957]) and to undergo molting (Held 1963, Amesbury 1980, Fletcher et al. 1989), and females need to reach the ocean to spawn their eggs (Reese and Kinsie 1968). There needs to be, therefore, a distinction between such "determinate" movement, which could see the individual ultimately returning to the same area, and "random" or migratory movements where an individual leaves an area indefi-

nately. A similar distinction was made by Hill (1978) for three classes of movements made by the crab *Scylla serrata*.

The frequency of foraging movements made by the coconut crabs seemed to be small, as few (< 10%) of the radio-tagged crabs were found out of their crevices on any one night. This is consistent with the percentage of tagged crabs found out on any one night (1–4%), but is much less than that calculated by Helfman (1973) for coconut crabs in Palau (15–75%), although using our criteria (number of marked crabs found/total marked) only 2–8% were found on any one night. By way of comparison, lobsters appear to forage on most nights (Jernakoff 1987), and consequently a very high percentage of tagged animals were observed out of their shelters. The radio-tracking of coconut crabs was, however, mostly done during the dry season, during which the rate of foraging may be reduced.

A control group of undisturbed crabs was lacking because of the logistic impossibility of studying the movement of coconut crabs that had not been caught and tagged. It was, therefore, difficult to determine how representative the results were of the natural situation. It is possible that, as with juvenile lobsters (Chittleborough 1974), the more the crabs are disturbed the more they move. Jernakoff et al. (1987) found this effect to be most pronounced in the first few days after release of tagged lobsters. This may explain why crabs that were introduced to a new area appeared to move farther or more frequently than was exhibited by locally caught individuals, because at least some movement would have been necessary to locate a new, unoccupied sheltering site. We can only speculate about the length of time a crab would normally remain in the one territory. The lack of a correlation between the time at liberty and the distance moved indicates that there is no consistent pattern of movement. Migrations from an area may be triggered by very different stimuli for each individual. Nonetheless, both the radio-tagging and mark-recapture data indicate that smaller crabs are more likely to move than larger crabs, possibly because the larger crabs are dominant in aggressive encounters (Helfman 1978).

The low rates of recaptures indicate that most of the marked individuals left the study area. This was in spite of the low density of crabs in these regions (generally < 1 crab per 27 m²). We observed no concomitant decline in catch rates at sites that were not exploited by collectors, so at least some immigration of crabs must have been occurring to replace those individuals that had left the area after marking. Helfman (1973) concluded that coconut crabs were nomadic, but were capable of establishing temporary residence in one area and remaining there if conditions were favorable. Irrespective of whether the movement of marked crabs found in this study is normal or merely a handling effect, it is clear that mark-recapture studies with coconut crabs will only be successful in areas where most of the crabs can be marked or the entire area can be searched, such as small islands. Consequently, in most locations we have been forced to use relative measures of density, for example Catch Per Unit Effort indices, to estimate stock abundance.

ACKNOWLEDGMENTS

We are grateful to the Fisheries Department, Republic of Vanuatu, for their support in this project, and special thanks are given to Alsen Obed and C. Schiller for help throughout the project and to S. Blight for preparing the figures. Comments from two anonymous referees improved the paper substantially.

LITERATURE CITED

- AMESBURY, S. S. 1980. Biological studies on the coconut crab (*Birgus latro*) in the Marianas Islands. Univ. Guam Mar. Lab. Tech. Rep. 66.
- BEGON, M. 1980. Investigating animal abundance: Capture-recapture for biologists. University Park Press, Baltimore.
- CHITTLEBOROUGH, R. G. 1974. Home range, homing, and dominance in juvenile western rock lobsters. Aust. J. Mar. Freshwater Res. 25:227–234.
- FLETCHER, W. J., I. W. BROWN, and D. R.

- FIELDER. 1990. Growth of the coconut crab *Birgus latro* in Vanuatu. *J. Exp. Mar. Biol. Ecol.* (in press).
- FLETCHER, W. J., D. R. FIELDER, and I. W. BROWN. 1989. A comparison of freeze and heat branding methods to mark the coconut crab *Birgus latro* (Crustacea, Anomura). *J. Exp. Mar. Biol. Ecol.* 127:245-251.
- GROSS, W. J. 1957. An analysis of response to osmotic stress in selected decapod Crustacea. *Biol. Bull. (Woods Hole, Mass.)* 112: 43-62.
- HARMS, J. W. 1937. Lebensableuf und Strammesgeschichte des *Birgus latro* L. von der Weihnachtsinsel. *Z. Naturwiss. (Jena)* 71: 1-34.
- HELD, E. E. 1963. Moulting behavior of *Birgus latro*. *Nature (London)* 200:799-800.
- HELFMAN, E. 1973. Ecology and behaviour of the coconut crab, *Birgus latro* (L.) M.S. thesis, University of Hawaii, Honolulu.
- . 1978. Agonistic behaviour of the coconut crab, *Birgus latro*. *Z. Tierpsychol.* 43:425-438.
- HILL, B. 1978. Activity, track and speed of movement of the crab *Scylla serrata* in an estuary. *Mar. Biol.* 47:135-141.
- JENNRICH, R. I. and F. B. TURNER. 1969. Measurement of non-circular home range. *J. Theor. Biol.* 22:227-237.
- JERNAKOFF, P. 1987. Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. *J. Exp. Mar. Biol. Ecol.* 113:125-144.
- JERNAKOFF, P., B. F. PHILLIPS, and R. A. MALLER. 1987. A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. *J. Exp. Mar. Biol. Ecol.* 113:9-21.
- MALLET, J., J. T. LONGINO, D. MURAWSKI, A. MURAWSKI, and A. S. DE GAMBOA. 1987. Handling effects in *Heliconius*: Where do all the butterflies go? *J. Anim. Ecol.* 56: 377-386.
- MORGAN, G. R. 1977. Locomotor activity in the western rock lobster *Panulirus longipes cygnus*. *Aust. J. Mar. Freshwater Res.* 29: 169-174.
- REESE, E. S. and R. A. KINSIE. 1968. The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridae). *Crustaceana Suppl. (Leiden)* 2:117-144.
- REYNE, A. 1939. On the food habits of the coconut crab (*Birgus latro* L.) with notes on its distribution. *Arch. Neer. Zool.* 3:282-320.