Sex Differences in Activity and Movements in the Pig-Nosed Turtle, *Carettochelys insculpta,* in the Wet-Dry Tropics of Australia

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Dry season movement patterns, home ranges, and activity was studied in a population of pig-nosed turtles (*Carettochelys insculpta*) in the wet-dry tropics of northern Australia. Compared to other turtles inhabiting lotic habitats, *C. insculpta* occupied considerably larger home ranges, covering up to 10 km of river. Of previously published factors influencing home range size, low productivity of the (micro) habitat may best explain the extensive home ranges in *C. insculpta.* Patchiness and low nutrient value of the chief food (aquatic vegetation) of *C. insculpta* may force turtles to cover large expanses of river to acquire sufficient energy for growth and reproduction. Females were more active, moved farther, and occupied larger home ranges than males. Home ranges of females comprised 1–4 activity centers, many of which were associated with thermal springs. We suggest that females may exhibit increased activity and movements relative to males because of sexual inequality in parental investment, where food is particularly limiting (e.g., in species with biennial reproduction). Biennial reproduction in the population allowed the examination of the influence of reproductive condition on home range size, movements, and activity. Reproductive condition did not influence home range or activity, but gravid turtles moved father between successive sightings than nongravid females. Individual data corroborate these findings, with females moving farther between successive sightings while gravid compared to while spent. Contrary to previous reports, turtles did not appear to move into estuarine areas or lowland floodplains during the wet season but moved into the riparian forest and possibly into wetlands adjacent to the main channel in the vicinity of their dry season home ranges.

KNOWLEDGE of movement patterns of animals is fundamental to understanding their life histories (Swingland and Greenwood, 1983; Gregory et al., 1987). Numerous studies have linked movements with functions such as food acquisition, aestivation, and reproduction, each of which influences lifetime reproductive success. In aquatic turtles, movements often differ between the sexes (e.g., MacCulloch and Secoy, 1983; Pluto and Bellis, 1988; but see Carter et al., 2000). Possible reasons include sex-related differences in habitat use (Plummer and Shirer, 1975; Plummer, 1977; Craig, 1992), or diet (reviewed in Lindeman, 2000), or differential reproductive strategies (e.g., nesting movements, Moll and Legler, 1971; Obbard and Brooks, 1980).

Morreale et al. (1984) generated a conceptual model termed the ''reproductive strategies hypothesis'' to explain differential movement and activity between the sexes. The model, which derives support from studies of aquatic turtles (Brown and Brooks, 1993; Jones, 1996; Thomas et al., 1999), predicts that (1) during the mating season, activity and movement should be greater in males than females, and (2) during the nesting season, activity and movement of females should equal or exceed that of males. Assumptions underlying the predictions are (1) males are more active to increase their chances of mating, (2) males move farther to increase their opportunities for multiple matings, (3) food resources used are similar between the sexes, and (4) during nesting, females make excursions associated with finding nest sites.

Although direct evidence is lacking for assumptions 1 and 2, most studies have shown that males tend to move farther than females (reviewed in Gibbons, 1986, Gibbons et al., 1990; Tuberville et al., 1996). Also, these assumptions are consistent with current theory (Trivers, 1972; Maynard Smith, 1978; Andersson, 1994). Assumption 3 is upheld in some species (Moll and Legler, 1971; Hart, 1983) but not others (Plummer and Farrar, 1981; Lindeman, 2000).

In most studies that have addressed assumption 4 (reviewed in Gibbons, 1986; Congdon et al., 1987), reasons for the difference in movements between the sexes cannot be readily identified (e.g., Thomas et al., 1999). Most turtles mate in spring and autumn (Gregory, 1982; Ernst et al., 1994), yet many nest in summer (reviewed in Ernst et al., 1994). Differences in movement and activity between the sexes, ac-

companied by seasonal changes in female movements associated with nesting are indicative but potentially confounded. Females may be moving more in agreement with assumption 4, or males may be moving less because females are unreceptive to mating at this time (Thomas et al., 1999). An unequivocal test of the idea that differential movements or activity between the sexes is a result of females searching for a nesting area would require a comparative study of the movements among males, gravid females, and nongravid adult females (e.g., a species exhibiting biennial reproduction). Comparison of the movements between gravid and nongravid adult females is less likely to be confounded than comparing males to females (Shine, 1980; Schwartzkopf, 1993).

In this study, we examine dry season movement patterns, home ranges, and activity in a population of pig-nosed turtles (*Carettochelys insculpta*) in the Daly River of tropical northern Australia. We used radio-telemetry to test the hypotheses that sex and reproductive condition influence home range size, movements, and activity of *C. insculpta* in ways predicted by the reproductive strategies hypothesis of Morreale et al. (1984). This species is ideal for such a study because it exhibits biennial reproduction, with approximately half of the adult females reproducing each year (unpubl. data), enabling a comparison between gravid and nongravid adult females. We also consider influences on home range size and compare our findings to those of other turtles and, in particular, species inhabiting lotic habitats. Finally, we examine a species-specific idea that Australian *C. insculpta* move into the lower estuarine floodplains during the wet season (Heaphy, 1990).

MATERIALS AND METHODS

We studied *C. insculpta* along an 11-km stretch of the Daly River near Oolloo Crossing (14°04′40″S, 131°15′00″E) in the Northern Territory, Australia, during the dry season (August to November) in 1996 and again during a single fly-over during the wet season of 1996–1997. The climate is typical of the wet-dry tropics of northern Australia (Taylor and Tulloch, 1985) with a mean monthly rainfall less than 7 mm from May to September, rising to a peak monthly average of 284 mm in February (Stn 014139/014941, Oolloo, 1962–1985). The river averaged approximately 50 m across and approximately 1.5 m in depth (deepest holes are up to 4 m deep). Secchi disk clarity was 1–4 m during the dry season but only a few centimeters during the wet season. Substrate was largely bedrock

and sand, and flow was moderate during the dry season.

Turtles were captured during the day with dipnets from a boat, and their sex was determined by inspection of tail length. Each turtle was fitted with a numbered cattle ear tag on the rear edge of the carapace. Cattle ear tags allowed identification from the boat without recapture (numbers can be read without capture). Curved carapace length (CL) and plastron length (PL) was measured to the nearest 0.1 cm with a tape and calipers. Females were x-rayed for the presence of shelled eggs using a portable x-ray machine (ExcelRay®). Radiographs were developed in a makeshift darkroom in the field.

Twenty turtles were fitted with radio-transmitters (Sirtrack®). Of these, eight were females subsequently found to be gravid, seven were females that failed to reproduce in that season ("nongravid" females), and five were males. Transmitters were mounted on aluminum plates (2.5 cm × 8 cm × 2 mm thick), and the unit was attached to the rear carapacial edge with surgical stainless-steel bolts, opposite the cattle ear tag. Bolts were fitted to two holes drilled through the edge of the marginal scutes. Wetsuit foam was used as a buffer between the transmitter mounting plates and the soft skin.

Turtles were released at the point of capture within 24 h. Markers were placed every 200 m for the 11-km stretch to facilitate the location of sightings. Locations of turtles were noted to the nearest 10 m by visual estimation of distance to markers.

Turtles were radio-tracked (Teleonics® TR4 receiver and Yagi antenna) by boat six days per week between 10 August and 1 December, 1996. This period included the nesting period (27 August to 30 September) and a post-nesting period (1 October to 29 November). Most (>95%) observations were made during the day. In most cases, we were able to see telemetered turtles. Date, time, location, microhabitat, activity, and depth were recorded with each fix. Turtles were scored as "active" if first observed swimming or crawling along the river bottom, or "inactive" if first seen sitting motionless on the river bottom (in association with logjams or other cover). Although this doubtless resulted in some error in assessing activity, the error would be expected to be similar between sexes. Microhabitat categories were ribbonweed bed (*Vallisneria* sp.), open sand flat, open rock flat, isolated log on sand/rock, and logjam. Ribbonweed is the primary dietary item of *C. insculpta* in the Daly River during the dry season (Heaphy, 1990; Welsh, 1999). Turtles were scored as using an

isolated log when part of the shell was under the log. Logjams were two or more abutting logs. Depth was estimated to the nearest 0.3 m using a metered weighted line.

Linear home range was defined for each turtle as the range spanned between the farthest upstream and downstream locations (Plummer et al., 1997). The 95th percentile was then taken to decrease sensitivity to outliers. Home range area was calculated by multiplying linear home range by the average width of the river in the study area (50 m). Turtle observations were plotted against location to examine relative dispersion and to identify centers of activity. We hypothesized that three types of resources could explain clumped distributions (food = ribbonweed beds, nesting habitat = beaches, and thermoregulation sites = thermal springs). Therefore, we mapped activity centers against locations of these resources.

We also calculated mean distance moved as the linear distance between successive sightings for each fix. This served as an estimate of distance per move. We did not adjust for time between sightings because most turtles were sighted each day.

To examine where turtles spent the wet season when the Daly overflows its banks, we radio-tracked the 20 turtles from a low-flying airplane equipped with a Global Positioning System. The flyover was made on 5 February when the river was at approximately 8 m above typical dry season river levels. The river had been in continuous flood beginning in late December and had reached a peak level of 18 m above normal dry season level on 5 January.

Among individuals, single-factor analysis of variance and analysis of covariance was used to determine the effects of body size, reproductive condition, and sex on home range size, movements, and number of beaches within a home range. Within individuals, we used paired *t*-tests to determine differences in home range, movements, and activity between the time females were gravid and the time females were spent (after eggs laid). All turtles were considered to have laid eggs by 15 October. This date is based on daily nest surveys conducted in a concurrent study on nest site choice (unpubl. data). We examined the independence of microhabitat use, activity, and sex by contingency table analysis. Assumptions of parametric tests were tested prior to analyses, and a 0.05 level of significance was used. Means are presented with their standard deviations, unless otherwise specified.

RESULTS

Home range size, movements, and activity.—Individual variation in number of fixes and home range size, movements, and activity are listed in Table 1. Asymptotes of change in linear home range size against number of fixes indicated that, on average, 24 fixes (observations) were needed for estimating linear home range size. After individuals with fewer than 24 observations had been discarded, the number of observations per individual did not influence linear home range size ($r^2 = 0.15$, $F_{1,17} = 2.90$, $P = 0.11$).

Linear home range size did not differ significantly between gravid and nongravid adult females (Table 2): thus, the two classes were pooled for comparing the sexes. Females had significantly longer linear home ranges than males (Table 2). Consequently, home range area was also larger in females (mean = 43.7 ± 17.27 ha, $n = 13$) than in males (mean = 16.2 ± 6.58 ha, $n = 5$). Mean differences in linear home range size were influenced by sex, over and above the effects of carapace length (ANCOVA, $F_{1,15} = 6.20$, $P = 0.025$). Males, but not females, had significantly larger linear home ranges while females were gravid, compared to when reproductive females were spent (Table 3). Linear home range size of females remained larger than that of males during the two months after the nesting season, although the difference only approached significance ($F_{1,13} = 4.42$, $P = 0.057$). Home range overlap, defined as the proportion of all turtles sharing a particular stretch of river with a given turtle, was high in both females (96.8 %) and males (84.6 %).

Gravid females moved farther between sightings, on average, than nongravid females, but the difference was not significant (Table 2). Although distance moved between sightings did not differ significantly between males and females, the difference approached significance, and on average females moved more than twice as far between sightings than males (Table 2). Both males and females covered longer distances between sightings while females were gravid than when females were spent (Table 3). Females continued to cover greater mean distances than males during the two months following nesting (females 334 ± 181.0 m; males 166 ± 58.8 m), although the difference only approached significance ($F_{1,14} = 4.67$, $P = 0.067$).

Females were more active than males during the day, when the majority of observations were made (Table 2). Activity was independent of reproductive condition among females (Table 2). In three cases with sufficient temporal data, there was no difference in activity of females while gravid, compared to when spent (Table 3). Males, but not females, were significantly more active when females were gravid, com-

TABLE 1. DESCRIPTIVE DATA FOR INDIVIDUAL *Carettochelys insculpta* OBTAINED BY RADIO-TELEMETRY. Distance data are means ± 1 SD. Sample sizes are in parentheses when not equal to number of fixes. Data are not included for F01 and F54 because of low number of fixes. Activity (%) is defined as the proportion of point locations in which turtles were "active" (see Materials and Methods). CL = carapace length, n/a = not applicable.

Turtle #	Sex	CL (cm)	Reproductive condition	# fixes	Linear home range (m)	Distance per move (m)	Activity (%)
F01	f	44.6	nongravid	11	—	—	—
F02	f	42.0	nongravid	95	7950	329.5 ± 830.05	76 (62)
F03	f	41.4	nongravid	51	6540	324.3 ± 759.10	75 (32)
F04	f	43.6	nongravid	72	7810	391.0 ± 527.55	72 (53)
F05	f	42.4	gravid	99	9850	228.0 ± 279.68	64 (78)
F07	f	46.2	gravid	19	5870	489.0 ± 868.82	71 (7)
F08	f	43.0	gravid	91	7405	523.4 ± 1019.72	61 (76)
F12	f	44.6	gravid	61	13890	1031.5 ± 1707.11	26 (35)
F16	f	43.6	gravid	29	12630	1452.1 ± 1879.04	35 (20)
F40	f	44.4	gravid	52	2450	249.0 ± 460.73	62 (34)
F54	f	44.5	nongravid	11	—	—	—
F64	f	40.9	gravid	31	9600	1297.3 ± 2370.78	53 (17)
F65	f	42.6	nongravid	102	8460	672.7 ± 1147.30	70 (69)
F67	f	40.2	gravid	100	7280	775.3 ± 1324.20	74 (72)
F69	f	44.5	nongravid	99	8250	463.0 ± 1052.73	74 (68)
M08	m	37.8	n/a	91	3955	259.2 ± 449.47	18 (79)
M52	m	37.5	n/a	89	3800	276.0 ± 434.16	61 (74)
M56	m	40.1	n/a	94	2185	212.4 ± 362.67	24 (80)
M62	m	40.1	n/a	96	4680	403.4 ± 658.59	10 (79)
M63	m	39.4	n/a	98	1535	210.0 ± 233.76	24 (84)

pared to when females were spent (Table 3). Greater activity in females persisted during the two months after the nesting season ($X^2 = 39.82$, df = 1, $P < 0.001$)

Activity centers and microhabitat use.—Pooled observations (point locations) for all radio-tracked turtles are compared to the locations of nesting beaches, ribbonweed beds, and thermal springs in Figure 1. Clustering was evident around thermal spring locations but may also be related to nesting beaches (Fig. 1). Most individual females had 1–4 discrete activity centers (areas with frequent usage), whereas males generally displayed one normally distributed activity center (Fig. 2).

Microhabitats occupied by males and females are shown in Figure 3. The major difference between sexes was the greater tendency for females to use open sand flats and for males to use isolated logs on sand/rock ($X^2 = 27.36$, df = 1, $P < 0.001$). In all observations, isolated logs were found at shallower depths than sand flats ($F_{1,630} = 3.86$, $P < 0.001$). The type of microhabitat used by females was independent of reproductive condition ($X^2 = 1.05$, df = 1, $P =$

TABLE 2. HOME RANGE SIZE, MOVEMENTS, AND ACTIVITY OF MALE AND FEMALE *Carettochelys insculpta*. Data are means ± 1 SD, or significance determined by ANOVA for home range and movements, or contingency analysis for activity. Numbers of animals are in parentheses.

Group	Linear home range length (km)	Distance per move (m)	Activity (%)
All females	8.3 ± 2.88 (13)	632.8 ± 399.16 (13)	67 ± 15.8 (13)
Gravid females	8.6 ± 3.69 (8)	755.7 ± 465.23 (8)	56 ± 20.9 (4)
Nongravid females	7.8 ± 0.75 (5)	436.1 ± 143.70 (5)	73 ± 2.4 (5)
Males	3.2 ± 1.32 (5)	272.2 ± 78.8 (5)	26 ± 8.9 (5)
Females vs males	$F_{1,18} = 4.49$, $P = 0.002**$	$F_{1,18} = 4.49$, $P = 0.066$	$\chi^2 = 33.79$, $P < 0.001***$
Gravid vs nongravid females	$F_{1,18} = 4.84$, $P = 0.638$	$F_{1,13} = 4.84$, $P = 0.169$	$\chi^2 = 2.26$, $P = 0.133$

TABLE 3. INFLUENCE OF FEMALE REPRODUCTIVE CONDITION ON HOME RANGE SIZE, MOVEMENTS, AND ACTIVITY OF MALE AND REPRODUCING FEMALE *Carettochelys insculpta*. Data are means ± 1 SD.

Variable	While females gravid	While females spent	n	Significance
Linear home range length (m)				
Females	5252 ± 2705.6	5561 ± 2965.4	4	$t = -0.725, P = 0.260$
Males	3052 ± 1239.3	1287 ± 824.8	5	$t = 3.117, P = 0.018$*
Distance per move (m)				
Females	715 ± 447.9	411 ± 200.2	5	$t = 2.655, P = 0.028$*
Males	464 ± 188.1	166 ± 58.8	5	$t = 3.494, P = 0.013$*
Activity (% active)				
Females	64.8 ± 11.92	68.5 ± 4.06	3	$t = -0.576, P = 0.312$
Males	32.2 ± 22.87	25.0 ± 18.68	5	$t = 2.395, P = 0.037$*

0.90). A three-way contingency analysis revealed that the difference in microhabitat use (open sand flat vs isolated log) between the sexes was not independent of activity ($X^2 = 12.72$, Mantel-Haenszel = 3.76, df = 2, $P < 0.001$).

Mean depth at the time of observations did not differ significantly between gravid and non-gravid females ($F_{1,650} = 3.86$, $P = 0.08$); thus, data were pooled for comparisons between sexes. Females were observed in deeper water than males (females = 1.47 ± 0.685 m, range = 0.2–4.0 m; males = 0.91 ± 0.470 m, range = 0.2–3.0 m; $F_{1,1018} = 3.85$, $P < 0.001$).

Movements associated with nesting.—Seven gravid females were linked to their nesting locations. Most turtles (87.5%) nested within the area they occupied 95% of the time (i.e., their home range). The exception was the second nest of F08, who was linked to both of her nests for the

year (Fig. 4). To lay her second nest, she apparently made a movement of 6 km, returning two days later to the area she had occupied prior to the foray (Fig. 4). Of 12 nesting events by 10 turtles with sufficient movement data ($n > 24$ fixes, Table 1), seven made upstream move-
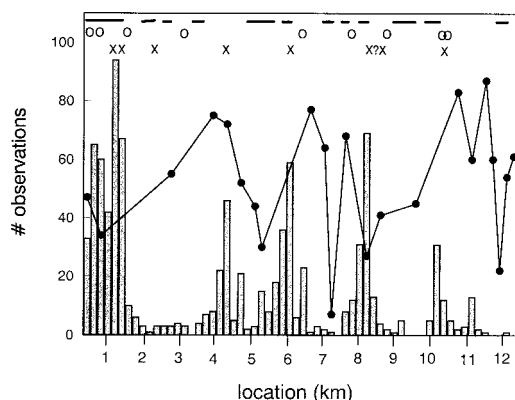

Fig. 1. Combined observations or activity centers of female *Carettochelys insculpta*, showing locations of thermal springs (X), dense ribbonweed beds (-), and nesting beaches (O). Each column bar represents a 200 m stretch of river.
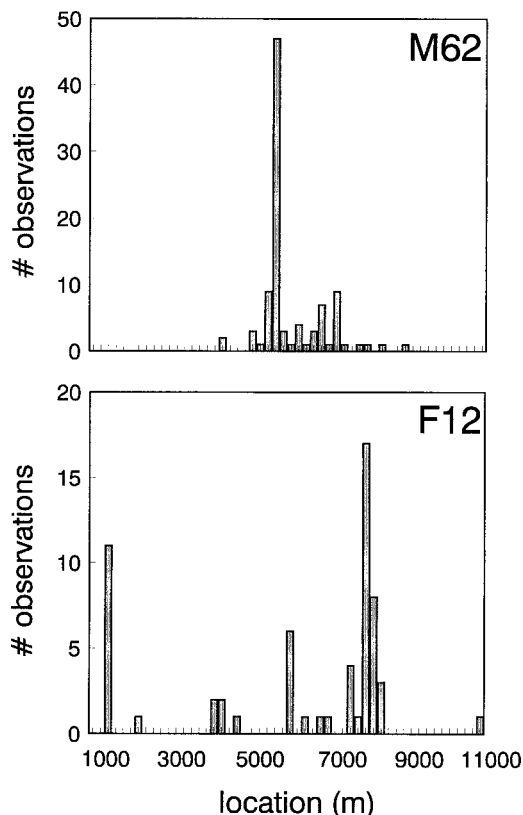

Fig. 2. Typical examples of dry season activity centers for individual male (M62) and female (F12) *Carettochelys insculpta*, showing larger home range and greater number of activity centers in females.
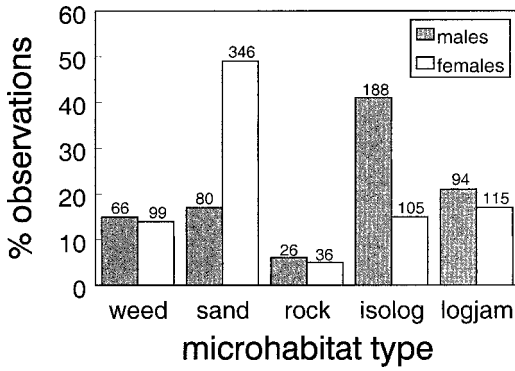
Fig. 3. Influence of sex on microhabitat use by *Carettochelys insculpta*: weed = ribbonweed bed (*Vallisneria spiralis*), sand = sand flat, rock = rock flat, isolog = isolated log. Numbers of observations are shown above each column.

ments just before nesting, one moved downstream, two did not move (>200 m), and two moved in both directions just before nesting.

The number of nesting beaches within a home range (defined as beaches used that year
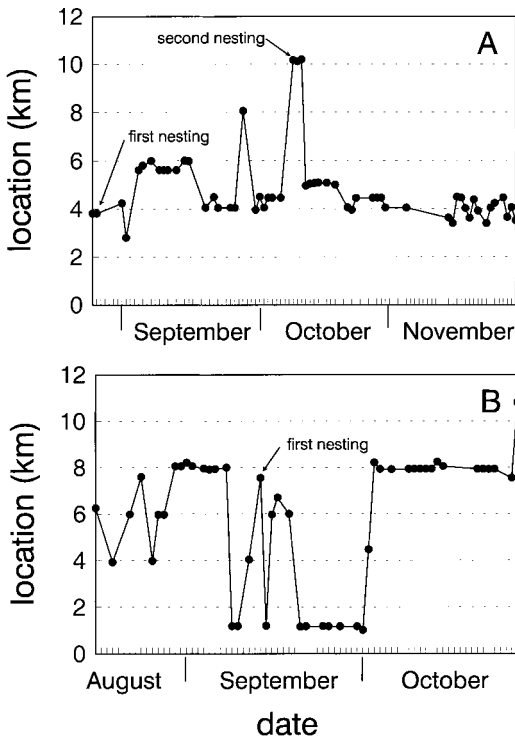

Fig. 4. Examples of sequential movements of two individual *Carettochelys insculpta*, showing nesting events (A, B) and fidelity to thermal springs (B) at the one and eight kilometer marks. Each dot represents a point location.
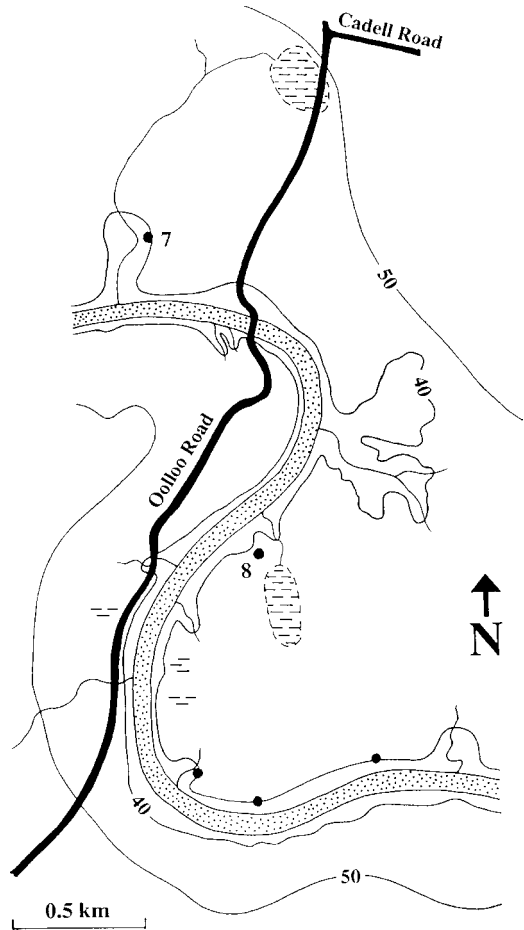

Fig. 5. Point locations of 18 *Carettochelys insculpta* during the wet season when the Daly River (stippled area) was in flood. ● indicates a turtle location or a group of seven or eight turtles. Note that two groups of turtles were near billabongs (surrounded by dashed lines), which become connected to the river during severe flooding. Numbered lines are contours.

by nesting turtles) did not differ between gravid and nongravid females ($F_{1,14} = 1.24$, $P = 0.28$). As expected due to range size, males had fewer beaches (1.4 ± 0.98 SD, range = 0–3, $n = 5$ turtles) within their home ranges than females (4.9 ± 1.57 SD, range = 2–7, $n = 15$).

Wet season locations.—Wet season locations, determined from the air in the fly-over on 5 February, 1997, were out of the main river channel (Fig. 5). The river was in flood on this day (fast flow and high) but was generally within its outer banks (<12 m, Fig. 6). Of the 18 turtles for which a signal was received, most were in two groups consisting of seven and eight turtles (Fig. 5). Both of these two groups were near
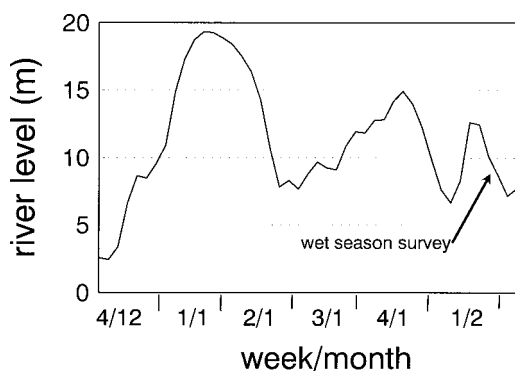
Fig. 6. Flood levels during the study (1996) at Dorisvale Crossing, near the study area. The arrow represents the flood level when the aerial survey was conducted.

billabongs. Eight turtles appeared to be associated with small creeks within 300 m of the river (Fig. 5). These creeks, which are dry during the dry season were in flood on 5 February according to river stage data. Turtles not associated with creeks appeared to occupy the flooded riparian zone within 200 m of the dry season river boundary.

During the wet season fly-over, all turtles were found either within ($n = 4$) or downstream of ($n = 14$) their dry season home range. Turtles downstream averaged 1.8 ± 1.70 km from the closest point of their dry season home range (range = 1.0–6.4 km). The turtles that were found within their dry season home range comprised three (previously) gravid females and one male. All transmitters fell off the turtles (by necrosis of the marginal bones) by April 1997 and were retrieved. Of the 18 transmitters recovered, 82% were found within the respective dry season home range of each turtle. Most transmitters ($n = 12$) were found in riparian forest out of the main channel, 15–39 m from the river's edge during the dry season. Five were found in the channel, two were found within a few meters of the river, and one was found in a creek 60 m from the river. One male died and was recovered, along with its transmitter, in riparian forest 45 m from the river. No other mortality was observed during the study.

Long-term site fidelity.—Of 150 *C. insculpta* marked in the study area in 1986–1988 by Heaphy (1990), 104 (69%) were recaptured during 1996–1998. The study area of the present study encompassed that of Heaphy (1990).

DISCUSSION

Sex differences and their significance.—In turtles, home range size, movements, and activity often differ between the sexes (Morreale et al., 1984). Most studies have found that movement and activity are greater in males than females (e.g., Pluto and Bellis, 1988; Rowe and Moll, 1991), whereas some studies have found the reverse (e.g., Gordon and MacCulloch, 1980; Ross and Anderson, 1990; Bodie and Semlitsch, 2000), and a few found no difference (e.g., Kramer, 1995; Jones, 1996; Carter et al., 2000). Current theory and available data on turtles suggest that differences in movement patterns and activity biased toward females can be explained by nesting excursions of those females (Morreale et al., 1984; but see Dodd, 1989). Although this pattern is sometimes obvious, as when females make abrupt movements just before nesting and then return, an unequivocal test of this prediction requires simultaneous comparison of movements and activity between gravid and nongravid females.

In the present study, females were more active, moved farther, and occupied home ranges twice the size of that of males (Table 2). These differences are not likely to be attributable to food type, because dry season food types do not differ between the sexes (Heaphy, 1990; Welsh, 1999). This assumption 3 of the reproductive strategies hypothesis (Morreale et al., 1984) is upheld, allowing us to address the model's predictions.

The model predicts that during the nesting season (first half of the study period, i.e., late August through to mid-October) females should equal or exceed males in activity, movements, and home range size, based on the assumption that females make excursions associated with choosing a nest site (Morreale et al., 1984). Several studies convincingly support this prediction (Ernst, 1970; Moll and Legler, 1971; Pluto and Bellis, 1988). However, our study found that gravid females did not differ significantly from nongravid females in home range size or activity (Table 2). Further, reproductive females did not possess larger home ranges while gravid compared to while spent, and the transition from gravid to spent was not associated to a difference in activity (Table 3). Consistent with this finding is the observation that gravid females generally nested within areas they already occupied; only one individual nested outside the area it otherwise occupied (Fig. 4). Finally, greater home range size, movements, and activity in females, relative to males, persisted after nesting was complete. Collectively, these results indicate that some factor other than nesting excursions must explain the differences between sexes in activity and movements in *C. insculpta*.

In theory, the difference between sexes could also be explained by males moving less during the nesting season, because females might not be receptive to mating (Morreale et al., 1984; Jones, 1996). Such data are difficult to obtain for turtles, but most mating activity reported occurs in spring and autumn (Gregory, 1982; Ernst et al., 1994). However, male *C. insculpta* actually had larger home ranges and moved farther (and thus were probably more active) while females were gravid than they did while females were spent (Table 3). We observed male *C. insculpta* accompanying gravid females near beaches at night during the nesting season, and in some cases males emerged from the water and nuzzled the sand where females had emerged. This is in contrast with male *Graptemys flavimaculata*, which were more sedentary during nesting (summer) than in autumn (Jones, 1996). Such differences may reflect variation in the chronology of mating. Timing of mating is unknown in *C. insculpta*, although there have been unconfirmed observations of mating in June and July (Heaphy, 1990). Nongravid females may be receptive during nesting in contrast to gravid females, and males may not be able to discriminate between the two female types. Or, females may become receptive just after laying.

An alternative hypothesis is that sexual size dimorphism accounts for the movement and activity differences (e.g., Schubauer et al., 1990). In the Daly River, female *C. insculpta* are approximately 50% larger than males (unpubl. data). However, ANCOVA indicated that home range size was influenced by sex, over and above any effect of body size. In general, vertebrates exhibit larger home ranges with larger body size, although this conclusion is largely based on across-species comparisons (Mace et al., 1983).

One possible explanation for the differences between males and females in activity and movements is related to energy acquisition. The study population exhibits biennial reproduction, with ca. half of females reproducing each year (unpubl. data). Assuming biennial reproduction in the population reflects a limiting food resource (Bull and Shine, 1979), females may need to maximize their time feeding relative to males, resulting in increased activity, movements, and larger home ranges. In this way, differences in activity and movements between the sexes would reflect sexual inequality in parental investment involved with gamete formation (Trivers, 1972; Andersson, 1994). Among adult female vertebrates, home range area is related to access to food, with the quality and density of food, coupled with the animal's energy requirements, being the major factors determining home range size (Mace et al., 1983).

If our hypothesis is validated by future work, an additional assumption should be included in the reproductive strategies model: that food (type, nutritional value, or abundance) is not particularly limiting to a measurable extent in reproductive output (e.g., biennial reproduction). This idea would be pertinent to turtles in general, because sex differences in movements and activity are not limited to aquatic species (e.g., Lue and Chen, 1999). A caveat, however, is that riverine turtles are habitat-constrained, having only two directions in which to forage. Confirmation of this phenomenon in *C. insculpta* would need to include (1) experimental evidence for phenotypic plasticity in clutch frequency (e.g., supplemental feeding), (2) a better understanding of the putative link between movement patterns and food availability, and (3) determination of activity patterns between sexes during the night. Our observations were biased toward daytime: males may have increased their activity during the night, relative to females. Turtles in the population are known to be active at night (Heaphy, 1990, pers. obs.).

Comparisons with other aquatic turtles.—*Carettochelys insculpta* occupied considerably larger home ranges than those reported for other lotic turtle species. Plummer et al. (1997) reviewed home range size for lotic turtles species, finding that most have home range areas of 0.5–4.0 ha, the maximum home range area being 11.6 ha (*Apalone mutica*). This figure is one-third of the mean home range calculated for *C. insculpta* (36 ha). The method could overestimate home range area in species that use one side of a large river (Plummer et al., 1997), because home range area was calculated by multiplying linear home range by width of stream. However, linear home range in *C. insculpta* (7.2 km) was also five times longer than the longest home range previously known (1.6 km, *Graptemys flavimaculata*, Jones, 1996). Further, stream width in the present study was approximately 50 m, and turtles were seen moving across the river in <1 min. Thus, we are not likely to have overestimated home range area in the present study using this method.

Plummer et al. (1997) also reviewed factors influencing home range size in turtles, citing body size, sex, reproductive condition, season, habitat productivity, habitat type, stream size, and methods. Which of these factors might explain the unusually large home ranges of *C. insculpta*? Although interspecific comparisons are

potentially confounded (e.g., by site, year, latitude), we can examine the apparent fit of these factors to home range size in *C. insculpta*.

At 5–11 kg and 37–45 cm carapace length (CL), Daly River *C. insculpta* are heavier and longer than most lotic species examined by Plummer et al. (1997). However, *C. insculpta* ranks near *Chelydra serpentina* in mass, and near *Apalone spinifera* in CL. Body size alone, therefore, cannot explain the extensive home ranges found in the present study. Although season may have influenced home range size in our study, we restrict our comparisons to dry season data, because we only tracked turtles once in the wet season. Stream size cannot explain the unusually large home range of *C. insculpta* in the present study. Using the regression equation of home range area against stream width (cf. Plummer et al., 1997), *C. insculpta* is predicted to have a home range size near 1.6 ha, compared to an actual home range area of 36 ha. Generally speaking, habitat type is not a factor, as our comparisons are restricted to lotic species. However, the distribution of microhabitats, particularly as related to productivity, could dictate home range size.

In the Daly River, *C. insculpta* is primarily herbivorous during the dry season (Heaphy, 1990; Welsh, 1999). Welsh (1999) found that ribbonweed (*Vallisneria spiralis*) comprised 74–90% of the total mass of dry season stomach contents of adult *C. insculpta* in the Daly River. Ribbonweed is patchily distributed along the river (unpubl. data), so turtles may need to cover great distances to forage and accumulate energy sufficient for reproduction. Data collected concurrent with the present study revealed that most *C. insculpta* in the Daly River exhibit biennial reproduction (unpubl. data). This fact, coupled with the relatively low available energy content of ribbonweed (Heaphy, 1990; Spencer et al., 1998), suggests that diet may limit reproduction in the population, as is apparently the case in the herbivorous sea turtle *Chelonia mydas* (Bjorndal, 1981). Large home ranges may, therefore, reflect movements between the scattered patches of the turtles' chief food during the dry season. This proposal is consistent with the finding that males had much smaller home ranges than females, given the greater relative energy demands of females. A study investigating the effect of supplemental feeding on the reproductive frequency of captive animals would provide a firmer basis for the above hypothesis.

Another possible reason for the extensive *C. insculpta* home ranges is related to method. Home range area can be underestimated in species inhabiting deeper rivers, relative to species occupying more shallow systems, because depth of water is not considered. Resources that turtles use are, in general, distributed in three-dimensional space. Food availability or abundance may covary with depth. In addition, depth may play a role in a turtle's perception of area, given that turtles swim through a range of depths. The Daly River averages approximately 1.5 m deep during the dry season, compared to much deeper systems in other studies of aquatic turtles (e.g., averaging several meters, Plummer and Shirer, 1975; Jones, 1996). This might also explain the long linear home range found in *A. spinifera* in a creek averaging 30 cm deep (Plummer et al., 1997). We recommend that future studies of home range in aquatic turtles should record and analyze depths as well as horizontal dimensions, as has been done in studies of marine mammals (e.g., Harcourt et al., 2000).

Activity centers and microhabitat use.—Visual inspection of combined point locations of females against locations of three potential resources reveals that turtles spent a considerable amount of time in areas near thermal springs (Fig. 1). During the dry season before the river warms to 30 C in September, turtles spend a substantial amount of time at thermal springs (Doody, 2000; Doody et al., 2001). The two known thermal springs that were not associated with high turtle activity were small springs in shallow water (2 km, 8.5 km marks, Fig. 1). The activity peak near the 8000 m mark was associated with deep water—there may be a thermal spring at this location that we did not detect (Figs. 1–2). Beach location may also have contributed to activity center location. Dense ribbonweed patches did not appear to be associated with centers of turtle activity but may be important at a larger scale. Stretches upstream of the study area with little or no ribbonweed were associated with very few egg clutches in 75 km nest surveys (unpubl. data). The influence of sex and reproductive condition on activity centers could not be determined because the sample sizes were too small.

Males and females used microhabitats with similar frequencies, except for open sand flats and isolated logs (Fig. 3). In comparison with females, males used isolated logs more, sand flats less, were found at shallower depths, and were less active during the daytime when most observations were made. Observations and analyses indicate that these differences were interrelated because the males often sat motionless against submerged isolated logs in shallow (<1 m) water. Thus, inactivity in males was probably responsible for sex differences in microhabitat,

and thus depth of observations. Male *Graptemys flavimaculata* used shallower depths and more snags than did females, but this difference was not attributable to activity (Jones, 1996).

Wet season locations.—Turtles did not appear to leave their dry season home ranges and move into estuarine areas during the wet season (Fig. 5), despite the occurrence of *C. insculpta* in estuarine areas in Papua New Guinea (Georges and Rose, 1993). The wet season aerial survey indicated that turtles moved out of the river channel during flooding (Figs. 5–6). Most turtles were clumped into two groups, each comprising males and gravid and nongravid females. The reason for this clumping is not known, but each group was near (group 1 = within 200 m, group 2 = within 800 m) a billabong or river swamp (Fig. 5). Turtles may have used these billabongs when water levels were higher weeks earlier (Fig. 6) and then followed receding water toward the riverbanks. Alho and Padua (1982) found *Podocnemis expansa* residing in lakes when the Amazon and its tributaries were high and returning to the river to nest when the water level dropped. Alternatively, clumping of *C. insculpta* could have occurred in response to some concentrated food source, such as flying fox colonies (Georges et al., 1989) or fig trees (Georges and Rose, 1993). The locations of the turtles at one point in the wet season relative to dry season home ranges indicated that turtles moved with the current downstream before leaving the river channel. Previous studies have reported downstream dispersal of freshwater turtles associated with periods of high water (Moll and Legler, 1971; Bury, 1972; Pluto and Bellis, 1988). However, few conclusions can be drawn from a single wet season survey. A radio-telemetry study during the wet season would be useful in completing our understanding of the movement patterns, diet, and other ecological attributes of *C. insculpta*.

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