

ECOLOGY OF ORIENTAL-AUSTRALIAN REAR-FANGED WATER SNAKES (COLUBRIDAE: HOMALOPSINAE) IN THE PASIR RIS PARK MANGROVE FOREST, SINGAPORE

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ABSTRACT. – We studied the ecology of four species of coastal marine homalopsine snakes (Oriental-Australian rear-fanged water snakes) in the Pasir Ris Park mangrove forest, Singapore, using survey methods and radiotelemetry. The snake assemblage at Pasir Ris (220 snakes collected) was dominated by *Cerberus rynchops* (72.7% of total snakes), a medium-sized piscivore. Three species of crustacean eaters were also present, but less common: *Gerarda prevostiana* (15.9% of total; medium-size, small head, slender body; diet of recently-molted crabs), *Fordonia leucobalia* (9.6% of total; broad head, stout body; diet of hard-shell crabs), and *Cantoria violacea* (1.8% of total; small head, slender, elongate body; diet of snapping shrimp). Size measurements indicated that sexual dimorphism was not pronounced, but we did find some sex differences in snout-vent length, tail length, and mass among the four species. Surveys along a 200 m boardwalk transect showed that *C. rynchops* exhibited a strong habitat association with mangrove forest areas dominated by open muddy pools (~100 m of the transect) compared to areas dominated by mud lobster (*Thalassina anomala*) mounds (~100 m of the transect). The crustacean-eaters were often observed in association with mud lobster mounds, but we found no significant difference in the use of the mud lobster mound habitat zone compared to the mud pool zone for these species. A survey of snake activity indicated that the mangrove homalopsines were strongly nocturnal and active throughout the night. *Gerarda prevostiana* increased activity during spring tides, but the other species did not. *Fordonia leucobalia* was the subject of a short-term (five-week) radiotelemetry study. The three male snakes monitored were relatively sedentary and moved short distances when they did move (range = 1.8 to 14.0 m). Typical of tropical aquatic snakes, the body temperatures of the snakes monitored were very stable (range = 26.3 - 29.0°C) and similar to the microhabitat temperatures recorded. However, we found that snake body temperatures were consistently higher than the microhabitat temperatures recorded during a 48-hour intensive monitoring period. Two of the monitored *F. leucobalia* resided in the mud lobster zone of the transect and made extensive use of mud lobster mounds (100% of telemetric locations). The snakes did not exhibit a significant preference for any particular size class of mud lobster mound, and mounds were used in approximately the same proportion as their abundance. We discuss the community ecology and conservation biology of coastal marine homalopsine snakes with respect to the special characteristics of the mangal forest ecosystem, particularly mud lobster mounds and their burrow complexes. The once extensive mangrove forests of Singapore have been reduced to a series of degraded patches. Despite its small size, the Pasir Ris Park mangrove forest supports a rich, diverse community indicating that even small patches of mangrove can be important reservoirs of biodiversity and deserve preservation.

KEY WORDS. – Homalopsinae, *Cantoria*, *Cerberus*, *Fordonia*, *Gerarda*, Pasir Ris, mangroves, water snakes, lobster mounds, *Thalassina*.

INTRODUCTION

The colubrid subfamily Homalopsinae (Oriental-Australian rear-fanged water snakes) includes ten genera and 34 species of snakes distributed from India across Southeast Asia to northern Australia (Gyi, 1970; Murphy & Voris, 1994). All

homalopsines are amphibious, usually associated with mud substrates, primarily nocturnal, and live at low elevations. Eight of the 34 species (24%) are coastal marine species living in mangrove forests, tidal mudflats, near-shore coastal waters, and estuarial habitats (Heatwole, 1999; Karns et al., 2000). The freshwater species are found in ponds, streams,

wetlands, agricultural wetlands (e.g., rice paddies), and lakes (Gyi, 1970). Most homalopsines eat fish, frogs, and tadpoles, but feeding on crustaceans is well documented in three of the coastal marine species (Voris & Murphy, 2002).

The Homalopsinae is characterized by a suite of features that adapt them for aquatic life (e.g., valvular nostrils). The species for which reproduction has been described are viviparous (Gyi, 1970). Homalopsines are opisthoglyphous (rear-fanged) and are considered mildly venomous (Minton, 1990). Homalopsines are relatively small in size (most species < 1 m adult snout-vent length). The homalopsines exhibit considerable morphological and ecological diversity for a small ophidian clade (Voris et al., 2002).

Despite their abundance and widespread distribution across the Oriental and Australian biogeographic regions, the homalopsines are a relatively understudied group of snakes. We have undertaken a series of autecological studies of homalopsine species, including *Cerberus rynchops* and *Bitia hydroides* in coastal peninsular Malaysia (Jayne et al., 1988, 1995), *Enhydryis plumbea* in agricultural wetlands in Malaysian Borneo (Karns et al., 1996; Voris & Karns, 1996), and *Enhydryis enhydryis*, *E. plumbea*, and *Homalopsis buccata* in a lake/wetland complex in southern Thailand (Murphy et al., 1999; Karns et al., 1999-2000). Our objective in these studies was to provide ecological profiles of representative taxa that cover the spectrum of environments in which homalopsines are found.

The mangal ecosystem (wetland community dominated by mangroves) is distributed throughout the tropics where average monthly minimum air temperatures are above 20°C (Bertness et al., 2000). Singapore is located 140 km north of the equator and at one time supported dense mangrove forests, especially on the northern and western coasts. The mangal in Singapore now consists of a series of fragmented and degraded patches of mangrove forest. Despite this history, some mangrove areas in Singapore still support a rich and diverse flora and fauna (Ng & Sivasothi, 1999a).

We report here on an ecological study of the four species of coastal marine homalopsines found in the mangrove forests of Singapore: *Cerberus rynchops* (dog-faced water snake), *Gerarda prevostiana* (Gerard's water snake), *Fordonia leucobalia* (crab-eating snake), and *Cantoria violacea* (Cantor's water snake). We studied this snake assemblage in the Pasir Ris Park mangrove forest during an eight-week period (February-March, 2001) and we documented species composition, age/size structure, habitat use, and activity patterns. One species, *F. leucobalia*, was the subject of a short-term (five-week) radiotelemetry study; we documented the movements, habitat utilization, and thermal ecology of three male *F. leucobalia*. We also investigated the relationship between snakes and the large mud mounds created by mud lobsters (*Thalassina anomala* and *T. gracilis*). We discuss the ecology of coastal marine homalopsine snakes with respect to the special characteristics of the mangal ecosystem.

MATERIALS AND METHODS

Study site. – Pasir Ris Park (1°22' 52.8"N, 103° 57'7.2"E) is located in northeastern Singapore (Ng & Sivasothi, 1999a). It is a 70.5 hectare urban park dominated by open lawns, walkways, and ornamental landscape plantings. The park is cut into three sections by the Api Api and Tampines rivers. A portion of the park sits on land reclaimed from the Johor Straits in 1978-79. Most of the existing coastal mangrove forest was destroyed during the reclamation process, but a five hectare patch of mature mangrove forest was preserved and developed into a park beginning in 1988. A channel system was constructed to ensure a tidal connection between the patch and the Tampines River, an adjacent one hectare area of vacant land was also inundated, and a boardwalk constructed along the edge of and into the mangrove patch. The Pasir Ris mangrove forest supports a rich community of at least 12 species of mangrove tree species (Ng & Sivasothi, 1999a). The normal pattern of tidal inundation has been modified by human activity, but spring tides still penetrate to the rear portion of the forest. The long-range future of the forest is uncertain due to freshwater inflow, invading freshwater species, and the small size of this mangrove forest fragment. Despite these problems, the Pasir Ris mangrove supports a diverse mangrove community, including four species of homalopsine snakes.

The fresh and saltwater influences of the Pasir Ris mangrove are reflected in the frog fauna that includes the freshwater *Microhyla heymonsi*, *Kaloula pulchra*, *Bufo melanostictus*, *Polypedates leucomystax*, and the saltwater tolerant *Rana cancrivora* (K. Lim, personal communication). Other reptiles reported from the mangrove portion of the park include the lizards *Varanus salvator*, *Hemidactylus frenatus*, *Lepidodactylus lugubris*, and *Calotes versicolor*, and the snake *Trimeresurus purpureomaculatus*. A variety of fish are found in the pools of Pasir Ris, the most noticeable being *Periophthalmodon schlosseri*, the giant mudskipper. A rich diversity of decapod crustaceans occurs in the Pasir Ris Park mangrove forest with burrowing and herbivorous sesarminae crabs (Grapsidae) being the most conspicuous crab group (Ng & Sivasothi, 1999b). Mud lobsters (Thalassinidea: *Thalassina anomala* and *T. gracilis*) create large mound structures (up to 3 m in diameter, reaching 2 m in height) along the landward edge of the mangrove forest (Ng & Kang, 1988).

Environmental monitoring. – We monitored the physical environment at Pasir Ris using several different models of electronic data loggers (Onset Computer Corp.). We monitored microclimate (shaded air temperature, relative humidity, and light intensity) and microhabitat temperatures at the site (15 cm into a crustacean burrow, on mud substrate, in water pool, and 15 cm into mud). Data loggers took measurements at one to four minute intervals over the duration of the study. We measured the salinity and pH of the water during both spring and neap tides using a Yellow Springs Instrument-30 salinity meter.

Survey methods. – We used a 200 m segment of the Pasir Ris mangrove forest boardwalk as a snake collecting transect; this boardwalk segment made a semi-circle through the main portion of the mangrove forest. We conducted snake surveys at Pasir Ris on a total of 12 nights between 7 February and 30 March, 2001. On 10 of the 12 survey nights we divided the transect into 20 m segments and identified the type of surface habitat (either extensive mud lobster mound field or open muddy pools with few lobster mounds) in each segment. The 20 m segments allowed assessment of snake habitat use and facilitated the return of snakes to their approximate area of capture. Snakes from all 12 survey nights ($n = 220$ snakes) were used to obtain size and sex statistics and to determine relative abundance. Habitat utilization analysis was based on the 10 nights that the transect was divided into 20 m segments ($n = 181$ snakes). A volunteer work force (10 to 14 persons) participated in the survey (average = 12/night). We attempted to collect by hand all snakes we observed, and noted the species, the time of collection, the 20 m segment of the boardwalk, and the microhabitat of every snake collected. Collected snakes were placed in numbered plastic bags, taken back to the laboratory, and processed the following day. The majority of collected snakes were usually returned to their capture site within 24 hours; some snakes were retained for physiological and behavioral experiments. In addition to the 12 survey nights on which snakes were collected with the assistance of volunteers, two nights were devoted to an intensive survey of snake activity patterns. During the intensive survey we identified and counted all snakes observed along the Pasir Ris boardwalk every three to four hours over a two-night period (21 March: one observer; 22 March: two observers). No snakes were collected during the intensive survey.

During processing, we weighed (± 0.1 g), measured snout-vent length (SVL) and tail length (± 0.1 cm), and sexed (when possible) each snake. We could not reliably identify the sex of *C. rynchops* individuals less than 35 cm SVL using external morphology. We could generally determine the sex of larger individuals of *F. leucobalia*, *G. prevostiana*, and *C. violacea* based on the enlarged tail base of males. Also, *F. leucobalia* has a conspicuous sexual dimorphism in anal plate scale morphology (personal observation). We checked snakes for prey items by standard massage and regurgitation methods; results of diet and feeding studies done in conjunction with this study are reported elsewhere (Jayne et al., 2002; Voris & Murphy, 2002). In order to identify previously captured snakes, we marked *G. prevostiana*, *F. leucobalia*, and *C. violacea* with PIT tags (passive integrative transponders, Avid Co.) for electronic identification during processing; we used a scale-marking system to identify *C. rynchops*.

Radiotelemetry. – We surgically implanted three male *F. leucobalia* (designated F264, F475, and F240) with temperature-sensitive radio transmitters (Holohil Systems, Ltd.: Model BD-2: 1.8 g, 4x8x15 mm). Only *F. leucobalia* was used for telemetric studies because some adults were sufficiently large and stout to accommodate a transmitter; the other species at Pasir Ris were too slender. We

anaesthetized snakes with Isoflurane and implanted the transmitters into the intraperitoneal cavity; the antenna was subdermal. The transmitter weight was 2.9% (F264), 3.1% (F475), and 3.4% (F240) of the body mass (see Table 2 for mass). Snakes were allowed to recover from surgery for four to seven days prior to release at their point of capture. Based on behavior and appearance, the snakes accommodated the transmitters without difficulty. We monitored two of the males (designated F264 and F475) over a five-week period (1 March to 7 April); one male (F240) was monitored over a three-week period (17 March to 7 April). We located snakes on approximately 60% of the days during this period (F264 = 57.9%; F240 = 63.6%, F475 = 57.9%). Despite concerns about the effect of salinity on transmitter signal, we relocated snakes in 89.8% of attempted locations ($n = 137$ attempts). We normally checked snakes once on any given day, but on some days we made more than one telemetric location per day; we refer to both of these types of observation as daily monitoring. Over a 48 hr period (21-22 March) we attempted to locate the three snakes every three to four hours; we refer to these observations as intensive monitoring. We combined movements from both daily and intensive monitoring to calculate basic movement statistics because the snakes were quite sedentary and duration of the intensive monitoring was short.

When we located telemetered snakes they were usually in a lobster mound or below the surface in the mud-root-tangle of the mangrove forest floor and not visible. Because of this concealment and the vagaries of signal transmission, we could not reliably locate snakes within a 0.2 m² patch. We marked each location with a dated, color-coded flag. Because we could not usually see the snake, we recorded microhabitat temperatures in the immediate vicinity of the snake with a digital thermometer (on mud substrate, in water pool, 15 cm into mud, and 15 cm into a crustacean burrow) to calculate the mean microhabitat temperature at the exact relocation site. We recorded the body temperature of the snakes using a pulse-interval-timer (AVM Instrument Co., Ltd.) connected to the radio receiver (Wildlife Materials, Inc.: Model TS 1000). Straight-line distances between consecutive locations in the field were measured with either a string-distance or an infrared-distance measuring device, and snake locations and movements were plotted onto scale maps of the study site. We constructed minimum convex polygons to describe snake movement areas and measured their areas on the scale maps using a scanner. Because the duration of our radiotelemetric monitoring was relatively short, we refer to the minimum convex polygons we constructed as short-term activity areas.

In order to facilitate comparison of movement data (Gregory et al., 1987; Macartney et al., 1988), we report movement as the mean distance per move (sum of straight line distances moved between consecutive locations/ total number of moves). Statistical tests follow Zar (1996) with significance levels set at $\alpha = 0.05$. We used the arc sine transformation on the ratio of snout-vent to tail length values to ensure normality. Means ± 1 SE are reported.

RESULTS

Physical environment at Pasir Ris. – During the February-March field season the mangrove forest at Pasir Ris exhibited uniform daily fluctuations in air temperature and relative humidity with predictable variation due to precipitation and cloud cover. A representative set of data logger measurements taken over a three-day period (21-23 March) is shown in Fig. 1. The first day-night cycle is a typical clear, sunny day with high temperatures (30 - 31°C) and relatively low humidity (75 - 80% RH) during the day and lower temperatures (24 - 26°C) and high humidity (90 - 100% RH) by early evening. Note the rapid change in conditions at dawn and dusk. This basic pattern was modified somewhat over the next two days by cloud cover and precipitation in the later afternoon (day 2) and the following morning (day 3).

Salinity recorded at 20 m intervals along the 200 m boardwalk transect at neap tide (mean = 18.8 ppt \pm 2.14, range = 2.9 - 29.3 ppt) was lower and more variable than during spring tide (mean = 25.5 ppt \pm 0.43, range 22.8 - 27.0 ppt). The pH recorded was circumneutral during both spring and neap tides (mean pH = 7.1 \pm 0.15, range = 6.6 - 8.0). The salinity in the Johor Straits between Singapore and Malaysia, the body of ocean water that feeds the Pasir Ris mangrove forest, is typically 28 to 30 ppt (Khuo, 1996).

Snake assemblage at Pasir Ris. – At Pasir Ris we collected 220 snakes (excluding recaptures and observations) representing four species of homalopsine snakes (Fig. 2). *Cerberus rynchops*, a piscivore, was the most abundant snake at Pasir Ris (mean number collected per survey = 13.3 \pm 1.51, range = 8 - 22, 72.7% of total snakes). The other three species were crustacean-eaters. Two of these species were regularly encountered, but in relatively low numbers. *Gerarda prevostiana* was the second most abundant snake (mean number collected per survey = 2.9 \pm 0.81, range = 0 - 8, 15.9% of total snakes). *Fordonia leucobalia* was similar in abundance to *G. prevostiana* (mean number collected per

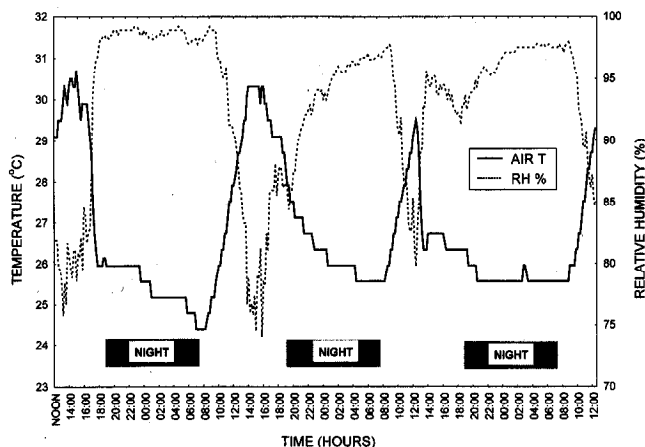


Fig. 1. Changes in air temperature and relative humidity over a three day period (21-23 March, 2001) in the Pasir Ris Park mangrove forest. Note the alternation of temperature and relative humidity over the day-night cycle. Measurements were taken by data loggers at four minute intervals.

survey = 1.8 \pm 0.33, range = 0 - 4, 9.6% of total snakes). *Cantoria violacea* was collected only four times during the study period (1.8% of total snakes). We observed no other species of snakes at the study site.

Population structure. – We obtained body measurements from 210 homalopsines at Pasir Ris (Table 1). Male (n = 24) and female (n = 41) *C. rynchops* did not differ significantly in SVL ($t = -0.37$, $df = 63$, $P > 0.05$) or mass ($t = -0.03$, $df = 63$, $P > 0.05$), but male tail length and the ratio of tail length to SVL were significantly different in males compared to females (tail length: $t = -4.65$, $df = 63$, $P < 0.001$; ratio: $t = 7.81$, $df = 63$, $P < 0.001$). The smallest *C. rynchops* collected at Pasir Ris measured 19.0 cm SVL and weighed 4.1 g. The ratio of male to female *C. rynchops* in this sample was 0.59:1.

The three crustacean-eaters at Pasir Ris were less commonly encountered than the piscivorous *C. rynchops* (Table 1). We did not observe a pronounced sexual dimorphism between males and females of *F. leucobalia* or *G. prevostiana*, although females of both species tended to be larger and stouter than males. Male (n = 21) and female (n = 10) *F. leucobalia* did not differ significantly in SVL ($t = 0.98$, $df = 13$, $P > 0.05$) or mass ($t = 0.98$, $df = 13$, $P > 0.05$), but tail length and the ratio of tail length to SVL did differ in males compared to females (tail length: $t = -4.60$, $df = 13$, $P < 0.001$; ratio: $t = -7.94$, $df = 13$, $P < 0.001$). Male (n = 9) and female (n = 6) *G. prevostiana* did not significantly differ in SVL ($t = 1.53$, $df = 29$, $P > 0.05$), in tail length ($t = 1.13$, $df = 29$, $P > 0.05$), or in the ratio of tail length to SVL ($t = -0.69$, $df = 29$, $P > 0.05$), but did differ in mass ($t = 2.53$, $df = 29$, $P < 0.05$). The male to female sex ratio observed in *F. leucobalia* was 1.5:1 and 2.1:1 for *G. prevostiana*.

Habitat utilization. – We observed conspicuous differences in the surface habitat of the mangrove forest along the 200 m section of boardwalk used as a survey transect (Fig. 3). Mud lobster mounds were abundant along the first 100 m of boardwalk, but were uncommon along the second 100 m segment. The second segment was generally more open and

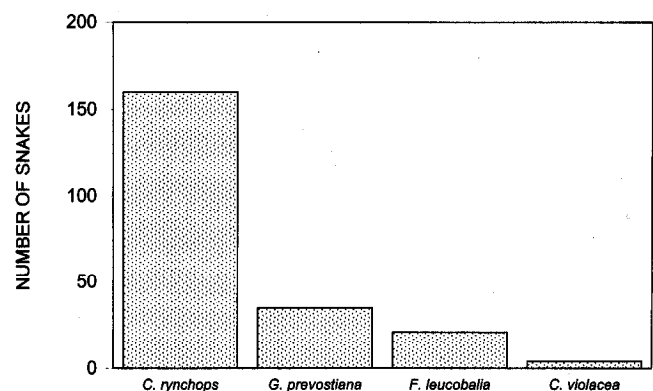


Fig. 2. Relative abundance of the four species of coastal marine homalopsine snakes found at Pasir Ris Park (n = 220 snakes). *Cerberus rynchops*, a piscivore, was the dominant species. The less abundant *Gerarda prevostiana*, *Fordonia leucobalia*, and *Cantoria violacea* are crustacean-eaters.

Table 1. Size and weight measurements for the four species of homalopsine snakes collected at Pasir Ris Park, Singapore. Numbers in parentheses following sex categories indicate the sample size. The mean \pm 1 SE is shown with the range in parentheses.

Species	Snout-vent Length (cm)	Tail Length ² (cm)	Ratio Tail: Snout-vent Length (%)	Mass (g)
<i>C. rynchops</i>				
Male (24)	40.1 \pm 1.12 (35.2 - 56.1)	10.9 \pm 0.31 (8.3 - 14.7)	27.2 \pm 0.36 (23.5 - 29.7)	36.6 \pm 2.60 (25.1 - 69.2)
Female (41)	39.6 \pm 0.73 (35.2 - 54.9)	9.4 \pm 0.15 (7.7 - 12.3)	23.9 \pm 0.2 (21.1 - 28.6)	36.5 \pm 2.35 (20.8 - 89.7)
Juvenile (91)	30.0 \pm 0.38 (19.0 - 34.7)	7.8 \pm 0.12 (4.6 - 9.8)	—	6.1 \pm 0.64 (4.1 - 30.6)
<i>G. prevostiana</i>				
Male (21)	35.3 \pm 0.70 (28.2 - 40.0)	5.4 \pm 0.10 (4.2 - 6.2)	15.3 \pm 0.26 (13.5 - 18.4)	19.6 \pm 1.20 (10.2 - 31.6)
Female (10)	37.7 \pm 1.65 (25.4 - 43.4)	5.6 \pm 0.24 (4.0 - 6.6)	15.0 \pm 0.33 (13.0 - 16.9)	26.8 \pm 3.30 (7.7 - 37.7)
<i>F. leucobalia</i>				
Male (9)	44.8 \pm 1.42 (39.4 - 52.8)	6.6 \pm 0.23 (5.7 - 8.2)	14.8 \pm 0.26 (13.5 - 15.9)	61.3 \pm 5.02 (40.5 - 91.5)
Female (6)	47.4 \pm 2.39 (42.7 - 58.9)	5.1 \pm 0.21 (4.6 - 5.8)	10.8 \pm 0.46 (9.8 - 12.6)	75.2 \pm 15.92 (48.9 - 152.3)
Juvenile (4)	21.1 \pm 0.71 (19.0 - 22.2)	2.5 \pm 0.06 (2.4 - 2.7)	—	6.8 \pm 0.55 (5.6 - 8.2)
<i>C. violacea</i>				
Female (1)	98.0	11.7	—	134.9
Male (2)	94.5	15.9	—	132.2
	90.9	15.5	—	127.0
Juvenile (1)	35.5	6.0	—	8.8

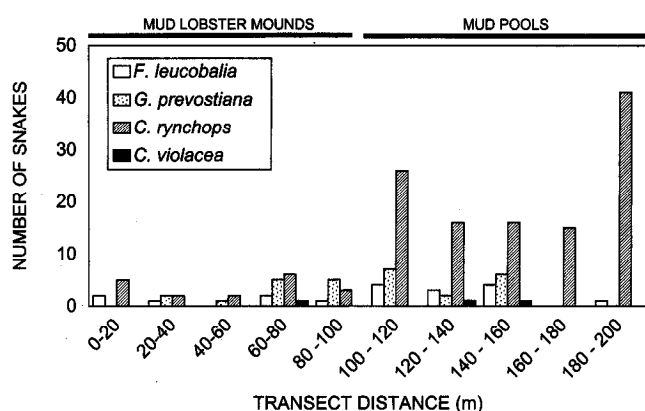


Fig. 3. Distribution of homalopsine snakes along a 200 m boardwalk transect in the Pasir Ris Park mangrove forest (n = 181 snakes). Mud lobster mounds were abundant along the first 100 m of the transect. The 100 to 200 m segment of the transect had relatively few lobster mounds and was dominated by muddy pools of water. *Cerberus rynchops* was particularly common in the mud pool habitat zone of the transect. The other three species were more uniformly distributed between the mud lobster mound and the mud pool habitat zones.

dominated by muddy pools. We found no significant difference between the number of snakes collected in the mud lobster mound zone compared to the mud pool zone for either *F. leucobalia* (6 vs.12, chi-square = 2.0, df = 1, P > 0.05) or for *G. prevostiana* (13 vs. 15, chi-square = 0.14, df = 1, P > 0.05). We did observe a significant difference in the number of *C. rynchops* collected in the mud lobster mound zone compared to the mud pool zone (18 vs. 114, chi-square = 69.82, df = 1, P < 0.001). *Cerberus rynchops* was particularly abundant along the last 20 m of the transect in a water-filled ditch adjacent to the boardwalk (n = 41, 31.1% of the total *C. rynchops* sample). We collected only three *C. violacea* during the habitat utilization survey (one in the mud lobster mound zone, two in the mud pool zone).

Activity patterns. – The coastal marine homalopsines observed in Singapore were strongly nocturnal. Observations made every three to four hours along the Pasir Ris boardwalk over a two-night period showed that snakes were active throughout the night (snakes were observed during every observation period) and there was a relatively abrupt period of emergence and disappearance at dawn and dusk (Fig. 4). We occasionally observed *C. rynchops* in pools during the day and activity increased in the later afternoon. We did

not observe *F. leucobalia* or *G. prevostiana* during the day; however, radiotelemetry showed one daytime movement by *F. leucobalia* (F240 moved 3.1 m, between 14:37 and 18:28, during the 48-hr intensive survey). On two occasions radiotelemetry allowed us to observe initiation of activity by *F. leucobalia* (F264) corresponding to sunset (at 19:40 and 19:42). We observed abrupt cessation of surface activity by *C. rynchops* at sunrise during the intensive survey. Observation of *C. rynchops* at another mangrove forest site, Sungei Buloh Nature Park, showed an abrupt increase in the number of *C. rynchops* observations corresponding with sunset.

Tidal cycles and rainfall may also influence snake activity patterns. The effects of the tidal cycle at Pasir Ris were modified by anthropogenic alterations of the local drainage. However, we found a significant difference (chi-square = 24.14, df = 1, P < 0.001) in the number of *G. prevostiana* collected during the two spring tide survey nights (full and new moon: 16 snakes) compared to the eight neap tide survey nights (half moon: 12 snakes). We detected no significant association between tide and snake activity for *C. rynchops* (2 spring tide nights = 24 snakes, 8 neap tide nights = 108 snakes; chi-square = 0.27, df = 1, P > 0.05) or *F. leucobalia* (2 spring tide nights = 3 snakes, 8 neap tide nights = 15 snakes; chi-square = 0.13, df = 1, P > 0.05). It was our qualitative impression that snake activity was higher on days with late afternoon or early evening showers; however, we could detect no significant difference in activity associated with precipitation for the three species (6 survey nights with rain in the afternoon or evening of the survey, 4 dry survey nights).

Movements. – Table 2 provides a summary of movement data for the three male *F. leucobalia* monitored by radiotelemetry. The three snakes exhibited variability in movement, but all were relatively sedentary (percentage of times snakes moved from previous telemetric location: mean = 29.1% ± 6.53, range = 17.4 - 40.0%). The three snakes

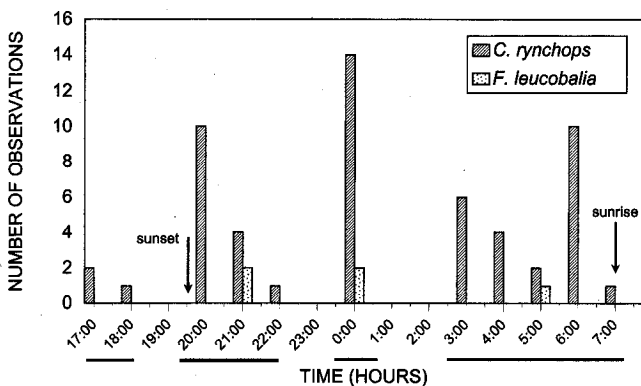


Fig. 4. Pattern of nocturnal-crepuscular activity for *Cerberus rynchops* and *Fordonia leucobalia* over a two-day period (21 March: one observer; 22 March: two observers; results from both nights pooled). The 200 m boardwalk transect in the Pasir Ris Park mangrove forest was checked every three to four hours on the two survey nights. The bold lines below the time intervals indicate the duration of the observation periods. Snakes were observed during every observation period.

moved relatively short distances (mean = 6.5 m ± 0.60, range = 1.6 - 14.0 m) and exhibited small short-term activity areas over the duration of the study (mean = 92.3 m² ± 16.08, range = 61.1 - 114.6 m²).

Two of the three telemetered snakes (F264, F240) were captured and released in areas of mud lobster mounds (within the first 40 m of the boardwalk transect). Telemetry movement maps (Fig. 5) show that these snakes were located

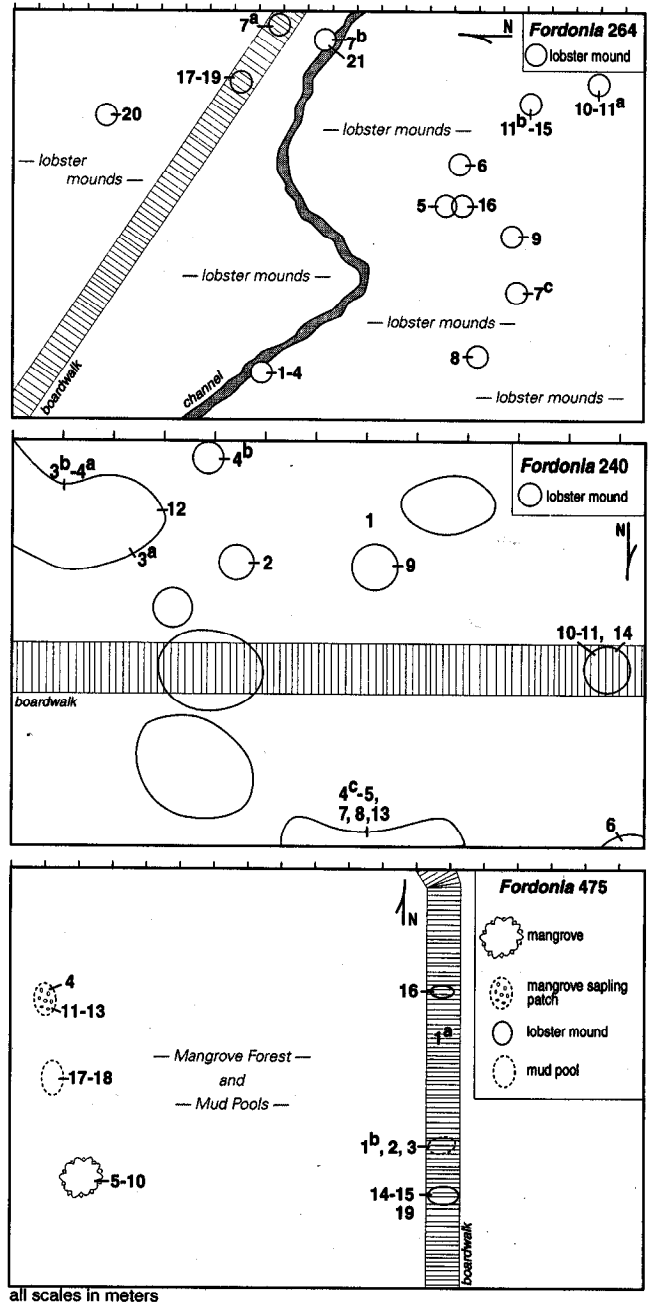


Fig 5. Movements of three male *Fordonia leucobalia* (F264, F240, F 475) in the Pasir Ris Park mangrove forest. Movements monitored by radiotelemetry over a three to five-week period (Table 2). Numbers indicate the number of days that the animal was relocated during this period and the sequence of movements. Superscripts indicate that the snake was located more than once on a particular day. Snake F264 and F240 were captured and released in areas with abundant mud lobster mounds; these snakes were associated with mud lobster mounds in 100% of the radiotelemetric relocations. Snake F475 was captured and released in an area of mud pools with relatively few mud lobster mounds.

Table 2. Movement data for male *Fordonia leucobalia* from Pasir Ris Park, Singapore. Snakes were monitored using radiotelemetry.

Snake (number days tracked)	SVL (cm) Mass (g)	Locations per attempted locations (%)	Number movements per locations (%)	Mean distance (m ± 1 SE) per movement (range)	Short-term Activity Area (m ²)
F264 (22)	47.6 61.9	47/52 (90.4)	14/47 (29.8)	6.6 ± 0.93 (1.8-13.0)	114.6
F240 (14)	45.0 57.3	30/31 (96.8)	12/30 (40.0)	5.0 ± 0.67 (1.6-9.2)	61.1
F475 (22)	47.6 53.7	46/54 (85.2)	8/46 (17.4)	8.8 ± 1.47 (3.0-14.0)	101.3

either on or in a lobster mound in 100% of the telemetric relocations for F264 (n = 47) and F240 (n = 30). When the position of the snake in a mound could be determined, we found that the snake was typically located in the flank of the mound toward the base. Snakes were observed foraging on mounds in a very slow, deliberate manner and appeared to be pressing their head and trunk into the substrate as they moved. They probed mound openings and would sometimes enter burrows; if disturbed they would quickly retreat into burrows. Snake F264 was observed approaching and tongue-flicking a sesarmin crab.

Snake F475 was captured and released (Fig. 5) in a relatively open area of mangrove and muddy pools with very few lobster mounds. This snake was monitored over a five-week period and found adjacent to (within 15 m of) the boardwalk in 58.7% of the locations. The snake was never observed on the surface, but found in the mud-root-tangle of the mangrove trees. The most frequent relocation site was among the roots of a small patch of young mangroves. Snake F475 was found under the boardwalk in 41.3% of the locations and was usually associated with two mud lobster mounds.

Table 2 includes movement data from both the daily and the 48-hour intensive telemetric monitoring. The intensive monitoring showed the same movement pattern as daily monitoring: snakes were sedentary and moved short distances if they did move. During the intensive monitoring F240 moved three times (1.6, 3.1, 7.9 m), F264 moved once (3.2 m), and F475 did not move (mean distance moved by all snakes during intensive monitoring = 4.0 m ± 1.37, n = 4; during daily monitoring = 6.9 m ± 0.64, n = 30).

We randomly sampled a series of 65 mounds in the mud lobster mound zone (Fig. 6) and compared them to the size (estimated as the volume of a right cone) of mounds used by F264 and F240 (n = 24 mounds). The majority of mounds (81.5%) in this random sample were relatively small (< 0.3 m³ in volume). The snakes did not exhibit a significant preference for any particular size class of mound (0 - 0.3 m³: 0.3 - 0.6 m³: > 0.60 m³). Mounds were used in approximately the same proportion as their abundance (chi-square = 2.81, df = 2, P > 0.05).

Snake thermal ecology. – Snake body temperatures recorded via telemetry (Fig. 7) showed a high degree of stability (mean

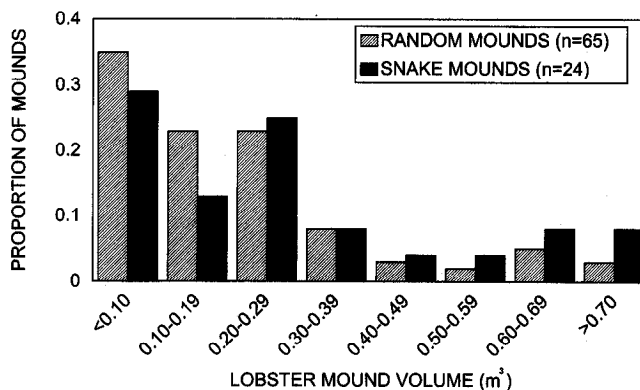


Fig. 6. Utilization of mud lobster (*Thalassina anomala*) mounds by *Fordonia leucobalia* in the Pasir Ris Park mangrove forest. The size of the 24 mud lobster mounds used by *F. leucobalia* during the radiotelemetry study was compared to a random sample of 65 mud lobster mounds from Pasir Ris Park. The proportion of random mounds and mounds used by snakes in each size category is shown. *Fordonia leucobalia* exhibited no significant preference for any particular size of mound. Mud lobster mound volume was calculated as the volume of a right cone.

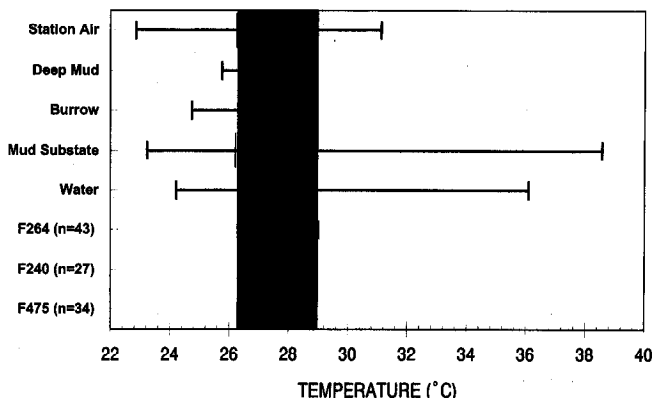


Fig. 7. Mean and range of five mangrove forest microhabitat temperatures compared to body temperatures recorded for three *Fordonia leucobalia* (F264, F240, F475). Body temperatures were recorded by radiotelemetry and microhabitat temperatures were recorded by data loggers (station air = shaded air temperature, deep mud = temperature 15 to 20 cm into mud, burrow = temperature 15 cm into a crustacean burrow, mud substrate = temperature on mud surface, water = temperature in a mangrove pool). The shaded area indicates the range of snake body temperatures.

= 28.0°C ± 0.05, range = 26.3 - 29.0°C, n = 105). The body temperatures of the three monitored *F. leucobalia* (shaded zone) are shown and overlap with the range of microhabitat temperatures recorded by data loggers. Mud substrate temperatures and the water temperatures recorded in a mangrove pool were more variable due to occasional exposure to patches of sunlight. The temperatures recorded 15 cm into a crustacean burrow and 15 to 20 cm deep in mud were less variable and similar to snake body temperatures.

Snake body temperatures monitored every three to four hours over a 48-hour (21-22 March) showed that the stability of snake body temperature persisted throughout the day-night cycle over this time period (Fig. 8). We found virtually no overlap between the body temperatures of the monitored snakes and the four microhabitat temperatures recorded by digital thermometer (on mud substrate, in water, 15 cm into burrow, 15 cm into mud) at the same time and location. We compared each snake body temperature to the mean microhabitat temperature (mean of the four microhabitat temperatures taken) at each snake location and found them to be significantly different during both the day (snake = 28.2°C ± 0.07, range = 27.8 - 28.8°C; microhabitat = 26.9°C ± 0.17, range = 26.1 - 29.2°C; paired t-test: $t = 6.16$, $df = 17$, $P < 0.001$) and the night (snake = 28.2°C ± 0.05, range = 27.8 - 28.8°C; microhabitat = 26.6°C ± 0.10, range = 26.0 - 27.4°C; paired t-test: $t = 12.73$, $df = 19$, $P < 0.001$).

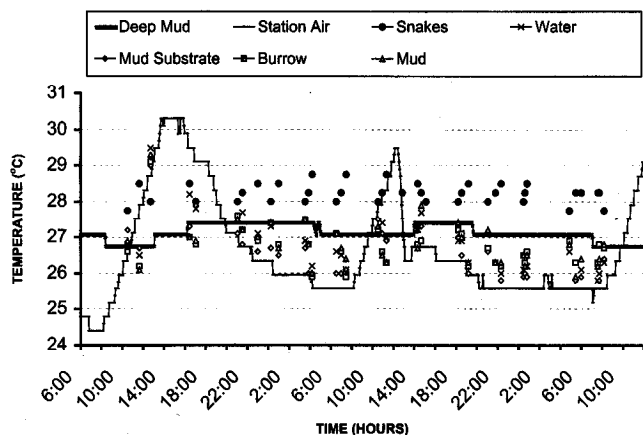


Fig. 8. Comparison of nocturnal-diurnal changes in microhabitat and snake body temperatures over a two-day period (21-22 March, 2001). The connected lines in the graph are data logger records of the temperature 15 to 20 cm into mud (deep mud) and shaded air temperature (station air). The solid circles are snake body temperatures (three male *Fordonia leucobalia*) recorded using radiotelemetry. The non-shaded symbols are four microhabitat temperatures recorded by digital thermometer in the immediate vicinity of a snake each time it was located (water = water in pool, mud substrate = on surface of the mud, burrow = 15 cm into a crustacean burrow, mud = 15 cm into mud). Note the stability of the snake body temperatures and that most snake body temperatures were greater than the microhabitat temperatures taken at the same time and place over the 48-hour period.

DISCUSSION

Community ecology. – The Pasir Ris Park snake community consists of a relatively abundant, medium-sized piscivore, *C. rynchops*, and three less common crustacean-eaters: *F. leucobalia* (broad head, stout body), *G. prevostiana* (medium-sized, small head, slender body), and *C. violacea* (small head, slender, elongate body). If crustacean-eaters are secretive and sedentary, as suggested by the telemetric monitoring of *F. leucobalia*, the relative abundance and habitat utilization comparisons (Fig. 2, 3) presented here may under-represent the crustacean-eating species. Another factor that may have influenced our snake observations was the boardwalk itself. It is not unusual for aquatic snakes to associate with man-made structures, and we do not know if the density of snakes was higher in the immediate vicinity of the boardwalk compared to areas away from the boardwalk. We also noted that larger *C. rynchops* (> 50 cm SVL) were conspicuously uncommon at Pasir Ris compared to other mangrove localities in Singapore (unpublished data).

A study of the diet and feeding behavior of the crustacean-eating homalopsines was done in conjunction with this study (Jayne et al., 2002) and data on the diet of homalopsines are summarized in Voris & Murphy (2002). Two of the homalopsine snakes at Pasir Ris, *G. prevostiana* and *F. leucobalia*, consume primarily herbivorous sesarminae crabs. *Gerarda prevostiana* specializes in recently molted crabs, whereas *F. leucobalia* eats hard-shell crabs. *Gerarda prevostiana* swallows small prey whole, but will rip apart and swallow the pieces of its larger prey; it may also pull off and eat the appendages of larger prey. *Fordonia leucobalia*, although it is a larger and stouter snake than *G. prevostiana* as an adult, is restricted in prey size by the hard shell of its prey. Similar to *G. prevostiana*, it is also reported to pull off the legs of larger crabs and eat them (Shine & Schwaner, 1985; Jayne et al., 2002). There may be more overlap in prey size between these species than would be predicted based on their body size differences because of the ability of *G. prevostiana* to tear apart its soft-bodied prey. These two species are feeding on the same food resource, crabs, but specializing on different phases of the ecdysis cycle of the prey species. Recent phylogenetic analysis based on mitochondrial DNA indicates that *G. prevostiana* and *F. leucobalia* are sister species (Voris et al., 2002). *Cantoria violacea* is also a crustacean-eater and specializes on snapping shrimp (*Alpheus* spp.).

Cerberus rynchops is a generalist piscivore that eats a variety of fish taxa. Other prey items that have been reported in its diet include frogs, tadpoles, and occasional crustaceans (Voris & Murphy, 2002). Field observations and stomach content analysis indicate that *C. rynchops* eats smaller fish and multiple prey items are often found in its gut (Jayne, 1988; HKV & DRK, personal observation).

Crustaceans undoubtedly influence the activity of homalopsine snakes in mangrove forests as both prey and predator. Crabs are opportunistic feeders and larger individuals have been observed to attack and feed on snakes

in the field and in staged laboratory encounters (Voris & Jeffries, 1995). We found dead homalopsines (*C. violacea*, *G. prevostiana*, *C. rynchops*) in Singapore mangrove forests that exhibited the signature chewing marks of crabs; however, this could be due to either scavenging or predation.

The diversity of largely diurnal vertebrate predators in mangrove forests may help explain the strongly nocturnal habits of the mangrove homalopsines. *Varanus salvator* is a common, upper trophic-level predator in the mangrove ecosystem in Singapore; its diet includes crustaceans, snakes, birds, and small mammals (Ng & Sivasothi, 1999b; Rashid & Diong, 1999). *Crocodylus porosus* feeds on crustaceans, fish, snakes, birds, and mammals, but it is now rare in Singaporean waters. Birds and fish are also important predators in the mangrove ecosystem. These predators move in and out of mangrove areas in response to tidal and seasonal fluctuations (Hutchings & Saenger, 1987; Hogarth, 1999).

Multi-species assemblages of saltwater tolerant snakes that live in coastal mangal and mudflat are an exclusively Old World phenomenon (Heatwole, 1999). A few species of natricines are found in saltwater marshes in the southeastern United States (*Nerodia clarkii taeniata*, *N. c. clarkii*, *N. sipedon williamengelsi*), and there is one saltwater tolerant natracine, *N. clarkii compressicauda*, found in the subtropical mangroves of Cuba and southern Florida, that has a niche similar to the homalopsines in this study (Heatwole, 1999). However, the snake assemblages associated with the mangal and mudflat environment in the neotropics are not truly residential when compared to the Old World coastal mangal and mudflat assemblages.

Movements and activity patterns. – Little information is available on the spatial ecology of homalopsine snakes. Short-term movements of five *Enhydris plumbea* monitored by radiotelemetry in a rice paddy wetland in Borneo (Voris & Karns, 1996) were similar to that of *F. leucobalia*; movements were short and the snakes were relatively sedentary (snakes monitored 7 to 10 days; days inactive = 46.6%; mean distance moved = 4.4 m). Two *Enhydris plumbea* in an extensive wetland meadow in southern Thailand (Karns et al., 1999-2000) were also relatively sedentary (snakes monitored 15-16 days, mean distance moved = 6.4 m). Five female and six male *Enhydris enhydris* at the same southern Thailand wetland site (snakes monitored for 8 - 19 days) exhibited more variable patterns of movements. Movements were dominated by short distance moves (< 10m), but punctuated by longer distance moves of up to 350 m in a 24-hr period (mean distance moved by males = 30.3 m; mean distance moved by females = 22.8 m).

Any consideration of the movements and activity patterns of mangal and mudflat snakes must take into account the tidal cycle and light levels. Jayne et al. (1988) and H. Voris (personal observation) observed that some species of coastal marine homalopsines (*F. leucobalia*, *C. rynchops*) actively forage along the moving tide line. We did not observe this at Pasir Ris because tidal effects were muted in the landward portion of the mangrove due to human disturbance. There

is evidence that some coastal marine reptiles may have an endogenous tidal foraging rhythm (Wikelski and Hau, 1995). Our observations on homalopsine activity patterns indicate that the day-night cycle is a primary environmental cue for the initiation of activity. A reduction in activity level as the full moon approaches has been reported for terrestrial snakes and for two aquatic snakes (Madsen & Osterkamp, 1982; Houston & Shine, 1994). In this study, *G. prevostiana* exhibited high levels of activity associated with spring tides under both the full and new moon suggesting that the tidal cycle was dominant over lunar light level.

Snake thermal ecology. – We have now collected thermal data from three species of homalopsines using radiotelemetry in Malaysian Borneo (*E. plumbea* in water buffalo wallows and streams: 4 snakes, mean temperature = 28.6°C, range = 25.5 - 32.2°C, n = 88; Voris & Karns, 1996), in southern Thailand (*E. enhydris* in mud-root-tangle along aquatic edges: 11 snakes, mean temperature = 30.4°C, range = 29.2 - 32.1°C, n = 110; Karns et al., 1999-2000), and in Singapore (*F. leucobalia* in mud lobster mounds and mangrove pools: mean temperature = 28.0°C, range = 26.3 - 29.0°C, n = 105). All three species exhibited relatively stable body temperatures, low variance in body temperatures, and body temperatures that did not vary greatly from the temperature of the microhabitat they utilized. These data are similar to those recorded for other tropical water snakes (e.g., Shine & Lambeck, 1985; Shine & Madsen, 1996) and are indicative of the highly stable thermal environments that are found in tropical wetlands. Shine and Madsen (1996) suggest that thermoregulation is not especially important for tropical reptiles.

The thermal data for *F. leucobalia* at Pasir Ris differ from our other homalopsine studies in the pronounced stability of the temperatures recorded, especially over the course of the day-night cycle. *Enhydris plumbea* and *E. enhydris* were monitored for two and six nights respectively, and although their body temperatures did not vary greatly, reflecting the high thermal inertia of their mud-water environments, the body temperatures did rise and fall in correspondence with the day-night temperature cycle and virtually all body temperatures recorded were within the range of microhabitat temperatures recorded at the same time and place (Murphy et al., 1999; HKV, DRK unpublished data). *Fordonia leucobalia* at Pasir Ris was different in that the day-night body temperatures recorded were very stable and significantly different from the microhabitat temperatures recorded at the same time that body temperature was recorded. However, caution is required in interpreting this difference; although there was virtually no overlap between the snake temperatures and microhabitat temperatures recorded, the mean difference was only 1.5°C. This difference may be a function of the temperature measurement instruments employed because we did not use snake models to measure environmental temperatures (Peterson et al., 1993). It is also possible that, because we did not usually see the telemetered snakes, the microhabitat temperatures we recorded by hand did not reflect the actual microhabitat temperatures in the mud lobster mounds and mud where the

snakes were located. Microbiological activity in the lobster mounds and mangrove forest mud may produce heat that is utilized by snakes and could account for the observed difference. The thermal dynamics of the mud lobster and mangrove mud environment deserve further investigation.

Habitat utilization. – Living in mangrove habitats poses physiological and ecological challenges for resident species, including salinity (Dunson & Dunson, 1979; Lillywhite & Ellis, 1994), changes in habitat structure and food availability associated with the tidal cycle, and habitat destruction by major storms (Berry, 1972; Hutchings & Saenger, 1987; Hogarth, 1999). Although a variety of reptiles (arboreal and amphibious snakes, lizards) and other vertebrates may utilize the mangrove forest on an occasional or regular basis (Hutchings & Saenger, 1987; Hogarth, 1999; Ng & Sivasothi, 1999b), relatively few species of reptiles can be considered residents of the mangrove similar to the homalopsine species in this study. Mangrove forest is a primary habitat for these homalopsines, but they also use tidal mudflats, *Nypa* forests, near-shore waters adjacent to the mangrove, as well as make limited use of freshwater-mangrove boundaries (Jayne et al., 1988; HKV, DRK, personal observation; natural history literature: e.g., Taylor, 1965). In general, coastal marine homalopsines can be considered as edge specialists of the mangal and mudflat terrestrial-marine ecotone.

Mud lobsters (*Thalassina anomala* and *T. gracilis*) eat organic material found in mangrove sediments and create extensive mound and burrow systems along the landward side of the mangrove forest. These mounds are used as a habitat and for foraging by a diversity of invertebrates, including flatworms, snails, insects, bivalves, and numerous species of crustaceans (Ng & Kang, 1988). The size and extent of mud lobster mound fields and burrow systems make them a significant landscape feature and provides important resources for resident mangal species.

Fordonia leucobalia made extensive use of mud lobster mounds at Pasir Ris where we observed both *F. leucobalia* and *G. prevostiana* foraging on mud lobster mounds. *Fordonia leucobalia*, *G. prevostiana*, *C. rynchops*, the mangrove skink (*Emoia atrocostata*), and the crab-eating frog (*Rana cancrivora*) have been excavated from lobster mounds in Singapore (Ng & Sivasothi, 1999b; B. Jayne, personal communication; HKV & DRK, personal observation). However, *F. leucobalia* is by no means restricted to lobster mounds and the landward portion of mangrove forests; it was found in similar abundance in mangrove areas with and without mud lobster mounds at Pasir Ris. It has also been observed foraging on tidal mud flats in Malaysia (B. Jayne, personal communication), in Australia (Shine, 1991), and in New Guinea (O'Shea, 1996). Use of crab burrows by *F. leucobalia* is noted in a number of natural history accounts (e.g., Kopstein, 1931; Hoesel, 1959; Gow, 1989; Cox, 1991).

Other species of homalopsines utilize particular landscape features as both habitat and as foraging sites, similar to the use of mud lobster mounds by *F. leucobalia*. *Enhydri-*

plumbea in Borneo heavily utilized water-buffalo wallows in pastures and rice paddys (Voris & Karns, 1996). In Thailand, *E. plumbea* used fish bays (excavated pits used to trap fish, typically 9 by 2 m in size) and *Enhydri-*

Conservation. – Although Pasir Ris is a small and disturbed remnant patch of mangrove forest it supports a diverse mangal community that includes apparently healthy populations of four species of homalopsine snakes, including the rare *C. violacea*. Mangrove is recognized as a critically and globally threatened ecosystem, and mangrove habitat is being lost at rates that exceed either tropical rainforests or coral reefs (Valiela et al., 2001). Estimates indicate that at least 35% of the world's mangrove forests have been lost in the last two decades, primarily to mariculture and harvest of forest products. In Singapore it is estimated that mangrove forest has been reduced from 13% of total land area in the 1820's to 0.5% today. From 1983 to 1990 mangrove in Singapore was reduced from 18 km² to 6 km² (Ng & Sivasothi, 1999a; Valiela et al., 2001). In Singapore, there are ongoing efforts to preserve and conserve the remaining patches of mangrove (Wee & Ng, 1994; Ng & Sivasothi, 1999a; L. Chan & N. Sivasothi, personal communication). The Pasir Ris mangrove forest demonstrates the value of conserving even small patches of mangrove forest.

In the early 1800's there was virtually continuous mangrove forest from the northeastern tip of Singapore along the northern and western coasts to the southwestern corner of the island including several large estuaries (Ng & Sivasothi, 1999a) and populations of mangrove snakes were presumably panmictic (free gene flow) throughout this mangrove corridor. As fragmentation of this mangrove border occurred, the predicted consequences would be loss of species richness in small patches, reduction of effective population size in fragments, and increased genetic drift resulting in a decrease in genetic variation within populations and an increase in variation among populations (Meffe & Carroll, 1997).

Mangrove homalopsines are coastal marine species and do not normally venture into open water; however, their saltwater tolerance would allow them to cross marine barriers in the absence of suitable mangrove habitat (Karns et al., 2000). There are large mangrove forests still remaining on some of the islands north of Singapore (Pulau Ubin and Pulau Tekong) and extensive mangrove forest is still found along the Malaysian coast. These may be source populations that supply waif snakes (and other organisms) across the narrow Johor Straits to the fragmented Singaporean mangrove forest. Occasional recruitment of new snakes into Singapore may help explain why the very small Pasir Ris mangrove forest is able to maintain populations of four species of homalopsines. The local biogeography and movements of organisms within and between mangrove patches around the southern tip of the Thai-Malay peninsula deserve further investigation.

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