

A MARK-RECAPTURE STUDY OF A DOG-FACED WATER SNAKE *CERBERUS SCHNEIDERII* (COLUBRIDAE: HOMALOPSIDAE) POPULATION IN SUNGEI BULOH WETLAND RESERVE, SINGAPORE

C. K. Chim

National Institute of Education, Nanyang Technological University, 1 Nanyang Walk, Singapore 637616

Present address: Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227

Email: tmsck@nus.edu.sg

C. H. Diong

National Institute of Education, Nanyang Technological University, 1 Nanyang Walk, Singapore 637616

ABSTRACT. — Ecological traits of a relatively sheltered population of the dog-faced water snake, *Cerberus schneiderii*, were determined or estimated using mark-recapture data. Monthly surveys were conducted at the man-made brackish ponds at Sungei Buloh Wetland Reserve, Singapore throughout the year 2006. Estimates of population density (102 snakes ha⁻¹), snake biomass (4.1 kg ha⁻¹) and relative abundance (5.4 snakes man-hour⁻¹) provided evidence of a large population. Sex ratio was almost 1:1. Snakes from a wide range (145–720 mm SVL) of body size were present. Even though neonates were rarely encountered, 88.7% of adult females have reached the size of sexual maturity (SVL = 336 mm SVL). There was no seasonal variation in the population's size structure, suggesting that recruitment occurred throughout the year. Most of the snakes were sedentary and more than 90% of them remained in the same pond that they were captured for the first time. During low tides, snakes had a tendency of congregating at the relatively deep waters close to the sluice gates and in the network of tidal streams and pools in the man-made ponds. The population exhibited sexual dimorphism, in terms of males having relatively longer tails and females possessing relatively wider heads.

KEY WORDS. — population size, sex ratio, size structure, sexual size dimorphism, spatial ecology, activity patterns

INTRODUCTION

Snakes are upper trophic level predators (see Weatherhead & Blouin-Demers, 2004) and can be especially abundant in natural environments (see Shine, 1986a; Plummer, 1997; Winne et al., 2005). As a result, these reptiles have a direct effect on prey population size. In an extreme case, an introduced species has resulted in the extinction of other animals (Savidge, 1987). Furthermore, snakes are prey to a variety of animals (Greene, 1997; Weatherhead & Blouin-Demers, 2004). Hence, population parameters (e.g., density, sex ratio, and size structure) collected from these ecologically important animals can indicate the general health of an ecosystem. These data are especially useful when the population is managed for harvesting or conservation (Houston & Shine, 1994c; Seigel et al., 1995; Roe et al., 2004; Stanford & King, 2004).

Mark-recapture technique is one of the most common field methods to collect ecological data of snake populations (e.g., Brown & Weatherhead, 1999a; Stanford & King, 2004;

Whiting et al., 2008), even though it requires considerable time and effort (Mertens, 1995). This technique is problematic for snakes that are rare or elusive, but is especially useful for abundant and highly mobile species. Passive integrated transponder (PIT) tags have revolutionised mark-recapture studies of snake populations because, unlike traditional tagging methods such as scale-clipping, they are tiny, reliable and durable (Mills et al., 1995). Although there are other techniques available to estimate abundance, mark-recapture studies have the additional capability of monitoring individual characteristics such as body growth and movements (Krebs, 1989).

Snake population processes are known to be affected by a host of environmental factors, including ambient temperature and rainfall (Brown & Shine, 2002, 2007). In temperate habitats, prey are usually more readily available in the summer, resulting in higher rates in feeding and body growth when compared to colder periods of the year. Seasonal fluctuations in snake activities were also observed in some populations in the tropics, specifically at wet-dry habitats where temperature

is high throughout the year while rainfall experiences extreme seasonality (e.g., Semlitsch et al., 1988; Madsen & Shine, 2000; Akani & Luiselli, 2001). Rainfall affects movements, habitat use, and resource availability in aquatic and semi-aquatic snakes directly by changing water levels (Saint Girons, 1972; Seigel et al., 1987; Houston & Shine, 1994c; Madsen & Shine, 1996; Whiting et al., 1997; Karns et al., 1999–2000). Ecological data are scarce for snake populations in tropical habitats that experience relatively little seasonal variations in both temperature and rainfall.

The island state of Singapore lies just one degree north of the equator, and has a tropical monsoon climate characterised by high ambient temperature (daily mean for each month ranges 26.4–28.3°C) and high rainfall levels (monthly mean ranges 107.4–329.5 mm) throughout the year (Meteorological Services Division, 2009). Preliminary studies showed that the dog-faced water snake, *Cerberus schneiderii*, is one of the most abundant aquatic snakes in mangrove ecosystems in Singapore, including the Sungei Buloh Wetland Reserve (SBWR). Since the brackish man-made ponds of SBWR do not dry up throughout the year, they are a source of abundant and continuous food supply to the snakes that inhabit the wetland. Based on the year-round favourable conditions available for body growth and reproduction, individuals in the *C. schneiderii* population at SBWR were expected to exhibit a wide range of body size, and to persist at high density. One of the objectives of this study is to test this hypothesis. In addition, this study aims to determine sexual dimorphism, growth rate, habitat utilisation, movement, activity patterns, and mortality in the population. Although ecological data are available for two populations of *C. schneiderii* (Jayne et al., 1988; Karns et al., 2002), there exist gaps in our knowledge on population structure (e.g., size structure). Life history traits tend to vary between populations of snakes (Voris & Jayne, 1979; Semlitsch & Moran, 1984; Seigel, 1992; Manjarrez, 1998; Blouin-Demers et al., 2002; Karns et al., 2005), and comparative studies of *C. schneiderii* populations in its range can provide a better understanding on how the species adapts to different environments (Parker & Plummer, 1987).

MATERIAL AND METHODS

Study species. — The dog-faced water snake, *Cerberus schneiderii*, is a member of Homalopsidae, which is a family of Oriental-Australian colubrids. This species was recently separated from *Cerberus rynchops* (Murphy et al., 2012), which was previously believed to occur from India across Southeast Asia to northern Australia and east in the Pacific to the Palau islands, encompassing almost the range of the entire family (Karns et al., 2000; Alfaro et al., 2004; Murphy, 2007). The revised distribution range of *C. schneiderii* includes almost the entire Southeast Asia, with the exception of Myanmar (Murphy et al., 2012). Diets of *C. schneiderii* comprised primarily fish and occasionally crustaceans (Jayne et al., 1988; Voris & Murphy, 2002). Many animals including the mangrove crab (*Scylla serrata*), the tiger shark (*Caracharhinus caustus*), and birds-of-prey (*Haliaeetus leucogaster*, *Haliastur Indus* and *Milvus migrans*) are known

to prey on *C. rynchops* and *C. schneiderii* (Murthy & Rao, 1986; Lye & Timms, 1987; Voris & Jeffries, 1995; Voris & Murphy, 2002). This medium-sized snake (145–720 mm SVL) gives birth throughout the year to 2–12 young (Chim & Diong, 2009). The activity of this nocturnal snake is most prominent during the period 1900–2200 hours and appears to be unaffected by physical environmental conditions such as tidal stages and rain (Jayne et al., 1988; Giesen, 1993; Karns et al., 2002).

Study area. — Field study was conducted at the Sungei Buloh Wetland Reserve (SBWR), which is situated in the north-western coast of the main Singapore island (1°26'49.8"N, 103°43'30.8"E; Fig. 1). Large areas of the wetland were cleared in the 1970s for prawn farming, but farming activities ended in 1989, and the 130-ha wetland was gazetted as a nature reserve in 2002 (Bird et al., 2004). This wetland reserve is dominated by mangroves and also consists of habitats such as brackish ponds, tidal mudflats, secondary forests, dykes, freshwater ponds, and grasslands.

All 10 brackish ponds in SBWR were surveyed for *Cerberus schneiderii* but systematic monthly sampling was conducted in only four of them ('A3-4', 'A6', 'C2-3', and 'C4-5'). The areas of ponds 'A3-4', 'A6', 'C2-3' and 'C4-5' are 7.7, 2.4, 2.5 and 2.8 ha, respectively. Total area of the four sampled ponds is 15.4 ha. Ponds 'A1', 'A2', 'A5', 'C1', 'C8' and 'C10' were not sampled as frequently because of logistic constraints. The ponds are relatively shallow (2 m max. depth) and support a wide variety of fishes (e.g., *Oryzias*

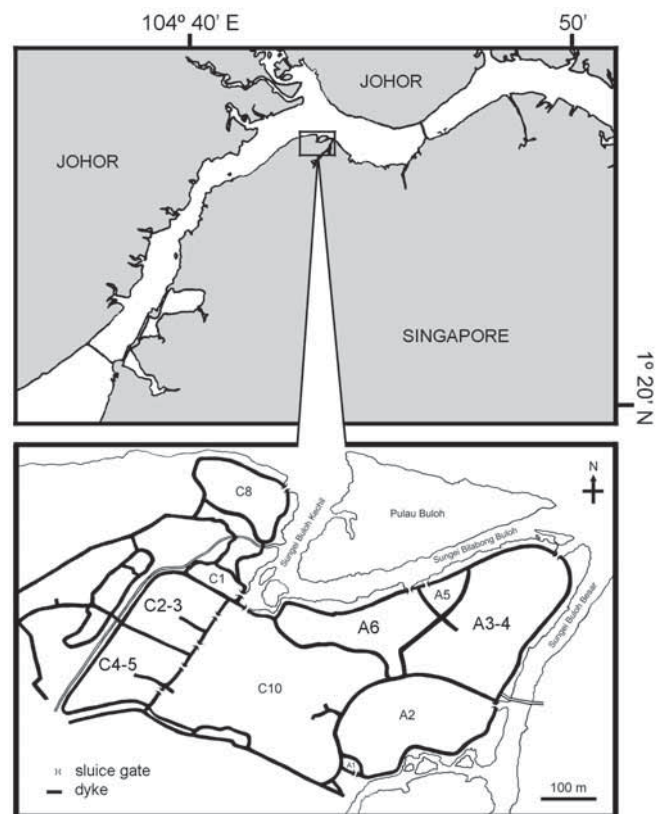


Fig. 1. Map of Sungei Buloh Wetland Reserve showing the locations of the four brackish ponds (A3-4, A6, C2-3 and C4-5) where *Cerberus schneiderii* individuals were collected.

javanicus and *Poecilia* spp.). Dykes separate the ponds from each other. Each pond has one or two openings leading to the sea. Ponds 'A3-4' and 'A6' have their water levels controlled artificially by sluice gates during the bird migratory season between Oct.–Mar. The water levels of ponds 'C2-3' and 'C4-5' are influenced entirely by tidal actions.

Although there are no distinct wet and dry periods, Singapore experiences two monsoon seasons: the Northeast Monsoon (Dec.–Mar.) with a rainfall peak, and the Southwest Monsoon (Jun.–Sep.) that is the drier period of the year. During the study period, mean monthly air temperature ranges 26.5–28.4°C and total monthly rainfall averages 229.4 ± 197.5 mm (range = 83.1–765.9 mm) (Singapore's Meteorological Services Department, National Environment Agency; Fig. 2a).

Data collection. — Brackish ponds were sampled for two hours during spring low tides on four to five consecutive days each month between 15 Jan. – 12 Dec. 2006. Snakes were located with headlights by three to five trained observers after dark, between 1900–2200 hours. Surveys were conducted by walking slowly and systematically in the brackish ponds. The duration of time spent and the number of observers deployed were recorded for each sampling session. As the activity of *C. schneiderii* may be influenced by moonlight as documented in the nocturnal fish-eating snakes, *Acrochordus arafurae* (Houston & Shine, 1994b) and *Lycodonomorphus bicolor* (Madsen & Osterkamp, 1982), sampling was conducted during the same moon phase, which is full moon in this study. As the surface area and profile of water bodies (e.g., tidal pools and tidal streams) change according to water level,

snakes were captured at similar tide levels. Snakes were collected by hand and held in cloth bags (68.5 × 47.0 cm).

For each snake captured, the microhabitat was recorded and later classified as 'in water' (when the snake is submerged in water), 'at water's edge' (when the snake is partially in water and partially on land), 'near water' (when the snake is approx. <1 m away from a water body) or 'on land' (when the snake is approx. >1 m away from a water body). The location of each snake was recorded using a handheld Global Positioning System (GPS) unit (Garmin GPSMAP 60CS). Displacement distance was calculated based on the linear distance between the coordinates of a capture and a subsequent recapture of the same individual. Monthly displacement was based on recaptures in consecutive months. The type of activity observed was also recorded for each capture. Activities were later classified as sedentary, burrowing, crawling, sidewinding, swimming, hunting, feeding, or moulting. A snake was classified as hunting when it was observed attacking a prey while a feeding snake was one that was swallowing a prey.

Snakes were transported to the university's IACUC Animal Research Facility at the National Institute of Education for processing within 24 h of capture. Individual snakes were sexed by manual hemipenial eversion, weighed, measured, palpated abdominally to assess stage of gravidity, collected for their food items by forced regurgitation, and tagged. Abdominal palpation was an accurate method of assessing the reproductive status in *C. schneiderii*, as verified by X-ray images taken from 10 individuals in a preliminary study. To obtain an unbiased true body weight (empty stomach), each snake was abdominally palpated to force it to excrete its faecal contents before it was weighed to the nearest 0.01 g using a top-loading digital scale (Scaltec SBA 51, Germany). Snout-vent length (SVL), tail length (TL) and head width (HW) of each snake was measured to the nearest 1 mm using a tailor's ruler taped to the bench top. Head width was measured at the widest part of the head (Shetty & Shine, 2002). Gravid snakes were not included in data analyses that involved body mass to prevent bias due to extra mass from the clutch. Body scars and tail stubs are indications of failed predation attempts (King, 1986) and were noted for each individual. Those without an intact tail were excluded from data analyses that involved tail length. To reduce measurement error and observer bias, processing of all snakes were performed by the same observer.

Individuals collected between Jan. 2006–Sep. 2006 were each given a unique mark. Prior to marking, each snake was first scanned using a Passive Integrated Transponder (PIT) reader (Trovan GR-250 High-Performance Portable Reader) to check if it had been tagged previously. Snakes were tagged by injecting a sterile PIT tag (Trovan ID 100 Implantable Transponder) subcutaneously into the lateral side of the mid-body. Although each PIT tag weighs only 0.05 g, individuals with body mass less than 10 g were not marked so as to prevent injury during the tagging procedure. Some gravid snakes were not marked because they were retained in captivity to collect data on reproductive output for another

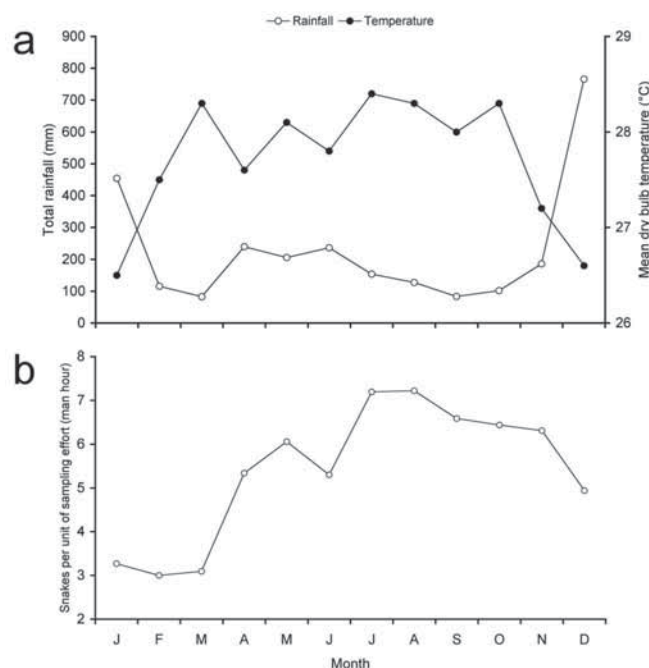


Fig. 2. Physical conditions (rainfall, air temperature) in relation to relative abundance of *Cerberus schneiderii* at Sungei Buloh Wetland Reserve between Jan.–Dec. 2006: a, total rainfall and mean dry bulb temperature at the Changi Meteorological Station, Singapore; b, relative abundance of snakes represented by the relative number of individuals captured (i.e., # captures (# hours × # observers)^{−1}) to standardise for sampling effort, which differed between months.

Table 1. Estimates of population size and biomass were obtained for *Cerberus schneiderii* using multiple recapture methods of Jolly-Seber, Schnabel and six 'close population' models in Program MARK. Densities were calculated using the surface area (15.4 ha) of ponds where snakes were captured. Biomass was calculated using mean snake body mass (39.99 g).

Model	Population size estimate	95% Confidence	AIC	Density (snakes ha ⁻¹)	Biomass (kg ha ⁻¹)
Jolly-Seber	872	575–910	—	57	2.3
Schnabel	1114	1043–1195	—	72	2.9
M ₀	1041	1015–1072	–389.85	68	2.7
M _t	1035	1010–1066	–635.03	67	2.7
M _b	1249	1152–1385	–441.06	81	3.2
M _h	1237	1153–1351	–568.86	80	3.2
M _{th}	1572	1340–1930	–905.60	102	4.1
M _{bh}	1304	1170–1508	–646.39	85	3.4

study. Tagged snakes were returned to their respective sites of capture within five days of capture.

Data analyses. — Mark-recapture data collected from 12 monthly sampling occasions were analysed using the Program MARK 5.1 (G. C. White, Colorado State University, CO, USA) to obtain population size estimates. Six different 'close population' models (Donovan & Alldredge, 2007) were used, each with a set of assumptions. The models are (1) M₀ (constant capture and recapture probabilities), (2) M_t (time variation in capture and recapture probabilities), (3) M_b (behaviour-based capture and recapture probabilities), (4) M_h (individual heterogeneity in capture and recapture probabilities), (5) M_{th} (time variation and individual heterogeneity in capture and recapture probabilities), and (6) M_{bh} (behaviour-based and individual heterogeneity in capture and recapture probabilities). The model with the lowest AIC value was considered the 'best model' because it best explained the variation in the data while using the fewest parameters (Cooch & White, 2006), and was used for population size estimation. For comparison, population size was also estimated by multiple-capture methods of Schnabel and Jolly-Seber (Caughley, 1977; Krebs, 1989). The number of snakes caught for each unit of sampling effort (total hours spent × number of observers deployed) was used as a measurement of relative abundance.

An analysis of covariance (ANCOVA) was performed using General Linear Model (GLM) to test for sexual differences in body mass, head width and tail length with SVL as a covariate. For each ANCOVA, 'SVL × Sex' was used to represent the slopes of the regressed lines of the two sexes, which were first tested for equality. The growth rate of an individual snake was based on the initial SVL (SVL₀) and the SVL after an one-month interval (SVL₁). An analysis of covariance (ANCOVA) was performed to test for sexual differences in growth rate. For each ANCOVA, 'SVL × SVL₀' was used to represent the slopes of the regressed lines of the two sexes, which were first tested for equality.

Statistical tests were performed using the software programmes Minitab 14 (Minitab Inc., State College, PA, USA) and SPSS (Statistical Package for Social Sciences) 11 (SPSS Inc., Chicago, IL, USA). Unless otherwise stated, sample means

were followed by ± s.d. When a χ^2 test with one degree of freedom was performed, the χ^2 value was calculated with Yate's correction of continuity. Variables were tested for homogeneity of variance using Levene's test prior to any parametric test. In cases of unequal variances, count data (e.g., recapture frequency) were square-root transformed before data analysis (see Zar, 1999). A statistically significant level of 0.05 was used throughout.

RESULTS

Population size, density, biomass and relative abundance.

— A total of 914 individuals (466 males and 448 females) were PIT-tagged between Jan.–Sep.2006. The Jolly-Seber and Schnabel methods gave a population size estimate of 872 and 1114 snakes, respectively. Among the six 'close population' models in MARK, the model M_{th} had the lowest AIC value (Table 1). This model provided a population size estimate of 1572 snakes (95% confidence = 1340–1930 snakes) or a density of 102 snakes ha⁻¹. Snake biomass in this population was estimated at 4.1 kg ha⁻¹, based on the mean snake body mass of 39.99 g (n = 1023). Relative abundance was lowest during the first three months of the study, between Jan.–Mar. (range = 3.00–3.27 snakes per man-hour). However, relative abundance increased dramatically to 4.94–7.22 snakes per man-hour between Apr.–Dec. (Fig. 2b). Mean relative abundance was 5.40 snakes per man-hour (n = 12 months).

Recapture frequency. — Among tagged individuals, 56.1% (n = 914) were recaptured at least once during the 12-month study period. Recapture frequency averaged 2.1 ± 1.4 times (n = 513). Individuals were recaptured up to eight times. Most of the individuals were recaptured only once; this constituted 44.4% of recaptures (Fig. 3). The interval between recaptures averaged two months and ranged from 1–10 months.

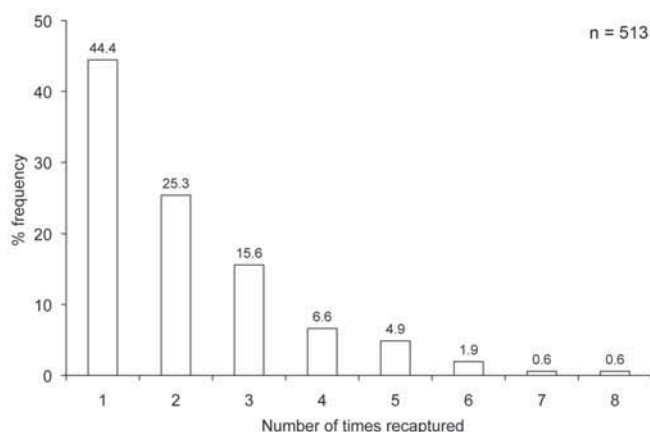
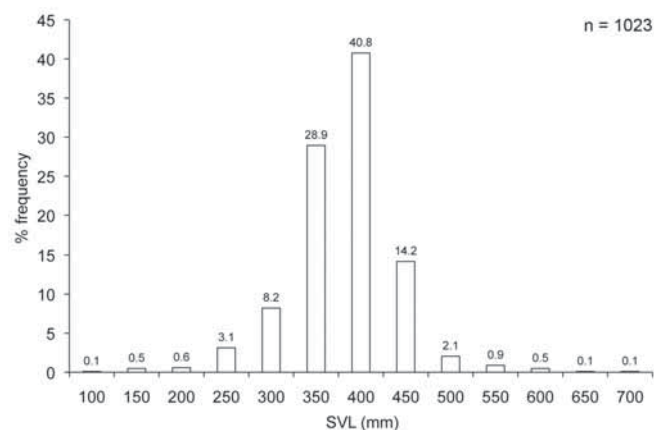
Sex ratio and size structure. — A total of 1023 individuals were captured between Jan.–Oct.2006, of which 501 were males and 522 were females. Sex ratio did not deviate significantly from 1:1 ($\chi^2 = 0.431$, df = 1, P = 0.512). Snout-vent length averaged 407 ± 59 mm (range = 145–720 mm; n = 1023). Body mass averaged 39.99 ± 18.95 g (range = 1.89–220.80 g; n = 1023). The population was dominated by

Table 2. Simple linear regressions of body mass (BM), tail length (TL) and head width (HW) against snout-vent length (SVL) for *Cerberus schneiderii* males (M) and females (F). Variables were \log_{10} -transformed before data analysis.

Variable	Sex	Regression equation	r^2	t	df	P
BM	M	$\text{Log}_{10}(\text{BM}) = 2.850\log_{10}(\text{SVL}) - 5.873$	0.912	107.316	1179	<0.001
	F	$\text{Log}_{10}(\text{BM}) = 2.908\log_{10}(\text{SVL}) - 6.038$	0.936	98.610	673	<0.001
TL	M	$\text{Log}_{10}(\text{TL}) = 1.030\log_{10}(\text{SVL}) - 0.634$	0.836	75.848	1181	<0.001
	F	$\text{Log}_{10}(\text{TL}) = 0.961\log_{10}(\text{SVL}) - 0.533$	0.855	76.377	1013	<0.001
HW	M	$\text{Log}_{10}(\text{HW}) = 1.021\log_{10}(\text{SVL}) - 1.709$	0.755	60.919	1201	<0.001
	F	$\text{Log}_{10}(\text{HW}) = 1.019\log_{10}(\text{SVL}) - 1.637$	0.934	118.113	1059	<0.001

snakes in the 350–400 mm SVL size classes (Figs. 4, 5), which constituted 69.7% of the samples. Snakes in the 100–300 mm SVL and 450–700 mm SVL size classes constituted 12.5% and 17.9% of the population, respectively. There was little monthly variation in population size structure throughout the study period (Fig. 5). The smallest gravid female captured had a SVL of 336 mm. Based on this body size, 88.7% (463 of 522) of individual females encountered in the field had already reached the size of sexual maturity.

Sexual size dimorphism. — Males ($\text{SVL} = 411.66 \pm 46.93$ mm) were generally larger than females ($\text{SVL} = 403.35 \pm 67.85$ mm) ($t = 2.268$, $\text{df} = 1021$, $P < 0.001$). However,

Fig. 3. Percentage frequency distribution of the number of times that tagged individuals of *Cerberus schneiderii* were recaptured.Fig. 4. Percentage frequency distribution of snout-vent length (SVL) of *Cerberus schneiderii*.

females attained larger maximum body size than males in SVL (720 mm vs 602 mm), as well as in body mass (220.80 g vs 117.47 g). In both sexes, body mass, tail length and head width increased linearly with SVL (Table 2; Fig. 6a–c). Males were relatively heavier than females (Table 3a). Tail length increased faster with increasing SVL in males than in females (Table 3b). Tail length contributed an average of 21.80 ± 0.90 % ($n = 1183$) of total body length in males compared to only 18.83 ± 0.93 % ($n = 1015$) in females. Females had relatively wider heads than males (Table 3c). There is a linear relationship between SVL_0 and SVL_1 in both sexes (males: $r^2 = 0.980$, $t = 116.902$, $\text{df} = 286$, $P < 0.001$; females: $r^2 = 0.979$, $t = 97.306$, $\text{df} = 208$, $P < 0.001$). Scatterplots and regression equations of these relationships are given in Fig. 7. Slopes of the regression lines of both sexes are significantly different ($F_{1,494} = 4.862$, $P = 0.028$). The regression line of females has a slightly steeper slope (1.001) compared to that of males (0.972), indicating that SVL increases at a faster rate in females.

Habitat utilisation. — The percentage of snakes found submerged in water, at the water's edge, near water bodies and on land was 49.5%, 41.2%, 1.0% and 8.3%, respectively ($n = 2262$; Fig. 8a). Male ($n = 1206$) and female ($n = 1056$) snakes were mostly found submerged in water (Fig. 8b, c). Females were found in water more frequently than males ($\chi^2 = 6.668$, $\text{df} = 1$, $P = 0.010$) while males were sighted more frequently at the water's edge than females ($\chi^2 = 12.084$, $\text{df} = 1$, $P < 0.001$). The frequencies of snakes found near water ($\chi^2 = 0.270$, $\text{df} = 1$, $P = 0.603$) and on land ($\chi^2 = 2.938$, $\text{df} = 1$, $P = 0.087$) were independent of sex.

Spatial distribution and dispersal. — During low tides, snakes aggregated in large numbers in the four brackish ponds (Fig. 9). Snakes were frequently encountered at the sluice gates where water was relatively deep. In each pond, snakes were also abundant along the perimeter closer to the sluice gates due to the presence of a network of tidal pools and streams. Relatively dry areas such as emerged mudflats were less densely populated with snakes. Some individuals were found on the dyke separating ponds 'A3-4' and 'A2' where there was a small man-made pool that often submerge during high tides.

Most of the tagged snakes (92.7%; $n = 531$) were recaptured in the same ponds where they were first captured. Only 7.3% of individuals were recaptured in a different pond. Most of the

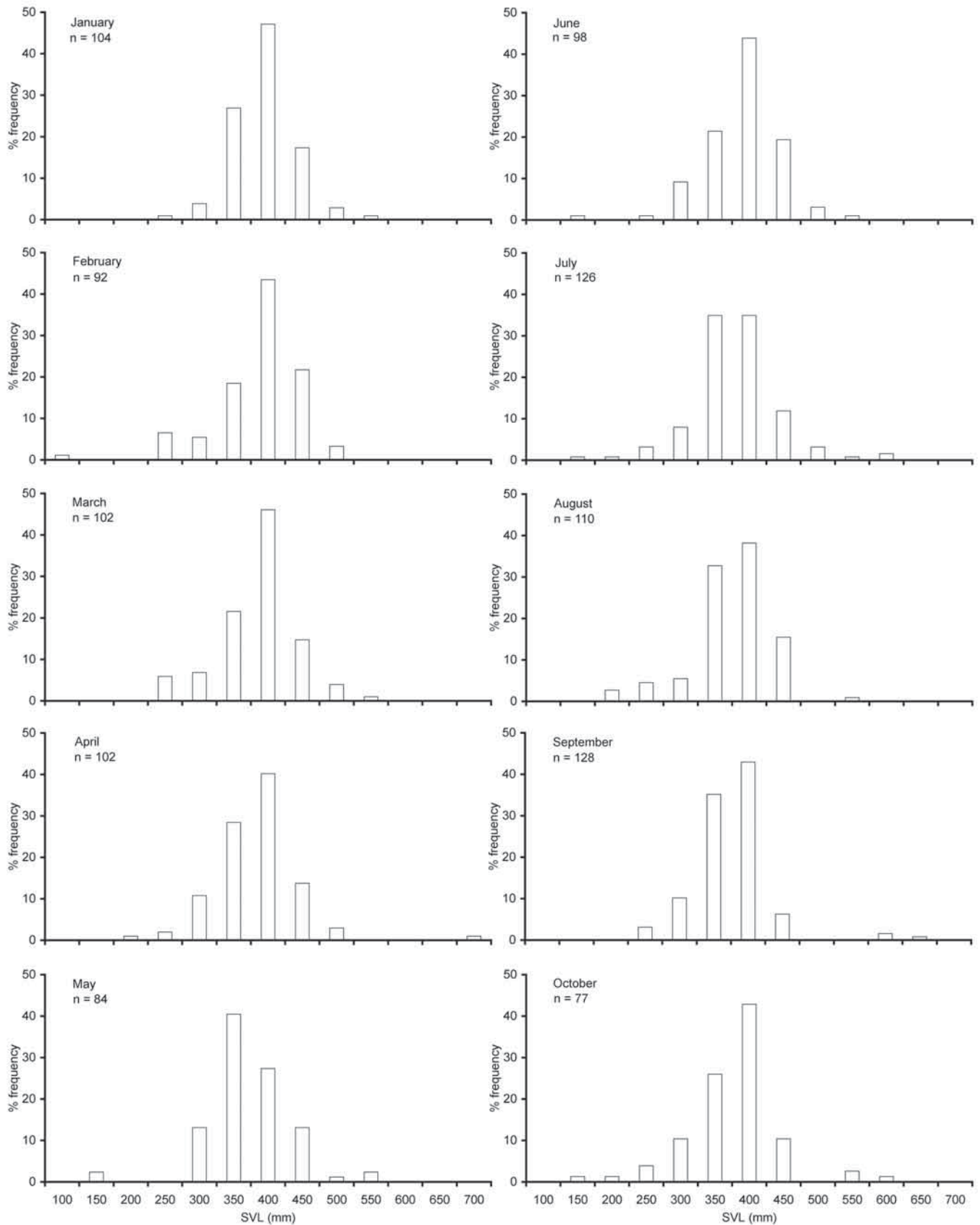


Fig. 5. Percentage frequency distribution of snout-vent length (SVL) of *Cerberus schneiderii* for each month between Jan.-Oct.2006.

Table 3. Results of ANCOVAs for the test of slopes and intercepts of regression lines of (a) body mass, (b) tail length and (c) head width of *Cerberus schneiderii* males and females with snout-vent length (SVL) as covariate. n.s., not significant; sig., significant. Variables were \log_{10} -transformed before data analysis.

Predictor	F	df	P	Result
(a) <i>Body mass</i>				
Sex	30.224	1, 1853	<0.001	Intercepts sig.
$\log_{10}(\text{SVL})$	21929.732	1, 1853	<0.001	
$\text{Sex} \times \log_{10}(\text{SVL})$	2.838	1, 1852	0.092	Slopes n.s.
(b) <i>Tail length</i>				
Sex	3.084	1, 2194	<0.079	
$\log_{10}(\text{SVL})$	11170.027	1, 2194	<0.001	
$\text{Sex} \times \log_{10}(\text{SVL})$	11.505	1, 2194	0.001	Slopes sig.
(c) <i>Head width</i>				
Sex	3908.939	1, 2261	<0.001	Intercepts sig.
$\log_{10}(\text{SVL})$	13579.150	1, 2261	<0.001	
$\text{Sex} \times \log_{10}(\text{SVL})$	0.066	1, 2260	0.797	Slopes n.s.

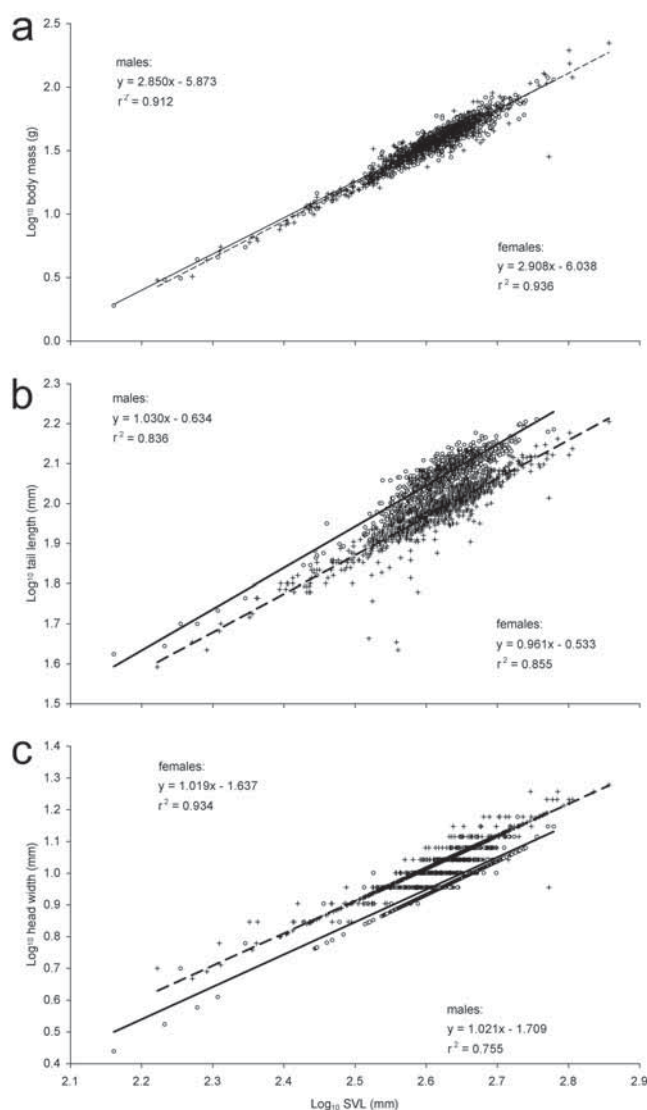


Fig. 6. *Cerberus schneiderii*. Scatterplots and fitted regression lines of: a, body mass; b, tail length; and c, head width against snout-vent length (SVL) for males (○, solid line) and females (+, dashed line). Variables were \log_{10} -transformed.

inter-pond movements were observed between ponds 'A3-4' and 'A6'. Twenty-five (13 males and 12 females) of these individuals moved from 'A6' to 'A3-4', while nine (4 males and 5 females) from 'A3-4' to 'A6' and one male from 'C2-3' to 'A3-4'. Four individuals (two males and two females) moved from 'A6' to 'A3-4' and were recaptured again at 'A6'. Most (74.4%; $n = 43$) of the inter-pond movements occurred between Apr.–Jun. (Table 4). Although snakes moved as much as 851 m away from their previous point of capture, most of them (89.6%; $n = 1087$ recaptures) had a displacement distance of less than 100 m (Fig. 10). Snakes moved an average of 197.63 ± 221.23 m ($n = 32$) in April, which was significantly higher than the mean displacement distance of snakes in the other ten months ($F_{1,499} = 13.781$, $P < 0.001$; Tukey's HSD Post-hoc test).

Examples from snakes that were recaptured between six and eight times showed that individuals were recaptured repeatedly at a small area for as long as 11-months (Fig. 11a–d). A male (PIT #6899BFE), two gravid snakes (#6328212 and #682D1CF) and a non-gravid female (#680C298), with SVL between 345 and 465 mm, spent 8–11 months in pond 'A3-4' and moved a maximum of 21–36 m. There were also

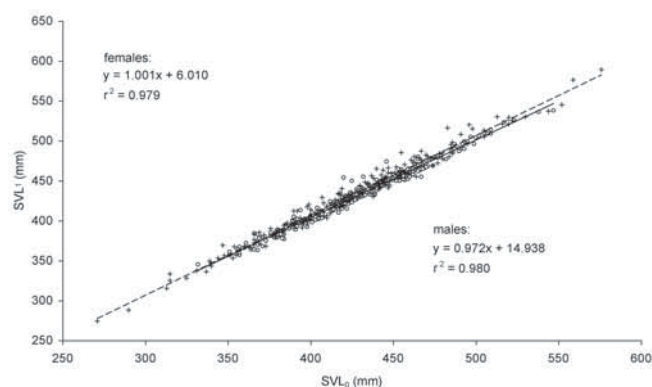
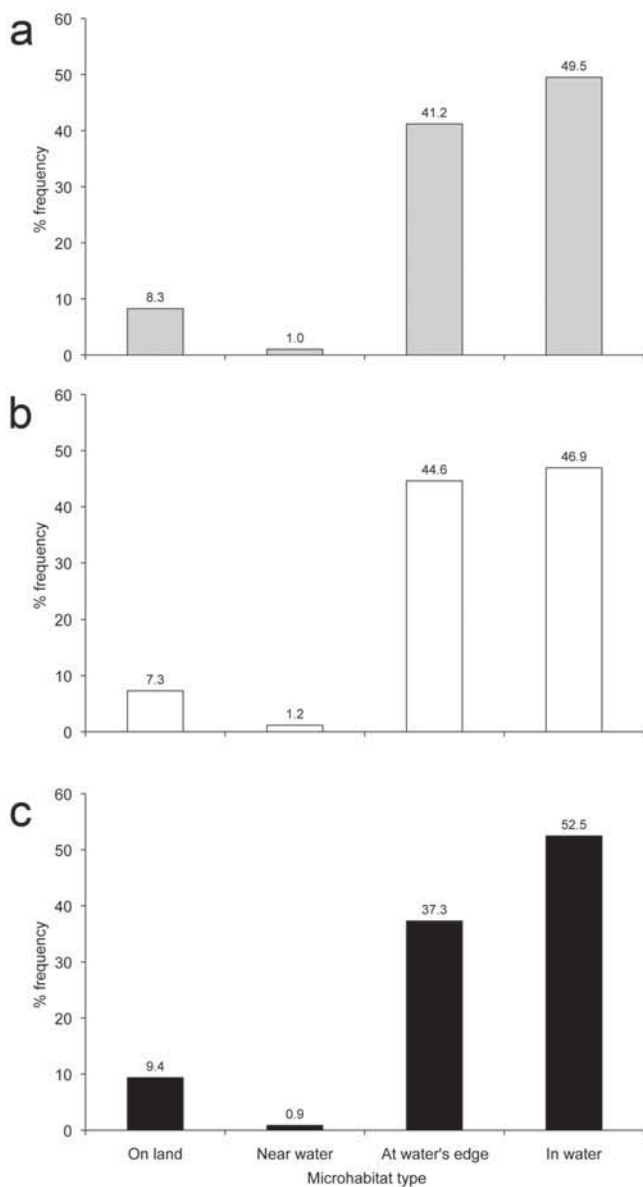


Fig. 7. *Cerberus schneiderii*. Scatterplots and fitted regression lines of initial snout-vent length (SVL₀) against 'SVL after one month' (SVL₁) for males (○, solid line) and females (+, dashed line).

Table 4. Number of inter-pond movements and displacement distances observed in *Cerberus schneiderii* for each month.

Month	Number of inter-pond movements	Capture-recapture linear distance		
		n	Mean \pm S. D. (m)	Range (m)
Feb.	0	40	32.20 \pm 43.17	4–209
Mar.	0	32	25.16 \pm 38.00	2–203
Apr.	17	32	197.63 \pm 221.23	4–851
May	5	45	39.42 \pm 82.61	2–528
Jun.	10	34	55.47 \pm 76.06	3–397
Jul.	4	56	39.11 \pm 38.76	6–217
Aug.	3	73	42.92 \pm 37.90	3–203
Sep.	2	70	33.66 \pm 44.74	2–276
Oct.	2	53	36.62 \pm 43.75	0–209
Nov.	0	31	42.26 \pm 50.41	2–178
Dec.	0	34	47.76 \pm 62.32	2–302
Total	43	500	49.26 \pm 84.11	0–851

Fig. 8. *Cerberus schneiderii*. Percentage frequency distribution of microhabitat types utilised by: a, all snakes (n = 2262); b, males (n = 1206); and c, females (n = 1056).

individuals that travelled for a relatively long distance to a new area and then remained there for up to eight months (Fig. 12a–c). Two males, one with a SVL of 466 mm (#680A445) and another with a 414 mm SVL (#680A2C9), moved from ponds ‘A6’ to ‘A3-4’ and remained in the new area for 5–8 months. A 417 mm (SVL) female (#680A377) that moved away from pond ‘A6’ in Jan. to pond ‘A3-4’ where it remained for seven months and was found to be gravid in Aug. Figure 12d shows a 384 mm (SVL) male (#680CAD9) that remained in the same area in pond ‘A3-4’ for seven months, then moved 148 m to pond ‘A3-4’ before returning to its initial site of capture after one month.

There was no relationship between snake body size (SVL) and their monthly displacement distance for males ($r^2 = 0.003$, $t = -0.853$, $df = 289$, $P = 0.394$), as well as females ($r^2 = 0.004$, $t = 0.888$, $df = 207$, $P = 0.376$). Maximum displacement distance for male snake was 851 m and 555 m for females. However, monthly displacements of males (mean = 48.94 ± 82.92 m, $n = 619$) and females (mean = 49.72 ± 85.93 m, $n = 468$) did not differ ($t = 0.102$, $df = 498$, $P = 0.919$). Among females, monthly displacements of non-gravid snakes (mean = 55.12 ± 98.94 m, $n = 121$) and gravid ones (mean = 42.28 ± 63.69 m, $n = 88$) were also not significantly different ($t = 1.067$, $df = 207$, $P = 0.287$).

Activity patterns. — Although 76.8% of snakes ($n = 2262$ captures and recaptures) were sedentary, the rest were observed performing activities including burrowing, crawling, sidewinding, swimming, hunting, feeding and moulting. No reproductive activities, such as courtship, mating and parturition, were observed in the field. The frequency of snakes observed swimming was significantly higher in males than in females while the frequency of other activities was independent of sex (Table 5).

Mortality and injury. — In spite spending of over 400 man-hours spent in the field, only one dead snake was encountered, which was lying with its ventral facing upwards. The carcass of this female snake looked fresh and did not have any obvious injury. Interestingly, a male snake of a similar body size was resting on top of it, in the same manner as

Table 5. Frequency of activities observed in *Cerberus schneiderii* at time of capture and recapture.

Activity	All snakes (%)	Male (%)	Female (%)	χ^2	P
Sedentary	1738 (76.8)	919 (76.3)	819 (77.5)	0.403	0.525
Burrowing	13 (0.6)	7 (0.6)	6 (0.6)	0.056	0.813
Crawling	13 (0.6)	9 (0.7)	4 (0.4)	0.771	0.380
Sidewinding	1 (0.0)	0 (0.0)	1 (0.1)	0.004	0.948
Swimming	122 (5.4)	78 (6.5)	44 (4.2)	5.446	0.020
Hunting	282 (12.5)	145 (12.0)	137 (13.4)	0.363	0.547
Feeding	90 (4.0)	45 (3.7)	45 (4.3)	0.278	0.598
Moulting	3 (0.1)	2 (0.2)	1 (0.1)	0.013	0.910
Total	2262	1205	1057		

male snakes that aligned their body along the length of the dorsal of female snakes just prior to copulation that we have observed in the laboratory.

Only 5.1% ($n = 914$) of tagged individuals had body scars or stubby tails. Of these, 14 were males whereas 33 were females. The frequency of snakes found to be injured was significantly higher in females than in males ($\chi^2 = 7.596$, $df = 1$, $P = 0.006$).

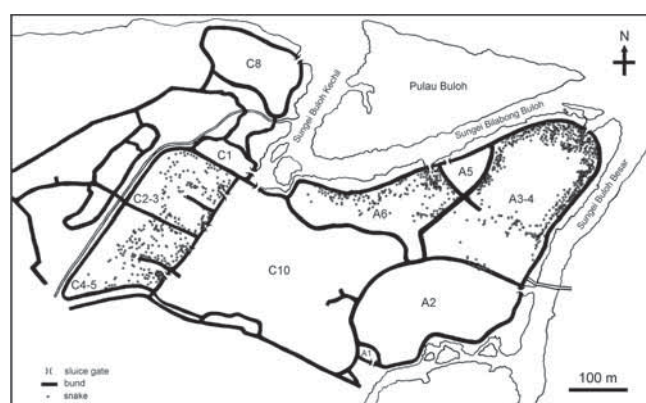


Fig. 9. Map showing the spatial distribution of *Cerberus schneiderii* in four brackish ponds ('A3-4', 'A6', 'C2-3' and 'C4-5') at Sungei Buloh Wetland Reserve. Each position was based on the GPS coordinates recorded for each snake captured ($n = 2258$).

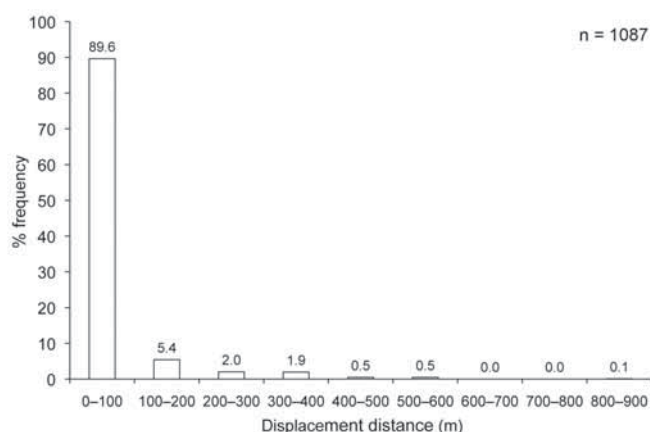


Fig. 10. *Cerberus schneiderii*. Percentage frequency of displacement distance, which was calculated as the shortest distance between two locations that an individual was captured and recaptured.

DISCUSSION

The size of the free-ranging population of *Cerberus schneiderii* at Sungei Buloh Wetland Reserve (SBWR) was estimated on the assumption of a closed system. Migrations and mortalities were rarely observed in the population during the 12-month study. Only one dead snake was found despite spending more than 400 man-hours in the field. Although snakes moved as much as 851 m away from their previous point of capture after one month, 89.6% of capture-recapture distances recorded were less than 100 m. Furthermore, only 7.3% of snakes were found to have travelled from one pond to another pond. The percentage of tagged snakes that were recaptured was high (56%), when compared to the recapture frequency of 20% reported for 35 species of snakes in 44 studies (Parker & Plummer, 1987). The high recapture frequency also allows the mark-recapture study to provide a robust estimate of the *C. schneiderii* population size.

Estimates of population density (102 snakes ha^{-1}), snake biomass (4.1 kg ha^{-1}) and relative abundance (5.4 snakes man-hour $^{-1}$) provided evidence of a large population. Unfortunately, these estimates are not available in other studies, so that meaningful comparisons on the population size of *C. schneiderii* can be made. Instead, studies in Muar, Malaysia (Jayne et al., 1988) and Pasir Ris, Singapore (Karns et al., 2002) provided population size estimates and the number of snakes captured per night, respectively. The population size estimated for SBWR was 1572 snakes (95% confidence = 1340–1930 snakes) whereas three estimates at Muar recorded 374, 426 and 1396 snakes. Even though the average number of snake catchers deployed per night at SBWR was one third of the number deployed at Pasir Ris (4 vs 12 people), the average number of snakes captured per night at SBWR was three times as many as the number captured at Pasir Ris (38 vs 13 snakes).

The abundance of *C. schneiderii* at SBWR was sustained by the presence of suitable microhabitats, a large supply of prey and relatively low levels of predators. Although snakes congregated at the deeper waters near the sluice gates during low tides, snakes were also commonly found at the network of tidal streams and tidal pools in the brackish ponds. These tidal streams and tidal pools retained brackish water and effectively increased the shoreline of the coastal mangrove habitat during low tides, which is necessary for this 'edge'

species to hunt and feed. A large percentage of snakes (41.2%) were observed utilising the water's edge of these water bodies. Snakes were also observed hiding inside crab burrows and rock crevices, which were aplenty in the brackish ponds. The stomach content of some snakes found inside crab burrows contained snapping shrimps, suggesting that this microhabitat is for refuge as well as for feeding. Other aquatic snakes, such as those from the genera *Nerodia* and *Regina*, are also known to utilise burrows of crustaceans (Kofron, 1978). High aquatic snake productivity is also observed in other human-modified wetlands, such as fish ponds and padi fields, and is often attributed to the significant amount of edge habitats that are created in the new landscapes (Fraker, 1970; Godley, 1980; Voris & Karns, 1996; Karns et al., 1999–2000). The ponds where snakes inhabit never dry out, hence food resources are available all year round. The fact that SBWR is a nature reserve also helped to maintain the health of the ecosystem. Prey abundance is a major factor that explained the high densities observed in other piscivorous snake populations (Hebrard & Mushinsky, 1978; Shine, 1986a). The semi-enclosed nature of the brackish ponds of SBWR could have sheltered *C. schneiderii* from aquatic and avian predators, as compared to the relatively open concept of the natural shorelines of the mangrove habitat. The injury frequency of 5.1% observed in the SBWR population is relatively low as compared to the frequencies of 10.3–50.0% documented for water snakes of the genera *Nerodia* and *Regina* in the United States (Mushinsky & Miller, 1993). As a nature reserve, SBWR protects *C. schneiderii* from anthropogenic threats that have been documented in other countries, including harvesting for its skin (Bauchot, 1994; Brooks et al., 2007) and killing it out of fear (Voris & Murphy, 2002).

Snakes in the SBWR population were largely sedentary, as indicated by the short distances travelled by tagged individuals, and also the high percentage (76.8%) of snakes that were not observed engaging in any activities. The low level of mobility in the population was due to the availability of abundant and predicted resources in the habitat. As prey was abundant in the nature reserve, snakes did not have to make spatial shifts in feeding areas in response to prey availability. The high population density and the fact that the snakes did not form breeding congregations suggest that the snakes did not have to travel long distances to seek for mates. As a live-bearing snake, it is not required for females to migrate in search for a nesting site for egg laying. In addition, it is also unnecessary for the female snake to disperse its offspring to other locations, as there were plenty of small prey, such as ricefishes and mollies, available to the neonates. Ambient temperature at the habitat was constantly high throughout the year, thus snakes did not have to migrate to hibernate or thermoregulate. It is, however, important to know that data on the spatial dispersal of *C. schneiderii* were based on capture-recaptures of more than 1-month interval, a time frame that is sufficiently long for snakes to travel long distances and then returned to their previous point of capture, thus resulting in the apparently short displacement distances. An individual that was tagged in this study displayed such a behaviour (Fig. 12d). To verify the homing capability of *C. schneiderii*, the locations of individuals will have to

be monitored at high resolutions using active transmitters. Homing was documented in other aquatic snakes including *Nerodia* (Natrix) sipedon sipedon (see Fraker, 1970) and *Laticauda colubrina* (see Shetty & Shine, 2002).

In contrast to this study's prediction, the *C. schneiderii* population at SBWR appears to exhibit some form of seasonality in snake abundance (Fig. 2b). Snakes were present throughout the year but were most common in Jul.–Nov., a phenomenon that was also observed in a *C. rynchops* population in Bombay, India (Whitaker, 1969). Snake abundance does not appear to follow the changes observed in Singapore's monthly rainfall and temperature. However, relatively low snake abundance coincided with the migratory bird season (Oct.–Mar.) in SBWR, when sluice gates of the ponds 'A3-4' and 'A6' were activated to control water at a low level for up to four consecutive days. It is possible that snakes left the ponds during the artificial drainage of water, and the majority did not manage to return to the ponds after the sluice gates were closed, resulting in a temporary decrease in abundance.

Based on snakes captured in the field, the sex ratio of the SBWR population was almost 1:1. Similarly, wild-caught females collected for a related study did not produce significantly different number of male and female neonates in captivity (Chim & Diong, 2009). This indicates that both sexes have a similar mortality rate. Snakes from a wide range (145–720 mm SVL) of body size were encountered. However, the population was dominated by snakes in the range of 350–450 mm SVL, constituting 69.7% of the population. The dependence on visual survey limited the chances of sampling small-sized snakes, which represented neonates and young juveniles. The lack of a mass emergence of neonates could also explain their apparent low abundance in the population. Large-sized individuals of aquatic snakes including *C. schneiderii* and *A. arafurae*, were known to utilise deeper waters more frequently than small-sized individuals, especially when in search of prey (Shine, 1986b; Jayne et al., 1988; Mills et al., 1995). This size-dependent behaviour suggests that large-sized snakes were apparently rare because they were difficult to spot when in relatively deep waters. Furthermore, large aquatic snakes swim faster than smaller ones (Weatherhead & Robertson, 1992) and thus are less likely to be captured.

Despite the wide geographical distribution and abundance of *C. schneiderii*, data on size structure are available for only one other population, which is also located in Singapore (see Karns et al., 2002). Snakes in the SBWR population had a larger body size than those in the Pasir Ris population (Table 6). The large body size observed in the SBWR population can be attributed to the same factors (i.e., abundant food and the lack of predators) that contributed to the large population size. However, it is important to note the large difference in sample sizes, as the much larger sample size in the present study provided it with a higher probability of capturing individuals from a wider range of body size. Although 88.7% of adult females in the population have reached the size of sexual maturity (SVL = 336 mm), neonates were

rarely encountered in the field. The apparently low level of recruitment does not reflect a low reproductive output, as indicated by the large number of snakes in the population.

Instead, it suggests that reproduction in the population is aseasonal. This observation was supported by the lack of seasonal variation in the population's size structure. Snakes

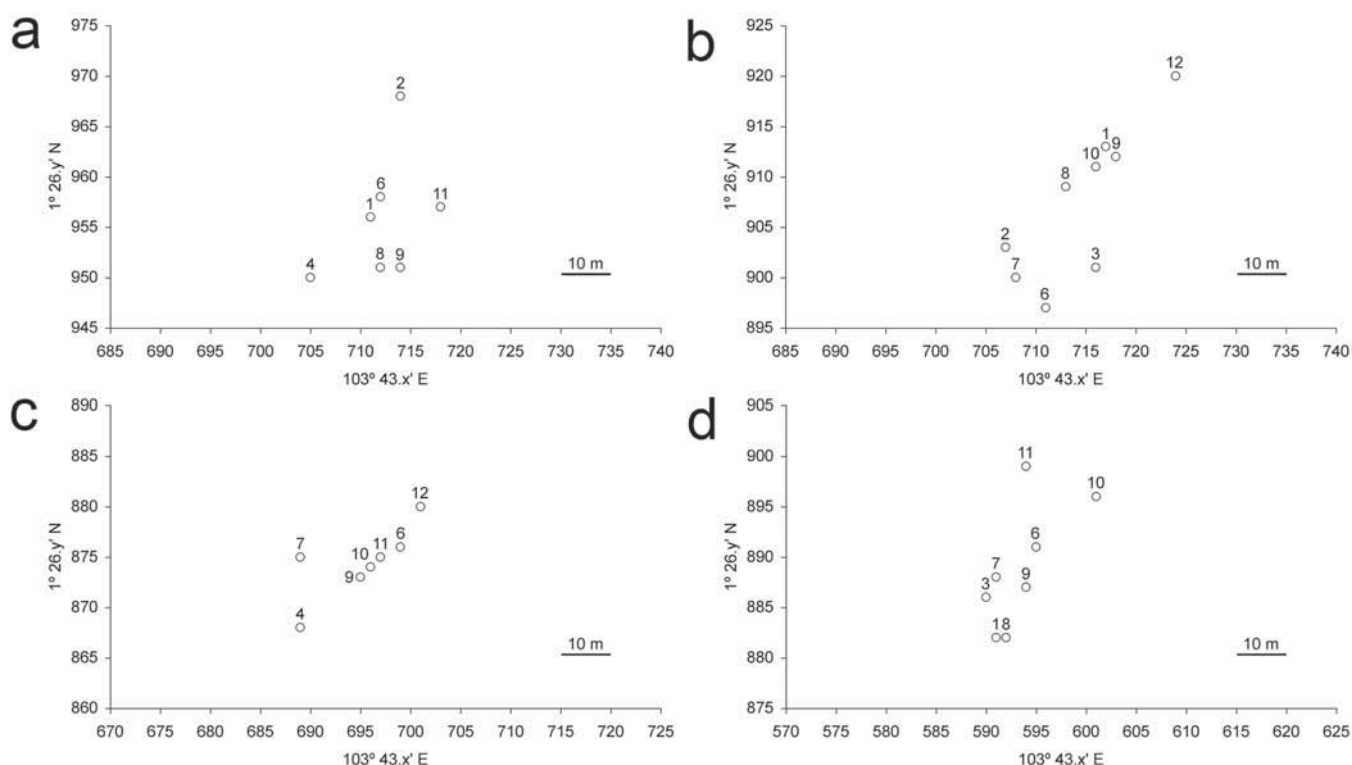


Fig. 11. Locations of *Cerberus schneiderii* individuals with PIT tags: a, #6899BFE; b, #6328212; c, #682D1CF; and d, #680C298. Each position was based on the GPS coordinates recorded from each capture. Number denotes the month of capture (i.e., 1=Jan., 2=Feb.,

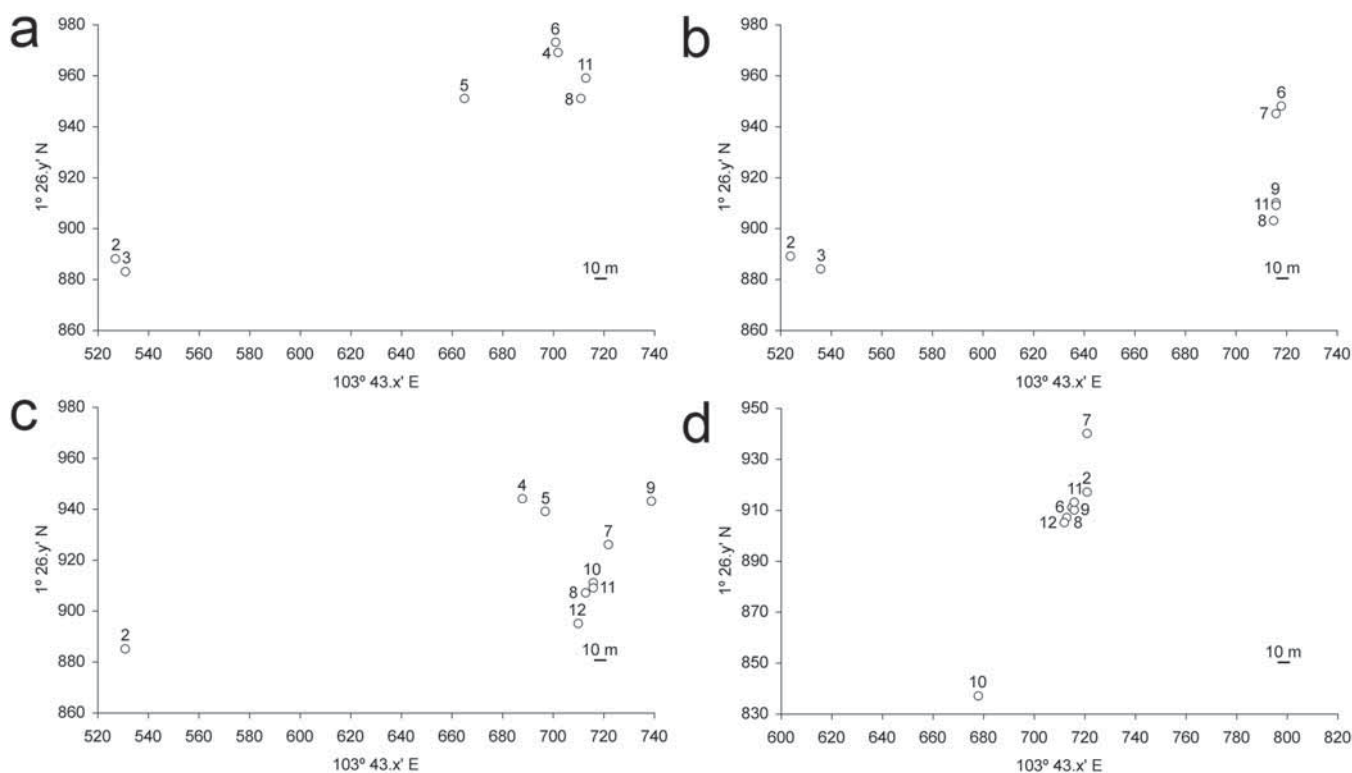


Fig. 12. Locations of *Cerberus schneiderii* individuals with PIT tags: a, #680A445; b, #680A2C9; c, #680A377; and d, #680CAD9. Each position was based on the GPS coordinates recorded from each capture. Number denotes the month of capture (i.e., 1=Jan., 2=Feb., 3=Mar., etc.).

Table 6. Snout-vent length (SVL) and body mass of *Cerberus schneiderii* males and females at Sungei Buloh Wetland Reserve (SBWR) and Pasir Ris Park.

Body size	Males		Females	
	SBWR	Pasir Ris	SBWR	Pasir Ris
<i>SVL (mm)</i>				
Mean	425 ± 1.3	401 ± 11.2	416 ± 2.0	396 ± 7.3
Range	145–602	352–561	167–720	352–549
n	1203	24	1061	41
<i>Body mass (g)</i>				
Mean	42.6 ± 0.36	36.6 ± 2.60	43.5 ± 0.68	36.5 ± 2.35
Range	1.9–117.5	25.1–69.2	3.0–220.8	20.8–89.7
n	1202	24	1059	41

were able to produce offspring all year round instead of during a particular time of the year, because food was abundant throughout the year.

Even though the brackish ponds were dominated by exposed mudflats during low tides, most snakes were observed utilising the limited amount of water bodies available to them. There were very few *C. schneiderii* encountered on land. Snakes occurred primarily inside water bodies (e.g., tidal pools and tidal streams) or at the water's edge, especially where debris or vegetation (e.g., mangrove roots and fallen leaves) provided abundant refuge, but were also encountered occasionally about 1 m away from these water bodies. *Cerberus schneiderii* frequently utilised microhabitats associated with water, probably due to their strong aquatic affinity and also because its diet consists entirely of aquatic prey (pers. obs.). In many instances when snakes were found at the water's edge, they were taking advantage of the shallow water to hunt for relatively small fishes. The water edges are also spatial magnets for other animals (Hunter, 1992) including aquatic snakes such as *A. arafurae* (Shine & Lambeck, 1985), *Enhydryis enhydryis* (Karns et al., 1999–2000), *Enhydryis plumbea* (Voris & Karns, 1996), and *Nerodia sipedon* (Tiebout & Cary, 1987). Snakes were also frequently observed swimming from deeper waters to the water's edge with prey in the mouth, presumably utilising the gentle gradient to aid ingestion of prey. When snakes beached on the banks of tidal pools and tidal streams, they were usually swallowing relatively large prey, which requires relatively long handling time.

The SBWR population exhibits sexual size dimorphism in terms of males having a larger body size and a relatively longer tail while females having a relatively wider head. In species with male combat, males are usually larger than conspecific females (Shine, 1978, 1994). Since combat for mates or territories has not been observed in *C. schneiderii*, males are unlikely to gain fitness advantage directly from an increase in body size. However, limited evidence provided by a study on *N. sipedon*, suggests that male mating success increases with body size (Weatherhead et al., 1995). Data from the present study showed that larger snakes have longer tails. In other snakes, a longer tail provides more space for

hemipenes, resulting in increased copulatory effectiveness and male reproductive success (Semlitsch & Gibbons, 1982; Shine et al., 1999). In the laboratory, *C. schneiderii* females were observed in a number of occasions twisting their bodies vigorously after a male has inserted its densely barbed hemipenis into the female's cloaca, apparently to detach from the male (pers. obs.). Furthermore, a longer tail increases a male's ability to displace the tails of his rivals from the vicinity of the female's cloaca during courtship, and thus increases its mating success (Shine et al., 1999). Thus, it is advantageous for *C. schneiderii* males to possess a relatively large body size because it provides them with reproductive fitness indirectly. Diet data collected from a related study showed that males had relatively small meals in high frequency whereas females had larger meals but in lower frequency (pers. obs.). The relatively wider head in females allow them to consumer larger prey. In many species of aquatic snakes, the females have a larger head or jaw than the males, allowing them to exploit larger prey than males and thus grow faster without foraging more frequently (e.g., Shine, 1986b; Brown & Weatherhead, 1999b; Seigel et al., 2000; Shetty & Shine, 2002).

Female dog-faced water snakes grew at a rate faster than their male counterparts, as observed in other aquatic snakes (e.g., King, 1986; Houston & Shine, 1994a; Brown & Weatherhead, 1999b). With a faster growing rate, females can attain a body size of sexual maturity early, and then produce more clutches in their lifetime. Furthermore, data from a related study showed that *C. schneiderii* females produce more and larger neonates when they grow to a larger body size (Chim & Diong, 2009). Thus, *C. schneiderii* females gain fitness advantage when they can grow at a fast rate.

ACKNOWLEDGEMENTS

We are indebted to the many volunteers, in particular Tay Ywee Chieh, Helen Wong, Ria Tan, and Chan Kwok Wai, who sacrificed their precious time to help in the field. The technical staff at the department of Natural Sciences and Science Education, National Institute of Education provided laboratory assistance. We thank the National Parks Board for

granting permission to use Sungei Buloh Wetland Reserve for our study. The Reserve's officer, Ramakrishnan Kolandavelu, was very helpful. Research protocols were approved by the Nanyang Technological University Institutional Animal Care and Use Committee. This study was funded by the Nanyang Technological University Academic Research Grant RF 06/02 DCH.

LITERATURE CITED

- Akani, G. C. & L. Luiselli, 2001. Ecological studies on a population of the water snake *Grayia mythii* in a rainforest swamp of the Niger Delta, Nigeria. *Contributions to Zoology*, **70**: 139–146.
- Alfaro, M. E., D. R. Karns, H. K. Voris, E. Abernathy & S. L. Sellins, 2004. Phylogeny of *Cerberus* (Serpentes: Homalopsinae) and phylogeography of *Cerberus rynchops*: Diversification of a coastal marine snake in Southeast Asia. *Journal of Biogeography*, **31**: 1277–1292.
- Bauchot, R., 1994. *Snakes: A Natural History*. Sterling Publishing Company, Inc., New York. 220 pp.
- Bird, M., S. Chua, L. K. Fildes, T. S. Teh & J. Lai, 2004. Evolution of the Sungei Buloh-Kranji mangrove coast, Singapore. *Applied Geography*, **24**: 181–198.
- Blouin-Demers, G., K. A. Prior & P. J. Weatherhead, 2002. Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. *Journal of Zoology (London)*, **256**: 1–10.
- Brooks, S. E., E. H. Allison & J. D. Reynolds, 2007. Vulnerability of Cambodian water snakes: Initial assessment of the impact of hunting at Tonle Sap Lake. *Biological Conservation*, **139**: 401–414.
- Brown, G. P. & R. Shine, 2002. Influence of weather conditions on activity of tropical snakes. *Austral Ecology*, **27**: 596–605.
- Brown, G. P. & R. Shine, 2007. Rain, prey and predators: Climatically driven shifts in frog abundance modify reproductive allometry in a tropical snake. *Oecologia*, **154**: 361–368.
- Brown, G. P. & P. J. Weatherhead, 1999a. Demography and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology*, **77**: 1358–1366.
- Brown, G. P. & P. J. Weatherhead, 1999b. Growth and sexual size dimorphism in northern water snakes (*Nerodia sipedon*). *Copeia*, **1999**: 723–732.
- Caughley, G., 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, New York. 234 pp.
- Chim, C. K. & C. H. Diong, 2009. Reproduction in a female population of the dog-faced water snake *Cerberus rynchops* (Homalopsidae) from the Sungei Buloh Wetland Reserve, Singapore. Joint Meeting of Ichthyologists and Herpetologists (JMIH) Abstract Book, Portland, 22–27 Jul. 2009. Abstract 405.
- Cooch, E. & G. White, 2006. *Program MARK: A Gentle Introduction (Fourth edition)*. <http://www.phidot.org/software/mark/docs/book>. (Accessed 2 Sep. 2006).
- Donovan, T. M. & M. Alldredge, 2007. *Exercises in Estimating and Monitoring Abundance*. <http://www.uvm.edu/envr/vtcfwru/spreadsheets/abundance/abundance.htm>. (Accessed 28 Jul. 2007).
- Fraker, M. A., 1970. Home range and homing in the watersnake, *Natrix sipedon sipedon*. *Copeia*, **1970**: 665–673.
- Giesen, W., 1993. Mass feeding by dog-faced water snakes (*Cerberus rynchops*) on Sumatran mudflats. *Malayan Nature Journal*, **46**: 265–266.
- Godley, J. S., 1980. Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. *Ecological Monographs*, **50**: 411–436.
- Greene, H. W., 1997. *Snakes: The Evolution of Mystery in Nature*. University of California Press, Berkeley. 351 pp.
- Hebrard, J. J. & H. R. Mushinsky, 1978. Habitat use by five sympatric water snakes in a Louisiana swamp. *Herpetologica*, **34**: 306–311.
- Houston, D. & R. Shine, 1994a. Low growth rates and delayed maturation in Arafura filesnakes (Serpentes: Acrochordidae) in tropical Australia. *Copeia*, **1994**: 726–731.
- Houston, D. & R. Shine, 1994b. Movement and activity patterns of Arafura filesnakes (Serpentes: Acrochordidae) in tropical Australia. *Herpetologica*, **50**: 349–357.
- Houston, D. & R. Shine, 1994c. Population demography of Arafura filesnakes (Serpentes: Acrochordidae) in tropical Australia. *Journal of Herpetology*, **28**: 273–280.
- Hunter, M. L. Jr., 1992. *Wildlife, Forests and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice Hall, Englewood Cliffs, New Jersey.
- Jayne, B. C., H. K. Voris & K. B. Heang, 1988. Diet, feeding behavior, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana*, **50**: 1–15.
- Karns, D. R., J. C. Murphy, H. K. Voris & J. S. Suddeth, 2005. Comparison of semi-aquatic snake communities associated with the Khorat Basin, Thailand. *The Natural History Journal of Chulalongkorn University*, **5**: 73–90.
- Karns, D. R., A. O'Bannon, H. K. Voris & L. A. Weigt, 2000. Biogeographical implications of mitochondrial DNA variation in the Bockadam snake (*Cerberus rynchops*, Serpentes: Homalopsinae) in Southeast Asia. *Journal of Biogeography*, **27**: 391–402.
- Karns, D. R., H. K. Voris, T. Chan-ard, J. C. Goodwin & J. C. Murphy, 1999–2000. The spatial ecology of the rainbow water snake, *Enhydryn enhydryn* (Homalopsinae) in Southern Thailand. *Herpetological Natural History*, **7**: 97–115.
- Karns, D. R., H. K. Voris & T. G. Goodwin, 2002. Ecology of Oriental-Australian rear-fanged water snakes (Colubridae: Homalopsinae) in the Pasir Ris Park Mangrove Forest, Singapore. *Raffles Bulletin of Zoology*, **50**: 487–498.
- King, R. B., 1986. Population ecology of the Lake Erie Water Snake, *Nerodia sipedon insularum*. *Copeia*, **1986**(3): 757–772.
- Kofron, C. P., 1978. Foods and habits of aquatic snakes (Reptilia, Serpentes) in a Louisiana Swamp. *Journal of Herpetology*, **12**: 543–554.
- Krebs, C. J., 1989. *Ecological Methodology*. Harper and Row Publishers, New York. 654 pp.
- Lye, J. M. & G. J. Timms, 1987. Predation on aquatic snakes by sharks from northern Australia. *Copeia*, **1987**: 802–803.
- Madsen, T. & M. Osterkamp, 1982. Notes on the biology of the fish-eating snake *Lycodonomorphus bicolor* in Lake Tanganyika. *Journal of Herpetology*, **16**: 185–188.
- Madsen, T. & R. Shine, 1996. Determinants of reproductive output in female water pythons (*Liasis fuscus*: Pythonidae). *Herpetologica*, **52**: 146–159.

- Madsen, T. & R. Shine, 2000. Rain, fish and snakes: Climatically driven population dynamics of Arafura filesnakes in tropical Australia. *Oecologia*, **124**: 208–215.
- Manjarrez, J., 1998. Ecology of the Mexican garter snake (*Thamnophis eques*) in Toluca, Mexico. *Journal of Herpetology*, **32**: 464–468.
- Mertens, D., 1995. Population structure and abundance of grass snakes, *Natrix natrix*, in Central Germany. *Journal of Herpetology*, **29**: 454–456.
- Meterological Services Division, 2009. *WEATHERwise* Singapore. Meterological Services Division, National Environment Agency, Singapore. <http://app2.nea.gov.sg/data/cmsresource/20090721544571208250.pdf>. (Accessed 10 Jun.2013).
- Mills, M. S., C. J. Hudson & H. J. Berna, 1995. Spatial ecology and movements of the brown water snake (*Nerodia taxispilota*). *Herpetologica*, **51**: 412–423.
- Murphy, J. C., 2007. *Homalopsid Snakes: Evolution in the Mud*. Kreiger Publishing Company, Florida. 260 pp.
- Murphy, J. C., H. K. Voris & D. R. Karns, 2012. The dog-faced water snakes, a revision of the genus *Cerberus* Cuvier, (Squamata, Serpentes, Homalopsidae), with the description of a new species. *Zootaxa*, **3484**: 1–34.
- Murthy, T. S. N. & K. V. R. Rao, 1986. Observations on some snake-eating birds of the Chilka Lagoon, Orissa. *Journal of the Bombay Natural History Society*, **85**: 620.
- Mushinsky, H. R. & D. E. Miller, 1993. Predation on water snakes: Ontogenetic and interspecific considerations. *Copeia*, **1993**: 660–665.
- Parker, W. S. & M. V. Plummer, 1987. Population ecology. In: Seigel, R. A., J. T. Collins & S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill, New York. Pp. 253–301.
- Plummer, M. V., 1997. Population ecology of green snakes (*Opheodrys aestivus*) revisited. *Herpetological Monographs*, **11**: 102–123.
- Roe, J. H., B. A. Kingsbury & N. R. Herbert, 2004. Comparative water snake ecology: Conservation of mobile animals that use temporally dynamic resources. *Biological Conservation*, **118**: 79–89.
- Saint Girons, H., 1972. Les serpents du Cambodge. *Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie*, **74**: 1–170.
- Savidge, J. A., 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology*, **68**: 660–668.
- Seigel, R. A., 1992. Ecology of a specialized predator: Regina grahmi in Missouri. *Journal of Herpetology*, **26**: 32–37.
- Seigel, R. A., N. B. Ford & L. A. Mahrt, 2000. Ecology of an aquatic snake (*Thamnophis marcianus*) in a desert environment: Implications of early timing of birth and geographic variation in reproduction. *American Midland Naturalist*, **143**: 453–462.
- Seigel, R. A., J. W. Gibbons & T. K. Lynch, 1995. Temporal changes in reptile population: Effects of a severe drought on aquatic snakes. *Herpetologica*, **51**: 424–434.
- Seigel, R. A., M. M. Huggins & N. B. Ford, 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, **73**: 481–485.
- Semlitsch, R. D. & J. W. Gibbons, 1982. Body size dimorphism and sexual selection in two species of water snakes. *Copeia*, **1982**: 974–976.
- Semlitsch, R. D. & G. B. Moran, 1984. Ecology of the redbelly snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. *The American Midland Naturalist*, **111**: 33–40.
- Semlitsch, R. D., J. H. K. Pechmann & J. W. Gibbons, 1988. Annual emergence of juvenile mud snakes (*Farancia abacura*) at aquatic habitats. *Copeia*, **1988**: 243–245.
- Shetty, S. & R. Shine, 2002. Sexual divergence in diets and morphology in Fijian sea snakes *Laticauda colubrina* (Laticaudinae). *Austral Ecology*, **27**: 77–84.
- Shine, R., 1978. Sexual size dimorphism and male combat in snakes. *Oecologia*, **33**: 269–277.
- Shine, R., 1986a. Ecology of a low-energy specialist: Food habits and reproductive biology of the Arafura filesnake (Acrochordidae). *Copeia*, **1986**: 424–437.
- Shine, R., 1986b. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia (Berlin)*, **69**: 260–267.
- Shine, R., 1994. Sexual size dimorphism in snakes revisited. *Copeia*, **1994**: 326–346.
- Shine, R. & R. Lambeck, 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes: Acrochordidae). *Herpetologica*, **41**: 351–361.
- Shine, R., M. M. Olsson, I. T. Moore, M. P. LeMaster & R. T. Mason, 1999. Why do male snakes have longer tails than females? *Proceedings of the Royal Society B: Biological Sciences*, **266**(1434): 2147–2151.
- Stanford, K. M. & R. B. King, 2004. Growth, survival and reproduction in a northern Illinois population of the plains gartersnake, *Thamnophis radix*. *Copeia*, **2004**: 465–478.
- Tiebout, H. M. III & J. R. Cary, 1987. Dynamic spatial ecology of the water snake, *Nerodia sipedon*. *Copeia*, **1987**: 1–18.
- Voris, H. K. & B. C. Jayne, 1979. Growth, reproduction and population structure of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia*, **1979**: 307–318.
- Voris, H. K. & W. B. Jeffries, 1995. Predation on marine snakes: A case for decapods supported by new observations from Thailand. *Journal of Tropical Ecology*, **11**: 569–576.
- Voris, H. K. & D. R. Karns, 1996. Habitat utilization, movements, and activity patterns of *Enhydris plumbea* (Serpentes: Homalopsinae) in a rice paddy wetland in Borneo. *Herpetological Natural History*, **4**: 111–126.
- Voris, H. K. & J. C. Murphy, 2002. The prey and predators of homalopsine snakes. *Journal of Natural History*, **36**: 1621–1632.
- Weatherhead, P. J. & G. Blouin-Demers, 2004. Understanding avian nest predation: Why ornithologists should study snakes. *Journal of Avian Biology*, **35**: 185–190.
- Weatherhead, P. J. & I. C. Robertson, 1992. Thermal constraints on swimming performance and escape response of northern water snakes (*Nerodia sipedon*). *Canadian Journal of Zoology*, **70**: 94–98.
- Weatherhead, P. J., F. E. Barry, G. P. Brown & M. R. L. Forbes, 1995. Sex ratios, mating behavior and sexual size dimorphism of the northern water snake, *Nerodia sipedon*. *Behavioral Ecology and Sociobiology*, **36**: 301–311.
- Whitaker, R., 1969. The dog-faced watersnake (*Cerberus rynchops*) in the Bombay area and notes on its habits. *Journal of the Bombay Natural History Society*, **66**: 386.

- Whiting, M. J., J. R. Dixon & B. D. Greene, 1997. Spatial ecology of the concho water snake (*Nerodia harteri paucimaculata*) in a large lake system. *Journal of Herpetology*, **31**: 327–335.
- Whiting, M. J., J. R. Dixon, B. D. Greene, J. M. Mueller, O. W. Thornton Jr., J. S. Hatfield, J. D. Nichols & J. E. Hines, 2008. Population dynamics of the concho water snake in rivers and reservoirs. *Copeia*, **2008**: 438–445.
- Winne, C. T., M. E. Dorcas & S. M. Poppy, 2005. Population structure, body size, and seasonal activity of black swamp snakes (*Seminatrix pygaea*). *Southeastern Naturalist*, **4**: 1–14.
- Zar, J. H., 1999. *Biostatistical Analysis*. 4th Edition). Prentice Hall, New Jersey. 663 pp.