



Niche partitioning and population structure of sympatric mud snakes (Homalopsidae) from Bangladesh

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Despite the greatest diversity of snakes being in the tropics, detailed ecological studies are rare, especially in tropical Asia. We studied the ecology of a coastal marine homalopsid (rear-fanged, aquatic snakes) assemblage in southeastern Bangladesh. Data were collected on community structure, resource partitioning (diet and habitat), body size and sexual size dimorphism. A total of 653 specimens belonging to three species were collected: *Cerberus rynchops* (81% of total capture), a medium-sized piscivorous snake, found to be the most abundant species in the study site followed by two crustacean eaters, *Gerada prevostiana* (13%) and *Fordonia leucobalia* (6%). The three species were relatively similar in terms of body size but were inconsistent with each other both in terms of morphological patterns and demography characteristics, with sex-ratio being equal in two species but female-biased in *G. prevostiana*. There was no apparent non-random resource partitioning along the microhabitat axis but a clear pattern of niche partitioning was observed along the food axis. Despite the very unusual evolutionary history of the Homalopsidae inside the group of the Colubroidea, our snake assemblage very closely resembled other communities of snakes worldwide.

Key words: Bangladesh, food niche, habitat, homalopsidae, mud snakes, population structure

INTRODUCTION

Snakes are among the few vertebrate groups which typically partition the food resource when sympatric (e.g., Luiselli, 2006a; Halstead et al., 2008; Steen et al., 1963), whereas most of the other groups usually partition the spatial resource (e.g., Pianka, 1986; McDonald, 2002). However, the relevant snake literature is taxonomically biased (most studies are on European and North-American Viperidae), with no information available concerning Typhlopidae and Homalopsidae (Luiselli, 2006a).

Homalopsidae includes some of the most atypical extant snakes. They are aquatic, rear-fanged species inhabiting marine, brackish and freshwater environments in the eastern hemisphere, roughly from the river Indus in Pakistan to Queensland in Australia (Murphy, 2007). They belong to the monophyletic Colubroidea group, and are characterised by several adaptations to both aquatic and terrestrial lifestyles. These adaptations include the presence of valvular nostrils, a shallow notch in the rostral scale and the ability to extend the glottis to the internal nares with nostrils and mouth forming a watertight seal (Murphy, 2007). The body architecture of these snakes is surprisingly variable; some species have a very short tail

(<8% of the snout-vent length), whereas others exhibit long tails (up to 59% of the body length; Murphy, 2007).

Despite their wide distribution and sometimes locally abundant occurrence in rice fields and other human-dominated environments, the ecological literature available on this group of snakes is still scarce (e.g., Berry & Lim, 1967; Murphy et al., 1999; Murphy, 2007). In this paper we aim to (i) provide ecological data on the community structure, food and habitat resource partitioning, and body size and sexual size dimorphism in an assemblage of homalopsid snakes from Bangladesh, and (ii) discuss these data in the light of general findings of community ecology of snakes (e.g., Luiselli 2006a).

MATERIALS AND METHODS

Study area

Our study was conducted at Sonadia Island, located in the far southeastern corner of Bangladesh, approximately nine kilometres northwest of Cox's Bazaar town. Sonadia is a ~4,900 ha barrier island separated from Moheshkhali Island by a tidal canal. The elevation of this island ranges from 0–4 metres and the depth of the mud varies from a few centimetres to few metres (CWBMP, 2006). The climate of the island is moist tropical maritime with high

temperatures year round. The island receives high rainfall concentrated in the monsoon period (June–September) and a dry period from November–March (CWBMP, 2006; average recorded annual rainfall 2,867–4,684 mm). The mean annual maximum and minimum temperatures recorded were recorded as 30.3–33°C and 19.3–22.4°C, respectively between 1987 and 1996 (CWBMP, 2006).

Sonadia Island comprises of a wide variety of habitat types, including mudflats, mangroves, intertidal mixed grassy vegetation, salt marshes, sand dunes, lagoons and sandy beaches (Chowdhury et al., 2011), and supports some of the last remaining patches of natural mangrove forest found in southeastern Bangladesh. The mangrove area is dominated by *Avicennia officinalis*, *A. marina*, *A. alba*, *Sonneratia apetala*, *Aegicerus corniculatum*, *Ceriops decandra* and *Aegialitis rotundifolia*. The salt marsh mostly consists of *Porteresia coarctata* and *Myristichia wighthenia* (CWBMP, 2006). We categorised the whole island into five different habitat types: 1) Open mudflat: open mudflat with no vegetation adjacent to tidal rivers inundated during high tides twice daily; a mean mud depth of 30 cm; 2) Mangrove mudflat: adjacent to open mudflats with a mean mud depth of 30 cm with densely planted secondary mangrove trees; 3) Intertidal mixed grassy vegetation: early succession mangrove forest dominated by mangrove saplings of less than 30 cm and mangrove shrubs and bushes with an average mud depth of 5 cm, mean elevation of 4 m asl. This area is inundated by flood water only during the spring tides; 4) Creek: narrow tidal creeks that passes through different habitat types; and 5) Salt marsh: grassy marshes adjacent to open and mangrove mudflats.

We conducted snake surveys at Sonadia Island on a total of 20 field days between 15 June and 17 August 2012. Snakes were surveyed during low tides during the day and at night. Snakes were collected using two different

methods commonly used for surveying aquatic snakes (McDiarmid et al., 2012): 1) opportunistically collected (OC) from the fishermen's stake net placed in the middle of a tidal canal during spring low tides, and 2) active searching in the intertidal zones using visual encounter survey techniques (VES, Doan, 2003), in two rectangular plots of dimension 1000x225 m and 550x700 m located near a fishing village. The dimension and location of the study plots were selected based on logistics and accessibility. The routes for VES inside those plots were selected using randomised walk designs (McDiarmid et al., 2012) and all efforts were made to cover different microhabitat types. In each plot, two surveyors walked the area at a standard pace visually examining the habitat for snakes.

Snakes were captured by hand, placed in snake bags and taken back to the field station for detailed data collection. Snakes captured during the day were processed the same evening and those captured at night were processed the following day. Diet was examined by palpating the snakes' abdomen until regurgitation of ingested food or defecation occurred. Food items were preserved in ethanol for later identification. Snakes were measured for snout-vent length (SVL) and tail length (TL) to the nearest 1 cm using a measuring tape, head length (HL) and head width (HW) to the nearest 0.5 cm using a slide calipers; and weighed to the nearest 1 g using a digital scale. Each snake was sexed using cloacal probing and individually marked by ventral scale-clipping following the protocol given by Dorcas & Wilson (2009). All snakes were released at the site of capture within 24 hours.

All statistical tests were two-tailed, with alpha set at 0.05. Eventual departure of adult sex-ratio from equality was evaluated by an observed-versus-expected χ^2 test; mean body size differences between sexes were assessed

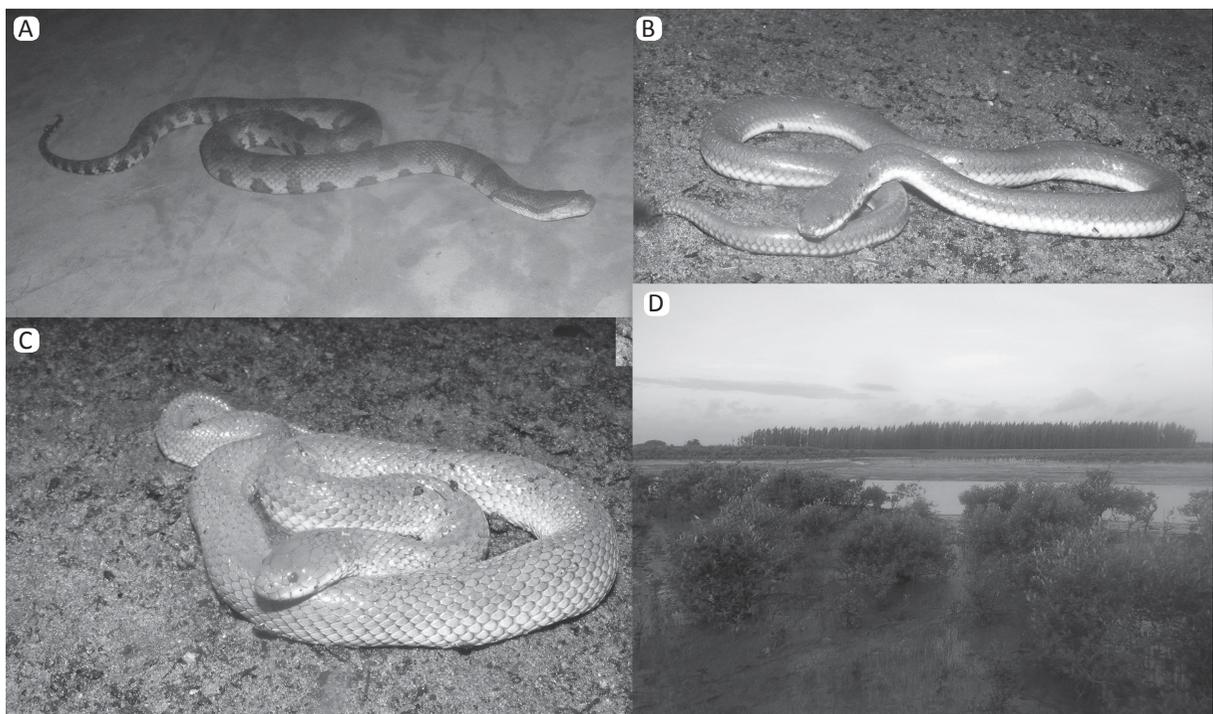


Fig. 1. The three study species: *Cerberus rynchops* (A), *Gerarda prevostiana* (B), *Fordonia leucobalia* (C) and their typical habitat (D).

by a Student *t*-test (means are followed by ±1 standard deviation). A one-way ANCOVA was used in order to test whether, for a given body length, males differed from females in tail length; a few evident outliers were removed from analyses due to the risk of biasing the analyses.

Habitat niche overlap between species was calculated by Pianka's (1986) overlap formula:

$$O_{xy} = \frac{\sum_{i=1}^n p_{xi} p_{yi}}{(\sum_{i=1}^n p_{xi}^2 \sum_{i=1}^n p_{yi}^2)^{1/2}}$$

where p_{xi} is the proportional utilisation of habitat *i* by form *x* and p_{yi} the proportional utilisation of habitat *i* by form *y*. Both indexes range from 0 (no prey in common in the habitat spectrum) to 1 (same habitat spectrum). We randomised the original species utilisation matrices by shuffling the original value among habitat resource states. We used two randomisation algorithms (RA2 and RA3) from Lawlor (1980), as they are particularly robust for niche overlap studies (Gotelli & Graves, 1996). RA2 tests for structure in the generalist-specialist nature of the resource utilisation matrix by conserving guild structure (i.e. keeping the zero states of the observed matrix), destroying observed niche breadth (Gotelli & Graves, 1996). RA3 tests for guild structure by conserving the niche breadth for each species, destroying the guild structure manifested by the resource utilisation matrix's zero structure (Gotelli & Graves, 1996). For each pair of species, 30,000 random Monte Carlo permutations were generated. Actual niche overlap values were then compared to the distributions of expected values. Structure was assumed when p (observed ≤ expected)

Table 1. Summary of the diet data recorded in the present study, and in comparison with the only other available study on resource partitioning patterns in the three studied species (Voris & Murphy, 2002).

Species	Diet (This Study)	Diet (Voris & Murphy, 2002)
<i>Fordonia leucobalia</i>	Crabs (Hardshelled) <i>Scylla olivacea</i> (n=2) <i>Ocyrode macrocera</i> (n=2) Gastropod (Cerithidae sp.) Unidentified crabs (n=2)	Crabs <i>Sarmiatium germaini</i> (Grapsidae), <i>Macrophthalmus</i> sp. Sesarmine crab (Grapsidae) <i>Dotilopsis brevitarsis</i> (Ocyropodidae) (3) <i>Uca</i> sp. (Ocyropodidae) ('many') <i>Thalassina anomala</i> (Thalassinidae)
<i>Gerarda prevostiana</i>	Crab (soft shelled) Unidentified (n=1)	<i>Dotilopsis</i> sp. (Ocyropodidae), crabs (4)
<i>Cerberus rynchops</i>	Fish <i>Apocryptes bato</i> (n=2) <i>Glossogobius giuis</i> (n=1) <i>Cirrhinius reba</i> (n=1) <i>Acentrogobius caninus</i> (n=1) <i>Acentrogobius</i> sp. (n=3) Unidentified Gobies (n=4) <i>Platycephalus indicus</i> (n=1) Anguillidae sp. (n=1)	<i>Caranx ire</i> <i>Amblygobius</i> sp., <i>Synodus evermanni</i> , <i>Alpheus</i> sp. (Alpheidae) Eels, gobies, apogonids, siganids Oxydercine gobies, other gobies, catfish, mullet <i>Periophthalmus</i> sp. <i>Arius</i> sp. (2), Eleotridae, <i>Tilapia mossambica</i>

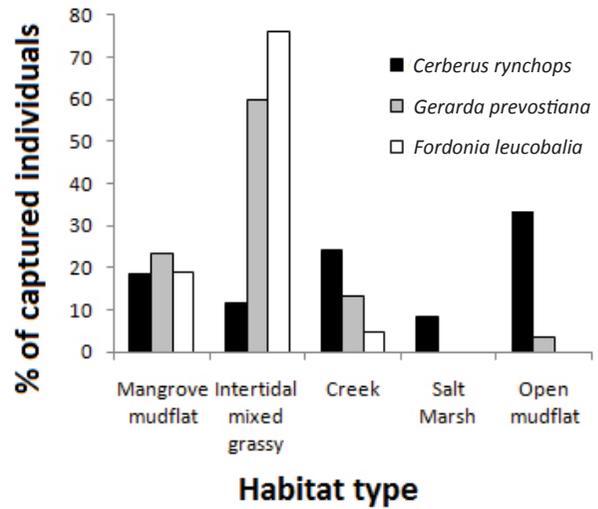


Fig. 2. Habitat use by sympatric Homalopsidae snakes at the study area, expressed in terms of percentage of individuals of each species found in each habitat type. Sample sizes: *Cerberus rynchops* n=207; *Gerarda prevostiana* n=30; *Fordonia leucobalia* n=21.

<0.05 (Gotelli & Graves, 1996). Equiprobable habitat resource use was assumed *a priori* in the analyses.

RESULTS

Habitat use and food niche

Excluding recaptures, 258 snakes belonging to three Homalopsidae species (*Cerberus rynchops*, *Gerarda prevostiana*, *Fordonia leucobalia*, Fig. 1) were used for habitat use analyses. *Cerberus rynchops* was the most abundant and generalist species in terms of microhabitat niche width, being recorded in all five habitat types

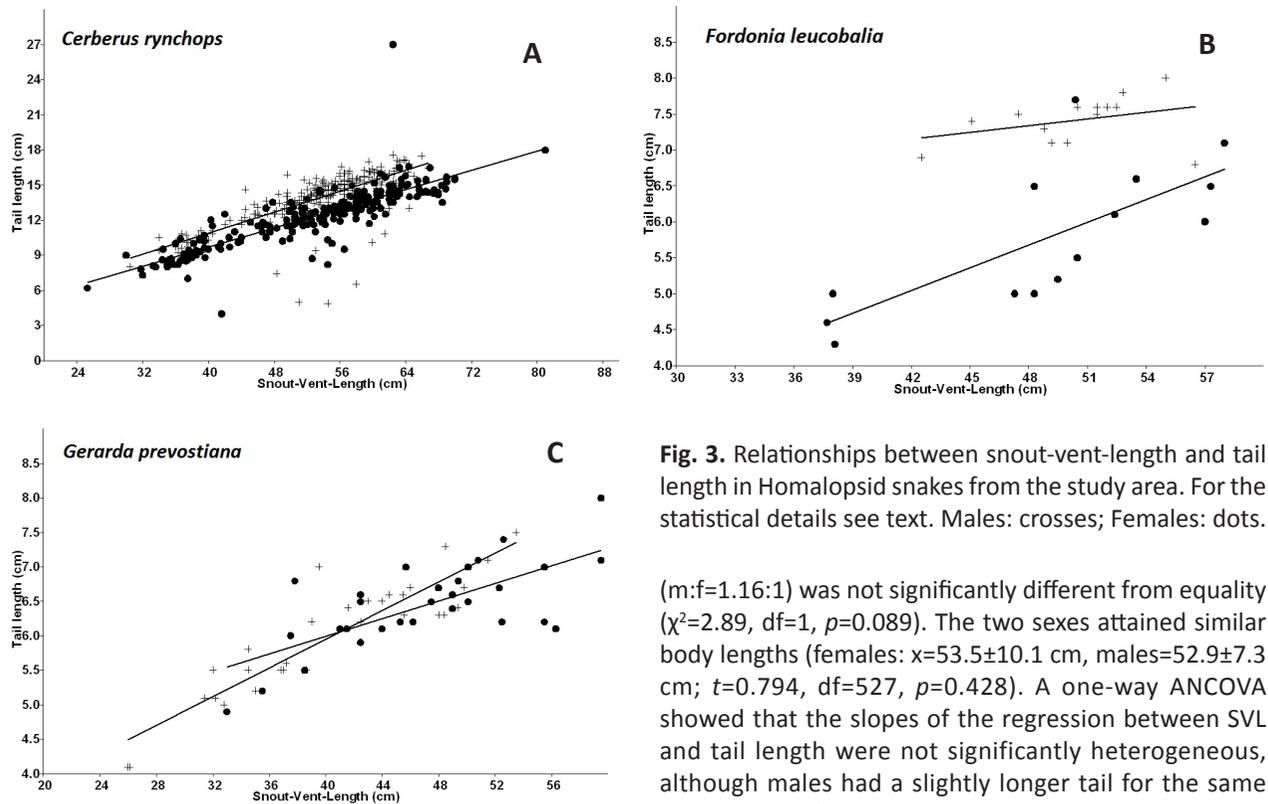


Fig. 3. Relationships between snout-vent-length and tail length in Homalopsid snakes from the study area. For the statistical details see text. Males: crosses; Females: dots.

(m:f=1.16:1) was not significantly different from equality ($\chi^2=2.89$, $df=1$, $p=0.089$). The two sexes attained similar body lengths (females: $x=53.5\pm 10.1$ cm, males= 52.9 ± 7.3 cm; $t=0.794$, $df=527$, $p=0.428$). A one-way ANCOVA showed that the slopes of the regression between SVL and tail length were not significantly heterogeneous, although males had a slightly longer tail for the same body length than females ($F_{1,523}=1.812$, $p=0.179$; Fig. 3A). The two sexes were similar in terms of body mass (females: $x=105.6\pm 52.4$ g, $n=242$, range=10–264 g; males= 100.4 ± 37.2 g, $n=282$, range=18–190 g; $t=1.329$, $df=522$, $p=0.182$).

Fordonia leucobalia. Overall, we captured 36 individuals (21 females, 14 males, two unsexed juveniles). Adult sex-ratio (0.67:1) was not skewed from equality (observed-versus-expected $\chi^2=1.57$, $df=1$, $p=0.210$). The two sexes attained similar sizes in terms of both SVL (males: $x=50.4\pm 3.7$ cm, $n=14$; females= 49.2 ± 6.4 cm, $n=21$; $t=0.603$, $df=33$, $p=0.550$) and body mass (males: $x=87.4\pm 18.3$ g, $n=14$; females= 85.6 ± 18.3 g, $n=21$; $t=0.182$, $df=33$, $p=0.856$). Males had slightly longer tails than females, but the slopes of the regression between SVL and tail length were not significantly heterogeneous between sexes (one-way ANCOVA: $F_{1,146}=0.480$, $p=0.492$, Fig. 3B).

Gerarda prevostiana. Eighty six snakes were captured (51 adult females, 28 adult males, seven unsexed juveniles). Adult sex-ratio (0.55:1) was significantly skewed towards females (observed-versus-expected $\chi^2=6.70$, $df=1$, $p<0.01$). Mean female SVL ($x=46.0\pm 7.2$ cm, $n=51$) exceeded that of males ($x=40.5\pm 7.4$ cm, $n=28$) at a statistically significant level ($t=3.327$, $df=77$, $p=0.001$); adult females also weighed significantly more than adult males (males: $x=35.2\pm 17.6$ g, $n=28$; females= 54.1 ± 26.3 g, $n=51$; $t=3.504$, $df=77$, $p<0.001$). However, males had significantly longer tails than females at same body lengths (one-way ANCOVA: $F_{1,79}=5.557$, $p=0.021$) (Fig. 3C).

with a relatively high number of individuals (Fig. 2). Conversely, the other two species were more specialised in terms of habitat use, with both *G. prevostiana* and *F. leucobalia* being linked especially to the two mangrove microhabitats (Fig. 2). Habitat niche overlap value was higher between *G. prevostiana* and *F. leucobalia* ($O=0.981$) than between each of these two species and *C. rynchops* (respectively, $O_{Gp,Cr}=0.474$, $O_{Fl,Cr}=0.399$). RA3 algorithm showed a random assemblage structure as for the habitat use is concerned (Observed mean index=0.598, Mean of simulated indices=0.497, Variance of simulated indices=0.017, $p_{(observed\leq expected)}=0.810$, $p_{(observed\geq expected)}=0.190$; Observed mean variance=0.114, Mean of simulated variances=0.063, Variance of simulated variances=0.002, $p_{(observed\leq expected)}=0.847$, $p_{(observed\geq expected)}=0.153$). An RA2 algorithm also confirmed the absence of habitat use structure for the assemblage under study (Observed mean index=0.598, Mean of simulated indices=0.662, Variance of simulated indices=0.015, $p_{(observed\leq expected)}=0.293$, $p_{(observed\geq expected)}=0.707$; Observed mean variance=0.114, Mean of simulated variances=0.029, Variance of simulated variances=0.001, $p_{(observed\leq expected)}=0.981$, $p_{(observed\geq expected)}=0.019$).

The food data collected in this study are presented in Table 1, together with comparative raw data reported in Voris & Murphy (2002), the only available previous study on the diet of the three studied species. *Cerberus rynchops* was typically piscivorous, *G. prevostiana* fed on soft-shelled crustaceans, and *F. leucobalia* on hard-shelled crustaceans.

Population structure

Cerberus rynchops. We captured and analysed 531 individuals (244 females, 283 males, three unsexed juveniles and an unsexed adult). The adult sex-ratio

DISCUSSION

We demonstrated that (i) the three species were relatively similar in terms of body size (with *Cerberus* being slightly

larger); (ii) the three species differed in morphological patterns (sexes attained at similar sizes in two species but females being larger than males in *G. prevostiana*) and demographic characteristics (equal sex-ratio being in two species, female-biased in *G. prevostiana*). The absence of a male-biased sexual size dimorphism in all study species may be correlated with the absence of male-male combat for access to females (Shine, 1978; 1993; 1994), and the female-biased sexual size dimorphism may be explained by the Darwin's fecundity advantage model (Shine, 1978; 1993; 2004). The longer tails of males for all species can be probably attributed to the increased space needed for hemipenes.

There was no non-random resource partitioning along the micro-habitat axis, whereas there was a clear niche partitioning along the food axis. Despite the peculiar evolutionary history of the Homalopsidae inside the group of the Colubroidea, our snake assemblage closely resembled other communities of snakes in that they partitioned the food but not the habitat resource (for a quantitative review see Luiselli, 2006a). The same pattern was also observed in an assemblage of colubrid aquatic snakes from tropical Nigeria (Luiselli, 2006b). This general pattern may be due to more intense interspecific competition along the food axis than along other niches (Luiselli, 2006a), or caused by phylogenetic inertia (Cadle & Greene, 1993). The presence of a phylogenetic signal behind the food niche partitioning pattern can be explored by examining the dietary preferences of other closely related species (Karns et al., 2002). However, both *Fordonia* and *Gerarda* are monotypic genera (Murphy, 2007), precluding comparisons with close relatives. *Fordonia* feeds almost exclusively on crabs also in areas where the other species may not be present (Shine, 1991), suggesting that ecological specialisation has a taxonomic basis. However, it should be noted that there are studies reporting frogs (Worrell, 1963), fish (Campden-Main, 1970) and even gastropods (Rahman & Reza, 2013) as occasional prey for *Fordonia*. The diet of *Gerarda* is less well known than that of *Fordonia* (Murphy, 2007). Available evidence suggest that it should feed only on soft-shelled crabs, and that it is one of the few known snake species which tears its food into pieces that can be swallowed (Murphy, 2007). The genus *Cerberus* includes three species, all of them being piscivorous (Murphy, 2007). We conclude that the apparent resource partitioning along the food axis was not caused by interspecific competition, but merely by the divergent evolutionary history of the three genera studied in this paper. The lack of structure along the microhabitat niche axis (consistent with other snake community studies; see Luiselli, 2006a) further suggests that interspecific competition should not be strong within mangrove snakes (Homalopsidae) assemblages.

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