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Morphology, Reproduction, and Diet of the Marine Homalopsine Snake *Bitia hydroides* in Peninsular Malaysia

BRUCE C. JAYNE, TODD J. WARD, AND HAROLD K. VORIS

Based on a collection from the Muar River estuary in western peninsular Malaysia, we quantified the morphology, reproductive effort and diet of the previously rare homalopsine snake *Bitia hydroides*. The dentition of *B. hydroides* is unusual because of enlarged anterior palatine teeth which have lengths that exceed those of all other teeth, including the posterior maxillary fangs. Enlarged palatine teeth have only been described previously for a single species of snake. Despite this unusual dentition, *B. hydroides* fed on oxydercine and bottom-dwelling species of gobies, which are consumed by sympatric species of marine snakes. Females were considerably larger than males. Reproduction was strongly seasonal and out of phase with that of the sympatric species of hydrophiids, and the size distribution of the snakes suggested that the age of first reproduction approximates one year. For 13 females, litter size ranged from 1–10 (\(\bar{x} = 4.2\)) and was significantly correlated with maternal size. Relative clutch mass ranged from 0.07–0.35 (\(\bar{x} = 0.22\)) and was not correlated with maternal size.

The homalopsine colubrid snakes consist of nearly three dozen species of which more than 20 belong to the genus *Enhydris* and eight belong to monotypic genera (Gyi, 1970). Homalopsins are uniformly associated with aquatic habitats, generally feed on frogs and fish, and show varying affinities for brackish water habitats (Smith, 1943; Gyi, 1970). The three homalopsine genera, *Cerberus*, *Fordonia*, and *Bitia* that reportedly have mainly marine and estuarine habitats can all be found in the Straits of Malacca between Sumatra and peninsular Malaysia. Currently, the biology of *Cerberus* is the best known of this group. *Cerberus* has a specialized salt gland (Dunson and Dunson, 1979), and many details of its diet and feeding behavior have been described (Jayne et al., 1988). *Fordonia* is a monotypic genus with numerous specializations associated with consuming crabs as its sole prey item (Gyi, 1970; Savitzky, 1988). *Bitia hydroides* belongs to another monotypic homalopsine genus with a morphology so distinct that its affinities with other homalopsine genera are far from clear (Gyi, 1970). Few aspects of the biology of *Bitia* have been well described because only a modest number have been collected previously. For example, Gyi (1970) examined only five specimens during his revision of the Homalopsinae. *Bitia* has been categorized as piscivorous although neither the species nor size of prey items has ever been documented (Gyi, 1970).

While performing fieldwork with marine snakes in the Straits of Malacca and near the Muar River estuary in Malaysia (Voris, 1985; Jayne et al., 1988), Jayne and Voris encountered unexpectedly large numbers of *Bitia hydroides*. The purpose of the present study is to document better the morphology and natural history of this species. In particular, we describe specialized dentition that is unique within homalopsines and rare for any snake taxon. We also

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from Muar and one from Parit Jawa. During 1985 and 1986, a total of 91 *Bitia hydrodes* were collected and preserved; and of those specimens, 18 individuals were neonates that were born while the maternal snakes were held in captivity for less than two weeks from the date of capture. In addition, 44 individuals were captured, measured, and then returned to the study site within 24 hr of capture. Thus, we had a total of 117 field-captured individuals for which we measured size, assessed reproductive condition and checked for prey items.

For each individual, we measured the snout–vent length (SVL) and tail length (TL) (± 5 and ± 1 mm for live and dead specimens, respectively), and we determined mass to the nearest 0.1 g using a top loading digital scale. Individuals that were preserved were killed with an injection of sodium pentobarbital before measuring. We usually removed and weighed the contents of the stomachs and oviducts (11 of 14 gravid individuals) before preservation. Animals that were not preserved were palpated manually to detect the presence of both prey and embryos. When stomach contents were detected, we gently forced the live snakes to regurgitate them. Dissections were used to determine the sex of the largest 23 male and largest 30 females that had been preserved. The sex of live individuals was determined subjectively based on the shape of the tail. For live neonatal snakes, the sex of individuals could not be determined reliably in the field, and we excluded these individuals from statistical analyses for which sex needed to be known.

In the laboratory, we counted ventral and subcaudal scales for all preserved specimens. For the 10 largest individuals of each sex, we also counted midbody dorsal scale rows and various cranial scales. The sex of the smallest individuals and embryos was determined from the number of subcaudal scales, which had non-overlapping ranges based on data from the specimens whose sex had been verified by dissection of the gonads. Because of some damage to specimens, the numbers of subcaudal and ventrals could not be determined for three of the 91 preserved specimens, and the sex could not be determined for two of these three individuals. For three females that had not had their reproductive tracts removed before preservation, we removed all of the embryos and yolk sacs from the preserved (70% ethanol) specimens, blotted off excess moisture, and determined the SVL of each embryo and the mass of each embryo plus its yolk sac. To determine reproductive effort, we used the combined data from fresh and preserved specimens to quantify such
parameters as the relative clutch mass [RCM = (total mass of reproductive material)/(maternal mass not including reproductive material)]. Oviducal eggs that appeared infertile were not included in measurements of either RCM or litter size.

We determined the numbers of teeth from two prepared skulls of large adult females (FMNH 229792, 229794), and tooth lengths were measured from the specimen having a greater number of intact teeth (FMNH 229792). We used a dissecting microscope with an ocular micrometer to quantify the straight-line distance (± 0.05 mm) from the anterior base to the tip of each undamaged tooth, and we counted tooth number from anterior to posterior within each toothed bone. When measurements were made for both the left and right teeth with homologous position, mean values were calculated.

For all statistical analyses, we used $P < 0.05$ as the criterion for significance. All log transformations were base-10, and all regressions used the least-squares method. For comparisons of meristic data between males and females, we use two-tailed t-tests. Unless otherwise stated, all snakes were from the 1985–1986 sample at Muar.

**Results**

*Size and postcranial morphology.*—For the 117 field-captured individuals (excluding those born in captivity), SVL ranged from 13.8–72.0 cm and mass ranged from 1.8–195 g (Fig. 1A). Analysis of covariance revealed that the slopes of the scaling relationships between SVL and mass or tail length (TL) differed significantly between males and females. Thus, we calculated regression coefficients ($\pm$ SE) separately for each sex. For 55 males, $\log(\text{mass}) = -2.661(\pm 0.063) + 2.545(\pm 0.043)\log(\text{SVL})$ [$r^2 = 0.99$], and for 68 females, the intercept and slope of this regression were $-2.868(\pm 0.052)$ and $2.723(\pm 0.033)$ [$r^2 = 0.99$], respectively. Both regression equations predict a mass of 2.2 g when SVL = 15 cm, whereas these scaling equations predict male and female masses of 26.0 and 31.2 g, respectively, for SVL = 40 cm. Hence, over the range of biologically meaningful values of SVL, females were more massive than equal length males, and the difference between the sexes increased with increasing SVL. The extent of sexual dimorphism in size is further illustrated in Figure 2. The greatest values of SVL and mass observed for males were 43 cm and 33 g, respectively, whereas we captured 41 females having both SVL and mass that exceeded those maximal values for males.

When expressed as a percentage of total length, the relative length of the tail of males (mean = 11.1%) was significantly greater than that of females (mean = 8.0%), with a value of 10% being exceeded by 92% of the males and only 4.5% of the females. For the same sample that was used to determine the scaling of mass, the slope and intercept for the scaling of log TL as a function of log SVL were $1.125(\pm 0.033)$ and $-1.089(\pm 0.048)$ for males and $0.897(\pm 0.024)$ and $-0.897(\pm 0.038)$ for females, respectively (Fig. 1B).

The postcranial meristic data for the entire sample of preserved specimens were within the
Fig. 2. Size distribution of all field-captured *Bitia hydroidea* (excluding captive-born individuals). Note the extent to which size of the females exceeds that of males.

range of values observed for 23 males and 30 females whose sex was verified by dissections, and the mean (SD; range) values that follow are for this subsample of 53 individuals. Males averaged 158 ventrals (2.73; 150–161) which was significantly less than the average of 161 (1.68; 157–164) for females. As might be expected from the sexual dimorphism in tail length, males averaged 35 subcaudals (1.33; 33–37) which was significantly greater than the average of 27 (0.96; 25–29) observed for females. Males and females did not differ significantly in the number of dorsal scale rows at midbody which averaged 39 (1.00; 37–40) for the pooled data. An unusual feature of the dorsal scales on the sides of *Bitia* is that, instead of adjacent scales overlapping longitudinally, there is a conspicuous area of exposed skin between the scales (Fig. 3).

Reproduction.—The SVL and mass (excluding that of embryos) of the smallest gravid female were 36.5 cm and 26 g, respectively. Of 28 females captured with SVL > 36.5, 14 individuals were gravid. One of those gravid females appeared to have inviable oviducal eggs, and this individual was excluded from further analysis of reproductive effort. The earliest date of capture of a gravid female was on the first day of collecting (20 Nov.), and the latest date of capture of a gravid female was on 18 Dec. As shown in Figure 4A, litter size varied from 1–10 (x = 4.2) and increased significantly with increased SVL (r² = 0.68). Clutch mass (Fig. 4B) averaged 14.5 g (range = 2.3–52 g) and increased significantly with increased SVL (r² = 0.53). Mean RCM was 0.22 (SD = 0.095; range = 0.08–0.35), and this estimate of RCM does not differ significantly from the slope of the regression predicting clutch mass from maternal mass [clutch mass = 0.209 (+ 0.053) mass − 0.029 (+ 4.44); r² = 0.58]. RCM was not significantly correlated with either maternal SVL (r = −0.20) or mass (r = −0.17). The mean value of RCM

Fig. 3. A female (SVL = 38.5 cm) *Bitia hydroidea* (FMNH 218878) captured at Parit Jawa, Malaysia. Note, even for the sides of the snake that are flexed, there are gaps between most of the adjacent dorsal scales.
of Bitia appears relatively low for a viviparous colubrid since it is exceeded by nine of 11 North American species of natricines whose reproductive efforts have been reviewed recently (Seigel et al., 1986). RCM per progeny showed a significant decrease with increased maternal SVL (Fig. 3C). The mean mass of progeny per litter ranged from 2.3–5.2 g (\( \bar{x} = 3.2 \) g), and this quantity was not significantly correlated with maternal size, litter size, or RCM.

Three gravid females captured between 1 and 18 Dec. gave birth in captivity between 18 and 20 Dec. The average SVL and mass of the newborns from these three litters were 16.1 cm (range = 15.5–16.8 cm) and 2.5 g (range = 2.1–3.0 g), respectively. Prior to 30 Dec., a total of 14 nongravid females with SVL > 36.5 cm were collected and preserved. Examinations of these 14 reproductive tracts for evidence of recent birth, such as enlarged and vascularized oviducts, suggested that seven of these individuals had recently given birth. Of 22 additional females (SVL = 40–72 cm) captured between 30 Dec. and 6 Feb., none was gravid or had enlarged follicles.

**Cranial morphology.**—Figure 5 illustrates the skull from the large adult female specimen (FMNH 229792, SVL = 62 cm) for which both the lengths and numbers of teeth were determined (Fig. 6). The dentition of Bitia shows the unusual derived feature of enlarged teeth on the anterior portion of the palatine (Fig. 5b–c). Remarkably, the fourth palatine tooth (3.1 mm) exceeded the length of the posterior maxillary fang (2.1 mm) by nearly 50% (Fig. 6). Furthermore, the posterior maxillary fang was also shorter than the fourth and longest (2.6 mm) tooth of the lower jaw (Fig. 5d). The pterygoid teeth were relatively small, with a gradual decrease in length posteriorly that contrasted with the maxilla, dentary, and palatine, all of which showed longitudinal discontinuities in tooth length (Fig. 6). Based on the left and right bones from two prepared skulls (FMNH 229792; 229794), the ranges in the numbers of teeth on the maxilla, palatine, pterygoid, and dentary were 13–14, 7–8, 19–23, and 18–23, respectively.

The dorsal orientation of the orbits is conspicuous in the skull (Fig. 5a) and reflects the position of the eyes in intact specimens (Fig. 3). The posterior portion of the dentary of Bitia appeared to be rather loosely attached to the compound bone (Fig. 5d). The braincase has both a well-developed sagittal crest (Fig. 5c) and a well-developed transverse supraoccipital crest (Fig. 5a). Similar to available illustrations of other piscivorous homalopsines (Gyi, 1970), the supratemporal of Bitia is strongly curved in the frontal plane such that it is concave medially (Fig. 5a).
Fig. 5. The skull and jaw of a large adult female *Bitia hydroides* (FMNH 229792). (a) Dorsal, (b) ventral, and (c) lateral views of the skull. (d) Lateral and (e) dorsal views of the right lower jaw. Note the enlarged teeth on both the palatine and lower jaw (scale bar = 1 cm).

*Bitia* has been described previously as having a head that is relatively indistinct from the neck (Smith, 1943; Gyi, 1970). However, this condition is only apparent in small individuals, and Figure 7 shows that the width of the head commonly exceeds that of the neck in larger specimens. Another conspicuous feature of external cephalic morphology is the relatively small eye (Fig. 3). *Bitia* also has valvular nostrils.

Males and females did not differ significantly in cephalic scutellation. For the combined sample of the 10 largest males and 10 largest females, all individuals had one loreal, one preocular scale, two postoculars, and two primary temporals on each side of the head; and all specimens had two pairs of chin shields. The numbers of supralabials, infralabials, gulars, and secondary temporals averaged 7.5 (range = 7–9), 10.7 (range = 10–12), 8.3 (range = 8–9), and 3 (range = 2–4), respectively.

**Diet.**—Of the 117 field-captured individuals (Fig. 2), we only found one prey item in each of six individuals (none of which were gravid). Three of these items could only be identified as the tail fin rays of fish of unknown taxonomic identity. Two individuals had consumed the goby species *Oxuderces dentatus*, and for one of these snakes (SVL = 16.5, mass = 3.0g), the prey item had a total length of 6.6 cm and a mass of 0.4 g. The remaining prey item (Fig. 6) found in a snake (SVL = 39 cm, mass = 26 g) was another goby (*Trypauchen raha*), which was the largest prey item consumed in terms of both absolute size (total length = 14 cm; mass = 9.1 g) and mass relative to that of the predator (38%). Although we offered several captive individuals (in Malaysia at the field site), a variety of sympatric species of oxydercine gobies (*Periopthalmus chrysospilos*, *Scartelaus pectinistrostris*, and *Ox-
Fig. 7. The largest prey item consumed by *Bitia hydroides* (FMNH 229783). Note the elongate shape of this burrowing goby (*Trypauchen raha*) which approximated 38% of the mass of the snake (shown) which consumed it. The large divisions on the ruler are cm.

uderces dentatus*), we were unsuccessful in eliciting feeding behavior in any *Bitia hydroides*.

**Discussion**

In the Muar estuary, stake nets in the main channel of the river have proven very effective for sampling the hydrophiid species (Voris, 1985). Based on a cumulative sample of approximately 1200 individuals, the hydrophiid species in order of abundance are as follows: *Enhydrina schistosa*, *Hydrophis melanomma*, *H. brookii*, *H. torquatus*, and *H. caerulescens* (Lemen and Voris, 1981). Over the same time interval of the hydrophiid sample, fewer than 10 *Acrochordus granulatus* were collected in the main channel of the Muar river (Voris and Glodek, 1980), and a single *A. granulatus* was obtained during 1984 through 1986 from a fisherman working the intertidal area where we collected the homalopsine snakes. In the intertidal zone at Muar, the homalopsine *Cerberus rynchops* was most abundant during 1984 through 1986, as indicated by more than 600 captures during approximately six months of collecting (Jayne et al., 1988). Furthermore, we did not capture all individuals of *C. rynchops* that were encountered during this time period.

*Bitia hydroides* was the second most abundant species in the intertidal zone at Muar, although only a single individual has been caught in the main channel of the river (sample summarized in Voris, 1985). A curious feature of the abundance of *B. hydroides* at Muar is that during 1984, when collecting methods were identical to those of 1985 and 1986, only a single *Bitia* was found, and it was an emaciated individual which appeared on the shore following a strong high tide. Both field trips included a period from 14 Jan. through 8 Feb. when only a single *Bitia* was captured in 1984 compared to 28 individuals captured and more than 20 sighted in 1986. During 1984, one *Fordinia leucobalia* was also collected at Muar, and one *Homalopsis buccata* was found in vegetative debris in the intertidal zone after a period of heavy rains that had markedly increased the discharge of the river. During 1985–1986, eight *Fordinia leucobalia* were sighted and/or collected at Muar. Consequently, the sporadic temporal occurrence of *Bitia* at Muar complicates determination of the rank order of abundance of the co-occurring species of marine snakes.

In the vicinity of Parit Jawa, *Cerberus rynchops* was most abundant, and more than 30 *Fordinia leucobalia* were collected, whereas only two *Bitia hydroides* were collected. At Parit Jawa, a large area of mangrove was closer to the collecting site than at Muar, and the discharge of the stream at Parit Jawa is very small compared to the Muar River; hence, these factors may contribute to different abundance of *Bitia* relative to *Fordinia* at these two sites.

A puzzling trait of *Bitia hydroides* is the markedly enlarged palatine teeth. To the best of our knowledge, the only other species of snake in the world with this condition is an unrelated African opisthoglyphous snake, *Pythonodipsas*, which preys on lizards using constriction (Marx et al., 1982). Despite the peculiar palatine dentition of *Bitia*, it preyed in part on *Oxuderces dentatus*, which is the dominant prey item of the co-occurring homalopsine *Cerberus rynchops* (Jayne et al., 1988). The elongate shape, scapulation, and relative size of *Trypauchen* are similar to many other species of gobies which are consumed by *Acrochordus granulatus* and to a lesser extent by three species of *Hydrophis* at Muar which also regularly consume eels (Voris and Glodek, 1980; Voris and Voris, 1983). Thus,
the specialized dentition of *Bitia* appears unlikely to be a prerequisite for consuming any of the species of prey observed for *Bitia*. Whether or not *Bitia* catches and consumes prey common to other marine snakes by using specialized behaviors remains an open question.

The foraging activity of *Cerberus rynchops* in this intertidal area commonly involves diverse modes of locomotion in mud of varying consistencies (Jayne et al., 1988). Similar to *Cerberus*, we observed *Bitia* using lateral undulatory swimming through water and loose mud and using proficient sidewinding on the surface of harder mud. Released specimens of *Bitia* readily burrowed into the mud that was hard enough to elicit sidewinding, whereas *Cerberus* usually only burrowed into the looser mud in which lateral undulatory locomotion was performed. Consequently, *Bitia* appeared to be a more proficient burrower than *Cerberus*, and the small eyes, smooth scales, and short tail of *Bitia* (Fig. 3) are all morphological specializations that are commonly associated with burrowing.

*Bitia* may be more nocturnal than *Cerberus*. Although we found more *Cerberus* than *Bitia* during daylight hours, both homalopsines were more abundant at night. The greater abundance of *Cerberus* could contribute to a perceived difference in the extent of nocturnality. The activity of both *Bitia* and *Cerberus* in the intertidal zone was also strongly influenced by the tidal cycle, as indicated by night collecting along the incoming tidal edge being particularly effective for both taxa.

Because only 5.1% (5.8% if gravid snakes excluded) of the *Bitia* collected had prey items, it is not clear whether this species normally forages in the regions where they were captured. In contrast to the low incidence of prey items in *Bitia*, samples of *Cerberus rynchops* and *Enhydrina schistosa* at Muar had values of 29.6% and 19.6%, respectively (Voris and Moffett, 1981; Jayne et al., 1988). Furthermore, nearly half of the *C. rynchops* with prey had more than one item in the stomach (Jayne et al., 1988). Hence, feeding rates may differ substantially among the different species of marine snakes.

Based on the capture dates of gravid females and neonatal snakes and the abrupt absence of gravid females, it appears that *Bitia hydroides* has a seasonal reproductive cycle, with births occurring from Nov. until late Dec. These dates of birth are out of phase with *Enhydrina schistosa*, *Hydropis melanoma*, and *H. brookii* in which parturition occurs from Feb. until mid-March (Voris and Jayne, 1979; Lemen and Voris, 1981). No evidence exists for seasonality in the reproduction of *Cerberus rynchops* (Jayne et al., 1988) and *Acrochordus granulatus* (Voris and Glodek, 1980) at Muar. Perhaps the different patterns of reproductive seasonality reflect independent invasions of the marine habitat by *Cerberus* and *Bitia*.

The distinct seasonality of reproduction of *Bitia hydroides* facilitates estimating age of first reproduction and early growth rates. Even when we subdivided the entire sample into the first and second portions of our collecting period, the size distributions of captured snakes always had two distinct modes that included males (Fig. 2). We interpret the modes with the two smallest SVLs to be neonates and one-year olds, respectively (Fig. 2). The mode of presumed one-year olds included gravid females, but not all females in this size group were gravid or had anatomical evidence of having reproduced. Thus, it appears likely that some female *Bitia* reproduce in their first year of life.

We subdivided the sample of neonatal *Bitia* into two temporally distinct subsamples (20 Nov.–18 Dec. and 6 Jan.–6 Feb.) and calculated the mean SVL and dates of capture of each subsample. We then divided the mean difference in SVL by the mean time difference, which yielded an estimated growth rate of 0.06 cm/day for neonates.

Voris and Jayne (1979) estimated an early growth rate of *Enhydrina schistosa* (0.12 cm/day) that is twice that of *Bitia hydroides* at Muar. Furthermore, it appears to take two years for female *E. schistosa* to mature. *Bitia hydroides* are born much smaller than *E. schistosa* (SVL = 16 vs 23 cm.; mass = 2.5 vs 11.4 g) and have slower growth, but *B. hydroides* attains sexual maturity at a younger age as a result of having a smaller size at maturity (SVL = 36 vs 73 cm; mass = 26 vs 200 g). Small adults *E. schistosa* (SVL = 73–83 cm) have litter sizes of 1–10 which is similar to *B. hydroides*, but large *E. schistosa* (SVL = 90–112 cm; mass = approximately 500–1000 g) can have nearly three times the litter size of the largest litter observed for *B. hydroides* (Voris and Jayne, 1979; Lemen and Voris, 1981). In contrast to the gobies consumed by *B. hydroides* (Fig. 7), *E. schistosa* is a specialist on primarily two species of catfish which are relatively stout for their mass compared to most gobies (Voris and Moffett, 1981; Voris and Voris, 1983). Such differences in prey species and their rates of consumption may be two of many factors that potentially cause the observed differences in growth rate and age at maturity of these two sympatric species of snakes.

We have detected minimal spatial overlap between the homalopsines and other marine snakes (Acrochordidae and Hydrophiidae) in the Muar estuary. In the main channel of the river in the Muar estuary, hydrophiids are abundant and
homalopsines are rare. Conversely, in the intertidal mudflat at Muar, homalopsines abound and hydrophids are completely absent. The primitive Ephalophis greyi of Australia is the only hydrophid known to occur regularly in intertidal mudflats (field notes for FMNH specimens), and this species consumes oxydercine gobies and has a superficial appearance intriguingly convergent with that of Bitia hydroides.

An unresolved issue for the Muar marine snake community is the extent to which either the hydrophids or the homalopsines occur in the region of permanent water (maximum depth approximately 2 m) between the intertidal area and the main channel. The low numbers of large Cerberus rynchops captured in the intertidal area combined with dietary information suggest that this homalopsine also occurs in deeper water (Jayne et al., 1988). The finding of a prey species (Trypauchen raha) not generally found in intertidal areas supports the possibility that Bitia exploits both intertidal and deeper water habitats. Another possibility for Bitia is that the intertidal zone is primarily exploited during the season of parturition. However, nearly equal numbers of males and females were collected (Fig. 2), suggesting that this habitat is not limited to gravid females and neonates.

In summary, of all the marine snake species found at Muar, the diet and habitat of Bitia hydroides were most similar to those of the numerically dominant homalopsine species Cerberus rynchops. Similar to the two dominant hydrophid species, the reproduction of Bitia was strongly seasonal. However, parturition of Bitia (Nov. through Dec.) was out of phase with that of all sympatric marine snake species. Furthermore, Bitia attains sexual maturity (1 yr) twice as quickly as the dominant sympatric species of hydrophids. For Bitia, we presently lack clear explanations both for the enlarged palatine teeth and for the sporadic occurrence in the intertidal area of this site. Perhaps future samples from intermediate water depths will resolve both of these issues.

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