



Morphology, reproduction and diet of the greater sea snake, *Hydrophis major* (Elapidae, Hydrophiinae)

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Abstract Although widespread, the large Hydrophiinae sea snake *Hydrophis major* is poorly known ecologically. We dissected 119 preserved specimens in museum collections to quantify body sizes and proportions, sexual dimorphism, reproductive biology and diet. The sexes mature at similar snout–vent lengths (SVLs, about 75 cm) and attain similar maximum sizes (females 123 cm vs. males 122 cm SVL), but females in our sample exhibited larger mean sizes than did males (means 98.8 vs. 93.1 cm SVL). The adult sex ratio in museum specimens was highly female-biased (64:30), and the high proportion of reproductive females during the austral summer suggests annual reproduction. At the same SVL, females had shorter tails and wider bodies than did males, but sex differences in other body proportions (e.g. tail shape, head dimensions, eye diameter) were minimal. Skin rugosity increased with SVL, was greater in males than females and was greater on the dorsal than the ventral surface of the body. Litter size averaged 4.9 offspring (range 2–10) and increased with maternal body size. Neonates were approximately 33 cm SVL. The only prey items found inside dissected snakes (and also, recorded as prey in free-ranging snakes in our New Caledonia field studies) were catfish (*Plotosus lineatus*), whereas previous studies have suggested a more diverse diet. Although *H. major* resembles its terrestrial

relatives in some respects, other characteristics (such as scale rugosity, low proportion of juveniles in collections, frequent production of small litters of large offspring) may reflect adaptation to marine habitats.

Keywords Dietary specialisation · *Disteira major* · Elapidae · Life-history · Olive-headed sea snake · Trophic ecology

Introduction

Rates of speciation are higher in the viviparous sea snakes (Hydrophiinae) than in any other extant group of reptiles. In particular, one clade of sea snakes—the *Hydrophis* group—contains more than 30 species despite originating less than eight million years ago (Sanders et al. 2013a, b; Lee et al. 2016); and those species span a wide range in terms of mean body sizes (< 1 m to > 3 m in length), body shapes (robust to highly elongate), diets (specialised to generalised) and habitat use (freshwater lakes, mangroves, coral reefs, open ocean) (Ukuwela et al. 2017; Sherratt et al. 2018). Although sea snakes thus offer exceptional opportunities to explore evolutionary processes, that opportunity has been taken up primarily by physiologists (e.g. for research on diving abilities and salt tolerances: Dunson and Dunson 1973; Heatwole 1978; Seymour 1982). Such work can be performed on recently captured snakes that are housed in the laboratory for short-term studies, whereas most types of ecological research in tropical marine systems require longer periods in the field—which is expensive, logistically challenging and can often be dangerous. As a result, detailed ecological data are lacking for almost all species of sea snakes. Quantitative analysis of Web of Science records confirms that recent

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decades have witnessed an explosion of research on terrestrial snakes, but no such increase for marine species. For example, a search of Web of Science reveals > 1500 references to garter snakes (*Thamnophis*) and > 3000 to rattlesnakes (*Crotalus*) but only 105 to the most speciose genus of sea snakes (*Hydrophis*) and 55 to the next largest marine genus (*Aipysurus*).

The paucity of ecological research on sea snakes means that even abundant and widespread taxa remain unstudied. One such species is the greater sea snake (or olive-headed sea snake), *Hydrophis major* (formerly allocated to the genus *Disteira*) (see Fig. 1). The species is common across much of its wide range, from New Guinea to tropical Australia and New Caledonia (e.g. Ward 2000, 2001; Elfes et al. 2013), but literature on the species' ecology is fragmentary. The most extensive data on diets and reproduction come from analyses of bycatch from prawn trawlers in Australian waters (Heatwole and Burns 1987; Ward 1996a, b; Fry et al. 2001; see also Lemen and Voris 1981; Marcos and Lanyon 2004; Lukoschek and Avise 2011). Feeding behaviour has been described from incidental observations (Heatwole et al. 1978; Letourneur and Briand 2012) as has a specimen's reaction to contact with an anemone (Goiran and Shine 2014). Studies in Western Australia have suggested that tide-related shifts in habitat

use reduce vulnerability to predation by sharks (Kerford et al. 2008; Wirsing and Heithaus 2009). All other reports, to our knowledge, are summaries in field guides and the like (e.g. Heatwole and Cogger 1994; Ineich and Rasmussen 1997; Ineich and Laboute 2002) or evaluations of trawler-bycatch issues (e.g. Ward 2000; Fry et al. 2001). To expand the database on the species, we examined preserved specimens of *Hydrophis major* to collect information on morphology, reproductive biology and diet.

Methods

We looked at all available *H. major* in the collections of the Australian Museum (Sydney) and the Northern Territory Museum (Darwin). Each specimen was measured for snout–vent length (SVL), tail length, maximum tail width and mean midbody diameter with a flexible measuring tape. We used callipers to measure head length (from the snout to the quadrate–articular joint), maximum head width and eye diameter. Sex was determined by tail shape and length, and by direct inspection of gonads via a midventral incision. Males were scored as adult if they had large turgid testes and/or thickened opaque efferent ducts (reflecting the presence of sperm); females were considered adult if they had large (> 20 mm) ovarian follicles and/or thickened muscular oviducts, or if they were at least 10 cm larger than the smallest adult female (the latter criterion allowed for adult but non-reproductive animals). Where palpation revealed the presence of a prey item, we made another incision to identify and measure the prey, and to determine the direction of ingestion (head-first vs. tail-first). In reproductive females, we counted enlarged ovarian follicles and oviductal embryos. We scored scale rugosity (Avolio et al. 2006a) on both the dorsal and ventral surfaces of the body, at three equidistant points (25, 50 and 75% of SVL). Rugosity at each point was rated on a four-point scale, from 0 (smooth) to 3 (highly rugose).

Continuous-variable data conformed to the assumptions of normality and variance homogeneity. We used Chi-squared tests to see if the relative numbers of adult males versus females differed from that expected under a null hypothesis of equal numbers, and logistic regression to see if the relative numbers of plotosid catfish versus other prey types differed between our datasets and previous reports. We used analysis of variance (ANOVA) to compare males and females for mean values of SVL, and analysis of covariance (ANCOVA) to compare males and females for relative body proportions [with SVL as covariate and the other dimensions (e.g. head length, midbody width) as the dependent variables]. We used head length as the covariate to compare the sexes in terms of head shape (with head width as the dependent variable) and eye size. For tail



Fig. 1 Greater sea snake, *Hydrophis major*, in Baie de Citrons, New Caledonia, photographed while **a** swimming and **b** feeding (Photographs by Claire Goiran)

shape, we compared males and females with tail length as covariate and tail width as dependent variable.

We assessed the relationship between litter size and maternal SVL with regression analysis. To examine sex differences in scale rugosity, we calculated mean rugosities (treating our scores as a continuous variable) for dorsal and ventral surfaces of each snake separately, and analysed those data using repeated-measures ANOVA (with sex as factor, SVL as covariate and dorsal/ventral as the repeated measure).

Results

Population structure

Of the 119 snakes examined (85 females, 34 males), 94 were adults (64 females and 30 males). Females significantly outnumbered males within our samples both of juveniles ($\chi^2 = 111.56$, $df = 1$, $P < 0.01$) and of adult snakes ($\chi^2 = 12.30$, $df = 1$, $P < 0.01$). For 64 adult snakes with data on month of collection, males and females tended to differ (males more common in first half of year, females in second half), but the effect did not attain statistical significance ($\chi^2 = 18.05$, $df = 10$, $P = 0.054$).

Sexual dimorphism

Juvenile males and females were more brightly banded than were adults, but with no overt sex difference in colour pattern either in adults or in juveniles. Both sexes matured at about 75 cm SVL (minima 76.5 cm in females, 78 cm in males) and reached similar maximum sizes (SVLs 123 cm in females, 122 cm in males). Mean adult SVL of adult females was larger than that of adult males (98.8 cm and 93.1 cm, respectively; ANOVA, $F_{1,93} = 6.10$, $P < 0.016$).

At the same SVL, females were thicker-bodied than were males (ANCOVA with sex as factor, SVL as covariate, body width as dependent variable: interaction sex*SVL NS; SVL effect, $F_{1,113} = 42.79$, $P < 0.0001$; sex effect, $F_{1,113} = 5.42$, $P < 0.022$) and had shorter tails (interaction SVL*sex NS; sex effect, $F_{1,116} = 37.02$, $P < 0.0001$; Fig. 2a). However, we detected no significant sex-based divergences in head length relative to SVL, tail width relative to tail length, head width relative to head length or eye diameter relative to head width (ANCOVA, all $P > 0.10$; Fig. 2b).

The scales of males were more rugose than were those of females ($F_{1,115} = 30.36$, $P < 0.0001$), and in both sexes the dorsal surface was more rugose than the ventral surface (especially in larger snakes; interaction SVL*dorsal/ventral, $F_{1,115} = 9.70$, $P < 0.002$). The increase in overall rugosity with increasing SVL was more rapid in males than

in females (interaction sex*SVL, $F_{1,115} = 6.38$, $P < 0.013$; see Fig. 2c, d).

Reproduction

Of the 64 adult females, 10 had been eviscerated so provided no reproductive data. Of the rest, 35 of 54 had enlarged follicles (10 mm and above) or were gravid. The largest sample sizes of adult-size females came from the period August to November, and comprised 18 reproductive animals (gravid, or follicles > 10 mm) and five non-reproductive animals (follicles < 10 mm).

Mean litter size averaged 4.9 offspring (range 2–10) and increased with maternal body size (SVL, $r^2 = 0.31$, $n = 31$, $P < 0.001$; see Fig. 3). The best information on size at birth comes from four full-term embryos removed from a gravid female in February; these ranged from 31 to 36.5 cm SVL. The smallest field-collected snake was 31 cm SVL, with two others < 36 cm. Thus, neonates appear to average about 33 cm SVL.

Feeding habits

We identified seven items in snake stomachs; all were striped eel catfish *Plotosus lineatus*, 230–380 mm long, and all had been swallowed head-first.

Discussion

Below, we evaluate our results in light of published information on *Hydrophis major* and other snake species, to identify consistencies, discrepancies and possible general trends in snake ecology that accompanied the transition from terrestrial to marine environments. Because methods of data collection influence sampling, the strongest comparison between terrestrial and marine species comes from the same method as used in the current study—examination of museum specimens of sea snakes versus terrestrial Australian snakes. Phylogenetic analyses identify the viviparous Australian elapids (notably the *Hemiaspis* lineage) as being closest to the origins of the marine hydrophiines (Keogh et al. 1998; Sanders et al. 2008, 2013a, b; JS Keogh, pers. comm.); and we have extensive ecological data from museum specimens of these taxa (Shine 1987, 1994b). Nonetheless, we recognise that the comparison may be confounded by differences in the methods used to collect museum specimens. Many sea snakes are taken as a bycatch of commercial fisheries, potentially generating biases in the sizes, sexes and reproductive condition of the animals obtained (e.g. Udyawer et al. 2016a).

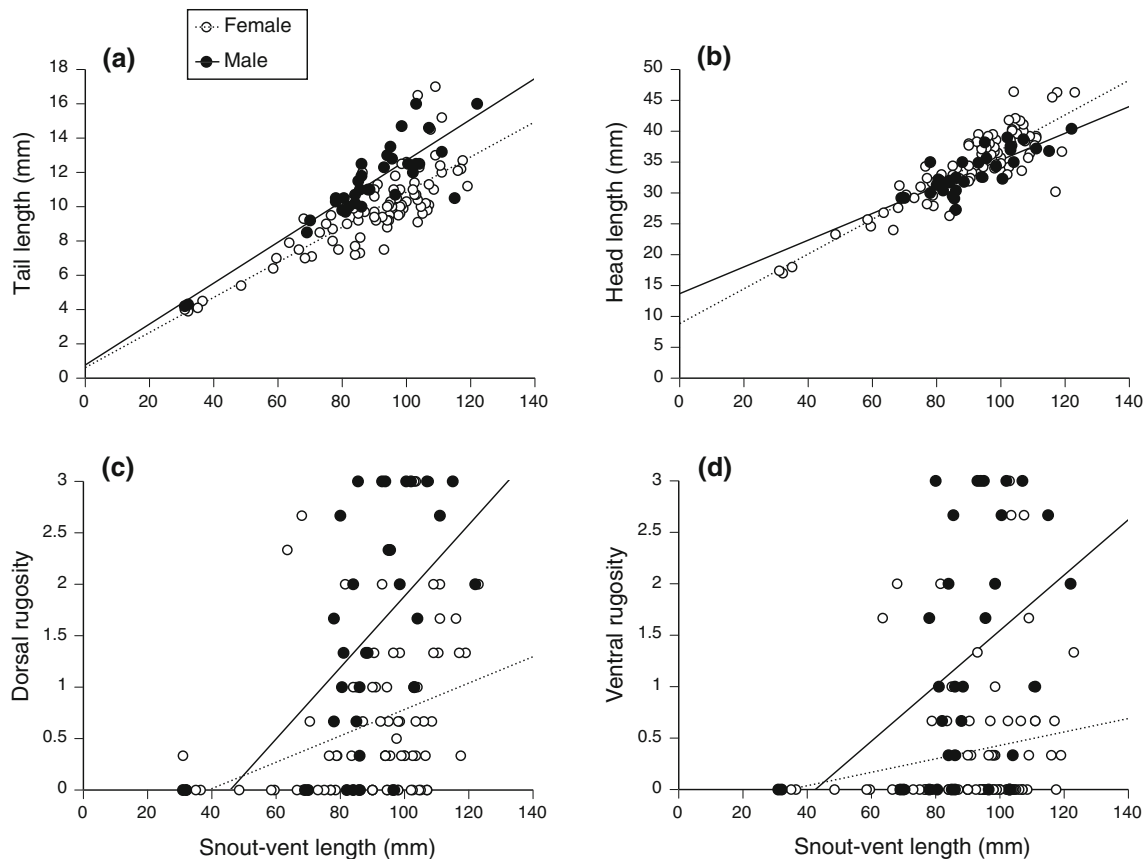


Fig. 2 Sex differences in morphological traits in greater sea snakes, *Hydrophis major*. Males have longer tails than do females at the same snout–vent length (a), but head lengths are similar between the sexes

(b). Scale rugosity increases with body size, and rugosity is higher in males than in females on both the dorsal surface of the body (c) and the ventral surface (d)

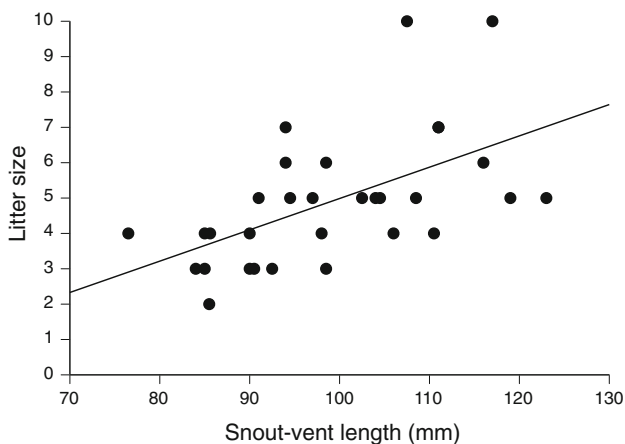


Fig. 3 Litter size relative to maternal body length in greater sea snakes, *Hydrophis major*

Population structure

Only 21% of the sample of *H. major* that we examined consisted of juvenile snakes, a pattern that is also seen in previous analyses of trawler bycatch both for this species (e.g. Kerford 2005) and for sea snakes in general (e.g.

Burns and Heatwole 2000; Fry et al. 2001). In contrast, juveniles typically comprise about 30% of samples in museum collections of terrestrial elapids, including those species most closely related to the marine hydrophiines (e.g. *Hemiaspis damelii* 33%, *H. signata* 32%: Shine 1987, 1994b). The scarcity of juvenile sea snakes might be due to life-history traits (e.g. low mean litter sizes: see below) and/or to ontogenetic divergence in habitats (whereby juveniles inhabit areas too shallow for trawlers to operate: Wassenberg et al. 1994; Udyawer et al. 2016a) and/or to the ability of smaller animals to escape through trawl mesh (Kerford 2005).

The highly female-biased sex ratio in our sample of *H. major* also differs from the situation seen in most terrestrial elapids, where both sexes are equally common or males outnumber females (e.g. museum collections of *Hemiaspis damelii*—56 adult males, 34 adult females; *H. signata*—123 males, 127 females: Shine 1987). Female-biased sex ratios are widespread in trawler-bycatch records of sea snakes (including *H. major*—Fry et al. 2001 reported 74 females, 48 males) and have been attributed to sex differences in habitat use (such that females congregate in areas that are also fished heavily: Fry et al. 2001). Alternatively

or additionally, decrements in swimming ability due to pregnancy (or increased body distension) may reduce the ability of gravid females to avoid or escape from nets, or behavioural shifts associated with reproduction may modify sex-specific vulnerability to capture (as reported for terrestrial snakes by Brown and Shine 2004). An underlying sex-ratio bias at the population level offers another explanation, but it is unlikely given equal numbers of males and females among late-stage embryos of at least one sea snake species (*H. schistosus*: Lemen and Voris 1981) as well as among snakes in general (e.g. Shine and Bull 1977). Detailed studies on free-ranging sea snakes (*Aipysurus laevis*, *Emydocephalus annulatus*) have reported strong sex-based divergences in habitat usage and feeding ecology seasonally (e.g. Lynch 1999; Goiran et al. 2013), suggesting that sex-based divergence in habitat use and activity patterns may be responsible for sex biases in capture rates. The sex difference in monthly dates of collection for adult male and female *H. major* in our sample fell just short of statistical significance, but our surveys of this species in shallow bays near Noumea, New Caledonia, show that males are seen most often in winter, and females in summer (Goiran and Shine, unpubl. data).

Sexual dimorphism

Our results on sexual size dimorphism support earlier reports that males and females of this species attain similar maximum lengths, but average adult body length is greater in females. Mean SVL of adult male *H. major* has been reported as 89.7 cm (Kerford 2005), 95.9 cm (Ward 2000), 87.8 cm (Shine 1991, 1994a, 1995) and 93.1 cm (current study). Mean SVL of adult females has been given as 97.7 cm (Kerford 2005), 100.2 cm (Ward 2000), 94 cm (Shine 1991, 1994a, 1995) and 98.8 cm (current study). Fry et al. (2001) reported minimum sizes at sexual maturity of 84 cm SVL in male *H. major*, and 71 cm in females (vs. 78 cm in males, 76.5 cm in females in the current analysis). In keeping with our own results, neither Kerford (2005) nor Shine (1991) found significant sexual dimorphism in dimensions of the head relative to the body in *H. major*. However, we found sex divergence both in relative tail length and in girth, whereas Kerford (2005) did not, perhaps reflecting the larger sample sizes available in our study.

Ward (2001) speculated that the evolutionary shift to marine habitats had modified sexual size dimorphism in snakes, with males larger than females in terrestrial species but the reverse in marine taxa. He attributed that shift to increased locomotor costs of pregnancy in marine snakes (as inferred by Shine 1988), favouring increased maternal body size to maintain swimming performance. The larger dataset now available weakens the putative link between

habitat and sexual size dimorphism. Some of the terrestrial species most closely related to marine hydrophiines show little sexual difference in mean adult body sizes (e.g. *Hemiaspis damelii* and *H. signata* differ in which sex attains larger mean adult size: Shine 1987, 1994a), and males average larger than females in some marine species (e.g. *Hydrophis hardwickii*: Shine 1994a). Likewise, even closely related species often differ in whether or not head sizes relative to body length diverge between conspecific males and females (Shine 1991). Given that diversity within lineages, it is difficult to identify any clear shifts in sexual dimorphism of body sizes or body proportions accompanying the shift from terrestrial to marine environments.

One trait that has clearly shifted, however, is rugosity of scales. Highly rugose and spinose scales are widespread in sea snakes but rare in terrestrial species (Avolio et al. 2006a). As is the case for *H. major*, the degree of rugosity in sea snakes generally increases with body size, is greater on the dorsal than the ventral surface and is greater in males than in females (Avolio et al. 2006a). The functional significance of that rugosity may relate to hydrodynamics and oxygen transfer across the skin (Avolio et al. 2006b) and/or to adaptations that facilitate a male clinging to a female during courtship (Shine 1993). More generally, the skin of a sea snake must deal with challenges (e.g. in salt and water flow, epifaunal fouling: Heatwole 1978, 1999; Pfaller et al. 2012; Lillywhite and Menon 2019) that are not relevant to terrestrial species. Future work to explore skin function and structure in sea snakes might clarify a range of marine innovations [including, for example, sensory papillae (Crowe-Riddell et al. 2016) and light-sensitive sections of skin (Zimmerman and Heatwole 1990)].

Reproductive output

Most viviparous sea snakes produce fewer larger offspring than do similarly-sized terrestrial species (Lemen and Voris 1981). At the same mean SVL as adult female *H. major* (98.8 cm SVL), terrestrial Australian elapids typically produce litters of about 20–30 small (< 25 cm SVL) neonates (Shine 1994b, 1995). In contrast, *H. major* produces about five offspring (means of 5—Shine 1995; 5.9—Ward 2001; 4.9—Fry et al. 2001; 4.7—Lukoschek and Avise 2011; 4.9—current study) of about 30–40 cm SVL [from late-stage embryos, 42.7 cm SVL, mass 39.6 g (Fry et al. 2001); 31–36.5 cm SVL (current study)]. The increased offspring size and decreased litter size may reflect a trade-off between these two parameters, due to limited space within a female's body and the impacts of bodily distension on hydrodynamics and thus swimming efficiency and effectiveness (Shine 1988). Plausibly, selection for larger offspring size (perhaps due to the

advantages of greater swimming ability and buoyancy control of neonates) has favoured an evolutionary reduction in litter size. That reduction has been exacerbated by the high locomotor costs of distension to the rear part of the mother's body (critical for swimming), further reducing litter volume relative to maternal body size (Shine 1988).

The putative role of maternal body volume in constraining total litter volume predicts that litter size and/or offspring size will increase in larger females. In keeping with that prediction, we found larger litters in larger female *H. major* (Fig. 3). Similar relationships have been documented in many other snakes, including sea snakes (e.g. Lemen and Voris 1981; Fry et al. 2001; contra speculations by Greer 1997) as well as their terrestrial relatives (e.g. *Hemiaspis* spp.—Shine 1987).

Most of the adult-size female *H. major* collected from August to November were reproductive (18 of 23 = 78%), as has also been reported in previous studies on this species (Fry et al. 2001) as well as on other sea snakes (Ward 2001). Although adult females of some sea snake species reproduce less-than-annually (e.g. Burns 1985), annual reproduction may be more common in marine snakes than in their terrestrial relatives (e.g. the proportion of adult-size female snakes that were reproductive averaged about 60–70% in the 52 terrestrial species reviewed by Shine 1986). Part of the disparity may, however, involve climatic factors. Sea snakes are almost exclusively tropical in distribution, whereas terrestrial snakes extend into much cooler regions; and reproductive frequencies of female snakes tend to be higher in warmer than in colder climates (e.g. Shine 1981; Bonnet et al. 1999). A scarcity of reproductive data for viviparous terrestrial snakes in the tropics renders comparisons difficult.

Composition of the diet

Many species of snakes exhibit a high degree of dietary specialisation, feeding only on a single type of prey (e.g. *Vermicella* feeding on typhlopids—Shine 1980) or a single ontogenetic stage of prey (e.g. *Emydocephalus* feeding on eggs of fishes—Goiran et al. 2013). In marine snakes, previous studies have suggested a near-dichotomous situation, with some species eating a wide phylogenetic assortment of fishes, whereas others take only a single type of prey (e.g. Voris and Voris 1983; Fry et al. 2001; Sanders et al. 2013a, b; Sherratt et al. 2018). Limited sample sizes make it difficult to determine dietary breadth in detail, let alone tease apart the degree to which diet is affected by factors such as snake sex, body size, habitat and locality (for an exception see Brischoux et al. 2007).

Available records of dietary composition of *H. major* are puzzling. Broad surveys based on dissection of snakes collected over a wide area have reported several types of

fishes in the diet. These fishes have included eel-tailed catfish (*Plotosus* spp.), nettle catfish [*Euristhmus nudiceps* (Plotosidae)] and pearlfish (*Carapus* spp., Carapidae—Voris 1972; Voris and Voris 1983), as well as an eel (Heatwole et al. 1978). Kerford (2005) reported that of seven gut contents from *H. major*, two were eels (Anguilliformes), one Perciform, three scorpionfish (Scorpaenidae) and one parrotfish (Scaridae). The quantitative analysis by Fry et al. (2001) reported that of 19 prey items, 93% by weight were *Euristhmus nudiceps*, 3% *Parachaeurichthys polynema* (tail-eyed goby, Gobiidae) and the remaining 4% were unidentified teleosts. These records suggest that *H. major* eats a variety of teleost taxa, mostly eel-tailed species.

In contrast, recent records of dietary items for *H. major*, mostly from New Caledonia, suggest a specialised diet that consists entirely of plotosid catfish (consistent with our dissections of Australian specimens in the current paper, which yielded seven records of predation on *Plotosus lineatus*). Letourneur and Briand (2012) reported four observations of predation on *Plotosus lineatus* in New Caledonia, and during fieldwork near Noumea we have witnessed a further 13 cases of predation or attempted predation on this species (see <https://la1ere.francetvinfo.fr/nouvellecaledonie/decouverte-hydrophis-major-576959.html>). To our knowledge, no other fish species have been observed to have been consumed by *H. major* in New Caledonia. That situation suggests a substantial difference between the importance of *P. lineatus* in the diet of *H. major* in Australia and New Caledonia (from the current study, 24 of 24 records, = 100%) versus published observations from a range of sites including Australian waters (1 of 30 records; $\chi^2 = 66.45$, $df = 1$, $P < 0.0001$). Our observations have included predation by juvenile as well as adult *H. major*, so geographic differences in the ontogenetic stages of snakes with food cannot explain this divergence. We do not know why diets appear to be more specialised in New Caledonia than elsewhere, but geographic variation in prey availability may be important. We also note a cautionary tale: sea snakes are notoriously difficult to identify correctly (Greer 1997), and the museum collections that we examined contained several mislabelled specimens (*H. elegans* wrongly identified as *H. major*). Also, some catfish taxa (e.g. *Plotosus lineatus* and *Euristhmus nudiceps*) can be difficult to distinguish (especially when part-digested). Thus, some of the disagreement about dietary specialisation might involve misidentification of snake or prey species.

In summary, our examination of preserved specimens in museum collections provides the most extensive data yet available on ecological characteristics of this large, abundant and widely distributed sea snake. Such studies cannot be a substitute for detailed work on the behaviour and

ecology of free-ranging snakes, but logistical constraints render dissection-based research easier and less expensive than fieldwork. The increasing application of new methods (including acoustic telemetry) to quantify habitat use and movement patterns in these poorly understood marine predators (e.g. Udyawer et al. 2015, 2016a, b) holds great promise. We already know that sea snakes play diverse ecological roles (e.g. Voris and Voris 1983; Sherratt et al. 2018) and may be in decline over much of their range (e.g. Goiran and Shine 2013; Lukoschek et al. 2013). To understand and address those declines, we need to know far more about the ecology of marine snakes than is currently the case.

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Author contributions All authors contributed to data collection. RS initiated the study, analysed the data and wrote the manuscript, with input from CG and TS.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Avolio C, Shine R, Pile A (2006a) Sexual dimorphism in scale rugosity in sea snakes (Hydrophiidae). *Biol J Linn Soc* 89:343–354
- Avolio C, Shine R, Pile AJ (2006b) The adaptive significance of sexually dimorphic scale rugosity in sea snakes. *Am Nat* 167:728–738
- Bonnet X, Shine R, Naulleau G, Lourdaux O (1999) What is the appropriate timescale for measuring “costs of reproduction” in a typical capital breeder, the asp viper? *Evol Ecol* 13:485–497
- Brischoux F, Bonnet X, Shine R (2007) Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. *Mar Ecol Prog Ser* 350:145–151
- Brown GP, Shine R (2004) Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis mairii*, Colubridae). *Behav Ecol Sociobiol* 56:257–262
- Burns GW (1985) The female reproductive cycle of the Olive Sea snake, *Aipysurus laevis* (Hydrophiidae). In: Grigg GC, Shine R, Ehmann H (eds) *Biology of Australasian frogs and reptiles*. Surrey Beatty, Sydney, pp 339–341
- Burns GW, Heatwole H (2000) Growth, sexual dimorphism, and population biology of the olive sea snake, *Aipysurus laevis*, on the Great Barrier Reef of Australia. *Amphibia-Reptilia* 21:289–300
- Crowe-Riddell JM, Snelling EP, Watson AP, Suh AK, Partridge JC, Sanders KL (2016) The evolution of scale sensilla in the transition from land to sea in elapid snakes. *Open Biol* 6:160054
- Dunson WA, Dunson MK (1973) Convergent evolution of sublingual salt glands in the marine file snake and the true sea snakes. *J Comp Physiol* 86:193–208
- Elfes CT, Livingstone SR, Lane A, Lukoschek V, Sanders KL, Courtney AJ, Gatus JL, Guinea M, Lobo AS, Milton D, Rasmussen AR (2013) Fascinating and forgotten: the conservation status of the world’s sea snakes. *Herpetol Conserv Biol* 8:37–52
- Fry GC, Milton DA, Wassenberg TJ (2001) The reproductive biology and diet of sea snake bycatch of prawn trawling in northern Australia: characteristics important for assessing the impacts on populations. *Pac Conserv Biol* 7:55–73
- Goiran C, Shine R (2013) Decline in sea snake abundance on a protected coral reef system in the New Caledonian Lagoon. *Coral Reefs* 32:281–284
- Goiran C, Shine R (2014) Reaction of a sea snake (*Hydrophis major*) to contact with a sea anemone. *Coral Reefs* 33:793
- Goiran C, Dubey S, Shine R (2013) Effects of season, sex and body size on the feeding ecology of turtle-headed sea snakes (*Emydocephalus annulatus*) on IndoPacific inshore coral reefs. *Coral Reefs* 32:527–538
- Greer AE (1997) *The biology and evolution of Australian snakes*. Surrey Beatty, Sydney
- Heatwole H (1978) Adaptations of marine snakes: unusual physiological strategies have enabled some snakes to live in a saltwater environment. *Am Sci* 66:594–604
- Heatwole H (1999) *Sea snakes*, 2nd edn. Krieger Publishing Company, Florida
- Heatwole H, Burns G (1987) *Final Report for National Parks and Wildlife Service Consultancy on Sea snake Populations*. Unpublished Report, Australian National parks and Wildlife Service, Canberra
- Heatwole H, Cogger HG (1994) *Sea snakes of Australia*. In: Gopalakrishnakone P (ed) *Sea snake toxinology*. Singapore University Press, Singapore, pp 167–205
- Heatwole H, Minton SA Jr, Taylor R, Taylor V (1978) Underwater observations on sea snake behaviour. *Rec Aust Mus* 31:737–761
- Ineich I, Rasmussen AR (1997) Sea snakes from New Caledonia and the Loyalty Islands (Elapidae, Laticaudinae and Hydrophiinae). *Zoosystema* 19:185–192
- Ineich I, Laboute P (2002) *Les serpents marins de Nouvelle-Calédonie*. IRD éditions, Paris
- Keogh JS, Shine R, Donnellan S (1998) Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (subfamily Hydrophiinae) based on cytochrome b and 16S rRNA sequences. *Mol Phylogenet Evol* 10:67–81
- Kerford M (2005) *The ecology of the bar bellied sea snake (Hydrophis elegans) in Shark Bay, Western Australia*. M.Sc. thesis, Biological Sciences, Simon Fraser University, p 85
- Kerford M, Wirsing AJ, Heithaus MR, Dill LM (2008) Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the bar-bellied sea snake *Hydrophis elegans*. *Mar Ecol Prog Ser* 358:289–294
- Lee MS, Sanders KL, King B, Palci A (2016) Diversification rates and phenotypic evolution in venomous snakes (Elapidae). *R Soc Open Sci* 3:150277
- Lemen CA, Voris HK (1981) A comparison of reproductive strategies among marine snakes. *J Anim Ecol* 50:89–101
- Letourneur Y, Briand MJ (2012) Catfish *Plotosus lineatus* are prey for the rare sea snake *Hydrophis major* in New Caledonia. *Coral Reefs* 31:349–349
- Lillywhite HB, Menon GK (2019) Structure and function of skin in the pelagic sea snake, *Hydrophis platurus*. *J Morphol* 280:544–554
- Lukoschek V, Avise JC (2011) Genetic monandry in 6 viviparous species of true sea snakes. *J Hered* 102:347–351

- Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M (2013) Enigmatic declines of Australia's sea snakes from a biodiversity hotspot. *Biol Conserv* 166:191–202
- Lynch TP (1999) The behavioural ecology of the Olive Sea snake, *Aipysurus laevis*. Ph.D. thesis, James Cook University, Townsville
- Marcos LA, Lanyon JM (2004) Dietary and morphometric analysis of three sea snake species caught as a single trawl by-catch assemblage around the Swain's Reefs, Southern Great Barrier Reef, Queensland. *Proc R Soc Qld* 111:63–71
- Pfaller JB, Frick MG, Brischoux F, Sheehy CM III, Lillywhite HB (2012) Marine snake epibiosis: a review and first report of decapods associated with *Pelamis platurus*. *Integr Comp Biol* 52:296–310
- Sanders KL, Lee MS, Leys R, Foster R, Keogh SJ (2008) Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *J Evol Biol* 21:682–695
- Sanders KL, Lee MS, Bertozzi T, Rasmussen AR (2013a) Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Mol Phylogenet Evol* 66:575–591
- Sanders KL, Rasmussen AR, Elmerberg J, De Silva A, Guinea ML, Lee MS (2013b) Recent rapid speciation and ecomorph divergence in Indo-Australian sea snakes. *Mol Ecol* 22:2742–2759
- Seymour RS (1982) Physiological adaptations to aquatic life. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, vol 13. Academic Press, New York, pp 1–51
- Sherratt E, Rasmussen AR, Sanders KL (2018) Trophic specialization drives morphological evolution in sea snakes. *R Soc Open Sci* 5:172141
- Shine R (1980) Reproduction, feeding and growth in the Australian burrowing snake *Vermicella annulata*. *J Herpetol* 14:71–77
- Shine R (1981) Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). *Copeia* 1981:14–25
- Shine R (1986) Ecology of a low-energy specialist: food habits and reproductive biology of the arafura filesnake (Acrochordidae). *Copeia* 1986:424–437
- Shine R (1987) Food habits and reproductive biology of Australian snakes of the genus *Hemiaspis* (Elapidae). *J Herpetol* 21:71–74
- Shine R (1988) Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* 42:17–27
- Shine R (1991) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am Nat* 138:103–122
- Shine R (1993) Sexual dimorphism in snakes. In: Collins JT, Seigel RA (eds) *Snakes: ecology and behavior*. McGraw-Hill, New York, pp 49–86
- Shine R (1994a) Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346
- Shine R (1994b) Allometric patterns in the ecology of Australian snakes. *Copeia* 1994:851–867
- Shine R (1995) *Australian snakes: a natural history*. Cornell University Press, Ithaca
- Shine R, Bull JJ (1977) Skewed sex ratios in snakes. *Copeia* 1977:228–234
- Udyawer V, Simpfendorfer CA, Heupel MR (2015) Diel patterns in three-dimensional use of space by sea snakes. *Animal Biotelemetry* 3:29
- Udyawer V, Simpfendorfer CA, Read M, Hamann M, Heupel MR (2016a) Exploring habitat selection in sea snakes using passive acoustic monitoring and Bayesian hierarchical models. *Mar Ecol Prog Ser* 546:249–262
- Udyawer V, Read M, Hamann M, Heupel MR, Simpfendorfer CA (2016b) Importance of shallow tidal habitats as refugia from trawl fishing for sea snakes. *J Herpetol* 50:527–533
- Ukuwela KD, Lee MS, Rasmussen AR, De Silva A, Sanders KL (2017) Biogeographic origins of the viviparous sea snake assemblage (Elapidae) of the Indian Ocean. *Ceylon J Sci* 46:101–110
- Voris HK (1972) The role of sea snakes (Hydrophiidae) in the trophic structure of coastal ocean communities. *J Mar Biol Assoc India* 14:429–442
- Voris HK, Voris HH (1983) Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioral and ecological relationships. *Am Zool* 23:411–425
- Ward TM (1996a) Sea snake by-catch of fish trawlers on the northern Australian continental shelf. *Mar Freshw Res* 47:625–630
- Ward TM (1996b) Sea snake by-catch of prawn trawlers on the northern Australian continental shelf. *Mar Freshw Res* 47:631–635
- Ward TM (2000) Factors affecting the catch rates and relative abundance of sea snakes in the by-catch of trawlers targeting tiger and endeavour prawns on the northern Australian continental shelf. *Mar Freshw Res* 51:155–164
- Ward TM (2001) Age structures and reproductive patterns of two species of sea snake, *Lapemis hardwickii* Grey (1836) and *Hydrophis elegans* (Grey 1842), incidentally captured by prawn trawlers in northern Australia. *Mar Freshw Res* 52:193–203
- Wassenberg TJ, Salini JP, Heatwole H, Kerr JD (1994) Incidental capture of sea-snakes (Hydrophiidae) by prawn trawlers in the Gulf of Carpentaria, Australia. *Mar Freshw Res* 45:429–443
- Wirsing AJ, Heithaus MR (2009) Olive-headed sea snakes *Distertia major* shift seagrass microhabitats to avoid shark predation. *Mar Ecol Prog Ser* 387:287–293
- Zimmerman K, Heatwole H (1990) Cutaneous photoreception: a new sensory mechanism for reptiles. *Copeia* 1990:860–862

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