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Niche partitioning within a population of seasnakes is constrained by ambient thermal homogeneity and small prey size

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In many populations of terrestrial snakes, an individual's phenotype (e.g. body size, sex, colour) affects its habitat use. One cause for that link is gape-limitation, which can result in larger snakes eating prey that are found in different habitats. A second factor involves thermoregulatory opportunities, whereby individuals select habitats based upon thermal conditions. These ideas predict minimal intraspecific variation in habitat use in a species that eats small prey and lives in a thermally uniform habitat – such as the seasnake *Emydocephalus annulatus*, that feeds on tiny fish eggs and lives in inshore coral-reefs. To test that prediction, we gathered data on water depths and substrate attributes for 1475 sightings of 128 free-ranging *E. annulatus* in a bay near Noumea, New Caledonia. Habitat selection varied among individuals, but with a preference for coral-dominated substrates. A snake's body size and reproductive state affected its detectability in deep water, but overall habitat use was not linked to snake body size, colour morph, sex, or pregnancy. A lack of ontogenetic shifts in habitat use allows extreme philopatry in *E. annulatus*, thereby reducing gene flow among populations and potentially, delaying recolonization after local extirpation events.

ADDITIONAL KEYWORDS: Elapidae – Hydrophiinae – New Caledonia – sexual dimorphism.

INTRODUCTION

Although ecological differences among individuals within the same population often are minor, a growing literature examines exceptions to that rule. For example, individuals may shift in dietary composition, foraging tactics, diel activity patterns and habitat use as they grow larger (e.g. Marques *et al.*, 2013), or as a function of their sex (Ruckstuhl *et al.*, 2005), morphology of feeding structures (Collins & Holomuzki, 1984), or colour (Wilson *et al.*, 2007; Isaac & Gregory, 2013). Likewise, an individual's use of habitats may be affected by its physiological state: for example, reproduction can induce long migrations to habitat types that facilitate mating and/or enhance the viability of offspring (e.g. Heatwole 1989; Sinsch, 1990; Stewart, 1997).

Many striking cases of intrapopulation divergence in ecological niches involve ectothermic species rather than endotherms, for three reasons. First, ectothermy allows a wide range of body sizes and shapes, whereas endothermy demands large size and a low ratio of surface area to volume (Pough, 1980). Thus, ectotherms can be ecologically independent over a wide range of body sizes (Lever, 2001). Almost inevitably, then, a neonate and a conspecific adult will differ in the food they consume, the predators that threaten them, the shelters they use, and the habitat features that provide other resources. Lability in body sizes can translate into extreme sexual size dimorphism, given divergent sex-specific selective pressures (e.g. Shine *et al.*, 1998; Rivas & Burghardt, 2001). Second, the low metabolic maintenance requirements of ectothermy allow niche specialization: an animal that feeds infrequently can target prey resources that are available only occasionally, or at specific sites (Pough, 1980). Lastly, many terrestrial ectotherms regulate their body temperatures by exploiting ambient thermal heterogeneity, moving in and out of sun-exposed sites (Chou *et al.*, 2019). Optimal body temperature shifts as a function of physiological state: for example, higher temperatures accelerate digestion and embryogenesis, and thus are often selected by

recently-fed and gravid ectotherms – with direct effects on habitat use (Reinert, 1984; Luiselli, 2006). The end result is that many populations of ectotherms contain individuals that diverge substantially from each other in niche dimensions such as habitat use, dietary composition and diel timing of activity (e.g. Wolf & Werner, 1994; Tanaka, 2007, 2009; Trullas *et al.*, 2007; Hyslop *et al.*, 2014; but see Luiselli *et al.*, 1994; Tu *et al.*, 2000).

Snakes provide many examples of intraspecific divergences in niche utilization (Shine & Wall, 2005). Compared to lizards, for example, snakes tend to exhibit larger adult body sizes (creating a wide range of body sizes within a population) and have lower metabolic rates, allowing specialized diets (Andrews & Pough, 1985; Greene, 1997). Most snakes take large prey items; and the maximum ingestible prey size is set by the dimensions of the snake's head (Pearson *et al.*, 2002; Filippi *et al.*, 2005). As a result, larger individuals have access to prey resources that cannot be swallowed by smaller conspecifics. Often, the prey consumed by adult snakes are found in different places, or are active at different times of day, than are the prey of younger conspecifics (Ayers & Shine, 1997; Shine *et al.*, 1998). Similarly, sex differences in diet, and in relative head size, are widespread in snakes (Shine, 1986, 1991; Houston & Shine, 1993; Luiselli & Angelici, 1998; Shine *et al.*, 2002; Glaudas *et al.*, 2008; Ford & Hampton, 2009).

In summary, two drivers of intraspecific niche differentiation in snakes appear to have been (a) prey large enough to cause gape-limitation, and (b) spatial and temporal heterogeneity in ambient temperatures. If those conditions are not satisfied, then, we should not see niche divergence. The role of gape-limitation is straightforward: if all available prey items are small enough to be eaten by all snakes, then a predator's body size is unlikely to affect its diet. Likewise, snakes that live in an environment with uniform ambient temperatures have no opportunity to modify their own body temperatures behaviourally (Daltry *et al.*, 1998). Snakes that lack gape-limitation and that inhabit thermally uniform

environments thus offer a way to test the hypothesis that these factors cause intraspecific niche divergence.

Marine snakes of the genus *Emydocephalus* offer an ideal system in this respect. They feed on tiny prey (the eggs of fishes) and live in coral-reef systems where temperatures are relatively invariant through space and across the diel cycle (Shine *et al.*, 2003). Although seasnakes of some species bask on the sea surface, most (including *E. annulatus*) do not do so (presumably because of the risk of predation: Heatwole *et al.*, 2012). Water conducts heat so effectively that thermal gradients are far weaker in marine systems than in many terrestrial situations (Rugenstein *et al.*, 2016); and hence, factors that affect heating rates and equilibrated temperatures of terrestrial snakes (such as body size and colour) have no impact on the temperature of seasnakes (Shine *et al.*, 2003).

A preliminary study of *Emydocephalus annulatus* reported little intraspecific niche divergence (Shine *et al.*, 2003), but that study was based on a small sample size. To convincingly support the null hypothesis – that a snake’s size, sex, colour and physiological state do *not* affect its habitat use – we need robust tests with large sample sizes. Otherwise, we risk accepting the null hypothesis simply because we lack the power to refute it (Aberson, 2019). Likewise, we need to individually identify animals so as to avoid pseudoreplication (i.e. to treat repeated sightings of the same animal as statistically independent). In the present paper, we describe habitat use in the same population of *Emydocephalus annulatus* as studied by Shine *et al.* (2003), but with information on individual identity and a 20-fold larger sample size ($N = 1475$ vs. 74 observations).

MATERIAL AND METHODS

SPECIES

Turtle-headed seasnakes (*E. annulatus*) are stout-bodied medium-sized hydrophiine elapids. Females grow larger than males (maxima 72.0 vs. 63.5 cm snout-vent length [SVL]) and produce litters of one to four neonates (approx. 30 cm SVL) in April-May on an approximately biennial schedule (R. Shine & C. Goiran, unpublished data). All size classes of *E. annulatus* feed only on the eggs of demersal-spawning blennies, gobies and damselfish, but foraging activity is curtailed in adult males during the mating season (in winter) and in females during late pregnancy (during late summer: Goiran *et al.*, 2013). Individuals vary in colour, but each retains the same colour throughout its life; most individuals in our study site are melanic, but some are brightly banded with black and white rings (Goiran *et al.*, 2017).

STUDY SITE

The Baie des Citrons is a small shallow bay beside the city of Noumea, New Caledonia (22°16'S, 166°26'E). Our study area is approximately 250 m long but is narrow (50 to 100 m wide at high tide; total area 0.03 km²), with sand substrate in deeper water, giving way to corals, coral rubble and rocks in shallower areas (see Fig. 1A, and Shine *et al.*, 2003 for description). The tidal range is usually less than 1.6 m, and adjacent headlands protect the bay from trade winds. Water depth at high tide across our study area ranges from 0.9 to 4.4 m (mean = 2.25 m, SD = 0.87 m) whereas water depths in which we recorded snakes, at the times we found them rather than at high tide, ranged from 0.3 to 4.0 m (mean = 1.49, SD = 0.65). The species has also been reported to occur in much deeper water (e.g., to at least 30 m: Ineich and Laboute 2002). Annual (January) mark-recapture trips have resulted in most snakes within this population carrying microchips (Trovan ID) for individual identification.

METHODS

We mapped substrate types and water depths in each 20 × 20-metre quadrat of the study site in December 2014, to create a detailed map. Within each 20 × 20-metre quadrat, we scored the percentage of substrate covered by rock, coral rubble, branching coral, non-branching coral, soft coral and algae. We also recorded water depth at high tide for each quadrat.

To quantify habitat use by snakes, we snorkelled through the study area on 312 days between March 2014 and August 2018. The number of divers per trip ranged from 1 to 12, but most sessions were conducted by a single person (CG). Snakes were hand-captured (Fig. 1B), and identified by implanted microchips (using a scanner inside a waterproof bag) before being released at the site of capture <1 min later. We then recorded the location (quadrat) and water depth in the site at the time of capture, and tidal stage (low, medium or high).

For statistical analysis, we combined habitat (substrate-type) categories into five groups: rock, sand plus coral rubble, soft coral plus algae, non-branching hard coral, and branching hard coral. The data on % coverage of each quadrat by each substrate type was $\ln(1+X)$ -transformed to improve normality and model convergence. We performed four general linear mixed model multiple regressions to analyse four dependent variables (snake body size, sex, coloration and pregnancy). We included seven habitat variables (five % substrate types, plus water depths at capture and at high tide) as independent variables in each analysis. Snake identification (ID) # was included as a random effect, to account for multiple captures of the same snake on different days. General linear mixed models were performed using Proc glimmix in SAS 9.4 (SAS Institute, Cary, NC). For the three binomial dependent variables (sex [male vs. female], colouration [banded vs. melanic], and pregnancy [yes vs. no]), we used a binary distribution with a logit link function. For the continuous dependent variable (SVL) we used a normal distribution with an identify link function.

To estimate consistency in the use of habitat features by individual snakes, we calculated repeatability of the seven physical characteristics (% rock, % algae plus soft coral, % non-

branching coral, % branching coral, % sand and rubble, water depth, and depth at high tide) recorded for the 110 individual snakes sighted more than once (2–47 times). To calculate the repeatability of each habitat feature we used generalized linear mixed models implemented in R package rptR (Stoffel *et al.*, 2017) with normal distributions and with individual snake ID as a random effect. The five substrate-type features (% rock, % algae plus soft coral, % non-branching coral, % branching coral, % sand plus rubble) were $\ln(1+X)$ -transformed to improve normality and model convergence. Standard errors around repeatability estimates were generated from 1000 bootstrap simulations and significance levels of repeatability estimates from 1000 randomized permutations (Nakagawa & Schielzeth, 2010).

To compare used versus available habitats, we calculated mean values for each quadrat and for each snake, and compared the two using MANOVA with substrate type as the repeated variable in JMP 13.0 (SAS Institute, Cary, NC). We also ran multiple regressions with $\ln(1+\%$ substrate type) as independent variables and frequency of use of each quadrat as the dependent variable, to see if frequently-used quadrats had distinctive habitat attributes.

RESULTS

SAMPLE SIZES AND MEAN VALUES

We obtained data on capture locations for 128 snakes, with 1 to 39 observations per animal (mean = 11.4 sightings per snake; total = 1475 observations). Animal ID was unknown for an additional 14 cases (snakes without microchips). Only 29 of the sightings (2%) were of juveniles ($N = 5$ individuals). For adult snakes, we obtained 832 records from 69 males, and 614 records from 57 females. The mean body lengths of snakes in our dataset (based upon measurements in January of the year they were recaptured) was 58.23 cm SVL (SE = 0.17, range 35–72 cm SVL). We made 203 observations of banded snakes (13.8% of the dataset) and 1272 observations of melanic snakes (86.2%).

Individual snakes varied considerably in the habitats that they occupied, reflecting small home ranges. Although each snake was captured an average of 11.4 times, those captures occurred within an average of 6.6 quadrats per snake, out of a total of 71 quadrats used by all snakes within the population. Thus, each individual snake used only a small part of the study area. Spatial variation in substrate types and water depths meant that this extreme philopatry was associated with significant repeatability in characteristics of habitat used by individual snakes (see Table 1).

OVERALL PATTERNS IN HABITAT USE

The usage of different habitats by snakes was correlated with the availability of those habitats (Fig. 2), but with a significant interaction between substrate type and usage (interaction $F_{4,192} = 3.66$, $P < 0.007$) because snakes were found over coral more often than expected by chance (Fig. 2). Mean water depths at sites where snakes were found did not differ significantly from site-wide mean values for water depth at the time of capture ($F_{1,197} = 0.37$, $P = 0.54$) or at high tide ($F_{1,195} = 0.74$, $P = 0.39$).

Another way to examine non-random habitat use is to look at predictors of the number of times a quadrat was used by snakes. In a multiple regression, the frequency of use of a quadrat was affected by the proportion of the substrate covered by algae plus soft coral ($P < 0.04$), branching coral ($P < 0.05$) and non-branching coral ($P < 0.005$).

RELATIONSHIPS BETWEEN SNAKE PHENOTYPE AND HABITAT USE

Our generalized linear mixed models revealed few significant links between most aspects of a snake's phenotype (colour, sex, SVL) and the substrate types and water depths where it was found (see Table 2). The only statistically significant associations were that snakes seen in deeper water tended to be larger, and that gravid snakes were found in shallower water than

were non-gravid females (means of 1.32 [SE = 0.04] vs. 1.56 [SE = 0.05] m; for comparison, mean water depth for males = 1.52 [SE = 0.02] m) (Table 2). Paradoxically, however, mean water depths at high tide were similar in sites where we found small versus large snakes, and where we found gravid versus non-gravid snakes (Table 2). Those conflicting results reflect the fact that we saw smaller snakes, and gravid female snakes, during low rather than high tides. For example, water depth at the time of sighting averaged 74.0% (SE = 0.02) of depth at high tide at the same site for non-gravid females, versus 65.0% (SE = 0.02) for gravid females (ANOVA $F_{1,321.1} = 8.87, P < 0.005$).

DISCUSSION

Our sightings and resightings of 128 specimens of turtle-headed seasnakes (1475 captures) show that individual snakes used only small areas, and hence differed significantly from each other in all of the attributes of habitat that we assessed. Nonetheless, that variation among individuals was largely independent of variation in phenotypic traits of the animals involved.

A previous analysis at the same site was based on 74 captures, without individual identification. The total number of animals used in Shine *et al.*'s (2003) study was around 40 to 50, based on proportions of newly-found versus resighted individuals after we commenced individual marking (e.g. resighted individuals comprised 35% of 66 snakes captured in 2004, and 42% of 72 snakes in 2005). Our results from the expanded dataset support the conclusion of Shine *et al.* (2003) that smaller snakes tend to be found in shallower water. However, we found no evidence for a sex difference in habitat breadth, nor for snakes to be found over coral rubble more often than expected by chance. Instead, a snake's sex and body size did not affect its habitat use; and coral substrates were used slightly more often than expected based on their availability.

Despite the large sample size, we detected only two non-random patterns in habitat use. First, gravid females were found in shallower water than were males or non-gravid females. This difference might be due either to an effect of pregnancy on habitat selection (as is common in terrestrial snakes: e.g. Charland & Gregory, 1995; Reinert & Zappalorti, 1998; Carfagno & Weatherhead, 2006; Waldron *et al.*, 2006), or to differential observability (gravid females are inactive [Goiran *et al.*, 2013], and thereby might be more difficult to see in deep water). In keeping with the latter hypothesis, the maximum water depth (i.e. at high tide) at sites where we found gravid females did not differ from the mean values for males or non-gravid females. This result suggests that pregnancy does not affect a snake's habitat selection, but does affect its probability of detection. The second non-random pattern was a trend for smaller snakes to be found in shallower water (as also detected by Shine *et al.* 2003), and may reflect size-dependent vulnerability to predatory fish species that are found in deeper water (e.g. Kerford *et al.*, 2008; Udyawer *et al.*, 2016a). In the case of *E. annulatus*, however, observability offers a more plausible explanation. A snake's body size was not associated with the depth at high tide of the site where we found it; instead, it was associated with depth at the time of sighting. Overall, then, the reduced rate at which we found small snakes and gravid snakes in deep water is due to difficulties in observing cryptic individuals in deeper water, rather than an underlying association between water depth and snake phenotypes.

The low level of intrapopulation niche partitioning within *E. annulatus* (but see Goiran *et al.*, 2013 for evidence of divergences in feeding rates and prey types) may be due primarily to the homogeneity of habitats across our study area. Thermal homogeneity precludes subgroups within the snake population (e.g. gravid females) from selecting sites that facilitate higher body temperatures. Food availability is similarly homogeneous: demersal-spawning fish occur across the entire study area, and their eggs are small enough to be consumed by even a neonate *E. annulatus* (Shine *et al.*, 2003). Likewise, the water is too shallow for

ingress by large sharks (important predators for seasnakes: Heatwole *et al.*, 1974; Kerford *et al.*, 2008; Masunaga *et al.*, 2008). Lastly, shallow water means that the risks of surfacing to breathe likely are minimal. Some seasnakes forage at much greater depths (e.g. Udyawer *et al.*, 2015; Cook *et al.*, 2016; Crowe-Riddell *et al.*, 2019).

Increasing the spatial variance in prey sizes, prey availability or predation risk could magnify opportunities for intrapopulation divergence in niche utilization. Thus, for example, sea kraits (*Laticauda* spp.) in the Baie des Citrons partition prey resources among age classes and sexes because predator body size constrains maximal ingestible prey size, and the ability to penetrate narrow coralline crevices to capture eels (Shine *et al.*, 2002; Brischoux *et al.*, 2009). Selection of shallow tidal habitats by gravid females and juveniles of other seasnake species (*Hydrophis curtus* and *H. elegans*) has been attributed to refuge from predation, habitat-specific prey availability, and the impairment of locomotory ability by pregnancy and small body size (Udyawer *et al.*, 2016a). Sex differences in habitat use are associated with reproductive activity in other seasnakes (*Aipysurus laevis*, *Hydrophis major*), with adult males utilizing shallow coralline habitats primarily while mate-searching (Lynch, 2000; Goiran & Shine, 2019).

Our analyses broadly support the a priori prediction of minimal intraspecific variation in habitat use in *Emydocephalus annulatus*. By reducing opportunities for behavioural thermoregulation, the low thermal heterogeneity in marine systems should weaken functional links between snake phenotypes and habitat attributes. At the same time, however, marine systems introduce another axis of habitat variation – water depth – that creates a mosaic of different patches that are optimal for animals of different sizes, sexes, or physiological states. For example, bodily distension by a large prey item or a developing litter may compromise hydrodynamics, thereby favouring selection of shallow-water microhabitats that do not require a snake to make extensive movements to reach the water surface to breathe (Udyawer

et al., 2016b). Such factors may be more important in deep-water sites than in our shallow study area (e.g. Udyawer *et al.*, 2015; Cook *et al.*, 2016; Crowe-Riddell *et al.*, 2019).

At present, we know too little about intrapopulation variation in ecological traits of marine snakes to make any broad comparisons between terrestrial and marine systems. However, that situation is changing rapidly, with acoustic telemetry (e.g. Udyawer *et al.*, 2016a, 2017) promising to enhance our understanding of seasnake ecology in the same way that other types of telemetry revolutionized our knowledge of terrestrial snakes (Shine & Bonnet, 2000). Citizen science also offers potential for studies of large mobile predators in marine habitats (Goiran & Shine, 2019). In addition, many terrestrial snake species provide opportunities to explore intrapopulation niche divergence in thermally homogeneous habitats (e.g. underground) and in the absence of gape-limitation (e.g. snakes that feed on insect eggs: Webb & Shine, 1993).

The lack of any strong ontogenetic shift in habitat use within *E. annulatus* fits well with the high degree of philopatry in our study population (Shine *et al.*, 2012; Lukoschek & Shine, 2012; and present study). The home range of a snake contains all of the resources it needs, and strong overlap in habitat use between males and females reduces the importance of long-distance mate-searching behaviour by males, as is common in other snake species (e.g. Lynch, 2000; Keogh *et al.*, 2007; Lane & Shine, 2011). Extreme philopatry creates an opportunity for genetic divergence among populations (Lukoschek & Shine, 2012). Also, the limited movements of individuals likely delay recolonization of sites after local extirpation by events such as coral bleaching. Hence, a lack of niche divergence among individuals within a population may translate into increased vulnerability to threats such as climate change.

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AUTHOR CONTRIBUTIONS

The project was initiated by CG and RS, CG gathered the data, RS and GPB conducted statistical analyses, all authors contributed to manuscript preparation.

CONFLICT OF INTEREST

We declare no conflict of interests.

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Table 1. Repeatability estimates of habitat features used by individual turtle-headed seasnakes (*Emydocephalus annulatus*) in the Baie des Citrons, Noumea. Bold font shows significant values at $P < 0.05$

Habitat characteristic	Repeatability (\pm SE)	<i>P</i>
Rock (%)	0.22 \pm 0.03	0.001
Algae plus soft coral (%)	0.19 \pm 0.03	0.001
Non-branching coral (%)	0.10 \pm 0.02	0.001
Branching coral (%)	0.13 \pm 0.03	0.001
Sand plus rubble (%)	0.10 \pm 0.02	0.001
Water depth (m)	0.16 \pm 0.03	0.001
Depth at high tide (m)	0.25 \pm 0.04	0.001

Table 2. Generalized linear mixed model results assessing habitat characteristics associated with different phenotypes of turtle-headed seasnakes (*Emydocephalus annulatus*) in the Baie des Citrons, Noumea. One dependent variable was continuous (snout-vent length [= SVL]) and the analysis was performed using a normal distribution and an identify link function. The remaining four dependent variables were binary [sex (male vs. female), colour morph (banded vs. black) and pregnancy (gravid vs. non-gravid)] and these analyses were performed using a binary distribution and a logit link function. Individual snake ID # was included as a random effect in all models and the Table shows type III tests of fixed effects. Snakes seen in deeper water tended to be larger. Females seen in shallower water were more likely to be pregnant. Bold font shows significance at $P < 0.05$

Independent variable	SVL		Sex		Colour		Pregnancy	
	$F_{1,1329}$	P	$F_{1,1323}$	P	$F_{1,1329}$	P	$F_{1,295}$	P
Rock (%)	1.74	0.187	0.04	0.843	1.62	0.203	0.42	0.518
Algae plus soft coral (%)	2.45	0.118	0.04	0.834	1.07	0.301	0.61	0.436
Non-branching coral (%)	0.22	0.638	0.05	0.816	0.44	0.505	0.84	0.360
Branching coral (%)	0.79	0.374	0.09	0.762	0.89	0.344	2.26	0.134
Sand plus rubble (%)	0.00	0.960	0.22	0.636	0.88	0.349	0.72	0.398
Water depth (m)	4.93	0.027	0.01	0.935	0.58	0.447	9.84	0.002
Depth at high tide (m)	0.56	0.456	0.15	0.699	0.60	0.440	0.82	0.365

Figure 1. (A) Aerial photograph of study site at Baie des Citrons (uniformly pale substrates on upper part of the photograph are sandy; darker strip in midline is coral; variegated area in shallows is dominated by coral rubble and rocks; and (B) turtle-headed seasnake (*Emydocephalus annulatus*) and snorkeller. Photograph by Pierre Larue (A), and (B) from <https://georep.nc/>

Figure 2. Availability of different substrate types in Baie des Citrons, compared to use of those substrates by turtle-headed seasnakes (*Emydocephalus annulatus*).