
Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern

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An individual's sex, body size and colour pattern can influence its habitat use, and such partitioning can have important ecological and evolutionary consequences. We studied a system very different from those that have attracted previous research on this topic: sea snakes (*Emydocephalus annulatus*) in shallow-water coral-reef areas of New Caledonia. The snakes used habitats non-randomly in terms of substrate types and water depths, with frequent use of coral-rubble areas that also contained the nests of fish (damselfish and blennies) whose eggs are eaten by these snakes. Mate-searching adult male snakes were found across a broader range of habitat types than were foraging females and juveniles. Smaller snakes were found in shallower water. Colour polymorphism was evident (melanism increased with body size, and was more common in males than in females) but did not affect habitat use. The effects of colour morph on operative temperatures of physical models (evident in terrestrial situations) disappeared under water. Habitat use in this population is affected by a snake's body size and sex, but not by colour. Studies of terrestrial snakes have emphasized thermal or camouflage benefits of colour polymorphism, but the superficially similar polymorphism in *E. annulatus* is not consistent with either of these hypotheses and thus challenges their generality. Similarly, there was no dietary difference between age or sex groups and thus dietary partitioning cannot explain the observed intraspecific habitat partitioning. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 80, 1–10.

ADDITIONAL KEYWORDS: dimorphism – Hydrophiidae – marine – niche – polymorphism.

INTRODUCTION

Frequently, a single population contains individuals that encompass a wide range of phenotypes in terms of factors such as sex, body size, colour, shape, locomotor abilities, dietary specialization, antipredator responses, and so forth (e.g. Brodie, 1989; Torre & Bosch, 1999; Kirkton & Schultz, 2001). Many environments are similarly heterogeneous, so that a given phenotype confers different fitness in one habitat type than in another; for example, a particular colour or shape may provide effective camouflage against only some kinds of background. In such situations, we expect natural selection to modify habitat-selection

behaviour such that individuals of different phenotypes use available habitats differently (Kirkton & Schultz, 2001; Telleria *et al.*, 2001; Rolando, 2002; Rossi *et al.*, 2002). Thus, an animal's phenotype can affect its probability of survival not only by direct processes, but also by modifying the times and places of fitness-relevant interactions. For example, an organism that matches its habitat selection to its phenotype may thereby modify its exposure to food, predators and/or conspecifics. Among the most important phenotypic traits in this respect are:

1 Body size – small animals may eat different types and sizes of prey, be vulnerable to a wider range of predators, and (because of higher surface area-to-volume ratio) heat, cool and exchange water with the surrounding environment more rapidly than do larger animals (Peters, 1983; Hatase *et al.*, 2002). Small individuals may fit more easily into small crevices inac-

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cessible to larger conspecifics, but social aggression may restrict smaller animals to suboptimal habitats (Law & Bradley, 1990; Golden, Smith & Rettig, 2001).

2 Sex – males and females differ in many attributes that can influence habitat use (Ruckstuhl & Neuhaus, 2001; McDonald, 2002). Most obviously, they differ in behaviour, with males sometimes moving over much larger areas than do females in the course of territorial defence or mate-searching. Such movements are likely to influence the amounts of time spent in different habitat types (Andersson, 1994; Sims, Nash & Morritt, 2001). Males and females also differ in body size in many taxa, and not infrequently in food habits, further favouring habitat subdivision within the population (Mushinsky, Hebrard & Vodopich, 1982; Mushinsky, 1987; Luiselli & Angelici, 1998; Bowyer *et al.*, 2002; Lesage *et al.*, 2002).

3 Colour – in a population with multiple colour morphs, individuals may select areas that provide effective camouflage (Endler, 1983; King, 1993a,b; Shine *et al.*, 1998), or facilitate the predator-escape behaviours most effective for an animal of their phenotype (Brodie, 1989). Because colour can also modify rates of thermal exchange, an animal's colour can influence the times and places that it is active (Peterson, Gibson & Dorcas, 1993).

Ectotherms offer excellent model systems to investigate this topic. Typically, a single population of ectotherms contains a much wider body-size range of ecologically independent individuals than is the case for endotherms (e.g. Pough, 1980; Vitt, 2000). Conspecific males and females often differ substantially in mean body sizes, adding another level of complexity. Thermal exchange with the environment plays a major role for many ectotherms, and colour polymorphism is common. Thus, we expect that a single population of ectotherms may often contain a high degree of phenotypic variation attributable to body size, sex and colour, and hence that intrapopulation variation in habitat use may be particularly important in such systems.

Despite these advantages, most studies on the relationship between phenotypic traits and habitat use within populations have been based on endothermic vertebrates (birds and mammals), typically in temperate-zone terrestrial habitats (e.g. Torre & Bosch, 1999; Telleria *et al.*, 2001; Bowyer *et al.*, 2002; McDonald, 2002; McLoughlin *et al.*, 2002; Rolando, 2002; Ruckstuhl & Neuhaus, 2002). We studied a system very different from these, involving sea snakes in tropical coral reefs. The species we studied displays a high degree of variation in body size and colour, with the sexes differing in both of these attributes. Thus, it provides a very different situation in which to investigate the ways in which an animal's phenotype influences its patterns of habitat use.

MATERIAL AND METHODS

STUDY SPECIES

Turtle-headed sea snakes, *Emydocephalus annulatus*, are medium-sized (up to 1 m total length: Ineich & Laboute, 2002) hydrophiid snakes, widely distributed in shallow-water reef habitats across the Pacific (Cogger, 1975; Ineich & Laboute, 2002). Phylogenetic analyses suggest that *Emydocephalus* is close to the base of the hydrophiid radiation (Rasmussen, 2002). Like all hydrophiids, *Emydocephalus* is viviparous, spends its entire life in the water, and is virtually incapable of terrestrial locomotion (Shine *et al.*, 2002a). *Emydocephalus annulatus* feeds exclusively on the eggs of small fish (Voris, 1966; McCosker, 1975; McCarthy, 1987), scraping the eggs from the substrate with enlarged supralabial scales (Guinea, 1996). In New Caledonia, these snakes consume the eggs of damselfish, blennies and gobies (Ineich & Laboute, 2002). Our fieldwork in June–July 2002 coincided with intense courtship activity by *E. annulatus*, and hence with cessation of feeding by adult males. Juveniles and adult females often (15 of 27 such animals) regurgitated prey items when handled, but no prey items were regurgitated by 38 adult males (R. Shine *et al.* unpubl. data).

STUDY AREA

We studied a population of *E. annulatus* in the Baie de Citrons, a tourist beach in Noumea, New Caledonia (22°16'S, 166°26'E). The study area (60 × 60 m) had a mosaic substrate dominated by rocks, sand and coral rubble (0.8–1.5 m deep at high tide), extending to live coral reef in deeper water (3–5 m deep at high tide; mean tidal range 0.9 m). The bay is protected from winds and swell from most directions, and thus the water is generally calm.

SURVEYS

Three people snorkelled over the site for 45–60 min observation sessions twice per day over the period 24 June to 4 July 2002, except for two days when storms decreased visibility and engendered a strong swell. Observations were concentrated on periods approximately 1 h before and 1 h following each high tide during daylight hours. When we found a snake we recorded the water depth and substrate characteristics (% cover of coral rubble, live coral, rocks and sand) of a 1-m² quadrat centred on a point directly beneath the snake's head at the time it was first seen. We also scored the overall colour (lightness) of the substrate within this quadrat on a five-point scale (0 = white, 5 = black). Some snakes were collected immediately after they were sighted, others were monitored for up

to 10 min with habitat data taken every 60 s (in which case we calculated average values for each snake over the entire observation period) and then captured, and some snakes were simply observed but not captured. Thus, our sample sizes for snake morphology differ from those for habitat records.

All captured snakes were measured (snout–vent length = SVL) and weighed. Sex could not be determined for neonatal snakes (<35 cm), but for all other snakes this was established based on relative tail length, rugosity of dorsal scales and presence of a rostral spine (both the latter traits characterize adult males: Guinea, 1996; pers. observ.). We marked snakes by scale-clipping before release, to ensure that no snake was scored more than once for any variable.

To quantify availability of different habitat types, we scored the same attributes (substrate, water depth) as above for 156 evenly spaced points along a series of transects running through the study area in a grid pattern. The transects were 5 m apart and parallel to each other, and we took habitat data at points 5 m apart along each transect. We also searched the study area for the fish species (damselfish of the genera *Amphiprion*, *Abudefduf*, *Chromis* and *Dascyllus* and blennies, *Salarias fasciatus*) whose eggs were being consumed by *E. annulatus*, and scored habitat attributes at 25 sites where we found these fish. We could not identify the species of fish eggs in gut contents, and base our identification of the relevant fish species on the fact that these taxa attacked *E. annulatus* that were ingesting eggs. We never saw attacks by fish on *E. annulatus* in any context other than when the snake had found a nest and was consuming eggs (see Ineich & Laboute, 2002 for photographs of this type of parental defence).

To test the hypothesis that the coloration of *E. annulatus* might influence its body-temperature regimes (as has been shown in studies of terrestrial snakes, e.g. Gibson & Falls, 1988; Peterson *et al.*, 1993), we constructed physical models consisting of copper tubes 200 mm long and 25 mm in diameter, and painted one of three colours (black, white or banded black-and-white with each band 20 mm in width). Two replicates of each of these models were deployed in deep water (2.6 m at low tide, 3.5 m at high tide), shallow water (0.6 m at low tide, 1.5 m at high tide) and on the ground surface a few hundred meters from the study site, in a location fully exposed to solar radiation. Data-loggers (thermochron iButton, Dallas Semiconductor) inside the sealed lumen of each model (i.e. in air not water) recorded temperatures every 5 min for 4 days.

The software program Statview 5 (SAS Institute, 1998) on a Macintosh G4 computer was used to analyze these data. Non-normally distributed variables (including all percentage measures) were transformed

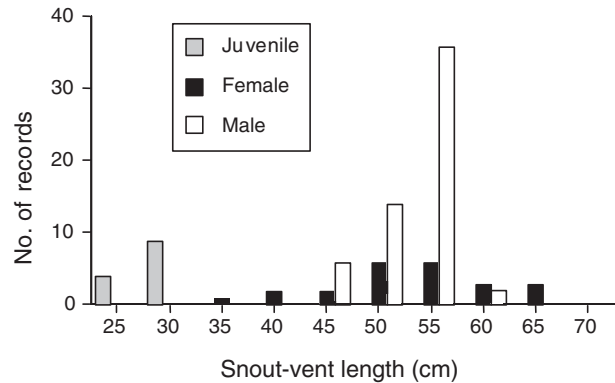


Figure 1. Body-size distributions of captured sea snakes, *Emydocephalus annulatus* according to age-sex class.

prior to analysis to normalize variances. To avoid artefactually 'significant' results due to multiple testing, we combined data for all measured groups into single analyses (rather than, for example, using a stepwise approach which would first compare snake locations to random locations, then examine different age-sex groups of snakes in another analysis). For the same reason, we report a MANOVA on the total data set, as well as the component ANOVAs on each variable.

RESULTS

E. ANNULATUS BODY SIZES

Body-size distributions of the captured *E. annulatus* were strongly bimodal, with one group of snakes with a SVL <35 cm and another peak around 50–60 cm (Fig. 1). The smaller sized group all had obvious umbilical scars and were certainly neonates; parturition in this population occurs in May and June (unpubl. data; P. Borsa, pers. comm.). The five largest snakes were all females (despite the overall sample size being much lower for this sex than for males), indicating that females attain larger body sizes. For simplicity, we refer to snakes >35 cm in size as 'adults'. This is undoubtedly true for males (all SVL >45 cm and with sexually dimorphic traits such as rugose dorsal scales and rostral spines: pers. observ.), but some of the smaller females were immature.

HABITAT AVAILABILITY AND USE

We obtained habitat data for 74 *E. annulatus*, primarily adult males ($N = 38$, vs. 20 females and 16 neonates). The MANOVA on five habitat attributes (four aspects of substrate composition, plus water depth) revealed significant differences among the five categories that we tested (transect points, fish, and juvenile, female and male snakes: Pillai trace = 0.34,

$F_{20,996} = 4.55, P < 0.0001$). Separate ANOVAs on transformed values of these variables showed that all differed significantly among the five groups (Table 1), but much more dramatically in some cases than others. For example, all three age-sex classes of snake were found in areas with less rock and more coral rubble as

the substrate than was the case for the study area overall (as quantified by the transect points: see Fig. 2). A similar divergence was evident in water depths, with adult snakes in deeper-than-random sites, and juveniles mostly in the shallows (Fig. 3, Table 1). Even within the relatively minor body-size

Table 1. Results of analysis of variance comparing habitat features of sites containing juvenile, adult female and adult male sea snakes (*Emydocephalus annulatus*), fish species whose eggs are eaten by these snakes, and a random selection of sites within the general study area

Variable	Mean values					<i>F</i>	<i>P</i>
	Random	Fish	Juvenile	Female	Male		
Arcsin percentage rubble	0.42 ^{a,b,c}	0.72 ^b	0.93 ^c	0.75 ^a	0.56 ^b	9.09	0.0001
Arcsin percentage coral	0.24 ^b	0.32	0.20 ^a	0.32	0.41 ^{a,b}	2.51	0.04
Arcsin percentage rock	0.28 ^{a,b,c}	0.16	0.02 ^a	0.06 ^b	0.03 ^c	8.50	0.0001
Arcsin percentage sand	0.17 ^{a,b}	0.03 ^a	0.06	0.03 ^b	0.14	2.57	0.04
Ln (1 + water depth)	0.69 ^{a,b}	0.75	0.66 ^c	0.91 ^a	0.95 ^{b,c}	3.39	0.01

The five groups (random, fish, juvenile snakes, female snakes, male snakes) were used as categories in a one-factor ANOVA for each habitat variable (4250 d.f. in each case). Superscripts indicate groups that differ significantly from each other ($P < 0.05$) using Fisher's PLSD posthoc tests. The text reports the results of the overall MANOVA from these analyses.

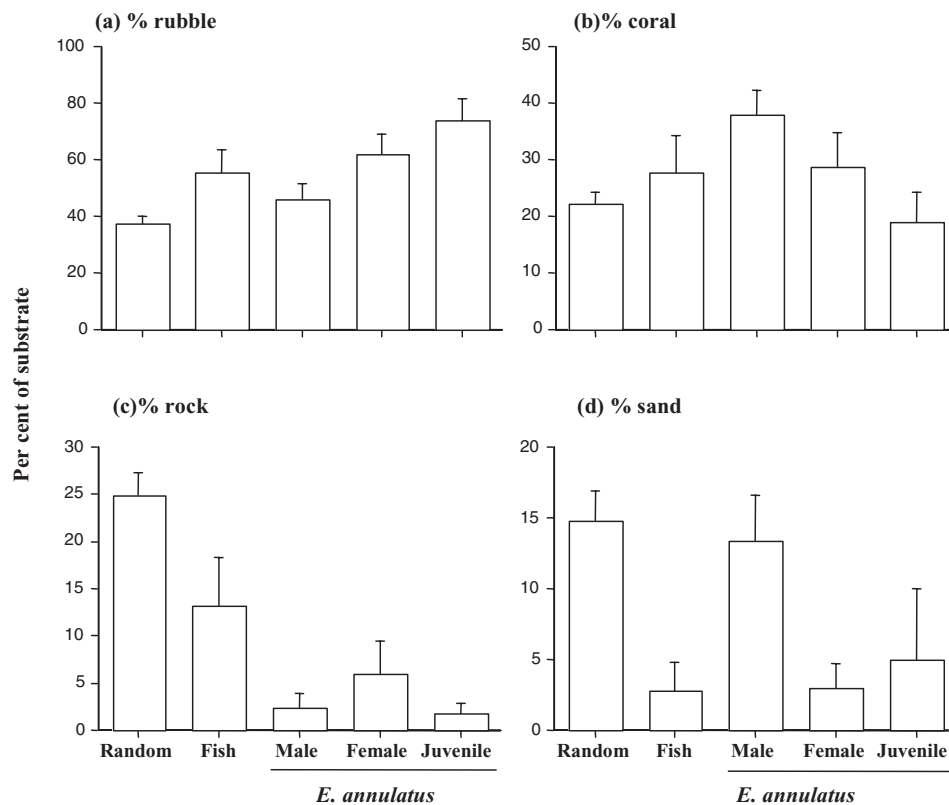


Figure 2. Substrate attributes at sites within the study area in the Baie de Citrons, New Caledonia, showing percentage of rubble (a), coral (b), rock (c) and sand (d). Data are shown separately for points along transects ('random'), to show habitat availability, and for sites where we recorded either *E. annulatus* of different age-sex classes, or fish species whose eggs are eaten by these snakes.

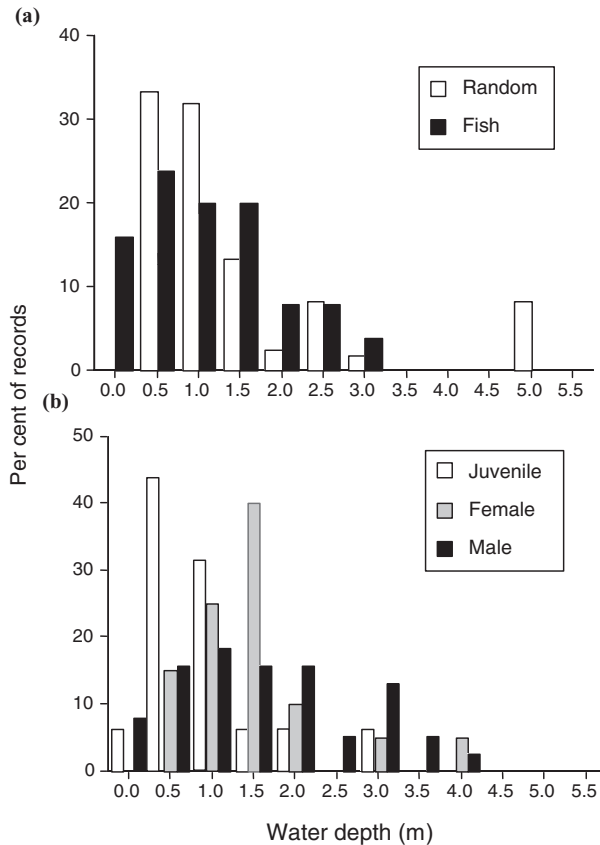


Figure 3. Water depths at sites within the study area in the Baie de Citrons, New Caledonia. Data are shown separately for points along transects ('random'), to show habitat availability, and for sites where we recorded either fish species whose eggs are eaten by *E. annulatus* (a) or *E. annulatus* of different age-sex classes (b). Horizontal axis shows minimum depth for each 50-cm category, i.e. 0.5 = 0.50–1.00 m, etc.

variation exhibited by juveniles, smaller snakes were found in shallower water (SVL vs. water depth, $N = 11$, $r^2 = 0.63$, $P < 0.004$).

Damselfish and blennies also used habitats non-randomly, avoiding sandy and rocky areas in favour of coral rubble (Fig. 2, Table 1). Despite the small sample size, differences were evident also between the sites where we recorded damselfish ($N = 18$) vs. those where blennies were found ($N = 7$; from MANOVA as above, Pillai trace = 0.44, $F_{5,19} = 2.96$, $P < 0.04$). Blennies were found in shallower areas (ANOVA, $F_{1,23} = 9.78$, $P < 0.005$) with more coral rubble ($F_{1,23} = 7.61$, $P < 0.02$) than were damselfish.

SIGNIFICANCE OF COLOUR VARIATION

We also gathered data on the colour of *E. annulatus*, and on the consequences of colour for operative tem-

peratures (as measured by physical models). The captured snakes ranged from uniformly black to brightly black-and-white banded (see Ineich & Laboute, 2002 for photographs of these morphs). Between these two extremes, many animals showed black bands against a more or less heavily melanized background. Among adult snakes, the uniformly black phase was more common in males than in females (52 of 63 vs. 13 of 24, $\chi^2 = 6.00$, 1 d.f., $P < 0.015$). Most striking, however, was that all neonates were banded (13 of 13; juveniles vs. pooled adults, $\chi^2 = 24.56$, 1 d.f., $P < 0.0001$). Thus, the degree of melanism increases ontogenetically, and males become darker at smaller body sizes than do females.

Comparisons of *E. annulatus* body colour to background (habitat) colour provided no evidence for colour-matching. Black and banded snakes were found in similar microhabitats (MANOVA as above, Pillai trace = 0.05, $F_{5,61} = 0.66$, $P = 0.65$; vs. mean habitat colour: $F_{1,65} = 3.35$, $P = 0.07$), and the small spatial scale of this habitat heterogeneity means that a foraging snake often moved from one extreme in background colour to the other in < 1 min (pers. observ.). Foraging snakes move almost continuously (R. Shine *et al.* unpubl. data), so that habitat selection on the basis of colour would be very difficult in this system (vs., for example, an ambush predator that can remain within the same habitat patch for long periods of time). Our physical models showed that the colour of a model affected its temperature (both the mean and the coefficient of variation) only when the model was out of water (Fig. 4). Models in terrestrial sites exposed to sunlight achieved higher more variable temperatures during the day, with black models hotter and more variable than those of other colours (Fig. 4). Underwater models maintained virtually constant temperatures, regardless of their depth, colour or the time of day (Fig. 4).

DISCUSSION

Habitat use by *E. annulatus* at the Baie de Citrons was non-random overall: all age-sex groups differed significantly from the distribution of available habitats, as indicated by the transect points (Table 1). The body size and sex of *E. annulatus* also influenced its use of habitats, but colour did not seem to play any significant role in this respect. Interpretation is complicated by interactions among these variables: females grow larger than males, snakes become darker in colour as they grow larger, and females make this transition more slowly than do males. Below, we examine these influences on habitat use in more detail.

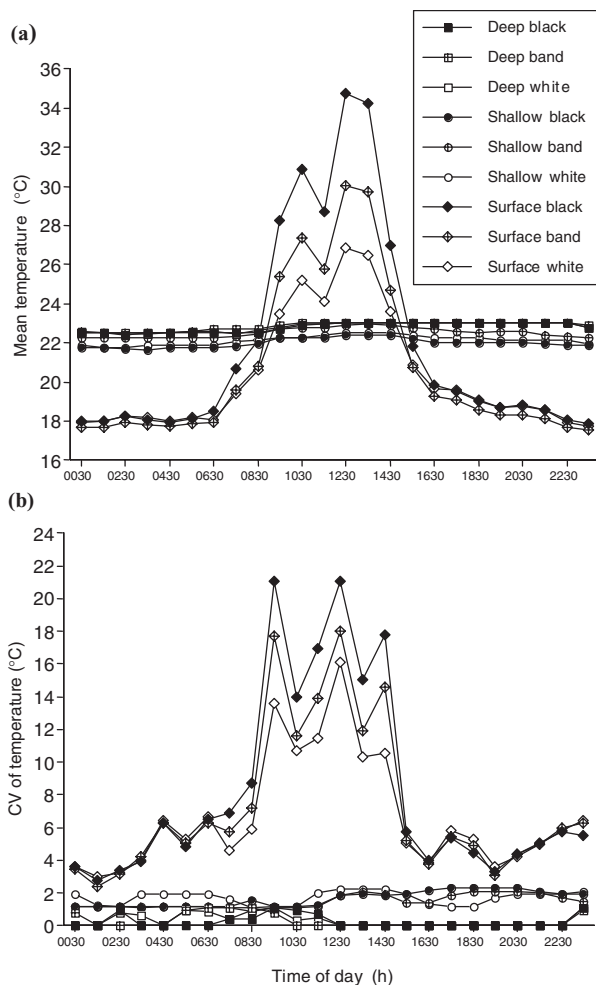


Figure 4. Hourly mean values (a) and hourly coefficients of variation (b) for temperatures measured inside physical models (copper tubes) of different colours (black, white, or banded black-and-white) placed either in deep water (3.5 m at high tide, 2.6 m at low tide), shallow water (1.5–0.6 m) or on the ground surface in an exposed position.

SEX

Juveniles and adult female *E. annulatus* were broadly similar to damselfish and blennies in habitat use (note the absence of statistically significant differences in habitat usage between fish and these categories of *E. annulatus* in Table 1). Most records for all three groups came from coral-rubble substrates (Fig. 2). Behavioural observations showed that juveniles and adult females spent most of their time foraging, moving relatively slowly ($<2 \text{ m min}^{-1}$) but almost continuously with their heads near the substrate, tongue-flicking frequently and stopping only to ingest eggs from fish nests (R. Shine *et al.* unpubl. data). This focus on feeding inevitably results in a close match between the distribution of prey and that of the predator.

In contrast, adult male *E. annulatus* swam more rapidly, did not feed, and actively courted any adult female that they encountered (R. Shine, unpubl. data). They thus used the available habitat at a larger 'grain size' than did females, searching for the relatively large females rather than the smaller and well-hidden fish nests. In consequence, male *E. annulatus* spent relatively less time in food-rich habitats than did females. The higher proportion of time spent over sandy substrates (Fig. 2) may reflect the greater contrast of the (dark) females against the (light) background in such areas, and hence the greater effectiveness of mate-searching in such habitats.

Sex differences in habitat use are very widespread among animal species, and reflect a combination of factors. Males forego feeding during the breeding season in many taxa, including endotherms as well as ectotherms (e.g. Le Bouef, 1974). Thus, shifts towards mate-searching over a broad range of habitats rather than foraging within more specific food-rich areas, as seen here in *E. annulatus*, may be widespread (Mace, 1979). In other cases, males continue to feed but do so on different food resources than do conspecific females (Clutton-Brock, Guinness & Albon, 1982), or bias habitat use towards sites that facilitate surveillance for rivals, access to receptive females, and so forth (e.g. Jennsen, 1970; Robertson, 1986; Andersson, 1994). In turn, occupancy of different habitat types may impose selective pressures that further exaggerate sexual dimorphism (e.g. Slatkin, 1984; Andersson, 1994).

BODY SIZE

Juvenile *E. annulatus* were found in shallower water than were larger conspecifics (Table 1, Fig. 3), and smaller juveniles were in shallower water than were larger juveniles. Similar ontogenetic shifts in habitat use in snakes, including other aquatic species, have generally been explained in terms of foraging biology. In at least five piscivorous lineages that represent phylogenetically independent invasions of aquatic habitats (acrochordids, homalopsine and natricine colubrids, hydrophiids, laticaudids), juveniles consume smaller fish than do adult conspecifics (Voris & Moffett, 1981; Mushinsky *et al.*, 1982; Jayne, Voris & Heang, 1988; Houston & Shine, 1993; Shetty & Shine, 2002). In some or all of these cases, the smaller snakes presumably obtain these prey in relatively shallow water. Correlated ontogenetic shifts in prey size and habitats also occur in terrestrial snakes. For example, juvenile tree boas (*Epicrates monensis*) used smaller thinner branches than did conspecific adults, matching the size distributions of available prey (Chandler & Tolson, 1990). Juvenile Chinese pit-vipers (*Gloydius shedaoensis*) are more arboreal than are adults, perhaps reflecting both the availability of smaller prey

(birds) in arboreal perches, and the greater ease with which prey can be captured from such perches (Shine *et al.*, 2002b). The direction of causation (habitat selection exposing the snakes to small prey, vs. a reliance on small prey driving habitat selection) is difficult to infer because of the correlation between prey size and habitat type.

Although most previous studies on snakes have explained ontogenetic shifts in foraging habitats in terms of ontogenetic shifts in diet, this explanation is not applicable to our data on *E. annulatus*. Most previously studied snake species take prey items that are large relative to the predator, and hence gape-limitation constrains maximum prey size. As a result, prey sizes (and often, types) shift dramatically with age (body size) within such populations (Greene, 1983; Mushinsky, 1987; Luiselli & Angelici, 1998). This is not the case with *E. annulatus*. The species feeds exclusively on tiny (<1 × 1 mm) fish eggs, with neonates taking the same-sized eggs as adults (R. Shine *et al.* unpubl. data). In consequence, the spatial distribution of suitably small prey items cannot be used to explain the ontogenetic shift in water depths within *E. annulatus*. Predation vulnerability may be more important. *Emydocephalus* are eaten by fish (especially, tiger sharks) in New Caledonia (Rancurel & Intes, 1982; Ineich & Laboute, 2002), and juveniles may be at particular risk in this respect. Larger fish are generally found in deeper water, so that the inshore habitats of neonatal snakes (mostly <1 m deep) may reduce their vulnerability.

Most endothermic vertebrates display a suite of life-history traits (notably, prolonged parent-offspring association and rapid growth to near-adult size prior to termination of parental care) that reduces the potential for ontogenetic shifts in habitat utilization (e.g. Clutton-Brock, 1991). Even in endotherms, however, detailed studies frequently report significant intrapopulation heterogeneity in patterns of habitat use (e.g. Rolando, 2002). The much wider size range of free-living individuals in ectotherm populations generates a corresponding diversity in phenotypic traits, and hence in the potential matching of individuals to specific microhabitats. Most obviously, small size may permit use of microhabitats (small holes, thin branches, etc.) unavailable to larger conspecifics. Prey availability, predator vulnerability, physical exchanges with the environment and social interactions also will often depend on body size. As a result, ontogenetic shifts in habitat use are probably the rule, not the exception, within ectotherms (Vitt, 2000).

COLOUR

Polymorphism in dorsal coloration is widespread in snakes, albeit often relatively subtle, and frequently

varying with age and/or sex (e.g. Shine, 1993; Shine *et al.*, 1998) and geographical location (e.g. Gibson & Falls, 1988; Barker & Barker, 1994; Nilson *et al.*, 1994; Johnston, 1996). Several attempts have been made to identify selective forces acting to maintain chromatic polymorphism in snake populations (e.g. King, 1993a,b; Shine & Madsen, 1994; King & Lawson, 1995; Lindell & Forsman, 1996). The most extensive literature concerns the occurrence of melanism in cool-climate populations of North American garter snakes (*Thamnophis sirtalis*) and European adders (*Vipera berus*), with many authors suggesting that melanism confers a thermal advantage (black snakes heat faster) but provides less effective camouflage against predation (e.g. Gibson & Falls, 1979; Andren & Nilson, 1981; Gibson & Falls, 1988; Madsen & Stille, 1988; Madsen, 1988; Luiselli, 1992; Bittner, King & Kerfin, 2002). Some cases offer strong parallels with the situation in *Emydocephalus*. For example, the pit-viper *Agkistrodon piscivorus leucostoma* shows an increase in melanism with age and a sex difference in the rate of this progression (females become darker at smaller sizes, perhaps reflecting thermal benefits during pregnancy: Zaidan, 2001).

Our data on *E. annulatus* (and the occurrence of sex dichromatism in at least three other hydrophiid species: Shine, 1993) offer a cautionary note to such interpretations. Although these colour polymorphisms are superficially similar to those in terrestrial snakes, the explanations widely accepted for this phenomenon in the latter group (e.g. Luiselli, 1995) are clearly not applicable. First, although darker colour can enhance rates of heating in a snake exposed to sunlight, even shallow water completely removes this effect (see Fig. 4; also Graham, 1974; Heatwole, 1981). Second, no sea snakes except the pelagic *Pelamis* are known to utilize ambush predation (Heatwole, 1999); instead, daily foraging activities typically place the animal in a wide range of microhabitats within short spaces of time (e.g. McCosker, 1975; Heatwole *et al.*, 1978). Thus, neither thermal advantages nor background colour-matching are likely to confer significant benefits or costs to specific colour morphs in sea snakes. It may well be true that such factors are important for terrestrial snakes, but the evolution of polymorphic colours in snakes that do not experience these costs and benefits suggests that other factors may be at work also, perhaps in terrestrial as well as aquatic systems. Morph frequencies show strong geographical variation within *Emydocephalus* (Ineich & Laboute, 2002), offering an opportunity to identify influences on colour patterns.

More generally, studies on 'neglected' systems such as sea snakes provide a valuable perspective on the generality of conclusions based on studies of more 'popular' systems. Intraspecific habitat partitioning is

undoubtedly widespread, and many of the factors that generate such divergences will be similar among disparate taxa. For example, it will often be true that traits such as an organism's sex, body size and colour influence the fitness benefits of occupying specific microhabitat types. Only by examining such influences within a broad ecological and phylogenetic perspective can we evaluate the generality of hypotheses proposed to explain these patterns. For example, spatial heterogeneity in prey size, operative temperature and background colour has been widely interpreted as a crucial factor generating intraspecific habitat divergence within reptile populations. In the *E. annulatus* population that we studied, such heterogeneity is either absent (food type, operative temperatures), or unlikely to affect fitness (background colour). This result not only means that we need to look for novel explanations for habitat partitioning in sea snakes, but also that some conclusions about terrestrial systems may need to be revisited.

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