



Phenotypic divergence between seasnake (*Emydocephalus annulatus*) populations from adjacent bays of the New Caledonian Lagoon

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Populations of widespread species often differ in phenotypic traits, although rarely in such a dramatic fashion as revealed by research on turtle-headed seasnakes (*Emydocephalus annulatus*). These snakes are highly philopatric, with mark–recapture studies showing that the interchange of individuals rarely occurs even between two adjacent bays (separated by < 1.2 km) in Noumea, New Caledonia. Data on > 500 field-captured snakes from these two bays reveal significant differences between these two locations in snake morphology (mean body length, relative tail length, head shape), colour, ecology (body condition, growth rate, incidence of algal fouling), behaviour (antipredator tactics), and locomotor performance. For some traits, the disparity was very marked (e.g. mean swimming speeds differed by > 30%). The causal bases for these phenotypic divergences may involve founder effects, local adaptation, and phenotypic plasticity. The spatial divergence in phenotypic traits offers a cautionary tale both for researchers (sampling of only a few populations may fail to provide a valid overview of the morphology, performance, and behaviour of a species) and managers (loss of local populations may eliminate distinctive genetic variation). © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 107, 824–832.

ADDITIONAL KEYWORDS: coral reef – ecological divergence – Elapidae – Hydrophiinae – local adaptation.

INTRODUCTION

Even if a species is widely and continuously distributed, detailed investigation often reveals sub-population structuring as a result of environmental heterogeneity through space or time (Hanski, 1999; Rocha *et al.*, 2002). Local populations may exhibit distinctive phenotypic traits as a result of developmental plasticity (the direct impact of local conditions such as temperature or food supply) and/or because genetically canalized traits differ among populations through processes such as founder effects, genetic drift or local adaptation (Ghalambor *et al.*, 2007; Aubret & Shine, 2009; Kim *et al.*, 2012). A diverse

suite of phenotypic traits can exhibit interpopulation divergence within wide-ranging species, and some of these patterns of divergence are so highly correlated with environmental conditions that they have been formalized as laws or rules (e.g. Bergmann's Rule: Husby, Hille, Visser & 2011; Rapoport's Rule: Gaston, Blackburn & Spicer, 1998). Understanding the spatial scale of phenotypic divergence between populations can clarify the proximate mechanisms responsible. Furthermore, intraspecific divergence in phenotypic traits enables researchers to conduct robust comparisons without the confounding problems introduced by interspecific differences. However, extensive population-specific variation also means that studies on any single population will underestimate morphological and ecological variation within the species as a whole (Daltry, Wuster & Thorpe, 1998; Lane & Shine,

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2011; Schilthuizen, Rutten & Haase, 2012), and that the loss of even a single population can eliminate genetic variation not present elsewhere within the range of a species.

Intuition suggests that aquatic habitats will facilitate the movement of organisms between suitable habitat patches. Dispersal costs are reduced by the buoyancy conferred by water, as well as the stability of thermal and hydric conditions through both time and space (Kritzer & Sale, 2006). Nonetheless, some marine species form relatively discrete subpopulations even in areas of superficially homogeneous habitat (Jones, Planes & Thorrold, 2005; Kritzer & Sale, 2006; Jones *et al.*, 2009). Our long-term mark-recapture studies have revealed such a situation in turtle-headed seasnakes (*Emydocephalus annulatus*) in the New Caledonian Lagoon (Lukoschek & Shine, 2012). In the course of ten censuses (> 800 recaptures) over eight years, we recorded only two snakes moving between adjacent bays < 1.2 km apart (travel time of a few hours at usual snake swimming speeds). Genetic data confirm that the two populations rarely exchange genes (Lukoschek & Shine, 2012), suggesting a potential for phenotypic divergence between the two populations, despite the similarity in environmental conditions to which they are exposed. The present study tests that prediction, and reveals strong phenotypic divergence between these two populations.

MATERIAL AND METHODS

SPECIES AND STUDY AREA

The turtle-headed seasnake, *Emydocephalus annulatus*, is an elapid snake within the aipysurine branch of the subfamily Hydrophiinae (Ineich & Laboute, 2002; Lukoschek & Keogh, 2006). This relatively small (up to 1 m in total length) species occurs in shallow coral-reef areas throughout the tropical Pacific (Lukoschek, Waycott & Marsh, 2007). Turtle-headed seasnakes have small fangs and tiny venom glands (Ineich & Laboute, 2002), and feed only on the eggs of demersal-spawning fishes (Voris, 1966; Ineich & Laboute, 2002; Shine, Shine & Shine, 2003b).

We have conducted ecological research on this taxon in two adjacent bays (Anse Vata and Baie des Citrons) beside the city of Noumea, in New Caledonia (Shine *et al.*, 2003a, b, 2004a, 2005; Shine, 2005; Avolio, Shine & Pile, 2006; Shine, Brischox & Pile, 2010; Brischox *et al.*, 2012) (Fig. 1). Both sites are areas (100 × 50 m) extending from the shoreline to deeper (> 2 m at low tide) water. The straightline distance between the two sites is 330 m, and the shortest aquatic connection (around an intervening headland) is 1.15 km. A snake could travel between

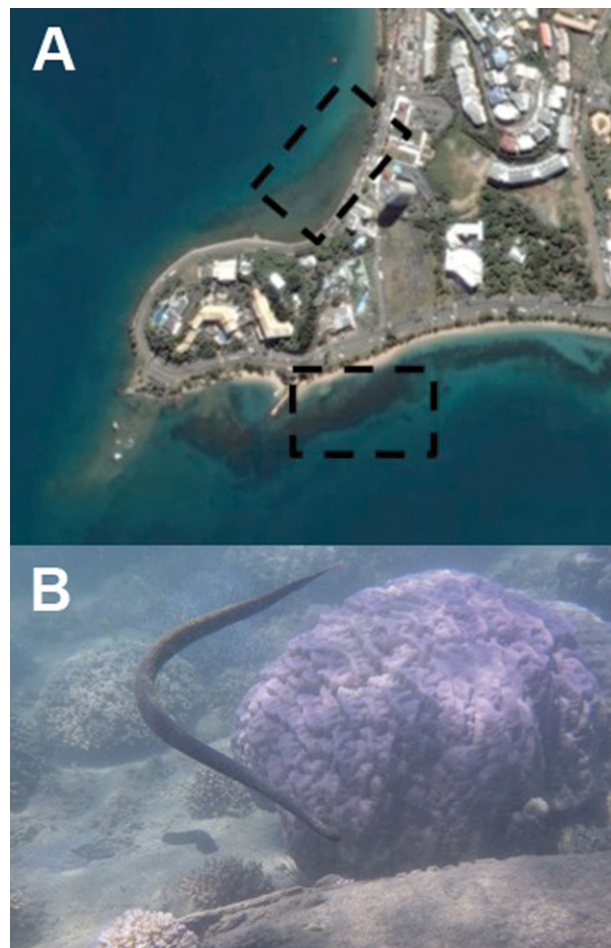


Figure 1. Study areas and species. A, aerial view showing the location of the two study sites in adjacent bays (upper, Baie des Citrons; lower, Anse Vata) of the New Caledonian Lagoon off Noumea. Both study sites (dotted outlines) are approximately 50 × 100 m in extent. B, a turtle-headed seasnake underwater.

the two sites in 38 min at maximum swimming speeds (30 m min⁻¹; see below), and in 5 to 10 h at speeds typical of snakes in the field (< 2 to 4 m min⁻¹; Shine, 2005; Avolio *et al.*, 2006; Lukoschek & Shine, 2012). The intervening area consists of shallow reef, where *E. annulatus* is common. Wind exposure is higher at Anse Vata than at Baie des Citrons, and the substrate at Anse Vata consists mostly of live coral, whereas Baie des Citrons is dominated by coral rubble (Shine *et al.*, 2003b).

WATER TEMPERATURE

Because ambient temperature is critical to ectotherm biology, including embryonic development (Du & Ji, 2006; Angilletta, 2009), we measured temperature regimes at both sites over the same 16-day period in

March 2011. Two miniature data-loggers (thermochron iButtons, Dallas Semiconductor) inside waterproof containers were placed on the substrate in shallow water (< 1 m) and deep water (2.5–3 m) at each site.

MARK–RECAPTURE STUDY

We snorkelled the study areas (Fig. 1) aiming to capture seasnakes during 10-day periods in every January from 2004 throughout 2011, and also in July 2004. The proportion of resident snakes caught each year (calculated from the rate at which the percentage of unmarked snakes declined during successive dives) averaged 85% at Anse Vata and 90% at Baie des Citrons. Captured snakes were returned to a nearby laboratory where we measured them [snout–vent length (SVL); tail length; head length (snout to end of quadrate) and width (widest point)], weighed them, and scored them for pregnancy (based on abdominal palpation) and algal cover (Shine *et al.*, 2010). We implanted individually-numbered passive integrated transponder tags subcutaneously near the cloaca, and the snake was then released at its site of capture. The analyses reported in the present study are based on data taken the first time an individual was captured, aiming to avoid pseudoreplication.

LOCOMOTOR PERFORMANCE

In January 2010, we measured locomotor performance of 56 snakes (35 from Anse Vata, 21 from Baie

des Citrons) before releasing them. Each snake was placed in a holding tank for at least 30 min to recover from handling, and then released at one end of the raceway (30 × 500 cm; depth of 50 cm) within a tank filled with fresh (circulating) sea-water at 25.1–26.0 °C. We recorded the time to travel successive 1-m lengths, as well as when the snake swam at the surface versus underwater, and how often it attempted to escape by climbing over the wall of the raceway. The snake was turned around at the end of each run, and the trial was repeated in the other direction. Analysis was based on 12 trials per snake (Shine *et al.*, 2010).

RESULTS

WATER TEMPERATURE

Temperatures in shallow water showed a strong diel cycle, peaking in the early afternoon, whereas deep-water temperatures were relatively stable (Fig. 2). An analysis of variance (ANOVA) revealed significant thermal variation among days ($F_{16,3003} = 170.08$, $P < 0.0001$) and as a function of time period within the day (time, nested within day: $F_{17,3003} = 47.38$, $P < 0.0001$), as well as between deep and shallow water (nested within site: $F_{2,3003} = 161.01$, $P < 0.0001$), although thermal regimes at the two sites were very similar ($F_{1,3003} = 0.39$, $P = 0.53$).

SNAKE POPULATION STRUCTURE

We captured more snakes at Anse Vata than at Baie des Citrons in seven of 8 years (means 89.6 versus

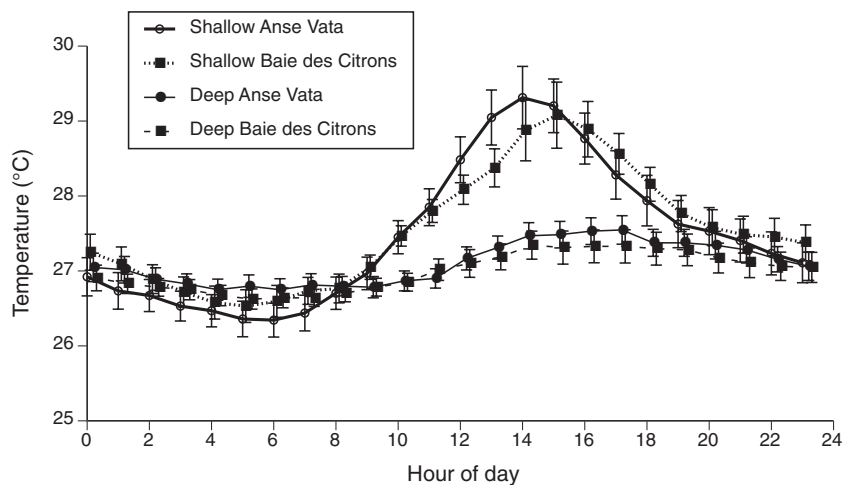


Figure 2. Thermal regimes in shallow (< 1 m at low tide) and deep (2–3 m) water at two study sites in the New Caledonian Lagoon, as measured over a 16-day period in March 2011. The graph shows the diel cycle in mean thermal profiles at Anse Vata and Baie des Citrons, based on two replicate data-loggers per depth per site (hourly mean and associated SE are shown).

54.9 snakes per site per year; thus comparing total numbers caught per year, $t = 3.26$, d.f. = 7, $P < 0.014$). Sex ratios were similar at the two sites, and close to equality: 49% male at Anse Vata (191 captures of males, 198 captures of females) and 54% male at Baie des Citrons (109 captures of males, 93 captures of females); comparing sex ratios at the two sites, Fisher's exact test, $P = 0.30$).

SNAKE BODY SIZE

In terms of SVL, females averaged larger than males (ANOVA: $F_{1,587} = 6.80$, $P < 0.01$), to a similar degree in both populations (interaction: $F_{1,587} = 1.00$, $P = 0.32$). Both sexes averaged larger in the Baie des Citrons population than the Anse Vata population ($F_{1,587} = 13.61$, $P < 0.001$; Fig. 3A). The same pattern was

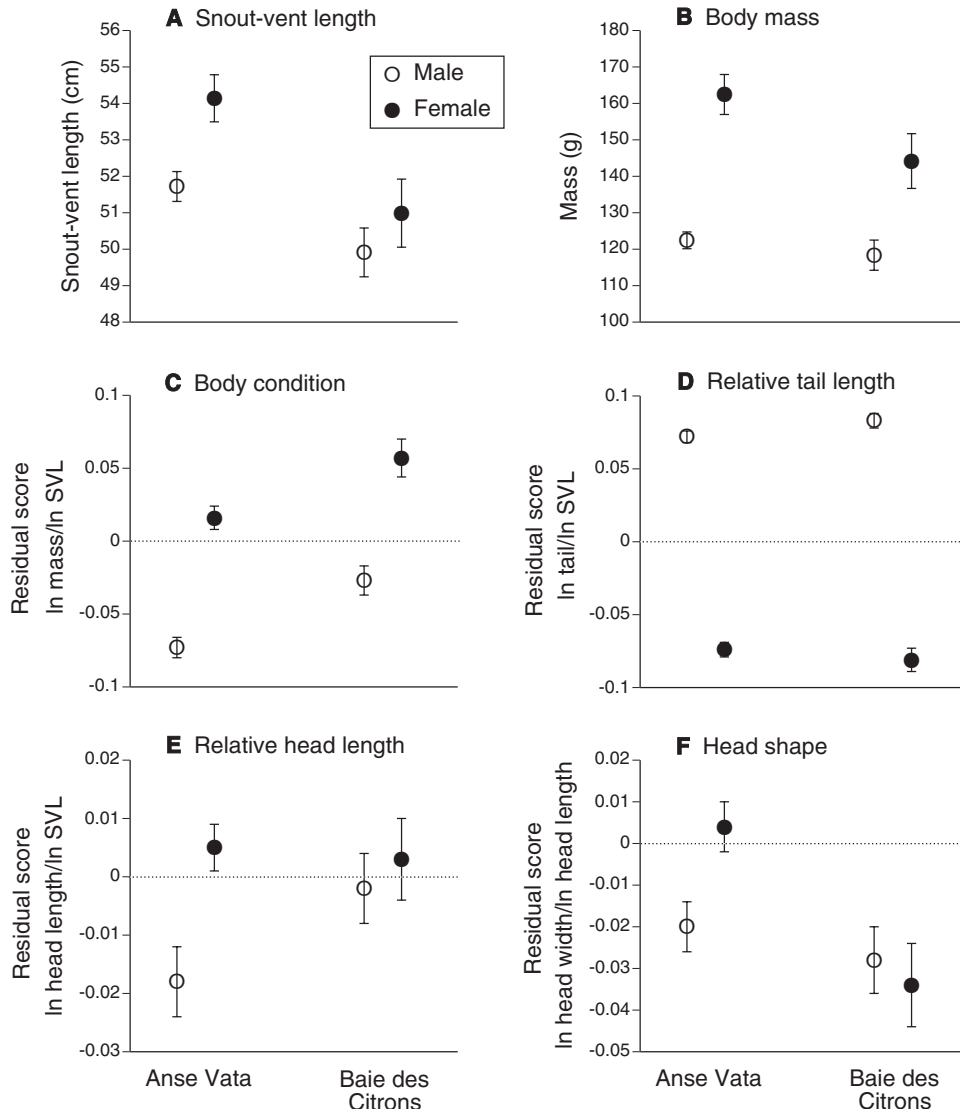


Figure 3. Effects of sex and location on morphological attributes of turtle-headed seasnakes, *Emydocephalus annulatus*, from two populations in the New Caledonian Lagoon. The graphs show mean values and associated SEs for snout-vent length (SVL) (A); body mass (B); body condition (based on residual scores from the general linear regression of ln mass on ln SVL) (C); relative tail length (based on residual scores from the general linear regression of ln tail length on ln SVL) (D); relative head length (based on residual scores from the general linear regression of ln head length on ln SVL) (E); and head shape (width relative to length based on residual scores from the general linear regression of ln head width on ln head length) (F). Note that (C) to (F) show residual scores for ease of interpretation, although the statistical tests in the present study are based on an analysis of covariance.

evident for body mass (sex effect: $F_{1,586} = 41.19$, $P < 0.001$; location effect: $F_{1,586} = 4.74$, $P < 0.03$; interaction: $F_{1,586} = 1.91$, $P = 0.17$; Fig. 3B).

SNAKE BODY SHAPE

Body condition (mass relative to SVL) was higher at Baie des Citrons (analysis of covariance with \ln SVL as covariate, \ln mass as dependent variable, after deleting the nonsignificant interaction between SVL and location, location effect: $F_{1,587} = 13.32$, $P < 0.0005$; Fig. 3C). Tail length relative to SVL differed strongly between the sexes (males have longer tails: $F_{1,558} = 12.85$, $P < 0.0005$) and snakes from Anse Vata had slightly (but significantly) shorter tails than did conspecifics from Baie des Citrons ($F_{1,608} = 9.02$, $P < 0.003$; Fig. 3D). Snakes in the two populations did not diverge significantly with respect to mean values for head length relative to SVL (location: $F_{1,558} = 0.07$, $P = 0.80$; Fig. 3E), although head shapes differed between snakes from the two areas (but not between the two sexes). Relative to head length, snakes from

Anse Vata had wider heads than did conspecifics from Baie des Citrons (location effect: $F_{1,555} = 8.70$, $P < 0.004$; Fig. 3F).

SNAKE COLORATION

In both populations, most individuals were black or showed slight banding, although some were boldly black-and-white banded (for a photograph, see Shine *et al.*, 2010). This banded morph was more common at Anse Vata (38 snakes; 9.8%) than at Baie des Citrons (nine snakes; 4.5%; logistic regression with sex and location as independent variables, banded or not as dependent variable; sex: $\chi^2 = 0.15$, d.f. = 1, $P = 0.70$; location: $\chi^2 = 7.55$, d.f. = 1, $P < 0.007$; Fig. 4A).

ALGAL FOULING

Snakes at Anse Vata were more likely to be covered by algae (70% of 389 captures) than were snakes at Baie des Citrons (54% of 200 captures; logistic regression with sex and location as independent variables,

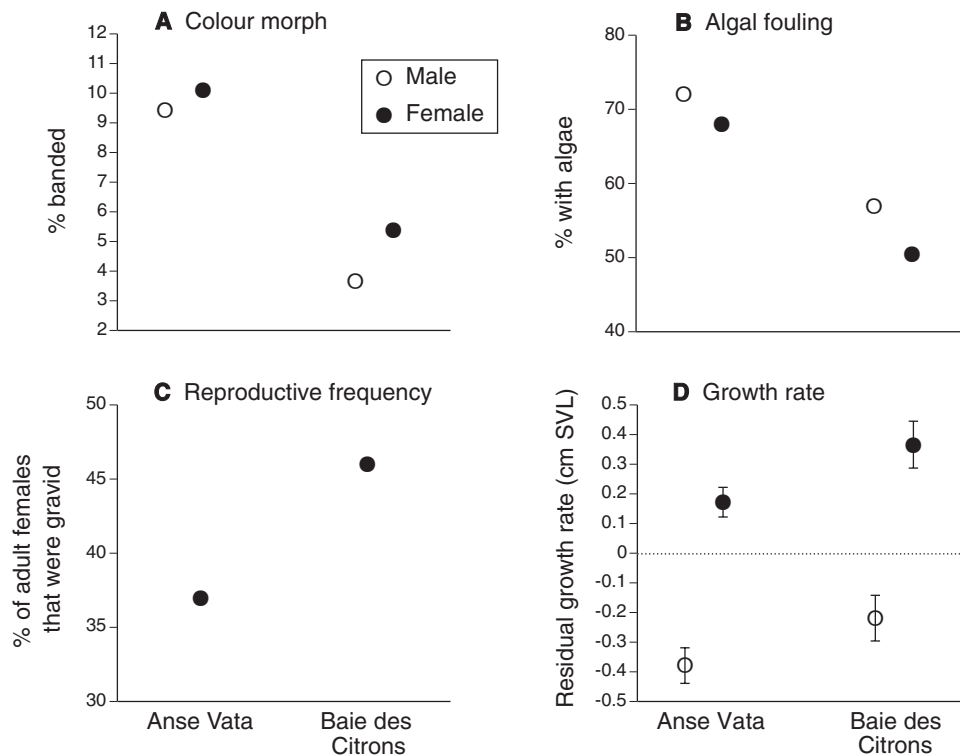


Figure 4. Effects of location on ecological attributes of turtle-headed seasnakes, *Emydocephalus annulatus*, from two populations in the New Caledonian Lagoon. The graphs show mean values and associated SEs for colour morph (frequency of highly banded snakes) (A); algal fouling (frequency of snakes exhibiting obvious algal coating) (B); reproductive frequency (proportion of adult-sized females that were gravid during January sampling) (C); and growth rate [based on residual scores from the general linear regression of snout–vent length (SVL) increment from one year to the next on mean SVL over that period] (D). This panel shows residual scores for ease of interpretation, although the statistical tests in the present study are based on an analysis of covariance.

algal cover or not as dependent variable; sex: $\chi^2 = 1.17$, d.f. = 1, $P = 0.28$; location: $\chi^2 = 12.59$, d.f. = 1, $P < 0.005$; Fig. 4B).

REPRODUCTIVE OUTPUT

Among adult-sized females (> 50 cm SVL), 37% of 122 Anse Vata females were gravid when first captured compared to 46% of 54 Baie des Citrons females (Fisher's exact test, $P = 0.25$; Fig. 4C). Mean litter sizes were similar in the two populations (1.74 and 1.70, respectively; $F_{1,192} = 0.15$, $P = 0.70$).

GROWTH RATE

We corrected for the ontogenetic decrease in annual growth rates by calculating residual scores of annual growth increment in SVL versus mean SVL over the recapture interval. These standardized mean annual growth increments were lower in males than females ($F_{1,464} = 74.58$, $P < 0.001$; Fig. 4D) and lower in Anse

Vata than in Baie des Citrons ($F_{1,464} = 7.24$, $P < 0.01$; interaction: $F_{1,464} = 0.07$, $P = 0.79$).

LOCOMOTOR SPEED

Including mean swimming speeds (in SVLs per second) on the water surface and underwater as dependent variables, a repeated-measures ANOVA showed that snakes from Anse Vata were approximately 40% slower than conspecifics from the Baie des Citrons (location effect: $F_{1,54} = 22.58$, $P < 0.0001$; other effects and interactions were nonsignificant; Fig. 5A). The same pattern was evident for maximum speeds (34% difference, location effect: $F_{1,54} = 18.27$, $P < 0.0001$; other effects and interactions were nonsignificant; Fig. 5B). Snakes from the two areas did not differ in their endurance (ability to maintain speeds across successive laps; repeated-measures ANOVA with speed in 12 successive laps as the dependent variable; location \times lap number $F_{11,1100} = 1.36$, $P = 0.19$).

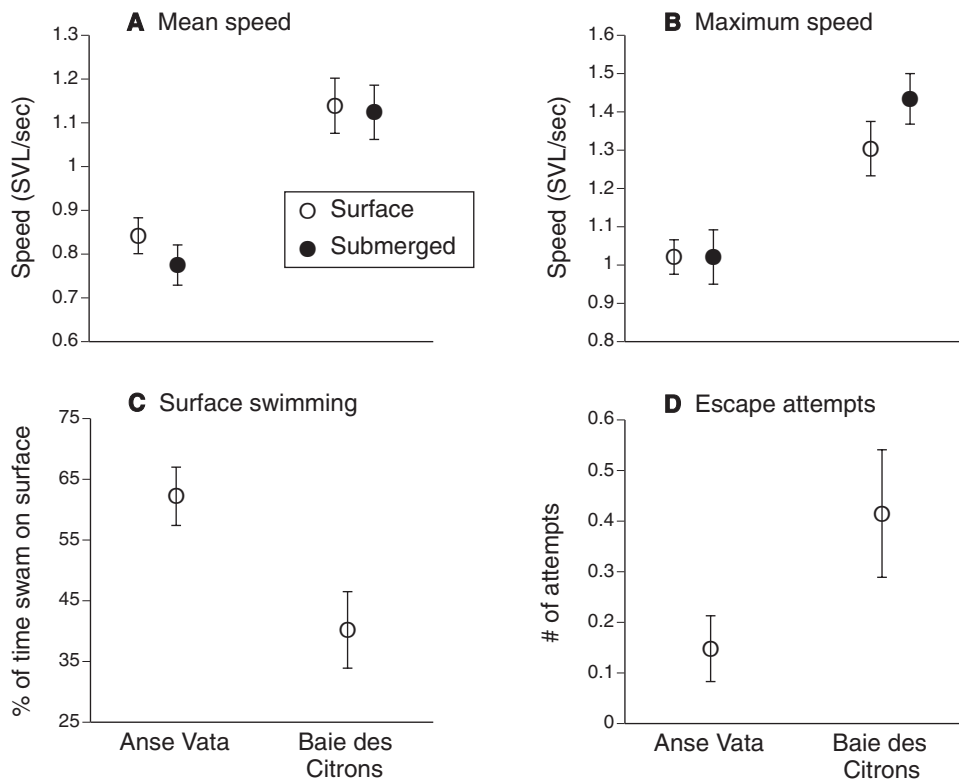


Figure 5. Effects of location on locomotor speeds and antipredator tactics of turtle-headed seasnakes, *Emydocephalus annulatus*, from two populations in the New Caledonian Lagoon. These data were taken during raceway trials on newly-captured snakes. The graphs show mean values and associated SEs for swimming speed [in snout–vent lengths (SVLs) per second], when snakes were swimming at the water surface (with their heads out) and submerged (A); maximum speeds recorded under these conditions (B); the proportion of time during trials that snakes swam with their heads out of water (C); and the number of times that snakes attempted to escape the raceway by climbing out over the walls (D).

ANTIPREDATOR TACTICS

Snakes from Anse Vata spent a higher proportion of the trial swimming along the water surface rather than submerged ($F_{1,100} = 7.94$, $P < 0.006$; Fig. 5C). Although they surfaced less often, snakes from the Baie des Citrons attempted to escape from the locomotor runway (by mounting the barrier) more often than did snakes from Anse Vata ($F_{1,100} = 4.20$, $P < 0.05$; Fig. 5D).

DISCUSSION

The present study identified significant phenotypic divergence in a wide range of traits between two populations of seasnakes. Despite the close proximity of our two collecting sites (a few hundred metres), they contain virtually separate populations of snakes. During our 8-year study, we recorded only two cases (out of 817 recaptures) of an individual snake moving from one area to the other (Lukoschek & Shine, 2012). Nonetheless, philopatry does not inevitably result in phenotypic divergence, and especially not in such a wide range of traits, nor to such a marked degree. Some of these divergences may reflect plastic responses to local conditions, and others are likely to be genetically-based.

Interpopulation divergence in phenotypic traits is common both in marine and terrestrial snakes but rarely as dramatic as that seen in the present study. Divergence can be especially strong in areas with spatial heterogeneity in climates (Gregory & Larsen, 1993), habitat types (Bronikowski & Arnold, 1999; Bronikowski, 2000) or food supply (Madsen & Shine, 1993; Boback, 2006; Aubret & Shine, 2009), or where phylogenetically distinct lineages come into contact and hybridize (Shine *et al.*, 2003c, 2004b). Although none of these factors apply (at least overtly) to our *Emydocephalus* populations, the snakes living in those two areas differ from each other in many respects.

Several of the interpopulation differences that we observed plausibly are phenotypically plastic responses related to foraging biology: snakes at the Baie des Citrons site may have greater food intake rates because prey are more common or because there is less competition from other snakes for those prey, or because calmer water conditions allow foraging under a wider range of conditions. Differences in water mixing also might influence rates of settlement and survival of larval fish (Grorud-Colvert & Sponaugle, 2011) and egg production by adult fishes, and thus influence the feeding and growth rates of snakes. Higher feeding rates could be the reason for the faster growth rates of Baie des Citrons snakes, which in turn might explain the lower rates of algal fouling

(because faster-growing snakes slough more often, thus losing the algae more often; Shine *et al.*, 2010). A lower mean body size, despite higher growth rates, suggests a higher recruitment of juvenile snakes into the Baie des Citrons population. Differences in body shape, such as relative head shapes and tail lengths, also might reflect differences in growth trajectories; in some reptiles, body proportions can be affected by growth rates and ages (Olsson & Shine, 1996).

Alternatively, or additionally, abiotic differences between the two sites may have influenced snake phenotypes. For example, subtle differences in the thermal regimes experienced by gravid females can affect the morphology of offspring, including traits such as relative tail length (Shine *et al.*, 1997; Lourdaï et al., 2004) and such incubation-induced effects can persist for long periods (Elphick & Shine, 1998). Wave action *per se* may have influenced feeding opportunities (see above). Differences in habitat also may play a role. For example, if snake colours are adaptive to camouflage (King, 1993), then background colour-matching might favour banded snakes more against the live coral of Anse Vata than the darker and more homogeneous coral rubble of Baie des Citrons.

Live coral also provides many more hiding places where a snake could escape predatory fish; and, thus, the snakes at Baie des Citrons may need to rely more on speed to escape predation than would their conspecifics at Anse Vata. That situation might result in higher locomotor abilities for the Baie des Citrons snakes, either through local adaptation, the selective mortality of slower individuals or a more frequent reliance on rapid locomotion (and thus, enhancement of swimming abilities: Houlihan & Laurent, 1987; Davison, 1989) as a result of more frequent encounters with predators. The shifts in antipredator tactics likely are secondary consequences of the difference in locomotor speeds. Studies on other reptiles show that individuals rely upon flight if they can move quickly, although they often resort to alternative tactics (e.g. swimming at the surface) if they are unable to maintain high speeds (Hertz, Huey & Nevo, 1982; Passek & Gillingham, 1997; Telemeco, Baird & Shine, 2011). Attempting to climb the raceway walls requires considerable strength, and was seen more often in the Baie des Citrons snakes than in Anse Vata conspecifics.

However, phenotypically plastic responses to local conditions cannot explain all of the interpopulation divergences revealed by the present study. A snake's colour phase is consistent throughout its life, based on long-term recapture records (R. Shine, unpubl. data) and is likely to have a genetic basis. The same is probably true for morphological traits such as relative tail length and head shape. Given the direct

evidence of genetic differentiation between the two populations (based on DNA sequence data: Lukoschek & Shine, 2012), the likeliest scenario is that the divergences we have recorded reflect a combination of developmentally plastic and genetically canalized traits. Although local adaptation offers a possible mechanism for genetic divergence, non-adaptive processes are perhaps more important in this system. Turtle-headed seasnakes are weak slow swimmers, and it is easy to imagine local populations being extirpated by the arrival of a novel predator, or by unusually rough seas during tropical storms. Frequent recolonization of sites by small numbers of founders could create the kinds of divergences that we have recorded in phenotypic traits. In keeping with this hypothesis, both of our study populations have experienced episodes of steep decline, followed by recruitment, over the course of our long-term mark-recapture study (R. Shine, unpubl. data).

The massive small-scale spatial heterogeneity that we documented in so many phenotypic traits has an obvious implication for conservation: the loss of even a single population may remove distinctive genetic variation from the gene pool of a species. Thus, managers need to maintain as many populations as possible, and cannot assume that individuals from adjacent sites, connected by suitable habitat corridors, are parts of a single genetically homogeneous population. A second implication concerns research methodology: we need to examine multiple populations if we are to obtain robust estimates of mean values for species traits. At the same time, spatial heterogeneity provides an excellent study system for exploring the proximate determinants of variation in such traits. Intraspecific comparisons have provided rich insights into life-history evolution in a diverse array of terrestrial reptile species, although they have relied upon comparisons between populations separated by very large distances (Tinkle & Ballinger, 1972; Du *et al.*, 2010) or inhabiting areas that impose very different selective forces (Bronikowski & Arnold, 1999; Bronikowski, 2000). The remarkably strong phenotypic divergence between seasnakes in adjacent bays of the New Caledonian Lagoon suggests an opportunity for comparisons at a much smaller spatial scale, without the numerous confounding factors that arise in broader-scale comparisons.

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