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Plasticity matches phenotype to local conditions despite genetic homogeneity across 13 snake populations

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In a widespread species, a matching of phenotypic traits to local environmental optima is generally attributed to site-specific adaptation. However, the same matching can occur via adaptive plasticity, without requiring genetic differences among populations. Adult sea kraits (*Laticauda saintgironsi*) are highly philopatric to small islands, but the entire population within the Neo-Caledonian Lagoon is genetically homogeneous because females migrate to the mainland to lay their eggs at communal sites; recruits disperse before settling, mixing up alleles. Consequently, any matching between local environments (e.g. prey sizes) and snake phenotypes (e.g. body sizes and relative jaw sizes (RJSs)) must be achieved via phenotypic plasticity rather than spatial heterogeneity in gene frequencies. We sampled 13 snake colonies spread along an approximately 200 km northwest–southeast gradient ($n > 4500$ individuals) to measure two morphological features that affect maximum ingestible prey size in gape-limited predators: body size and RJS. As proxies of habitat quality (HQ), we used protection status, fishing pressure and lagoon characteristics (lagoon width and distance of islands to the barrier reef). In both sexes, spatial variation in body sizes and RJSs was linked to HQ; albeit in different ways, consistent with sex-based divergences in foraging ecology. Strong spatial divergence in morphology among snake colonies, despite genetic homogeneity, supports the idea that phenotypic plasticity can facilitate speciation by creating multiple phenotypically distinct subpopulations shaped by their environment.

1. Introduction

The phenotype of an individual reflects not only its genotype, but also the way in which local conditions (e.g. experiences early in life) shape the translation of that genotype into measurable characteristics of the individual [1,2]. By generating phenotypic variation across a species' range, developmental plasticity in response to spatially heterogeneous environments can facilitate subsequent speciation and ultimately may impact biological diversification [3–5]. That is, site-specific environmental conditions can generate site-specific phenotypes via modifying developmental trajectories, generating phenotypically distinct subpopulations. If gene flow is low between sites with differing phenotypic optima, those subpopulations may continue to diverge under genetic assimilation (whereby facultatively expressed traits become constitutively expressed: [6,7]). Differential selection may further impact allelic frequencies, increasing genetic differentiation among subpopulations and eventually resulting in speciation [3].

Although the concept of adaptive phenotypic plasticity generating spatial variation is straightforward, empirical evidence that population divergence can be initiated by adaptive phenotypic plasticity is rare. In most situations, local populations that are exposed to differing conditions are likely to also be at least partially isolated in terms of gene flow. As a result, differentiation

among subpopulations will be the result of two processes acting simultaneously: adaptive plasticity, and site-specific shifts in allelic frequencies [8–12]. To tease apart their respective contributions, we need to control the role of each factor; and thus, such studies are usually conducted in captivity [13–15].

Although phenotypic plasticity provides an effective way to deal with unpredictably changing circumstances, canalization of trait expression (loss of plasticity) may confer advantages in more stable circumstances by allowing optimization of traits and functions, and buffering deleterious developmental deviations [16,17]. Thus, even if spatial heterogeneity in phenotypic traits is initially generated by plasticity, the proximate mechanisms causing that variation will shift through time to reflect increasing canalization (genetic assimilation)—that is, the spatial heterogeneity in traits will come to be underpinned by spatial heterogeneity in allelic frequencies. Unsurprisingly, then, empirical evidence that phenotypic plasticity can produce divergent adaptive phenotypes across populations of free-ranging individuals is scarce [18,19].

Owing to strong biomechanical constraints, skeletal structures provide good model systems with which to explore adaptive changes [20]. The skeleton of vertebrates is a complex structure that relies upon highly stabilized developmental processes (e.g. homeogenes that determine skeletal patterning)—but that nonetheless responds to environmental pressures [21–23]. Complex genetic, molecular and cellular mechanisms underpin the phenotypic plasticity of skeletal traits in vertebrates [24–26]. Inevitably, though, evidence on the role of skeletal plasticity in producing phenotypic variation across populations (especially, in the absence of genetic heterogeneity) has rarely been obtained in natural settings [4].

Snakes are highly plastic organisms [27–30], and their relatively simple morphology facilitates studies on adaptive phenotypic plasticity in skeletal traits [31]. In snakes, two main skeletal structures are known to respond to environmental conditions: the number of vertebrae and the dimensions of the trophic apparatus (jaws). The number of somites can be influenced by ambient temperature during embryonic development [32]. Relative jaw size (RJS), a crucial feature in gape-limited predators, is affected by the sizes of prey items that a snake encounters as it grows, such that snakes develop larger jaws (relative to body length) if they frequently attempt to ingest very large prey [31,33–35].

Geographical variation in both body size and RJS are widespread in various snake lineages, within as well as among species [30,31,36–41]. However, the respective influences of local (genetically based) adaptation versus plasticity have not been examined, because too few populations have been studied and/or because rates of genetic exchange among populations have not been known. In this study, we exploited an opportunity to examine the influence of environmental conditions on the morphology of sea snakes (*Laticauda saintgironsi*), independent of local genetic adaptation. Studies on this system have shown a combination of spatial (among-island) heterogeneity in the mean body sizes, but a lack of genetic divergence [42–44]. The large dataset (approx. 4500 individuals) and the wide area surveyed (13 sites spread over more than 200 km) enabled us to assess if spatial variation in food resources influences trophic morphology in a gape-limited predator, in the absence of significant spatial divergence in allelic frequencies.
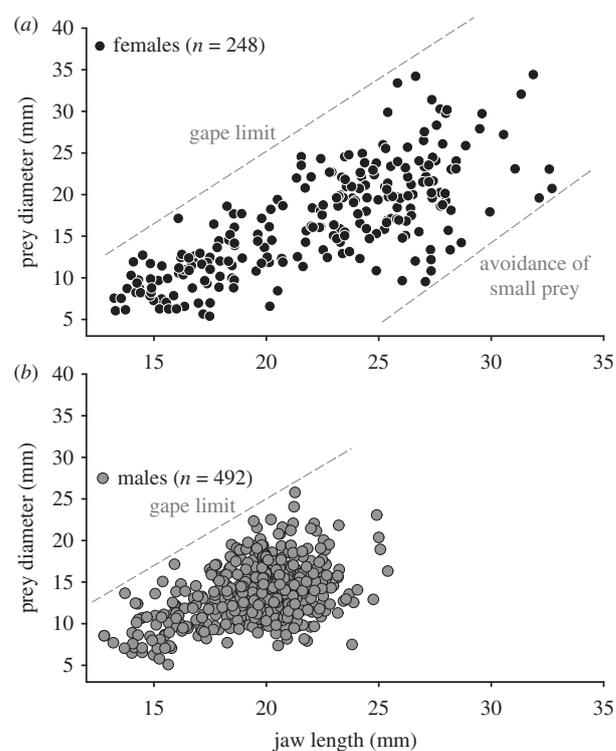

Figure 1. The maximal diameter of the fish ingested by sea kraits (*y*-axis) was measured in the field (see [48] for details) and values were plotted against snake jaw length (*x*-axis). (*a*,*b*) Data for females and males, respectively. The data reveal an upper limit for prey size that increases with jaw size: the maximal prey diameter ingestible by snakes is shown by the upper dashed grey line (gape limit). This result reflects the strong distension of the tropic apparatus in individuals with very large prey in their mouth, as depicted in the electronic supplementary material, figure S1. Also, the largest females did not consume small prey (prey avoidance area, lower dashed grey line) showing an ontogenetic diet shift; by contrast, large males continue to consume small prey (ontogenetic telescope pattern, [47]).

2. Material and methods

(a) Study species and study sites

Sea kraits are large (more than 1.5 m) banded hydrophiine elapid snakes that spend approximately half of their time foraging at sea and half of their time on land (e.g. for digestion, mating and to lay their eggs [45,46]). Sea kraits feed on more than 30 anguilliform fish species spanning a wide range of body sizes, and swallow them whole. Some of the fish consumed are so large that they pose a substantial physical challenge for the trophic apparatus, constraining maximal prey size ([47]; figure 1; electronic supplementary material, figure S1). The yellow sea krait (*L. saintgironsi*) is endemic to New Caledonia, where it is abundant on many small islets within the extensive Neo-Caledonian Lagoon [49]. Females attain larger body sizes than do males (mean adult snout–vent lengths (SVLs) 91 ± 9 cm and 73 ± 5 cm, respectively; maximal SVLs 130 cm versus 98 cm, respectively; $n = 6836$ individuals; X. Bonnet, F. Brischoux 2012, unpublished data).

Adult sea kraits are highly philopatric [46,50] and they forage around their home colony (one-third of prey taken less than 4 km from the shore [48,51]) as well as over a larger area (approx. 30 km radius [48]). Female sea kraits often undertake long foraging trips (greater than one week) and can dive as deep as 80 m, crossing the barrier reef to forage outside the lagoon in search of large prey [48,52]. Stomach content studies combined with stable isotope analyses have shown that body size (and hence sex) influences the diet, trophic level (i.e. sexes differ in δ^{15}N signatures) and foraging area (i.e. sex differ in δ^{14}C signatures) [53]. Males feed mostly

Table 1. Outcome of GLM with SVL (cm) as the dependent variable, and site ($n = 13$, figure 3) and sex as the factors.

	SS	d.f.	MS	F	*p*-value
intercept	8 694 896	1	8 694 896	243 899 0	<0.001
site	18 842	12	1570	44.0	<0.001
sex	109 531	1	109 531	3072.4	<0.001
site*sex	2329	12	194	5.4	<0.001
error	187 802	5268	36		

on small moray eels (e.g. *Gymnothorax chilospilus*, 65% of prey), whereas females consume a diverse array of moray and conger eels (no species exceeds 14% of the total number of prey) [53]. Large females avoid small prey, whereas males do not (figure 1). Because diving performance scales closely with body mass in air-breathing marine animals [54], the larger body size of females explains their ability to undertake prolonged dives to capture large fishes in deep water [48,53], and thus the sex divergence in diet.

In the lagoon of New Caledonia, sea kraits are apex predators in complex food-webs largely dependent on sedentary organisms [55]. Hard-bottom habitats colonized by live coral support a greater diversity and higher biomass of fishes than do non-coralline hard-bottom and soft-bottom habitats [56]. Both abundance and body size of demersal fishes increase from coastal zones to the barrier reef, and also from south to north along the lagoon [57,58]. Assemblages of the anguilliform fishes exploited by sea kraits also vary among sites [59], and are related to the width of the lagoon (and hence the surface area over which snakes can forage [48]) and the distance to the barrier reef (and hence the complexity of substrates over which snakes can forage [53,58]). In New Caledonia, professional and recreational fishing reduces fish abundance and diversity [60,61] and is spatially heterogenous. For example, recreational fishing exceeds offtake by professionals near popular islets [62] and remoteness to the main market places (i.e. Nouméa) is associated with lower fishing pressure [63]. Tourism, snorkeling and boat traffic degrade marine habitats around the islets where sea kraits capture many of their prey [48,64]. Thus, fish assemblages are negatively affected by recreational activities in such sites, as well as by spatially variable pollution by mining-produced trace elements (e.g. Ni, Cr) [65]. Because both contamination and recreational fishing are more intensive in coastal areas than in remote sites, we cannot partition their respective influences.

We studied 13 colonies of *L. saintgironsi* on a 200 km gradient along the western coast of New Caledonia (electronic supplementary material, figure S2). In order to compare the 13 sites, we first considered four main parameters (electronic supplementary material, table S1). For each site (colony) we took into account: (i) protection status, (ii) fishing pressure, (iii) the straight-line distance from the site to the barrier reef, and (iv) lagoon width using a straight-line from the nearest mainland coastline to the barrier reef passing through the site. Protection status and fishing impact were coded as follows: 1 to 4 for increasing protection status and −3 to 0 for decreasing fishing pressure [62]. To standardize the four parameters, the distance from site to the barrier reef and lagoon width were scaled to range from 0 to 3 (values, in km, divided by 7.66 and 16.66, respectively). Because we had no *a priori* prediction about the relative contributions of protection status, fishing impact and bottom habitats on the foraging success of sea kraits, we arbitrarily partitioned their influence to one-third each (we merged the distance to the barrier reef and lagoon width into a single

parameter, scaled to range from 0 to 3. The sum of the three final parameters provided an index of habitat quality (HQ; electronic supplementary material, table S1). For example, remote sites in strictly protected marine areas with abundant reef structures were allocated a high HQ-score. For several analyses, we used a crude geographical metric along the studied gradient (grey arrow in the electronic supplementary material, figure S2) by ranking each site using +1 increments from the first to the last site (i.e. Ile Verte was numbered 1, Ténia 2, Mba 3,… Brosse 11, Améré 12 and Kié 13). This metric allowed us to consider the northwest to southeast pattern of increasing abundance of fishes in the lagoon [57,58].

(b) Phenotypic traits

Snakes were caught by hand (sea kraits are docile and can be manipulated with ease). We recorded SVL and total length (TL) using a flexible ruler to the nearest 5 mm. Jaw length (JL) was measured with a digital caliper as the distance from the tip of the snout to the quadrato-mandibular joint to the nearest 0.1 mm, with the snake's mouth kept closed. The difficulties of obtaining accurate measurements in living animals were compensated for by wide variation in morphology and by large sample sizes. The stomach region of each snake was palpated to detect recently ingested prey, allowing us to distinguish even small items (greater than 2 g). The maximal diameter of undigested prey was recorded with digital calipers [48]. Each individual was permanently marked and then released at the place of capture. Recaptures were excluded from the analyses in this paper, such that each individual was included only once. In this study, we focus on adults because juveniles do not exhibit such a strong sexual dimorphism in trophic morphology, nor can these individuals in this dispersive life-stage be confidently allocated to a specific colony [42,43,48,50,53].

(c) Analyses

Comparisons of body size (SVL) and RJS (JL scaled by body size) were performed using generalized linear models (GLMs). SVL or jaw size were included as the dependent variable, site ($n = 13$) and sex were the factors; for RJS, SVL was used as a covariate. The correlation between jaw size and SVL was strong and linear ($R^2 = 0.84$, $F_{1,4687} = 24\,927.3$, $p < 0.001$; electronic supplementary material, figure S3). Thus, it was not necessary to transform the variables prior to analyses. In order to minimize the number of factors included in our analyses, we also calculated residuals from the regression between jaw size versus body size as a measure of RJS. Residuals were calculated independently in males and in females in the analyses where sexes were considered separately in order to reduce extraneous variation. For metrics based on ranking (crude geographical and habitat quality), we used non-parametric tests. SVL was more often recorded than jaw size, generating differences in sample sizes for these two traits. Statistical tests were performed with STATISTICA 13.5.0.17 (2018 TIBCO Software).
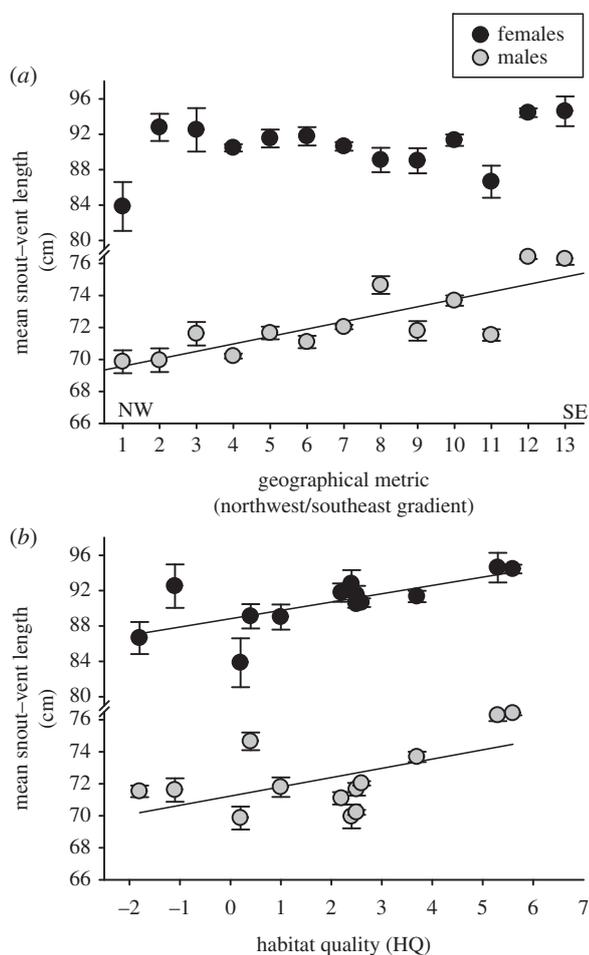
Figure 2. Relationship between body size (SVL) of sea kraits and (*a*) a metric of distance along the northwest/southwest geographical gradient within the Neo-Caledonian Lagoon, and (*b*) habitat quality. The points show mean values (±s.e.) for males and females at each of 13 colonies of sea kraits. (*a*) Spearman rank order correlation in males $\rho = 0.81$, $p < 0.05$, in females $\rho = 0.20$, $P > 0.05$. (*b*) Spearman rank order correlations: in males $\rho = 0.57$, $p < 0.05$, in females $\rho = 0.62$, $p < 0.05$ ($n = 13$ sites). See text for definition of metric of distance and of habitat quality.

3. Results

(a) Spatial variation in body size

The mean body size varied among sites, with a significant interaction with sex (table 1). Thus, the degree of sexual size dimorphism varied across sites. The mean SVL positively correlated with our geographical metric (position along the northwest–southeast transect within the lagoon) in males but not in females (Spearman rank order correlation in males $\rho = 0.81$, $p < 0.05$, in females $\rho = 0.20$, $p > 0.05$; figure 2). Male SVL tended to increase towards the southeast: HQ (electronic supplementary material, table S1) positively correlated with the mean SVL in both sexes ($\rho = 0.57$, $p < 0.05$ in males, $\rho = 0.62$, $p < 0.05$ in females; figure 2).

(b) Spatial variation in relative jaw size

Jaw size scaled by body size (RJS) varied among sites with significant interactions with sex (table 2). On average, females exhibited larger RJS than did males (23.1 ± 0.1 mm (±s.e.) in females and 22.0 ± 0.0 mm in males). Because body size, RJS and trophic ecology all diverged between the sexes, and because of strong interactions between sex and site (table 2), we considered each sex separately.

Table 2. Outcome of GLM with jaw size (mm) as the dependent variable, sites ($n = 13$, figure 3) and sex as the factors and SVL (cm) implemented as a continuous covariate.

	SS	d.f.	MS	F	*p*-value
intercept	571.4	1	571.4	457.2	<0.001
SVL	6990.6	1	6990.6	5592.9	<0.001
site	72.9	12	6.1	4.9	<0.001
sex	181.5	1	181.5	145.2	<0.001
site*sex	138.5	12	11.5	9.2	<0.001
site*sex*SVL	139.5	12	11.6	9.3	<0.001
error	5808.4	4647	1.3		

Table 3. Outcome of ANOVAs performed separately in males and in females with RJS (residuals) as the dependent variable, sites ($n = 13$, figure 3) as the factor.

	SS	d.f.	MS	F	*p*-value
males					
intercept	15.0	1	15.0	14.3	<0.001
site	177.6	12	14.8	14.1	<0.001
error	3449.7	3294	1.0		
females					
intercept	0.1	1	0.0	0.0	0.866
site	68.9	12	5.7	3.3	<0.001
error	2373.8	1366	1.7		

In both sexes, we found a significant site effect on RJS (table 3 and figure 3). RJS did not correlate significantly with the geographical metric (position within the lagoon) in males, but was negatively correlated with this index in females (Spearman rank order correlation, respectively, in males $\rho = 0.17$, $p > 0.05$, in females $\rho = -0.67$, $p < 0.05$; figure 3; electronic supplementary material, figure S4).

Across the 13 colonies of sea kraits, the mean body size was not correlated with the mean RJS ($\rho = 0.27$, $p > 0.05$ and $\rho = 0.01$, $p > 0.05$ in females and males, respectively).

(c) Influence of habitat quality on relative jaw size

HQ positively correlated with RJS in males ($\rho = 0.56$, $p < 0.05$) but not in females ($\rho = -0.05$, $p > 0.05$; figure 4). Because males feed on small prey captured in shallow water, whereas females can exploit the barrier reef and forage in deep water, we examined the effect of distance to barrier reef and lagoon width versus protection status and fishing pressure. In males, lower fishing pressure (note that this score was negatively coded, electronic supplementary material, table S1) was associated with higher RJS ($\rho = 0.64$, $p < 0.05$; figure 4); this effect was not significant with increasing protection status ($\rho = 0.53$, $p > 0.05$). The distance to barrier reef or lagoon width did not correlate with RJS ($\rho = 0.21$, $p > 0.05$ and $\rho = -0.11$, $p > 0.05$, respectively). By contrast, females exhibited significant correlations between RJS and distance to barrier reef and lagoon width (respectively, $\rho = -0.58$, $p < 0.05$ and $\rho = -0.62$, $p < 0.05$;
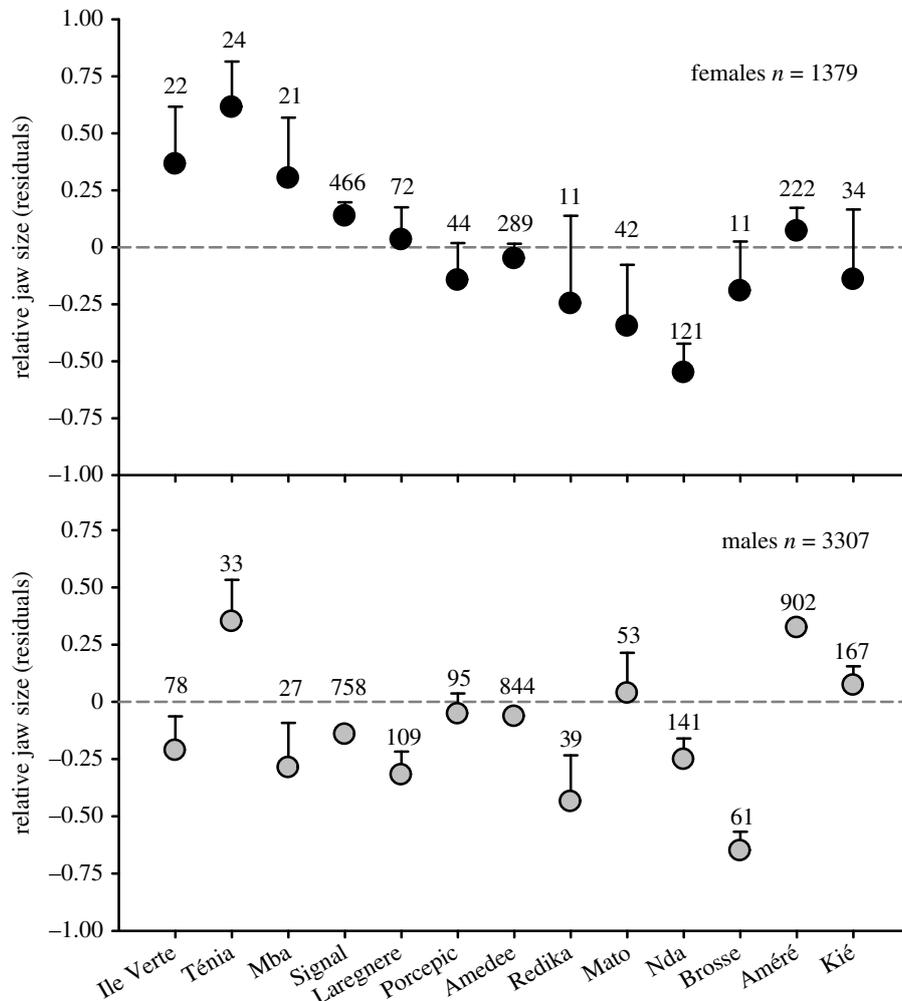
Figure 3. Mean RJS (residuals) of sea kraits was calculated separately for females (top panel) and males (lower panel) at each site (*x*-axis). Means are expressed ± s.e., with sample sizes. Dashed grey lines indicate the mean value (centred to zero by definition). The 13 sites are ordered following the northwest/southeast gradient (electronic supplementary material, figure S2). In females but not in males, RJS decreased significantly along this gradient (see text).

figure 4). RJS was largest in females from colonies near the barrier reef in narrower parts of the lagoon.

4. Discussion

Using a spectrum of colonies spread across a wide geographical gradient, our results show that body size and RJS in sea snakes are correlated with (i.e. respond to) spatially variable environmental conditions. The phenotypic variations that we have documented fit well with the hypothesis that increasing prey availability promotes both somatic growth and the development of the trophic apparatus.

The impact of food intake on growth rate and body size is straightforward and uncontroversial, but the idea of food-induced phenotypic plasticity in RJSs of snakes is less clearcut. Some of the experimental studies that have manipulated prey size for captive animals have concluded that RJS responds to food treatment [31,33–35,39], whereas others have found no such effect [66–69]. Some of those null results may reflect logistical constraints (sample sizes, durations of research), rendering it difficult to reach any conclusions on the generality of this form of phenotypic plasticity in snakes. By contrast, detailed field and laboratory investigations of teleost fishes have revealed how bony components of the trophic apparatus respond to different foraging challenges [70,71]. Environmentally induced mechanisms of bone deposition

have been deciphered using transgenic zebrafish [71]. Our own current study is limited to broad phenotypic traits, but may nonetheless provide insights into how the ability to ingest large prey has contributed to the evolutionary diversification of a highly speciose lineage of vertebrates (more than 3700 terrestrial, amphibious or truly marine snake species) [72].

Our work exploits the opportunity provided by multiple colonies of sea kraits that experience contrasting trophic conditions but yet are genetically homogeneous [44,59]. Long-term mark–recaptures show that, at least in adults, each colony functions independently from the others [43]. Well-identified groups of individuals are thus exposed to unique local conditions over long periods, probably throughout their adult lives [59]. Recruitment to these populations depends on supply from exogenous communal laying sites [42], followed by long-distance dispersal of juveniles across the lagoon, sometimes to islands more than 50 km away from the natal site. Even the few colonies where local reproduction is sufficient for population maintenance are not isolated. Indeed, some subadults and adults (less than 5%) leave their home island to resettle in a new home islet (maximal distance travelled more than 100 km; X. Bonnet, F. Brischoux 2012, unpublished data). Overall, high rates of juvenile dispersal and occasional adult dispersal maintain genetic homogeneity despite substantial genetic diversity
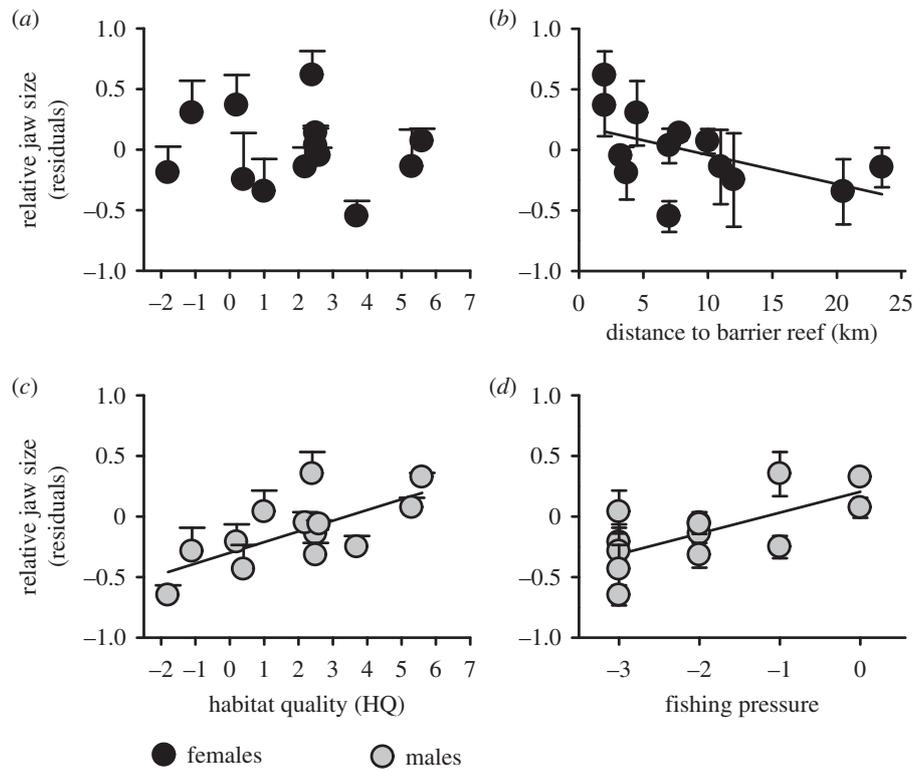
Figure 4. Relationship between RJS (residuals) and (*a,c*) habitat quality in both sexes, (*b*) distance from colony to the barrier reef of females, and (*d*) fishing pressure of males in 13 colonies of sea kraits. Each point shows the mean value (±s.e.) (see text for statistics).

[44]. The lack of geographical genetic structure among discrete colonies exposed to spatially heterogeneous local conditions provides a large-scale natural experiment on the potential impact of plasticity. Our conclusions are supported by large sample sizes, multiple sites, sex-specific responses, long-term exposure to local conditions (i.e. years in adults) and evidence that swallowing large prey exerts strong mechanical forces on the trophic apparatus.

HQ correlated with body size in both sexes (figure 2), as expected if more food promotes faster growth and higher survival rates (and thus, greater mean age). High rates of growth also might indirectly affect RJS [67,69]. Nonetheless, the lack of significant correlation between the mean body size and the mean RJS across sites suggests that effects of food supply on rates of growth of the body versus the jaws (relative to body size) were at least partly uncoupled. That uncoupling fits with the fact that abundant prey does not always imply large prey: indeed, in some well-protected sites (highest HQ) with abundant food, most prey items were small [59]. Such a situation may favour rapid growth of the body, but not necessarily trigger an equivalent growth rate of the jaws. Moreover, sex divergences in the relationship between the mean body size and the mean RJS among sites suggest that diversity of the diet (small prey versus wide range of prey size) influences spatial variation in RJS [39]. Males feed primarily on one moray eel species (lipspot moray, *G. chilospilus*) that lives in shallow waters, usually less than 5 m deep [73]. Thus, male snakes forage in shallow water close to their home islet, increasing their sensitivity to local factors that influence fish abundance (protection status of the colony, local fishing pressure and the broad northwest/ southeast gradient). In our analyses, these factors were correlated with body size and RJS of males. By contrast, female snakes feed on a wide range of prey [53], undertake long

foraging trips to various habitats including deep bottoms outside the lagoon [52,53], large individuals avoid small prey in this sex only (figure 1); and consistent with that foraging biology, body size and RJS in females were influenced by lagoon width and distance to the barrier reef rather than by the more locally acting factors that influenced males.

Our data do not allow us to test the hypothesis that the spatial variation in snake trophic morphology is adaptive [31,74], although that explanation is plausible (e.g. differential RJS might facilitate niche partitioning; [75]). However, the situation that we have described fits well with models that predict that if early steps of speciation involve phenotypic plasticity, we should not see genetic differentiation among populations at this point [5]. We provide empirical evidence that developmental plasticity may contribute to the early stage of divergence in fitness-relevant morphology among populations. Future studies could usefully explore the degree to which morphological variation maps onto individual variation in performance (e.g. maximal ingestible prey size) and correlates of fitness (e.g. rates of survival and reproductive success). Because many snake species occur on small semi-isolated islands (e.g. [76]), there is also the potential for research on systems in which some populations are linked by high gene flow whereas others are not. Such a system might clarify the mechanisms and time courses over which adaptive genetically based variation replaces plasticity as a source of fitness-relevant morphological variation among populations (e.g. [7,30]).

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