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ORIGINAL ARTICLE

# Phenotypic variation contrasts with genetic homogeneity across scattered sea snake colonies

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## ABSTRACT

**Aim** In philopatric species distributed across wide geographical areas, each population is influenced by local factors. We assessed the expected spatial genetic and phenotypic structure across a set of colonies of a highly philopatric sea snake.

**Location** South Lagoon of New Caledonia, Western Pacific Ocean.

**Methods** We used body size ($N = 4915$ individuals) to assess phenotypic variations across 11 islet colonies of the amphibious sea kraits (*L. saintgironsi*) spread throughout the South Lagoon of New Caledonia. We also used 11 microsatellite markers in a subsample of 302 individuals to examine the demographic history and genetic structure.

**Results** A major colonization event and rapid population expansion occurred during the mid-Pleistocene. Mean body size increased significantly along the north–south gradient investigated, suggesting that each colony is relatively independent and responds to local conditions. However, our data revealed a total lack of genetic structure despite a substantial genetic diversity.

**Main conclusions** A peculiar reproductive system likely underlies this pattern that combines a marked phenotypic gradient with a lack of geographical genetic structure. Gravid females from colonies scattered throughout the South Lagoon converge towards few communal coastal nesting sites to lay their eggs. Hatchlings disperse randomly in the lagoon and supply islets with recruits. This process homogenizes the overall genetic structure. However, because when settled snakes are philopatric, the mean body size of each colony presumably reflects the influence of local conditions. This system resembles those documented in various organisms (e.g. fish) but was not previously described in any amniotic lineage.

**Keywords**

**body size, communal coastal nurseries, demographic history, microsatellites, population structure, sea kraits**

## INTRODUCTION

Understanding how populations respond to changing environments, colonize new habitats, persist, or decline is a crucial albeit complex issue in evolutionary biology and conservation (Reed *et al.*, 2011). Since the advances in molecular biology, genetic markers offer powerful tools to investigate this kind of topics and notably to study genetic population structure (Allendorf *et al.*, 2010). However, phenotypic data remain essential when population structure results from phenotypic plasticity whereby environmental factors generate morphological divergences among genetically homogeneous populations (Thibert-Plante & Hendry, 2010). Phenotypic traits are an outcome of numerous interactions between genes and the environment and thus provide a global assessment of population structure over large spatial and time-scales (Klingenberg *et al.*, 2001).

In widely distributed species, individuals tend to aggregate in areas where environmental conditions are most suitable. This spatial structure favours the emergence of distinct

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populations, and promotes the expression of local phenotypic and genetic responses (Young *et al.*, 1996). However, phenotypic and spatial genetic responses are not necessarily parallel. Phenotypic plasticity can lead to strong phenotypic variations despite gene flow that homogenizes genetic structures, whereas substantial inter-population divergences caused by genetic barrier may remain undetectable using morphological traits (Knowlton, 1993; Baker *et al.*, 2003). Teasing apart the contribution of phenotypic plasticity versus genetic differentiation is important to assess population functioning and distributional patterns. As a result, combining phenotypic and genetic information across relevant geographical scales represents a valuable approach to examine population biogeographical patterns (Guillot *et al.*, 2012).

Organisms that form colonies in small islands scattered in the oceanic matrix offer valuable opportunities to assess the influence of population fragmentation on both phenotypic and genetic traits (Losos *et al.*, 1997; Lind & Johansson, 2007). Amphibious sea snakes (sea kraits, Elapids, *Laticauda* spp.) represent typical examples of such systems because populations are represented by discrete colonies spread in the coral reef archipelagos of the Western Pacific Ocean (Heatwole, 1999). Like many other marine tetrapods (e.g. seabirds, seals), sea kraits are predators that forage at sea but return to coastal colonies to reproduce (Heatwole, 1999). Sea kraits exhibit a strong dependence for terrestrial habitats (Bonnet *et al.*, 2005; Bonnet, 2012) and display a high degree of philopatry for their home islet (Shetty & Shine, 2002; Brischoux *et al.*, 2009a), in combination these traits may foster genetic and phenotypic divergences among colonies. Indeed, each colony is tightly associated with a specific environment that characterizes each islet (e.g. topography, surrounding seafloors; Andréfouët & Torres-Pulliza, 2004).

At a wide biogeographical scale, the highest values of marine snake species richness occur across the Sunda and Sahul shelves (Brischoux *et al.*, 2012). Two species (*L. laticaudata*, *L. colubrina*) followed a south-eastern route and reached the lagoon of New Caledonia during the Quaternary. Subsequent closing of oceanic routes caused by post-glacial transgressions favoured the emergence of endemic species (Cogger & Heatwole, 2006; Lane & Shine, 2011a). As a result a set of morphologically and genetically distinct species range across a wide biogeographical gradient; *L. saintgironsi* occupies an intermediate position between *L. colubrina* and *L. frontalis*, two closely related species. Numerous sea krait colonies are spread along this colonization route in the vast and elongated lagoon of New Caledonia (> 800 km north–south; 24,000 km$^2$); they offer a suitable system to examine the possible influence of environmental factors on genetic and phenotypic traits.

A mark recapture study of *L. saintgironsi* in the South Lagoon of New Caledonia has revealed a peculiar population functioning system: hundreds of reproductive females from various colonies migrate to very localized costal sites to lay their eggs, and then return home. Thousands of neonates hatch in communal coastal nurseries and later disperse in the South Lagoon (Bonnet *et al.*, 2014). This breeding system where offspring sired by adults from distinct colonies disperse from a single breeding ground may promote genetic mixing among colonies if juvenile dispersal is random. However, different mechanisms such as canalized propagule dispersal and natal homing may prevent population mixing. Indeed, most field studies in fully marine species that breed in communal sites reported marked spatial genetic structure (SGS). For instance, kin recognition among settling larvae of colonial ascidians results in the assembly of colonies that contain closely related individuals (Grosberg & Quinn, 1986). Similarly, philopatric larval dispersal promotes isolation by distance (IBD) in sponges (Blanquer *et al.*, 2009) and natal homing maintains SGS in many anadromous fish and whales (Hasler & Scholz, 1983; Baker *et al.*, 2013). However, the impact of communal nurseries on SGS and on spatial phenotypic structure (SPS) across colonies remains an unexplored issue in sea kraits, and thus more generally in amphibious marine vertebrates.

In this study, we used microsatellite markers to assess the genetic structure of 11 yellow sea krait colonies distributed in the South Lagoon of New Caledonia. Yellow sea kraits exhibit pronounced terrestrial habits (Bonnet *et al.*, 2005; Bonnet, 2012) and a very high degree of philopatry towards their home colony and for their familiar refuges (Brischoux *et al.*, 2009a). Thus, historical events combined with pronounced terrestrial habits and high degree of philopatry toward familiar refuges in yellow sea kraits should favour population fragmentation and spatial structuring compared to other sea krait species that may cross the ocean matrix more easily (Lane & Shine, 2011a). Accordingly, a significant SGS was expected along the north–south distribution axis of the populations. Besides, previous genetic investigations suggested spatially oriented sex-biased dispersal among six colonies of yellow and blue sea kraits (*L. saintgironsi* and *L. laticaudata*) sampled in New Caledonia; indicating possible geographical genetic structure (Lane & Shine, 2011b). Further, SGS was documented in other marine and terrestrial snake species (Pernetta *et al.*, 2011; Lukoschek & Shine, 2012).

Because the study zone spreads over 200 km along a relatively narrow north–south elongated area, we also expected phenotypic variations along this geographical axis. Major habitat differences exist among colonies in terms of, inter alia, reef structures, islet morphology, surrounding sea floors or prey diversity (Andréfouët & Torres-Pulliza, 2004; Brischoux *et al.*, 2009b). These spatial factors generate marked variations in terms of age structures among colonies (Bonnet *et al.*, 2015), but a possible impact on phenotypic variations has not been assessed yet. Because body size influences fecundity, survival or foraging success in snakes and because it varies across populations (Shine, 1990) we used snout to vent length (SVL) as a key integrative phenotypic trait (Feldman & Meiri, 2012).

Overall, based on these results, we expected marked SGS and SPS across scattered colonies of yellow sea kraits. However, the possible influence of communal breeding sites and




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associated neonatal dispersal throughout the South Lagoon on phenotypic and genetic structure was not easily predictable. Combining genetic and phenotypic markers this study aims to assess this issue and to examine the global functioning of sea snake colonies spread across a wide geographical area.

## MATERIALS AND METHODS

### Study system

We sampled 11 populations of *L. saintgironsi* distributed in the South Lagoon of New Caledonia following a north-west–south-east gradient along the western coast of the mainland (Fig. 1). The coast and the open ocean delimit an elongated study area (> 200 km), relatively narrow northward (< 3 km wide) and wider southward (*c.* 25 km). Previous studies revealed that the mean foraging radius of sea kraits around their home islet is relatively small, 15–20 km on average (Brischoux *et al.*, 2007). This information is important to select a relevant spatial scale for inter-population comparisons. The study site extends over 200 km and the studied colonies were scattered along this wide geographical gradient (Fig. 1).

### Phenotypic assessment

A total of 4915 adult snakes (1462 females and 3453 males) were captured by hand, sexed, and measured to the nearest 0.5 cm. Each snake was permanently individually marked and rapidly released. The sex of each individual was included as a factor in the analyses. We considered a broad north–south gradient (dashed arrow in Fig. 1) to assess possible geographical trend in mean body size: we ranked the populations along this broad axis. Using Euclidian geographical distances between sites provided similar results. However, this latter test confers important weight to the most remote islet; thus, to avoid possible outlier effect we used the most parsimonious ranking approach. Body size data did not exhibit skewed distribution, sample size was large, and none of the conditions for the application of parametric *F*-tests were violated; hence we used analyses of variances for body size comparisons among colonies (each individual was represented only once).

### Genetic analysis

#### *Tissue collection and microsatellite amplification*

In 2011 and 2012, we gathered biological tissues in a subsample of 302 snakes randomly selected among the snakes measured for SVL, including all age and sex classes. We collected the external portion of 1–4 ventral scales preserved in 95% ethanol or in dimethylsulfoxyde. DNA was extracted with a Chelex protocol (Walsh *et al.*, 1991). All samples were genotyped using 10 microsatellite markers developed for *L. saintgironsi* (i.e. Lati_D120, Lati_D105), for *L. laticaudata* (i.e. Lati_B2, Lati_D2, Lati_D108) and for both species (i.e. Lati_A115, Lati_A8, Lati_C10, Lati_D4,Lati_D6) (Lane *et al.*, 2008) (Table 1). The relevant DNA fragments were amplified using polymerase chain reaction (PCR) performed in three multiplexes using the QIAGEN multiplex kit. PCR amplifications of loci: Lati_B2, Lati_A115, Lati_A8, Lati_D108, Lati_D2 were grouped in the multiplex 1; loci Lati_C10, Lati_D4, Lati_D6 were grouped in the multiplex 2 and Lati_D120, Lati_D105 were grouped in the multiplex 3.

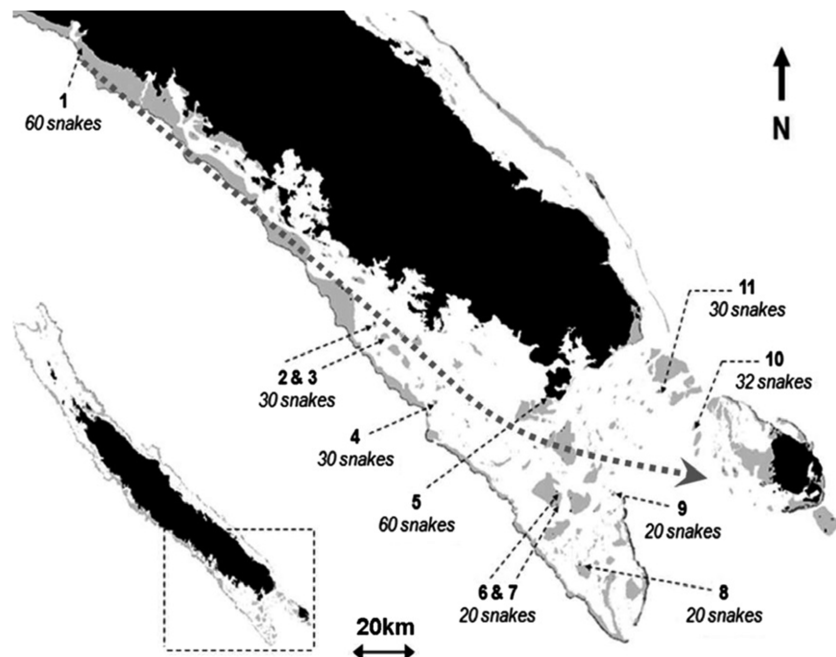


**Figure 1** Map of the South Lagoon of New Caledonia with the 11 islets visited and the number of yellow sea kraits (*Laticauda saintgironsi*) collected for genetic analyses. (1) Ile Verte, (2) Signal, (3) Larégnère, (4) Amédée, (5) Ile Ouen, (6) Uatérembi, (7) Ua, (8) N'da, (9) N'do, (10) N'dié, (11) Améré. The land areas are represented in black, coral reefs in light grey and the limit of the lagoon in grey. In italics sample size is indicated for each islet or group of islets. The dashed arrow indicates the geographical axis along which the populations are distributed we used for several analyses. The arrow also represents a segment of the colonization route followed by sea kraits during the Quaternary (see text).


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**Table 1** Genetic diversity for the nine localities of yellow sea krait (*Laticauda saintgironsi*), estimated using 10 microsatellite loci. Allelic richness (*AR*), expected heterozygosity ($H_e$) and FIS value. FIS significantly different from 0 are indicated in italics and bold (*P* value threshold adjusted with the Bonferroni correction: $P = 0.0005$).

| | | Améré | N'Die | N'Do | N'Da | Ua/Uatérembi | Amédée | Signal/Larégnère | Ouen | ÎleVerte | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Lati_A8 | AR | 9.094 | 10.087 | 9.692 | 10.787 | 10.876 | 9.748 | 8.188 | 10.537 | 11.131 | 10.016 |
| | $H_e$ | 0.884 | 0.891 | 0.876 | 0.885 | 0.907 | 0.867 | 0.864 | 0.882 | 0.900 | 0.884 |
| | $F_{is}$ | −0.053 | −0.052 | −0.027 | 0.107 | −0.048 | 0.192 | 0.112 | 0.044 | −0.037 | 0.026 |
| Lati_A115 | AR | 2.987 | 2.828 | 2.900 | 3.892 | 2.000 | 2.844 | 3.688 | 3.551 | 3.024 | 3.079 |
| | $H_e$ | 0.571 | 0.505 | 0.536 | 0.578 | 0.508 | 0.541 | 0.570 | 0.566 | 0.536 | 0.546 |
| | $F_{is}$ | 0.000 | −0.086 | 0.066 | 0.134 | −0.280 | 0.138 | 0.065 | ***−0.135*** | 0.037 | −0.007 |
| Lati_B2 | AR | 8.546 | 9.840 | 10.600 | 9.841 | 9.769 | 9.987 | 8.381 | 9.163 | 8.160 | 9.365 |
| | $H_e$ | 0.873 | 0.883 | 0.893 | 0.870 | 0.841 | 0.883 | 0.866 | 0.871 | 0.860 | 0.871 |
| | $F_{is}$ | 0.092 | −0.023 | −0.063 | 0.032 | 0.167 | 0.057 | −0.001 | 0.098 | 0.108 | 0.052 |
| Lati_C10 | AR | 12.472 | 11.861 | 9.785 | 11.392 | 11.384 | 14.138 | 12.933 | 12.198 | 11.879 | 12.005 |
| | $H_e$ | 0.857 | 0.872 | 0.813 | 0.879 | 0.828 | 0.902 | 0.900 | 0.851 | 0.873 | 0.864 |
| | $F_{is}$ | 0.027 | 0.212 | −0.165 | 0.147 | −0.027 | 0.002 | 0.157 | 0.006 | 0.122 | 0.053 |
| Lati_D2 | AR | 6.581 | 6.519 | 6.800 | 5.000 | 5.800 | 5.597 | 5.444 | 6.247 | 5.472 | 5.940 |
| | $H_e$ | 0.802 | 0.814 | 0.833 | 0.759 | 0.755 | 0.790 | 0.781 | 0.784 | 0.769 | 0.787 |
| | $F_{is}$ | −0.161 | −0.065 | 0.160 | 0.029 | −0.192 | −0.098 | −0.152 | 0.173 | 0.003 | −0.034 |
| Lati_D4 | AR | 6.874 | 6.487 | 6.942 | 7.600 | 4.992 | 5.687 | 5.197 | 5.432 | 6.465 | 6.186 |
| | $H_e$ | 0.778 | 0.764 | 0.692 | 0.784 | 0.729 | 0.756 | 0.744 | 0.782 | 0.796 | 0.758 |
| | $F_{is}$ | 0.036 | 0.018 | −0.370 | −0.084 | −0.235 | 0.118 | 0.014 | 0.006 | −0.089 | −0.065 |
| Lati_D6 | AR | 8.686 | 8.067 | 7.000 | 6.892 | 8.700 | 8.994 | 8.363 | 8.067 | 7.029 | 7.978 |
| | $H_e$ | 0.858 | 0.829 | 0.855 | 0.836 | 0.825 | 0.861 | 0.866 | 0.830 | 0.833 | 0.844 |
| | $F_{is}$ | −0.040 | ***−0.123*** | 0.025 | 0.282 | −0.030 | ***0.032*** | −0.001 | 0.041 | −0.100 | 0.010 |
| Lati_D108 | AR | 7.121 | 6.199 | 5.000 | 6.000 | 5.900 | 5.599 | 6.598 | 5.725 | 5.811 | 5.995 |
| | $H_e$ | 0.813 | 0.801 | 0.811 | 0.820 | 0.814 | 0.758 | 0.797 | 0.799 | 0.803 | 0.802 |
| | $F_{is}$ | 0.166 | 0.126 | 0.157 | 0.187 | −0.044 | 0.077 | −0.062 | 0.092 | 0.198 | 0.100 |
| Lati_D105 | AR | 6.589 | 5.570 | 6.984 | 5.999 | 6.000 | 7.760 | 6.984 | 6.623 | 6.694 | 6.578 |
| | $H_e$ | 0.818 | 0.743 | 0.822 | 0.785 | 0.818 | 0.853 | 0.793 | 0.777 | 0.774 | 0.798 |
| | $F_{is}$ | −0.091 | −0.114 | −0.094 | −0.006 | −0.100 | 0.101 | 0.201 | ***0.185*** | −0.033 | 0.005 |
| LatiD_120 | AR | 5.983 | 6.919 | 6.000 | 5.992 | 6.900 | 6.441 | 6.807 | 6.694 | 6.748 | 6.498 |
| | $H_e$ | 0.820 | 0.838 | 0.839 | 0.788 | 0.833 | 0.811 | 0.790 | 0.825 | 0.827 | 0.819 |
| | $F_{is}$ | −0.045 | −0.039 | 0.122 | −0.205 | −0.141 | −0.027 | −0.048 | −0.025 | 0.052 | −0.040 |
| Mean | AR | 7.493 | 7.438 | 7.170 | 7.340 | 7.232 | 7.680 | 7.258 | 7.424 | 7.241 | |
| | $H_e$ | 0.807 | 0.794 | 0.797 | 0.798 | 0.786 | 0.802 | 0.797 | 0.797 | 0.797 | |
| | $F_{is}$ | −0.007 | −0.015 | −0.019 | 0.062 | −0.093 | 0.059 | 0.029 | 0.049 | 0.026 | |

These multiplexes were carried out according to the manufacturer's standard microsatellite amplification protocol in the final volume of 10 μL and with 57 °C for annealing temperature. PCR products were sent to Genoscreen (Lille, France) for electrophoresis on an automatic sequencer (ABI). Genotypes were determined using the GENEMAPPER 3.7 software (Applied Biosystems, Foster city, CA, USA). Following preliminary analyses (data not shown) and due to low sample size in few islets, we pooled individuals from very close colonies: Signal with Larégnère (sites 2 and 3, separated by 4.2 km), and Ua with Uatérembi (sites 6 and 7, separated by 3.2 km, Fig. 1), decreasing the number of populations implemented in the analyses from 11 to 9.

### Genetic diversity

We used the software MICRO-CHECKER (Oosterhout *et al.*, 2004) to identify the presence of null alleles or scoring errors due to stuttering. Departures from Hardy–Weinberg expectations and linkage disequilibria are tested using exact tests, based on Markov chain (1000 permutations) as implemented in the software FSTAT 2.9.3.2. (Goudet, 2001). We adjusted the levels of significance for multiple tests using standard Bonferroni correction. We estimated the polymorphism over all loci for each population using the allelic richness (AR) expected heterozygosity (He) and the inbreeding coefficient FIS (FSTAT v.2.9.3.2, 1000 permutations). We performed Friedman tests with AR and He in each of the nine populations in order to detect possible differences in the distribution of the genetic variability.

### Genetic structuring

We computed pairwise $F_{ST}$ values between cohorts (i.e. neonates, juveniles and adults), between both sexes of each colonies and finally between colonies regardless sex and cohorts. These values and their associated significance were computed and tested using global tests implemented in FSTAT 2.9.3.2 with a level of significance adjusted for multiple tests using standard Bonferroni correction. The genetic structuring of


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these different groups was also analysed at an individual scale using Bayesian clustering approach implemented in the software STRUCTURE which allows estimating both the number of genetic populations (i.e. K clusters) and the admixture coefficient of individuals to be assigned to the estimated clusters (Pritchard *et al.*, 2000). We choose the admixture model and the option of correlated allele frequencies among colonies. We replicated 20 independent runs for each value of K genetic clusters (with $K$ varying from 1 to 9) with a total number of 1,000,000 iterations and a burn-in of 1000. To determine the number of genetic clusters from STRUCTURE analyses, we used STRUCTURE HARVESTER program (Earl & VonHoldt, 2011) in order to compare the mean likelihood and variance per $K$ values computed from the 20 independent runs. Finally, we combined Euclidian and genetic distances (i.e. Log 10 transform genetic distances) into simple Mantel test, using Allele In Space (Miller, 2005). We used this individual based method in order to test IBD between colonies and both sexes. Using broad ranking distance instead of Euclidian distance also provided similar results.

### *Demographic changes over time*

To reconstruct the demographic history of yellow sea kraits in our study area, we sampled randomly 45 individuals among the islets and we used the method of Storz & Beaumont (2002) implemented in the MSVAR 1.3 (Storz & Beaumont, 2002). This likelihood-based Bayesian method is known for producing robust reconstructions of the demographic history of populations (Beaumont, 2004; Girod *et al.*, 2011). MSVAR assumes the last ancestral population of size $N_1$ (ancestral size) began to decrease or increase exponentially some time during evolutionary history ($t_a$ generation ago) to the current population size $N_0$ (current size). Thus, MSVAR uses a coalescence-based framework under the stepwise mutation model in order to estimate $N_0$, $N_1$ and the time $T$ since the population started changing in size. This method analyses the allelic distribution and prior information for $N_0$, $N_1$ and $T$ whose distributions were assumed to be lognormal. The means and standard deviations of these prior lognormal distributions were themselves drawn from prior (i.e. hyperprior) distributions. For all simulations we used a generation time of 2 years, the mean age for reproductive maturity in females of *L. saintgironsi* (XB, FB & TF, unpublished data). We performed five independent runs (i.e. replicates) with different random seeds and uninformative hyperpriors (see Table S1 in Appendix in Supporting Information). Markov chains were run for $5 \times 10^9$ steps and thinned by $5 \times 10^4$ to get a total of 100,000 draws from the posterior distribution to prevent autocorrelation. We discarded the first 10% of the chains to avoid bias in parameter estimates resulting from the starting conditions. We used the statistic of Gelman & Rubin (1992) (G & R diagnostic) which observed the variance between and within multiple chains to control and test the convergence of the five independent chains (Gelman & Rubin, 1992). Smooth posterior distributions were estimated from the raw MSVAR data using the local regression as implemented in the Locfit R package.

## RESULTS

### Body size

Mean adult body size (SVL) averaged 78.5 ± 10.6 cm. Females were larger than males in all colonies ($F_{1,4893} = 805.33$, $P < 0.001$; and $P < 0.001$ in all *post hoc* tests; Fig. 2). We found strong differences in mean adult body size across sites (ANOVA with SVL as the dependent variable, sex and colonies as factors; $F_{10,4893} = 4.06$, $P < 0.001$; Fig. 2). Using geographical ranking of the colonies, we observed a strong spatial effect on the average body size of both males and females: snakes were smaller at the northern extremity of the gradient compared to the southern extremity (mean body size correlated with geographical ranking value, $r = 0.78$, $F_{1,9} = 13.74$, $P = 0.005$ and $r = 0.80$, $F_{1,9} = 15.52$, $P = 0.003$ in females and males respectively; Fig. 2). An inspection of the pattern suggests that colonies with larger females also sheltered larger males; this trend was supported by an ANCOVA with no difference between the sexes regarding the north–south increase in body size (i.e. parallel trends) (SVL as the dependent variable, sex as a main factor and geographical ranking as a covariate, slopes: $F_{1,418} = 0.08$, $P = 0.788$; Fig. 2).

### Genetic structure

Results showed no evidence for linkage disequilibrium ($P$-value threshold after Bonferroni correction = 0.001). We detected some null alleles but all were randomly distributed across loci and colonies. Among 90 tests, only four FIS values were significantly different from 0 ($P$-value threshold

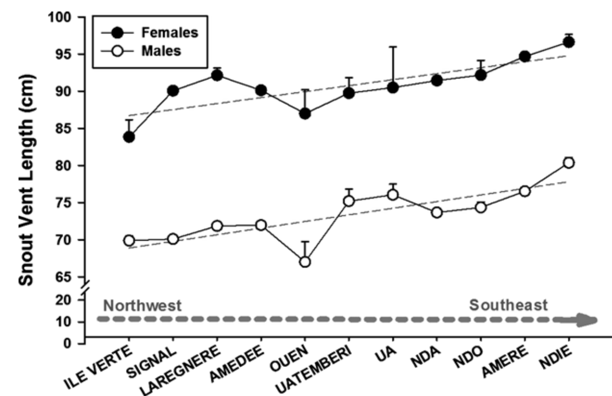


**Figure 2** Mean body size (SVL, snout vent length) of adult yellow sea kraits (*Laticauda saintgironsi*) measured in the 11 islets visited. The grey dashed line represent the geographical gradient presented in Fig. 1 (> 200 km). Data for females (black circles) and males (open circles) are provided. Error bars indicate standard deviations. The black dashed lines illustrate the trend with increasing mean body size from northern to southern colonies.


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after Bonferroni correction = 0.0005) but all were randomly distributed and did not affect the Hardy–Weinberg equilibrium at a global level (Table 1).

### *Population genetic diversity*

All microsatellite loci were highly polymorphic with an allelic richness (AR) ranging from 2 to 14.138 and a genetic diversity ($H_e$) ranging from 0.505 to 0.907 across colonies (Table 1). Both AR and $H_e$ were similar across populations (Friedman tests, $P = 0.99$ for $H_e$ and $P = 0.75$ for AR). This suggests a very strong genetic homogeneity across colonies.

### *Population genetic structure*

We did not detect evidence for genetic structure for any of the analysed groups. Indeed, $F_{ST}$ values revealed no significant genetic differentiation between the colonies regardless of sex and cohorts (mean $F_{ST} = 0.0029$, $P$ values > 0.001) (Table 2). This absence of genetic differentiation is also found between males (mean $F_{ST} = 0.003$, $P$ values > 0.001), females (mean $F_{ST} = 0.001$, $P$ values > 0.001) and different cohorts (mean $F_{ST} = 0.0016$, $P$ values > 0.001 for neonates, mean $F_{ST} = 0.0069$, $P$ values > 0.001 for juveniles and mean $F_{ST} = 0.0003$, $P$ values > 0.001 for adults). In agreement with these results, Bayesian clustering method, implemented in STRUCTURE program, indicated a weak genetic structure with the highest mean likelihood for only one cluster ($K = 1$) whatever the group of individuals taken into account. This suggests a very strong genetic homogeneity within the set of colonies occurring in the South Lagoon of New Caledonia. Moreover, the test for IBD showed a total lack of correlation between the Euclidian geographical distances and the genetic distance (between colonies: $r^2 = 0.001$, Mantel test, $P = 0.987$; for males: $r^2 = 0.028$, Mantel test, $P = 0.929$; and for females: $r^2 = 0.034$, Mantel test, $P = 0.954$).

### *Demographic history*

Using different prior and hyperprior sets, we observed a strong convergence of the five independent chains (G and R diagnostic = 1.04). Posteriors indicated that yellow sea kraits underwent population growth with a current population size ($N_0$) larger than the ancestral one ($N_1$) (Fig. 3a). Indeed, estimates indicated a current effective population size $N_0$ with a median values ranging from 32,419 to 41,722 and an ancestral population $N_1$ with a median values ranging from 411 to 1334 (depending on the run taken into account) (Fig. 3b). According to these time estimates, Yellow sea kraits population increased around 30,000 years ago (mid-Pleistocene) in the South Lagoon of New Caledonia (Fig. 3c).

## DISCUSSION

Our results revealed a strong dissociation between SGS and SPS: significant variations of mean body size along a north–south gradient were matched to a lack of genetic structure. To our knowledge, this contrasted pattern was not previously observed in marine tetrapods or in any snake species. Instead, strong phenotypic and genetic structuring effects caused by local factors have previously been documented in snakes (Kuriyama *et al.*, 2011; Pernetta *et al.*, 2011). Sea kraits are major colonial predators that are widely distributed in the western Pacific. Our results thus suggest that the mechanisms that underpin adaptation of colonies to local conditions, which in turn influence species distribution, are more diverse than previously described.

Highly significant differences in mean adult body size among colonies were observed in both sexes, following similar geographical gradient with larger snakes in the southern part of the study area. In snakes, mean body size is a major trait that typically varies among populations (Pearson *et al.*, 2002; Bronikowski & Vleck, 2010; Aubret, 2013). Body size is a complex feature controlled by many genes localized on different chromosomes (including mitochondrial genome) and controlled by many physiological factors (Karsenty & Wagner, 2002). Thus, the geographical gradient we observed in both sexes cannot be explained by a random effect, and thus was likely associated with a north–south environmental gradient (e.g. ambient temperatures, prey availability; Kuriyama *et al.*, 2011; Aubret, 2013). The observed differences in mean body size also imply limited (or lack of) exchanges of adults across colonies, a result in strong accordance with the marked philopatric habits of this species (Brischoux *et al.*, 2009a) and with the marked spatial differences in age structures across colonies (Bonnet *et al.*, 2015).

**Table 2** Absolute $F_{ST}$ values between the localities (below diagonal) and the associated $P$-values (in italics and above diagonal). Significance level (0.001) was adjusted with Bonferroni correction.

| | Améré | N'Dié | N'Do | N'Da | Ua/Uatérembi | Amédée | Signal/Larégnère | Ouen | Ile Verte |
|---|---|---|---|---|---|---|---|---|---|
| Améré | | *0.989* | *0.901* | *0.344* | *0.108* | *0.669* | *0.672* | *0.094* | *0.443* |
| N'Dié | 0.0037 | | *0.918* | *0.969* | *0.225* | *0.715* | *0.831* | *0.958* | *0.337* |
| N'Do | 0.0054 | 0.0024 | | *0.846* | *0.047* | *0.879* | *0.257* | *0.541* | *0.312* |
| N'Da | 0.0001 | 0.0068 | 0.0038 | | *0.549* | *0.990* | *0.875* | *0.995* | *0.547* |
| Ua/Uatérembi | 0.0003 | 0.0019 | 0.0046 | 0.0003 | | *0.265* | *0.086* | *0.386* | *0.004* |
| Amédée | 0.0036 | 0.0022 | 0.0041 | 0.0056 | 0.0039 | | *0.689* | *0.943* | *0.175* |
| Signal/Larégnère | 0.0016 | 0.0037 | 0.0004 | 0.0066 | 0.0084 | 0.0051 | | *0.475* | *0.136* |
| Ouen | 0.0006 | 0.0031 | 0.0018 | 0.0058 | 0.0002 | 0.0001 | 0.001 | | *0.237* |
| Ile Verte | 0.0031 | 0.0009 | 0.0033 | 0.0005 | 0.0052 | 0.0029 | 0.0012 | 0.0004 | |


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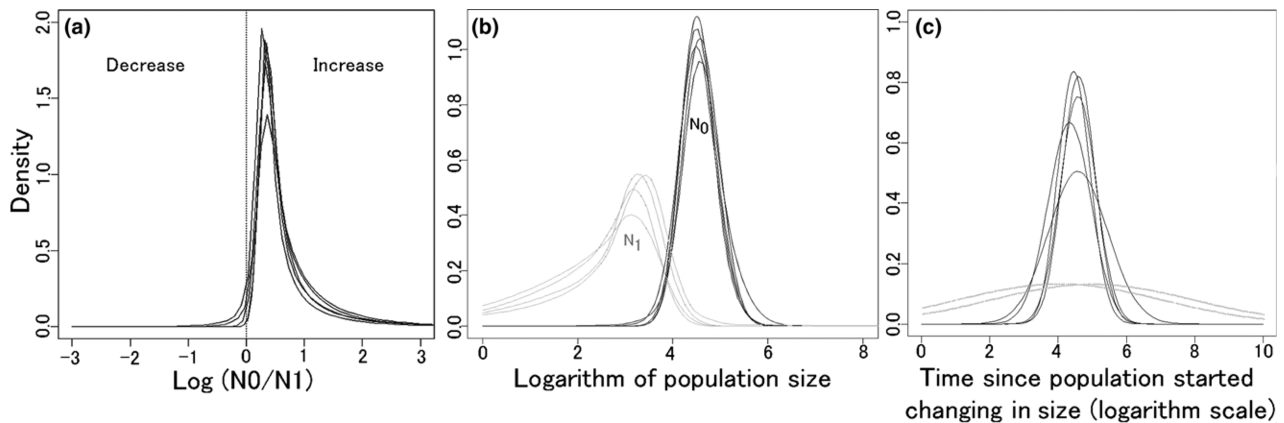


**Figure 3** Population history of yellow sea kraits (*Laticauda saintgironsi*) in south New Caledonia inferred from genetic analyses. (a) Demographic analysis results obtained using MSVAR. The set of solid curves corresponds to the posterior distributions (multiple independent runs) of the effective population size change; log ($N_0/N_1$). Log ($N_0/N_1$) represents the ratio of estimated current ($N_0$) to ancestral ($N_1$) population sizes. The dotted vertical line corresponds to a lack of change in effective population size: log ($N_0/N_1$) = 0. This figure suggests that the effective population size of yellow sea kraits, endemic of the Southern Lagoon of New Caledonia, increased. (b) Solid curves correspond to the posterior distributions (multiple independent runs) for current ($N_0$, black lines) and ancestral ($N_1$, grey lines) effective population size of the yellow sea kraits (*Laticauda saintgironsi*). We did not represent the priors and hyperpriors distribution in this figure for purposes of clarity but these are displayed in the Supporting Information. Also, this figure reveals that the current population size ($N_0$) is larger than the ancestral population ($N_0$) sizes, suggesting a population expansion. (c) Time since population started changing in size ($T$). Solid curves correspond to the posterior distributions (multiple independent runs) for time since population increase. The grey dashed lines represent the different prior distributions for $T$. This figure suggests that the population expansion occurred during the Holocene period (see text for details).

Genetic investigations performed in a random subset of individuals measured for SVL revealed a total lack of SGS. Although phenotypic variations are not necessarily mirrored by variations at neutral genetic markers, this result was unexpected as previous investigations in sea kraits revealed correlations between genetic and geographical differentiation (Lane & Shine, 2011a). Further, previously reported values for the IBD test (close to significance Mantel test; $r = 0.570$, $P = 0.09$, $N = 6$ colonies, based on mitochondrial data; Lane & Shine, 2011b) differ from our results from individuals based approach that strongly suggest a lack of effect ($r = 0.003$, $P = 0.99$, $N = 9$ colonies, based on microsatellites data). Below we review possible explanations for these discrepancies and for the dissociation between phenotypic and microsatellite data.

## Methodological issues

In this study we used a larger sample size, more loci, more sampling sites compared to previous genetic investigations in sea kraits, and we added phenotypic measurements on a large sample size. Although substantial genetic diversity was detected, the results indicated a total lack of IBD and no genetic structure among colonies. Our demographic analyses also inferred a population expansion during the mid-Pleistocene. Even if the quality of estimates is considered less precise for expanding population than for population contraction, the method we used is efficient to detect population expansion (Chikhi *et al.*, 2010). Moreover, the very low level of population genetic differentiation we found suggests that spurious bottleneck effects were unlikely and that the population expansion cannot result from a genetic substructure (Chikhi *et al.*, 2010). Considering the large sample sizes and wide spatial scale used in the current study, the inferences presented were likely robust.

## The role of coastal nurseries

*L. saintgironsi* are proficient swimmers (Brischoux *et al.*, 2007) and few juveniles have been observed travelling over long distance between colonies (> 80 km, Bonnet *et al.*, 2014; unpublished data), and these dispersing juveniles could contribute to the homogenized allelic distribution among colonies. However, another nonexclusive process may well be involved. Most juveniles hatch on few nursery spots where they stay during several months before dispersing (Bonnet *et al.*, 2014). If juvenile dispersal is random; nurseries may thus represent major inter-colony mixing sites. Our genetic data fit well with these observations. Indeed, the lack of SGS held true even when individual age was included as a factor in the analyses. Therefore, yellow sea kraits exhibit a peculiar breeding system: like many fish species, adults converge towards spawning grounds (Domeier & Colin, 1997), but in this snake species random juvenile dispersal entail a lack of SGS across colonies.

Marked SPS (i.e. the increase in mean body size towards southern colonies) presumably reflects gradual variations in local conditions, notably food availability (Pearson *et al.*,


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2002; Aubret, 2013). Coralline reef structures where yellow sea kraits forage are especially abundant in the southern part of our study area (Andréfouët & Torres-Pulliza, 2004). Accordingly, the main (preferred) prey species of sea kraits are also more abundant for the southern populations (Brischoux *et al.*, 2009b). These results suggest that phenotypic plasticity may account for the body size variations observed (Madsen & Shine, 1993; Shine, 2005). Snakes are highly plastic organisms with respect to environmental factors (Ford & Seigel, 1989; Aubret *et al.*, 2004; Bronikowski & Vleck, 2010). Similar results were reported in barnacles where strong differences in shells' morphology were observed among colonies despite a lack of SGS (Cheang *et al.*, 2013). Moreover, as phenotypic plasticity is able to limit genetic differentiation among individuals (Pertoldi *et al.*, 2007), it may have hampered genetic structure establishment.

### Demographic history

Our results indicate that yellow sea kraits experienced a major population size increase in the South Lagoon of New Caledonia during the mid-Pleistocene, a period characterized by periodic climatic oscillations that strongly influenced the distribution range and demographic history of many organisms, including snakes (Karns *et al.*, 2000). These results are in accordance with those reported by Lane & Shine (2011a): Quaternary climatic fluctuations influenced colonization episode of the Laticaudine sea snakes subfamily explaining, in the South Pacific, current patterns of genetic diversity. Indeed, Lane & Shine (2011a) previously suggested that *L. frontalis*, endemic species of Vanuatu Islands, is derived from a small founding population of *L. saintgironsi* through a colonization episode during the Last Glacial Maximum: *L. saintgironsi* that displays marked terrestrial habits might have taken advantages of low sea level with abundant emergent lands to find a route to Vanuatu (Lane & Shine, 2011a). Likely, the past major population increase of the yellow sea kraits in New Caledonia might be derived from northern populations of *L. colubrina* that colonized New Caledonia during Quaternary (Lane & Shine, 2011a). For the yellow sea kraits, the current and high overall genetic diversity combined with a lack of genetic structure suggests that an important population growth followed colonization episode and limited the loss of genetic diversity by reducing the founder effect and the genetic drift (Nei *et al.*, 1975). Moreover, after undergoing a bottleneck and associated genetic variability depletion (i.e. 'genetic revolution'), some populations might find a new ecological niche and may gradually accumulate a novel genetic variability (Provine, 2004). Recent studies on other elapid sea snakes from New Caledonia (*Emydocephalus annulatus*) (Lukoschek & Shine, 2012) and Ryukyu-Taiwan region (*Laticaudata laticaudata* and *Laticaudata semifasciata*) (Tandavanitj *et al.*, 2013) showed a significant genetic differentiation associated with a low dispersal and a limited gene flow between much closer populations. The existence of communal nurseries offers a possible mechanism to explain the high overall genetic diversity, lack of SGS, and the likely limited genetic drift that in turn could produce the peculiar assemblage of historical, phenotypic and genetic patterns we found.

### Conclusion

The presence of the endemic *L. saintgironsi* in New Caledonia likely dates from colonization during the Mid-Pleistocene. The observed contrast between phenotypic and genetic patterns might be the outcome of an initial rapid population expansion following a colonization episode combined with a particular reproductive system relying on communal nurseries associated with marked phenotypic response allowing local specializations. Relatively similar patterns are known in fish and invertebrates but were not until now described in any amniotic lineage.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Details of the priors and hyperpriors' distribution for the Storz & Beaumont (2002) method.

## BIOSKETCHES

**Nicolas Bech** is a population geneticist working on the impact of the landscape on population structure and **Thomas Foucart** is a PhD student working on evolution of the viviparity.

Author contributions: X.B. and F.B. conceive the idea; X.B., F.B. and T.F. participated to fieldwork and sampling; N.B., X.B., D.B. and T.F. analysed the data. All authors contributed equally to the paper's redaction.

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