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Spatial variation in age structure among colonies of a marine snake: the influence of ectothermy

Xavier Bonnet[1]*, François Brischoux[1], David Pinaud[1], Catherine Louise Michel[1], Jean Clobert[2], Richard Shine[3] and Thomas Fauvel[1,4]

[1]*Centre d'Etudes Biologiques de Chizé, UMR 7372-CNRS Université de La Rochelle, Villiers-en-Bois 79360, France;* [2]*Station d'Ecologie Expérimentale du CNRS à Moulis USR 2936, Moulis, Saint-Girons 09200, France;* [3]*School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia; and* [4]*Université Pierre et Marie Curie, Paris 75005, France*

Abstract

1. Several tetrapod lineages that have evolved to exploit marine environments (e.g. seals, seabirds, sea kraits) continue to rely upon land for reproduction and, thus, form dense colonies on suitable islands.

2. In birds and mammals (endotherms), the offspring cannot survive without their parents. Terrestrial colonies contain all age classes. In reptiles (ectotherms), this constraint is relaxed, because offspring are independent from birth. Hence, each age class has the potential to select sites with characteristics that favour them.

3. Our studies of sea snakes (sea kraits) in the lagoon of New Caledonia reveal marked spatial heterogeneity in age structure among colonies.

4. Sea krait colonies exhibit the endothermic 'seal–seabird' pattern (mixed-age classes within populations) only where the lagoon is narrow. Where the lagoon is wide, most snake colonies are comprised primarily of a single age cohort. Nurseries are located near the coast, adult colonies offshore and mixed colonies in-between.

5. We suggest that ectothermy allows individuals to utilize habitats that are best suited to their own ecological requirements, a flexibility not available to endothermic marine taxa with obligate parental care.

Key-words: colony, dispersal, *Laticauda*, marine tetrapods, population, sea snakes

Introduction

Although amniotic vertebrates (mammals and reptiles *lato sensu*, including birds) are predominately terrestrial, representatives of all major lineages have secondarily returned to marine habitats (Vermeij & Dudley 2000). Some, such as cetaceans, sirenians and hydrophiine sea snakes, complete their life cycles without leaving the water; they are truly marine animals. Many others, however, retain their ancestral dependence upon land for breeding. These amphibious tetrapods (seabirds, pinnipeds, marine turtles, marine iguanas and sea kraits) exploit the rich nutritional resources of the ocean, but must commute between land and sea to breed. Despite their phylogenetic diversity, most of these amphibious marine tetrapods breed in dense coastal colonies. These colonial marine tetrapods are central-place foragers, returning to terrestrial sites between successive foraging trips (Boyd 2002; Brischoux, Bonnet & Shine 2007). It is generally assumed that coloniality in amphibious marine tetrapods results from a scarcity of suitable terrestrial sites close to oceanic foraging grounds (Varela, Danchin & Wagner 2007).

Large coastal colonies of amphibious marine tetrapods are relatively independent functional units. In seabirds, pinnipeds and marine reptiles, individuals tend to be highly philopatric towards their home colony (Inchausti & Weimerskirch 2002; Shetty & Shine 2002; Wolf & Trillmich 2007). Even in colonies where many juveniles disperse (e.g. in seals, Testa 1987), females remain philopatric and reproduction occurs in their home colony (Pomeroy *et al.* 2001; Fabiani *et al.* 2006). Similar patterns also appear to be typical of aquatic reptiles that aggregate along shorelines (Trillmich & Trillmich 1984; Shetty & Shine 2002; King, Queral-Regil & Stanford 2006). For example, resource acquisition and predator

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*Correspondence author. E-mail: bonnet@cebc.cnrs.fr

avoidance favour colonial habits with high site fidelity in female Galapagos iguanas (Trillmich & Trillmich 1984; Wikelski, Carbone & Trillmich 1996), although males occasionally disperse to neighbouring colonies (Rassmann *et al.* 1997). Sea turtles also exhibit strong philopatry, returning to their natal coastal site to lay their eggs on sandy beaches in-between long bouts of oceanic foraging, sometimes over large distances (Lutz & Musick 1996). Coastal colonies of marine tetrapods often include a range of age classes, that is, adults as well as their offspring. In most seabirds, seals and iguanas, the juveniles remain in their home colony with the adults for prolonged periods. These striking similarities between different lineages of secondarily marine tetrapods suggest strong links between amphibious life, coastal habitats, foraging strategies and population functioning.

Boyd (2002) proposed that in seabirds and marine mammals, large foraging ranges (e.g. as in albatrosses and large phocid seals) enable individuals to integrate environmental variability over large scales and hence to remain philopatric to their home colonies even when resource availability fluctuates in nearby waters. In contrast, short-ranging (coastal) foragers such as terns and fur seals are forced to disperse more often in order to cope with environmental variability. Thus, although environmental constraints (especially resource availability) can influence population biology (Martin 1995; Weimerskirch *et al.* 1997), the relative autonomy of each colony is a central characteristic of amphibious marine tetrapods.

The lineages of secondarily marine tetrapods include both endotherms (mammals and avian reptiles) and ectotherms (squamate reptiles and chelonians). The strong physiological differences between these two metabolic modes (Brand *et al.* 1991; Turner, Hulbert & Else 2005) are associated with massive shifts in most life-history traits (Pough 1980; Bonnet, Bradshaw & Shine 1998; Brischoux *et al.* 2008). However, the possible impact of metabolic mode on population age structure has not been considered. In this study, we ask 'do environmental factors affect age composition in colonies of amphibious marine tetrapods?' To tease apart the influence of landscape spatial variability on population functioning, many confounding variables must be considered (Clobert *et al.* 2001). To do this, we need to focus on a single colony-forming species within a region that is climatically homogeneous, but provides spatial variation in aspects such as proximity to food resources. To reliably quantify spatial variation in population structure, we need many colonies, as well as many individuals within each colony. Only then can we ask how a species' biology influences the structure of its populations in this colonial system.

In this study, we exploited exactly this situation. For 11 years, we have monitored numerous colonies of an amphibious sea snake (the yellow-banded sea krait *Laticauda saintgironsi*) in the highly heterogeneous landscape offered by the lagoon of New Caledonia. Our analysis is facilitated by broad similarities in climate, a lack of strong genetic differentiation among these snake colonies (Lane & Shine 2011), the ease of obtaining large sample sizes (Bonnet 2012) and of allocating individuals to age classes (Brischoux, Bonnet & Shine 2009c; Bonnet *et al.* 2014a). Importantly, the metabolic mode of sea kraits differs considerably from that of the amphibious birds and mammals that have been the major focus of previous research. In colonial seabirds and mammals, prolonged parental care (due to constraints of endothermy on minimum effective body size for independent ecological functioning: Pough 1980) results in colonies that contain all age groups, from newborn or newly hatched young through to breeding adults. As ectotherms, sea kraits do not face this constraint on minimum effective body size. First, these snakes do not incubate their eggs; successful embryonic development depends primarily on the thermal and hydric conditions of the nest (Packard & Packard 1988). Secondly, sea kraits produce offspring that are small relative to adult size (about 5% of maternal mass) and that function independently from the time of hatching. All size and age classes of sea kraits feed primarily upon anguilliform fishes, but because of their small body sizes, neonatal sea kraits eat different sizes of eels than do conspecific adult snakes (Brischoux, Bonnet & Pinaud 2009b). Those prey resources are likely to be found in different places, and hence, we might expect optimal feeding grounds to differ between adult and juvenile snakes (Brischoux, Bonnet & Legagneux 2009a). Thus, ontogenetic niche divergence in sea kraits might favour spatial divergence between laying vs. foraging sites and in the foraging locations (and hence, home islands) of different age groups within the sea krait population. Such spatial divergence can occur, however, only if the array of local sites is diverse enough to include some that are best suited for young snakes, some for juveniles and some for adults. To address these issues, we quantified variation in age structure among snake colonies, examined how this variation correlates with characteristics of the surrounding habitat and evaluated alternative hypotheses on the causal mechanisms underlying this demographic variation.

Materials and methods

STUDY SITES AND STUDY SPECIES

The lagoon of New Caledonia is one of the largest in the world (24 000 km^2, 16 000 km of barrier reef) and is a biodiversity hot spot (listed on the UNESCO World Heritage List). This landscape is highly heterogeneous due to differing levels and directions of exposure to oceanic waves, the uneven spatial distribution of reefs, variation in width of the lagoon (extending <2 km to > 50 km from the main island) and the variable density of islets suitable for sea krait colonies (Andréfouët & Torres-Pulliza 2004; Bonnet 2012).

From 2002 to 2012, we monitored 41 colonies of an abundant sea krait species (yellow-banded sea krait: *L. saintgironsi*) through a long-term recapture programme (Bonnet 2012). Of these sites, 33 were in the south-west of the lagoon (30 islets and three coastal sites) and eight were further north (five islets and three coastal sites; see Fig. 1). Like many other amphibious marine tetrapods, sea kraits forage at sea but return to their home island to digest their prey (once every fortnight, approximately) and to reproduce (mate and lay eggs) (Saint-Girons 1964; Heatwole 1999; Shetty & Shine 2002; Brischoux, Bonnet & Shine 2007). Adults exhibit a high site fidelity to their home islet (Shetty & Shine 2002; Brischoux, Bonnet & Shine 2009c), but our recapture records include a few animals that were marked on one island but recaptured on another (<2% of individuals, X. Bonnet, T. Fauvel & F. Brischoux unpublished data). Sea kraits catch about one-third of their prey <1 km from their home islet, and most of the rest within about 15 km (Brischoux, Bonnet & Shine 2007). Islets are typically separated by greater distances (Fig. 1), facilitating delineation of sea krait populations at this spatial scale (i.e. an islet and its surrounding reefs).

FIELD METHODS

Sea kraits are very docile, so they were captured by hand, sexed, measured for body size [snout vent length, SVL (±0·5 cm) by gently stretching individuals on a flexible ruler], weighed and palpated to determine feeding and reproductive status (see Brischoux & Bonnet 2009 and Bonnet 2012 for details of field procedures). From 2002 to 2012, we captured 8835 yellow sea kraits (8620 marked individuals + 215 snakes captured and measured but not marked) and we recaptured 2656 snakes (total number of observations 11 491; Bonnet *et al.* 2015).

ANALYSES

Age structures across populations

Except for snakes captured and marked very early in life, the actual age of each snake was unknown. However, our long-term study enabled us to assign individuals to three main age classes using SVL and sex (Brischoux, Bonnet & Shine 2009c; Bonnet *et al.* 2014a for details): (i) young of the year (SVL < 50 cm), (ii) juvenile (2–3 years of age) males (50 cm < SVL < 63 cm) and juvenile females (50 cm < SVL < 75 cm), (iii) adult males (SVL > 63 cm) and adult females (SVL > 75 cm). This method relies on the fact that snakes grow rapidly after birth and continue to grow throughout their lives. In snakes, growth rate can be influenced by site, body condition and sex (Bronikowski 2000; Aubret *et al.* 2005; Bonnet *et al.* 2011). Our analyses detected these effects in sea kraits (unpublished data). The estimated age of each individual may have been influenced by these factors, as well as by sampling date (because reproduction is seasonal: Brischoux & Bonnet 2009). We took the sampling-date bias into account by standardizing the estimated age to a single date by subtracting or adding the number of days between capture and the first of October (the beginning of the breeding season). That standardization did not change any of our results. At all sites that were intensively monitored over long periods (e.g. 2002–2012), the age structure remained stable over time, regardless of the sampling date (Bonnet *et al.* 2014a). Consequently, we adopted a parsimonious approach. Our analyses used individual body size as an index of age without further correction.

Spatial and environmental variables

We selected the following environmental variables, based on their plausible influence on snake foraging success, reproduction and thus population age structure:

1. The distance from a site to the nearest shore of any of the three large continental and mountainous islands of the lagoon (i.e. mainland: the main island, the île Ouen and the île des Pins, Fig. 1), henceforth called 'distance to the coast'.
2. The distance from a site to the deep open ocean or to the barrier reef (i.e. outside the lagoon), henceforth called

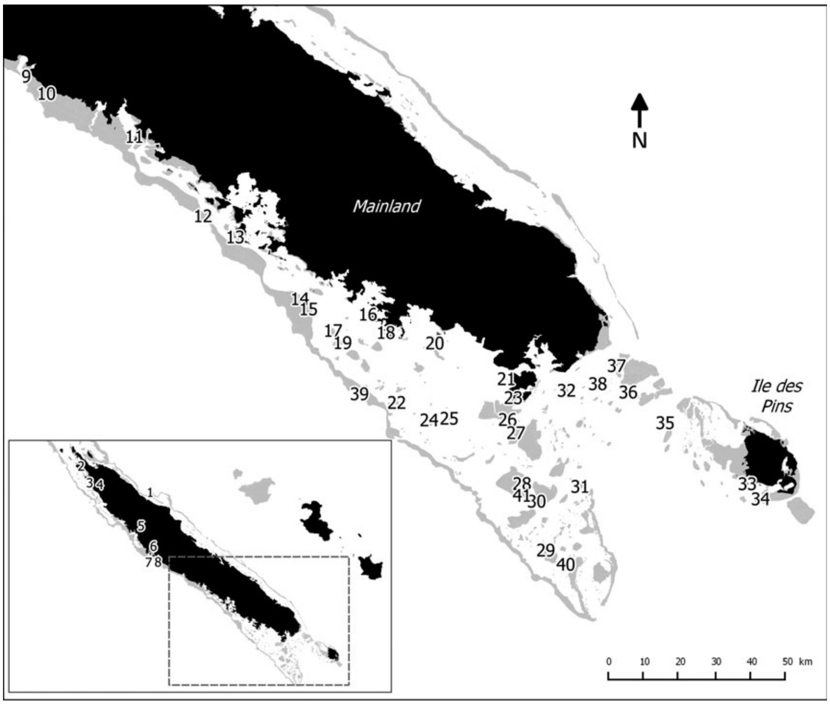

Fig. 1. Maps of New Caledonia with the sampled sites (sea krait colonies); the northern sites are indicated in the small global map; most sites (9-41) were located on the south-western part (enlarged map indicated with a dashed line square). Correspondence between site number and localities are as follow: (1) Hienghène, (2) Ouanné, (3) Table, (4) Pandop, (5) Foué, (6) Grimault, (7) Didot, (8) Contrariété, (9) Ile Verte, (10) Eori, (11) Ghero, (12) Tenia, (13) Petit Tenia, (14) Mba, (15) Mbo, (16) Kuendu, (17) Signal, (18) Nouméa/Baie des Citrons, (19) Larégnère, (20) Porc-Epic, (21) Tioaé, (22) Amédée, (23) Ile Ouen, (24) Atiré, (25) Rédika, (26) Uo, (27) Mato, (28) Uatérembi, (29) N'da, (30) Gi, (31) N'do, (32) Ugo, (33) Bayonnaise, (34) Brosse, (35) N'dié, (36) Améré, (37) Kié, (38) Nouaré, (39) Ever Prosperity, (40) Koko, (41) Ua. Mainland is indicated in black, grey areas represent coral reefs; the dark grey line represents the outer barrier reef.

'distance to the ocean'. These two-first variables are commonly used in analyses of coral reef ecology, as they influence factors such as rainfall, humidity, salinity, wind exposure, soil and contaminant inputs, and biodiversity (Hemminga *et al.* 1994; Dornelas, Connolly & Hughes 2006; Bonnet *et al.* 2014b). Furthermore, deep water (> 100 m) and land act as barriers to movement and dispersal for sea kraits.

3 Availability of rocks and boulders on/or near the shore that provide terrestrial shelters for sea kraits (Bonnet *et al.* 2009), henceforth called 'rock abundance'. Rocky areas with abundant crevices presumably offer suitable nesting sites (Bonnet *et al.* 2014a). Eggs and small snakes are particularly sensitive to dehydration and overheating; large rocks (30 cm < diameter to > > 1 m; see Bonnet *et al.* 2009 for details) buffer thermal and hydric variations. The availability of these major shelters was scored at each site, using a scale ranging from 1 (no large rocks, e.g. sandy beaches only) to 5 (large rocks present on 100% of the shore).

4 The surface area of shallow-water habitat (i.e. 'hunting grounds') available within the snake's foraging range (i.e. the lagoon surface, excluding land and ocean, within a 15 km radius around the site).

5 The surface area of hard bottom (i.e. coral, the preferred feeding habitat of *L. saintgironsi*: Brischoux, Bonnet & Shine 2007) within the foraging range (15 km) from each site. This parameter was determined using a reef-structure data base (Andréfouët & Torres-Pulliza 2004).

6 A Shannon diversity index of the surface covered by different lagoon-substrate types ('reef-structure diversity') within the same range around each site as described above. We used the classification of reef structures (level 4) provided in a comprehensive atlas of the lagoon of New Caledonia (Andréfouët & Torres-Pulliza 2004), with a spatial resolution of 100 m. A higher diversity of reef structures on the sea floor may facilitate niche partitioning among age or sex classes of the sea kraits (Brischoux, Bonnet & Shine 2007; Brischoux, Bonnet & Legagneux 2009a).

7 As a proxy of food availability, we used the mean body condition index of the snakes calculated for each site ('mean trophic condition'). Prey availability increases foraging success and hence the proportion of individuals with a prey in the stomach, as well as body stores (Naulleau & Bonnet 1996). Average body condition (mass relative to SVL) of freshly captured snakes incorporates the effects of both these traits and thus is positively influenced by prey availability. Body condition was calculated as residual scores from the general linear regression between log-body mass against log-body length (SVL). We used only adult males because neonates, juveniles and adult females were not present at all sites (Bonnet *et al.* 2014a). In addition, adult males forage primarily around their colony, whereas neonates, juveniles and gravid females tend to disperse or migrate throughout the lagoon (Bonnet *et al.* 2014a).

Possible effects of spatial autocorrelation were assessed during the modelling procedure (see below).

Statistical modelling of the age structure of snake populations

The age structure of sea krait populations was compared to spatial and environmental variables using multinomial loglinear models (Venables & Ripley 2002). The response variable was the number of individuals in each age class (adult, juvenile, neonate) observed in each site. Recaptures were omitted to avoid pseudo-replicates. Because information was lacking for some individuals, our analyses are based on data for 8833 snakes. The total number of snakes observed at each site was explicitly taken into account to model the relative occurrence of each age class (the adult class was used as a reference, see Tables 2 and 3) and include the relative weight of each site in terms of observation number. Namely, the null model was 'the proportion of each age class hold constant', that is independent from environmental variables. Explanatory variables were standardized, allowing a direct comparison of their relative influence on the proportions of individuals among the different age classes. The multinomial loglinear model was fitted via neural networks using the package 'NNET' (Venables & Ripley 2002). A stepwise selected model procedure was performed using AIC (Akaike 1974), beginning with the complete model and repeatedly dropping non-significant terms in order to retain the most parsimonious model at the end of the selection process. The AIC of the final model was also compared to the AIC of the null (i.e. constant) model. Independence and distribution of the model's residuals were checked, as was the possible influence of spatial autocorrelation (using Moran's test under the package 'SPDEP': Burnham & Anderson 2002; Bivand 2014).

Results

None of the model's residuals tested were spatially autocorrelated (Moran's tests, all $P > 0{\cdot}25$). All the explanatory variables were retained in the final model through the iterative stepwise AIC model selection procedure (Table 1). Comparison of the relative influence of the estimated parameters (Tables 2 and 3) suggests that the three age classes of sea kraits are sensitive to different

Table 1. Results from the stepwise selection model procedure performed using AIC, beginning with the complete model and repeatedly dropping single terms in order to retain the most parsimonious model at the end of the selection process. The AIC of the final model was also compared to the AIC of the null (i.e. constant) model. This procedure was used to examine the influence of spatial and environmental variables (first column) on the age structure of 41 sea krait populations. The response variable was the number of individuals in each age class (adult, juvenile, neonate) observed in each site ($N = 8833$ snakes). Explanatory (environmental) variables were standardized, allowing a direct comparison of their relative influence (Tables 2 and 3). The multinomial loglinear model was fitted via neural networks using the package 'NNET'

Variable effect	d.f.	AIC	δ-AIC
Constant	2	11916·947	3319·356
All variables	16	8597·591	0
Hunting grounds	14	8601·598	4·007
Reef-structure diversity	14	8602·425	4·834
Distance to the ocean	14	8626·307	28·716
Distance to the coast	14	8638·878	41·287
Surface of hard bottom	14	8641·119	43·528
Mean trophic condition	14	8747·739	150·148
Rock abundance	14	8756·770	159·179

Table 2. Parameters estimation for the final model studying the influence of explanatory (environmental) variables (first column) on the distribution of neonate yellow-banded sea kraits across colonies

	Estimate	SE	CI 2·5%	CI 97·5%	Odds-ratio	Absolute effect	Relative effect
Intercept	−3·2330320	0·13635581	−3·50028456	−2·9657796	0·03943774	3·2330	
Distance to the coast	−1·4429264	0·2896691	−2·01066742	−0·8751854	0·2362354	1·4429	1
Rock abundance	1·0323689	0·13735595	0·76315613	1·3015816	2·807709	1·0324	0·71546886
Mean trophic condition	−0·8302491	0·09781816	−1·02196918	−0·638529	0·4359407	0·8302	0·57539255
Distance to the ocean	0·7064787	0·17034398	0·37261059	1·0403467	2·0268415	0·7065	0·4896152
Surface of hard bottom	0·7048757	0·10187778	0·5051989	0·9045525	2·0235951	0·7049	0·48850425
Hunting grounds	−0·2248784	0·2104477 0	−0·63734839	0·1875915	0·7986133	0·2249	0·15584884
Reef-structure diversity	0·1836145	0·07868473	0·02939525	0·3378337	1·201553	0·1836	0·12725147

Table 3. Parameters estimation for the final model studying the influence of explanatory (environmental) variables (first column) on the distribution of juvenile yellow-banded sea kraits across colonies

	Estimate	SE	CI 2·5%	CI 97·5%	Odds-ratio	Absolute effect	Relative effect
Intercept	−2·218122	0·06537464	−2·3462539	−2·08999001	0·10881327	2·2181	
Rock abundance	0·8242919	0·08114662	0·66524746	0·98333638	2·280266	0·8243	1
Mean trophic condition	−0·500085	0·05868491	−0·61510532	−0·38506471	0·6064791	0·5001	0·606684355
Distance to the coast	−0·3705282	0·1165345	−0·59893158	−0·14212479	0·6903696	0·3705	0·449510907
Distance to the ocean	−0·3178895	0·08661268	−0·48764722	−0·14813174	0·7276832	0·3179	0·385651612
Hunting grounds	0·2889763	0·1162179 0	0·06119343	0·51675908	1·33506	0·2890	0·350575203
Reef-structure diversity	0·1221723	0·05438344	0·01558272	0·22876188	1·129949	0·1222	0·14821485
Surface of hard bottom	−0·03288355	0·06590034	−0·16204584	0·09627874	0·9676512	0·0329	0·039893089

environmental variables. The distribution of neonates across colonies was determined by the distance to the coast (strongest effect), by rock abundance and to a lower extent by the other variables (Table 2). Neonates were concentrated at sites near or on the mainland shore (Table 2 and Fig. 2); their abundance decreased with increasing distance to the coast, and they were completely absent from sites >20 km from the coast (Fig. S1, Supporting information). Neonates were most abundant in sites with many beach rocks, but less common in sites where adult male conspecifics were in good body condition (Table 2 and Fig. 2). The availability of extensive hunting grounds and reef structures was less important for neonate snakes. The distribution of juveniles was broadly similar to that of neonates in these respects (Fig. 2), but with a different ranking of the importance of the first three variables retained. For juvenile snakes, rock abundance was the first-ranked predictor of abundance (Table 3). The occurrence of juveniles decreased with increasing distance from the coast, but in a more gradual fashion than was true for neonates (Fig. 2). Adult snakes exhibited the opposite (i.e. complementary) pattern, increasing in abundance in sites that were further from the coast (Fig. 2).

tOverall, most young sea kraits were found in rocky sites close to the mainland. Where the lagoon is wide, the mean age of snakes within a colony increased rapidly with the first few kilometres off the coast and then plateaued (Fig. 2). Despite intensive sampling, few neonate or juveniles were found on islets more than 10 km offshore, and none were found more than 20 km from the mainland. For example, on Améré islet (Site 38, Fig. 1), we captured 1425 sea kraits (+449 recaptures), including >100 gravid females, and observed many matings, but we never found any young of the year. Where the lagoon is narrow, these spatial effects were not observed. All sites were close both to the mainland and to the barrier reef and often sheltered mixed-age populations of snakes (Fig. 3). Where the lagoon exhibited intermediate width, we observed intermediate trends (e.g. site 17, Figs 3 and S1, Supporting information).

Discussion

Populations of endothermic amphibious marine tetrapods (seabirds and seals) typically function as self-contained breeding colonies and thus contain individuals of all age classes. In contrast, the populations of sea kraits that we studied displayed a wide range of age structures. Some colonies consisted exclusively of adult snakes, whereas others were composed primarily of young of the year. We also recorded many intermediate conditions between these two extremes, with all age classes represented at some sites (Fig. 3). The temporal stability of population structures combined with the very narrow age structure of several colonies (e.g. all adults, or almost all neonates) shows that no individual in such a system lives throughout its life in the same colony, at least where the lagoon is wide. Instead, sea kraits move in age-assorted cohorts from one site to another as they grow larger (Bonnet *et al.* 2014a).

The striking spatial segregation pattern of age-assorted snake colonies in the widest parts of the lagoon cannot be explained by differential age-specific mortality or

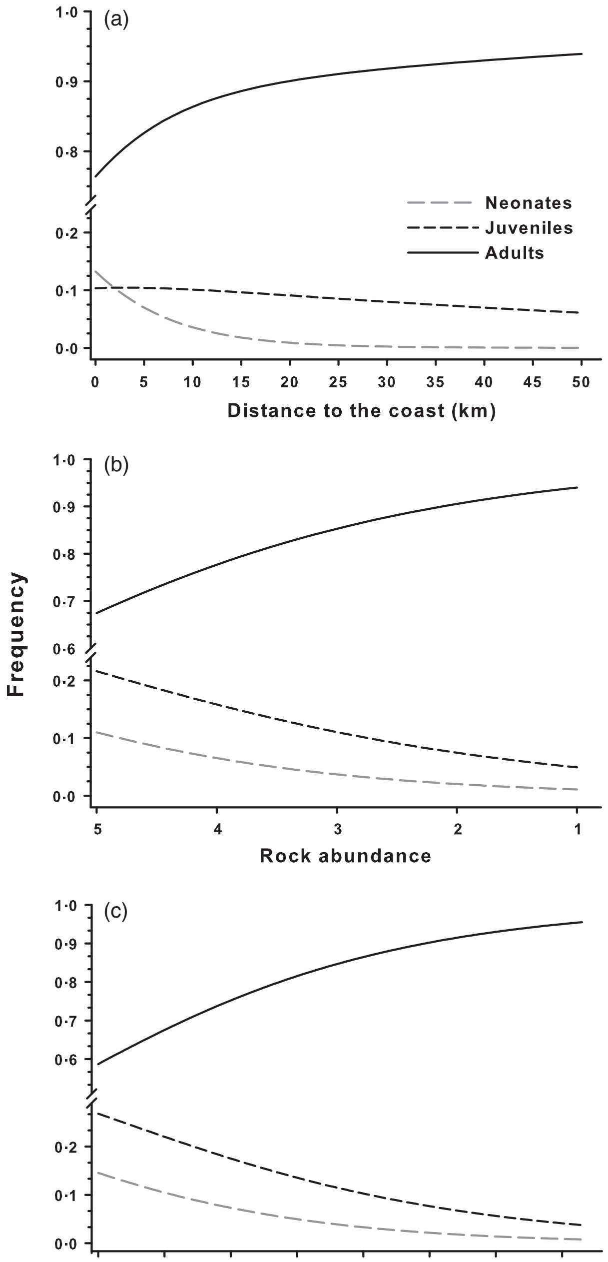

Fig. 2. Influence of the main environmental variables (*X*-axes, see Tables 2 and 3) on the relative distribution (*Y*-axis, frequency was estimated using multinomial log-linear models) of neonate, juvenile and adult yellow-banded sea kraits ($N = 8833$) across 41 colonies in the lagoon of New Caledonia. Neonates, and to a lesser instant juveniles, concentrate at sites near the mainland shore (a) with many beach rocks (b). Adults are more common in sites where adult males are in good body condition (b). All *X*-axes were organized to display increasing lagoon width from left to right (note the inversed scale for rock abundance).

catchability. Neonates and juveniles were easily observed in some sites, but totally absent in other islets, and this pattern was stable over years (Bonnet *et al.* 2014a; current study). What mechanisms are responsible for this divergence in age structure among snake colonies? One possibility involves ontogenetic shifts in foraging biology between juveniles and adults, such that each age class selects specific foraging areas and hence is found on adjacent terrestrial sites. This hypothesis was poorly supported. In yellow-banded sea kraits, individuals from all age classes feed mainly on a single prey species (the moray eel *Gymonothorax chilospilus*; Brischoux, Bonnet & Shine 2009c) that occurs in all the sites sampled (Brischoux, Bonnet & Legagneux 2009a), including coastal nurseries (Bonnet *et al.* 2014a). The distribution and abundance of these eels are likely influenced by the reef structures of the lagoon (their habitat), causing geographic variation in the diet of the snakes (Brischoux, Bonnet & Legagneux 2009a), but reef-structure variables had relatively little influence on the age structure of snake colonies. Indeed, neonates were relatively uncommon in sites where the body condition of adult male conspecifics (and thus presumably food availability) was high (Table 2 and Fig. 2).

Alternatively, some sites may be well suited to egg laying (Bonnet *et al.* 2014a), whereas others may provide better foraging opportunities for older (hence larger) snakes. In our data, the age gradient is very steep: neonates were essentially restricted to a few kilometres of the mainland. We never found neonate or juvenile snakes on any remote offshore islets. Our analyses also revealed that environmental variables associated with the availability of foraging grounds (e.g. surface area of hard-bottom habitat) were less important for predicting population age structure than was the distance from the mainland. Despite limited direct evidence (i.e. recaptures of animals moving from inshore to offshore islets as they grow larger; Bonnet *et al.* 2014a), these patterns suggest a segregation between coastal laying sites (containing primarily neonates and juveniles, and visited by gravid females) vs. offshore adult colonies (where philopatric adults forage around their home islet), rather than a niche partitioning between juveniles and adults. This ontogenetic gradient implies a functional connection between coastal nurseries through to distant offshore islets, via the progressive dispersal of juvenile snakes away from coastal nurseries as they grow older. That inference is supported by detailed examination of a major nursery (Bonnet *et al.* 2014a). A similar type of population functioning is seen in fully aquatic organisms. For example, many reef fish exhibit complex ontogenetic migratory events, sometimes over great distances and between very different habitats; juveniles and adults do not necessarily live at the same place, and a few breeding sites can supply recruits for many adult populations (Nagelkerken *et al.* 2000; Mumby *et al.* 2004; Kritzer & Sale 2006). This kind of spatial connection between reproduction and recruitment has not been documented for marine tetrapods in previous work, but reports of age-specific populations of sea turtles in foraging areas (Musick & Limpus 1997) suggest that a similar system may occur in marine chelonians also.

Interestingly, sea krait colonies in narrow parts of the lagoon exhibit a classical ‘seal – seabird’ pattern: all age

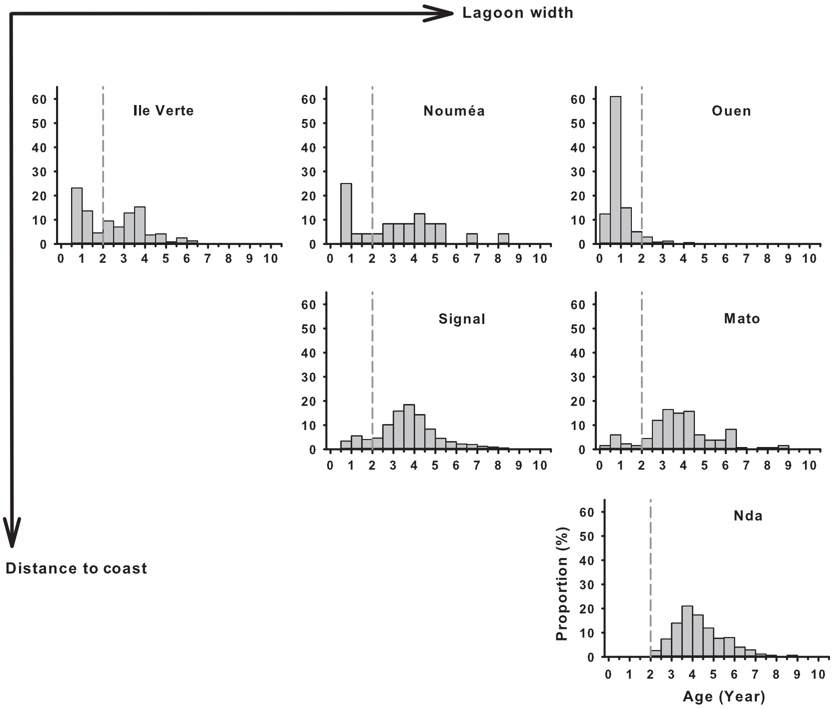

Fig. 3. Spatial variation (frequency, *Y*-axis) in the body size (snout vent length, SVL, *X*-axis) structure in a subset of sea krait colonies that illustrate the diversity of situations revealed by our study. Body size was used as a proxy of age (see text). Where the lagoon is narrow (e.g. Ile Verte site 9, Fig. 1), all age classes are well represented within the same population. Where the lagoon is wide, age structure shifts from juvenile to adult along a colony gradient from the coast to far offshore (e.g. from Ile Ouen site 23, Mato site 27 to N'da site 30, Fig. 1). Coastal colonies contain mostly juveniles (Ouen), whereas offshore colonies contain only adults (N'Da). Intermediate situations are observed in intermediate areas (Mato). In an area where the lagoon is of medium width (e.g. from Nouméa site 18 to Signal site 17, Fig. 1), we observed intermediate situation colonies. The dashed grey line indicates a crude maturity threshold (Bonnet *et al.* 2014a).

classes are well represented, unlike the spatial divergence in age structure typical of snake colonies in wider parts of the lagoon. Thus, snake population structure varies in relation to major landscape characteristics. Where the lagoon is narrow, dispersal is constrained because the deep ocean constitutes a dispersal barrier on the coast–ocean axis (sea kraits generally swim along the bottom of the water column) and few suitable sites are available. Hence, snakes of all age classes cohabit in a single colony. In such a population, suitable nesting sites must be available either within the home islet or on the nearby coast (from which neonates could easily reach the islet colony). Where the lagoon is broader, dispersing snakes have access to more islets and foraging grounds, enabling the age classes to segregate along a coast-to-ocean gradient.

The restriction of egg laying to coastal sites (i.e. mainland and islands close to the mainland) may reflect more favourable thermal and hydric conditions. Especially in the mainland areas, abundant rainfall and deep crevices in the igneous substrate provide suitable nesting sites (Tu, Fong & Lue 1990) that provide the thermostability and high humidity essential for successful embryonic development. Two governmental weather stations situated on the mainland coast and offshore near the barrier reef (Nouméa vs. Amédée Island, Fig. 1) show that rainfall is higher on the mainland than the lagoon: 10 326 mm vs. 7917 mm per year on average. The flat sandy islets of the remote areas of the wide lagoon may offer very few (if any) egg-laying sites. Where the lagoon is wide, we suggest that gravid sea kraits females undertake long trips in order to deposit their eggs into precisely selected nesting sites (Bonnet, Naulleau & Shine 1999; Bonnet *et al.* 2014a). The importance of appropriate rocky shelter for neonates and juveniles (and perhaps for incubating eggs) was supported by the strong influence of rock abundance in our results. Signal islet (site 17 Fig. 1,) is the only sandy-coralline flat offshore islet (15 km from the coast) where neonates are regularly observed (Figs 3 and S1, Supporting information). This islet is unique for another reason: many large rocks were deposited on the shore for the production of lime in past centuries. Consequently, Signal islet exhibits an artificially high 'rock abundance' score, providing many well-buffered shelters for snakes from all age classes (Bonnet *et al.* 2009).

One corollary of our results is that gravid female sea kraits return to the offshore islets after laying. Ontogenetic partitioning of the ecological niche is widespread in ectothermic vertebrates, especially in snakes (Shine & Wall 2007). Indeed, the wide range of body sizes within a snake population is often associated with shifts in diet and microhabitat selection, such that a single population can contain individuals with different niche requirements. The novel feature of sea kraits is that they are colonial, and the spatial scale of ontogenetic segregation is far greater than the scale of the distances between adjacent colonies (especially if the developing eggs are considered as a specific age class). The ultimate consequence of this process is a complex, flexible system, with a network of colonies connected by directional (offshore) dispersal of juvenile snakes, a mosaic of a few coastal sites dominated by juveniles, a large number of remote islets dominated by philopatric adults and a flow of gravid females between mainland and island sites to maintain the flow of juveniles.

Although the broad-scale population functioning dynamics that we describe have not been reported in previous studies of marine amphibious vertebrates, we doubt that sea kraits are unique in this respect. The intensive post-natal parental care of endothermic species canalizes the population structure of seabirds and pinnipeds, because neonates cannot survive in the absence of at least one parent. In contrast, the lack of post-natal parental care in most ectotherms allows greater flexibility. The adult females can lay their eggs in sites that are well suited for incubation but apparently less favourable for adults (which are rarely found on the mainland shore), and the adults themselves can live in areas that facilitate foraging but lack the resources needed for successful incubation.

A similar flexibility may influence population structure and generate spatial heterogeneity in age distributions in many species that are not marine. For example, reproducing females of many terrestrial reptile species leave their usual home ranges to travel to incubation sites that provide thermal and hydric benefits to the developing offspring (Packard & Packard 1988). Most amphibian species with aquatic eggs and larvae, but terrestrial adults, show a clear spatial separation between breeding sites (dominated by young of the year) and the surrounding habitat matrix (dominated by older animals) (Semlitsch 2008). In all of these cases, a lack of parental care removes the need for adults and offspring to cohabit and, thus, allows other ecological advantages of age-dependent habitat selection to enforce spatial separation along ontogenetic lines. The sea kraits of New Caledonia provide a particularly striking example of this phenomenon and of the kinds of ecological constraints that may reduce or intensify the degree to which multiple of age classes coexist within a single population.

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Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.p70r4 (Bonnet *et al.* 2015).

References

Akaike, H. (1974) A new look at the statistical model identification. *Automatic Control, IEEE Transactions on*, **19**, 719–723.

Andréfouët, S. & Torres-Pulliza, D. (2004) *Atlas des récifs coralliens de Nouvelle-Calédonie*. IFRECOR Nouvelle-Calédonie, IRD, Nouméa.

Aubret, F., Bonnet, X., Shine, R. & Maumelat, S. (2005) Why do female ball pythons (*Python regius*) coil so tightly around their eggs? *Evolutionary Ecology Research*, **7**, 743–758.

Bivand, R. (2014) *spdep: Spatial Dependence: Weighting Schemes, Statistics and Models. R Package Version 0.5-71.* http://cran.cnr.berkeley.edu/web/packages/spdep/spdep.pdf.

Bonnet, X. (2012) Long-term field study of sea kraits in New Caledonia: fundamental issues and conservation. *Integrative and Comparative Biology*, **52**, 281–295.

Bonnet, X., Bradshaw, S.D. & Shine, R. (1998) Capital versus income breeding: an ectothemic perspective. *Oikos*, **83**, 333–341.

Bonnet, X., Naulleau, G. & Shine, R. (1999) The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation*, **89**, 39–50.

Bonnet, X., Brischoux, F., Pearson, D. & Rivalan, P. (2009) Beach rock as a keystone habitat for amphibious sea snakes. *Environmental Conservation*, **36**, 62–70.

Bonnet, X., Lorioux, S., Pearson, D., Aubret, F., Bradshaw, D., Delmas, V. *et al.* (2011) Which proximate factor determines sexual size dimorphism in tiger snakes? *Biological Journal of the Linnean Society*, **103**, 668–680.

Bonnet, X., Brischoux, F., Bonnet, C., Plichon, P. & Fauvel, T. (2014a) Coastal nurseries and their importance for conservation of sea kraits. *PLoS One*, **9**, 1–6.

Bonnet, X., Briand, M.J., Brischoux, F., Letourneur, Y., Fauvel, T. & Bustamante, P. (2014b) Anguilliform fish reveal large scale contamination by mine trace elements in the coral reefs of New Caledonia. *Science of the Total Environment*, **470**, 876–882.

Bonnet, X., Brischoux, F., Pinaud, D., Michel, C.L., Clobert, J., Shine, R. *et al.* (2015) Data from: Spatial variation in age structure among colonies of a marine snake: the influence of ectothermy. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.p70r4

Boyd, I.L. (2002) The measurement of dispersal by sea birds and seals: implications for understanding their ecology. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails), pp. 72–88. Blackwell Science, Oxford, UK.

Brand, M.D., Couture, P., Else, P.L., Withers, K.W. & Hulbert, A.J. (1991) Evolution of energy metabolism. Proton permeability of the inner membrane of liver mitochondria is greater in a mammal than in a reptile. *Biochemical Journal*, **275**, 81–86.

Brischoux, F. & Bonnet, X. (2009) Life history of sea kraits in New Caledonia. *Memoires du Muséum National D'Histoire Naturelle*, **198**, 133–147.

Brischoux, F., Bonnet, X. & Legagneux, P. (2009a) Are sea snakes pertinent bio-indicators for coral reefs? A comparison between species and sites. *Marine Biology*, **156**, 1985–1992.

Brischoux, F., Bonnet, X. & Pinaud, D. (2009b) Fine scale site fidelity in sea kraits: implications for conservation. *Biodiversity and Conservation*, **18**, 2473–2481.

Brischoux, F., Bonnet, X. & Shine, R. (2007) Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. *Marine Ecology Progress Series*, **350**, 145–151.

Brischoux, F., Bonnet, X. & Shine, R. (2009c) Determinants of dietary specialization: a comparison of sympatric species of sea snakes. *Oikos*, **118**, 145–151.

Brischoux, F., Bonnet, X., Cook, T.R. & Shine, R. (2008) Allometry of diving capacities: ectothermy versus endothermy. *Journal of Evolutionary Biology*, **21**, 324–329.

Bronikowski, A.M. (2000) Experimental evidence for the adaptive evolution of growth rate in the garter snake Thamnophis elegans. *Evolution*, **54**, 1760–1767.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, NY.

Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. (2001) *Dispersal.* Oxford University Press, Oxford.

Dornelas, M., Connolly, S.R. & Hughes, T.P. (2006) Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, **440**, 80–82.

Fabiani, A., Galimberti, F., Sanvito, S. & Hoelzel, A.R. (2006) Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour*, **72**, 617–626.

Heatwole, H. (1999) *Sea Snakes*. Australian Natural History Series, University of New South Wales, Sydney, NSW.

Hemminga, M.A., Slim, F., Kazungu, J., Ganssen, G.M., Nieuwenhuize, J. & Kruyt, N.M. (1994) Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series*, **106**, 291–301.

Inchausti, P. & Weimerskirch, H. (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, **71**, 765–770.

King, R.B., Queral-Regil, A. & Stanford, K.M. (2006) Population size and recovery criteria of the threatened Lake Erie watersnake: integrating multiple methods of population estimation. *Herpetological Monographs*, **20**, 83–104.

Kritzer, J.P. & Sale, P.F. (2006) The metapopulation Ecology of coral fishes. *Marine Metapopulations* (eds J.P. Kritzer & P.F. Sale), pp. 31–68. Marine Metapopulations, Burlington, Massachusetts.

Lane, A. & Shine, R. (2011) Phylogenetic relationships within laticaudine sea kraits (Elapidae). *Molecular Phylogenetics and Evolution*, **59**, 567–577.

Lutz, P.L. & Musick, J.A. (eds.) (1996) *The Biology of Sea Turtles*. CRC Marine Biology Series, CRC Press, Boca Raton, Florida.

Martin, T. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.

Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A. *et al*. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533–536.

Musick, J.A. & Limpus, C.J. (1997) Habitat utilization and migration in juvenile sea turtles. *The Biology of Sea Turtles* (eds P. Lutz & J.A. Musick), pp. 137–163. CRC Press, Boca Raton, Florida.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T. & den Hartog, C. (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science*, **51**, 31–44.

Naulleau, G. & Bonnet, X. (1996) Body condition threshold for breeding in a viviparous snake. *Oecologia*, **107**, 301–306.

Packard, G.C. & Packard, M.J. (1988) The physiological ecology of reptilian eggs and embryos. *The Biology of the Reptilia 16* (eds C. Gans & R.B. Huey), pp. 523–605. Alan R Liss, Washington.

Pomeroy, P.P., Wilmer, J.W., Amos, W. & Twiss, S.D. (2001) Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**, 711–717.

Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *American Naturalist*, **115**, 92–112.

Rassmann, K., Tautz, D., Trillmich, F. & Gliddon, C. (1997) The microevolution of the Galápagos marine iguana *Amblyrhynchus cristatus* assessed by nuclear and mitochondrial genetic analyses. *Molecular Ecology*, **6**, 437–452.

Saint-Girons, H. (1964) Notes sur l'écologie et la structure des populations des Laticaudinae (Serpentes: Hydrophiidae) en Nouvelle-Calédonie. *Revue d'Ecologie, Terre et Vie*, **111**, 185–214.

Semlitsch, R.D. (2008) Differentiating migration and dispersal processes for pond-breeding amphibians. *The Journal of Wildlife Management*, **72**, 260–267.

Shetty, S. & Shine, R. (2002) Philopatry and homing behaviour of sea snakes (*Laticauda colubrina*) from two adjacent islands in Fiji. *Conservation Biology*, **16**, 1422–1426.

Shine, R. & Wall, M. (2007) Why is intraspecific niche partitioning more common in snakes than in lizards? *Lizard Ecology* (eds S.M. Reilly, L.B. McBrayer & D.B. Miles), pp. 173–208. Cambridge University Press, Cambridge.

Testa, J.W. (1987) Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddelli*). *Canadian Journal of Zoology*, **65**, 1091–1099.

Trillmich, F. & Trillmich, K.G.K. (1984) The mating system of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biological Journal of the Linnean Society*, **21**, 209–216.

Tu, M.C., Fong, S.C. & Lue, K.Y. (1990) Reproductive biology of the sea snake, *Laticauda semifasciata*, in Taiwan. *Journal of Herpetology*, **24**, 119–126.

Turner, N., Hulbert, A.J. & Else, P.L. (2005) Sodium pump molecular activity and membrane lipid composition in two disparate ectotherms and comparison with endotherms. *Journal of Comparative Physiology B*, **175**, 77–85.

Varela, S.A.M., Danchin, E. & Wagner, R.H. (2007) Does predation select for or against avian coloniality? A comparative analysis. *Journal of Evolutionary Biology*, **20**, 1490–1503.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, Verlag, NY.

Vermeij, G.J. & Dudley, R. (2000) Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biological Journal of the Linnean Society*, **20**, 541–554.

Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F. & Ridoux, V. (1997) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology*, **78**, 2051–2063.

Wikelski, M., Carbone, C. & Trillmich, F. (1996) Lekking in marine iguanas: female grouping and male reproductive strategies. *Animal Behaviour*, **52**, 581–596.

Wolf, J.B.W. & Trillmich, F. (2007) Fine-scale site fidelity in a breeding colony of the Galápagos sea lion (*Zalophus californianus wollebaeki*): a prerequisite for social networking? *Oecologia*, **152**, 553–567.

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Supporting Information

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

Fig. S1. The population structure of the 41 sites sampled is represented by the different pie charts (see figure 1). The size of each pie is proportional to sample size. Note that remote sites of the wide south-western lagoon are represented almost exclusively by adults but neonates are totally lacking. Neonates are found on sites near the mainland coasts.