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Do researchers impact their study populations? Assessing the effect of field procedures in a long term population monitoring of sea kraits

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Abstract. Long term population monitoring is essential to ecological studies; however, field procedures may disturb individuals. Assessing this topic is important in worldwide declining taxa such as reptiles. Previous studies focussed on animal welfare issues and examined short-term effects (e.g. increase of stress hormones due to handling). Long-term effects with possible consequences at the population level remain poorly investigated. In the present study, we evaluated the effects of widely used field procedures (e.g. handling, marking, forced regurgitation) both on short-term (hormonal stress response) and on long-term (changes in body condition, survival) scales in two intensively monitored populations of sea kraits (*Laticauda* spp.) in New Caledonia. Focusing on the most intensively monitored sites, from 2002 to 2012, we gathered approximately 11 200 captures/recaptures on 4500 individuals. Each snake was individually marked (scale clipping + branding) and subjected to various measurements (e.g. body size, head morphology, palpation). In addition, a subsample of more than 500 snakes was forced to regurgitate their prey for dietary analyses. Handling caused a significant stress hormonal response, however we found no detrimental long-term effect on body condition. Forced regurgitation did not cause any significant effect on both body condition one year later and survival. These results suggest that the strong short-term stress provoked by field procedures did not translate into negative effects on the population. Although similar analyses are required to test the validity of our conclusions in other species, our results suggest distinguishing welfare and population issues to evaluate the potential impact of population surveys.

Keywords: corticosterone, ethics, *Laticauda*, long-term survey, methods, sea snakes, survival analysis.

Introduction

The impact of data collection on free ranging animals is an important issue. The use of non-invasive methods should be promoted, and indeed, various techniques have been developed to minimize the negative influence of researches. For instance, observations from distance or collection of faeces are useful methods in field ecology that do not entail disturbance (Taberlet, Waits and Luikart, 1999; Monestiez et al., 2006). However, non-invasive techniques do not provide a panacea preventing intrusive investigations. In fact, most field research is based on biometric and physiological measurements, bio-logging, or mark-recapture programs; all of which necessitate handling of individuals (sometimes during prolonged periods), and thus most field procedures inevitably inflict a substantial stress to the individuals. In addition, handling and various techniques deprive the subject from energy resources either directly (e.g. blood sampling, forced regurgitation) or indirectly via missed foraging opportunities during restraining and recovery period (e.g. following surgery).

Assessing the consequences of manipulation on individuals is necessary for several reasons. First, most species are threatened and any population impact of field research must be carefully evaluated. Second, animal welfare issues are essential for environmental education, public awareness, and to limit possible negative consequences induced by stress (e.g. depletion of immunity). Finally we need to quantify how much the estimations of demographic parameters in wild populations are biased by the stress we induce.

Field ecology of non-avian reptiles (e.g. lizards, snakes, tortoises) heavily depends on

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manipulations; many species are secretive and captured in their shelters or using trap systems. In most cases, individuals are captured, measured, marked, released, and recaptured repeatedly. Indeed identification from distance is usually impossible and continuous growth requires repeated size-measurements. Further, individuals can be blood sampled (e.g. for DNA or physiological investigations) or fitted with electronic devices. Several studies examining the possible impact of field research provided contrasted outcomes, ranging from an absence of effects (e.g. Lagarde et al., 2008 for radio-tracking; Keck, 1994 for PIT tags in snakes) to significant effects (e.g. McCarthy and Parris, 2004 for toe-clipping). The discrepancies between these conclusions likely reflect the use of various animal species (hence wide range of sensitiveness) combined with various and not easily comparable techniques. Importantly, previous studies focussed on short-term issues (e.g. locomotor performances, individual welfare, stress) while long-term effects at the population scale remain poorly explored. Consequently, there is a need for a better assessment of these questions. For instance, the impact of one of the most widely used field techniques, forced regurgitation, has not been investigated yet.

The concerns about potential impact of forced regurgitation apply with force on snakes. Most species feed infrequently on large prey that are swallowed whole (Carpenter, 1952). Forced regurgitation likely entails a massive energy loss (i.e. loss of a large prey and digestive fluids, wasted specific dynamic action; Secor and Diamond, 1997) associated with a major perturbation of the day-to-day life of the subject. Indeed, a snake deprived from its prey can be constrained to undertake a compensatory foraging activity followed by an extended digestion episode, all of which may affect survival (e.g., increased predation risks). Thus, a long lasting decrease in body condition and/or survival could result from the stressful loss of a meal provoked by the researchers. Although forced regurgitation represents a considerable source of stress it may not necessarily induce negative impact over long term. Snakes are particularly tolerant to both fasting and manipulation; they may well withstand short-term perturbation without long-term consequences.

Since 2002, we conducted intensive field studies on two species of amphibious sea kraits (*Laticauda saingironsi* and *Laticauda laticaudata*, Bonnet, 2012). Our research involved forced regurgitation on a very large number of individuals ($N > 2000$) whereas most individuals ($N > 22\,500$ captures, including snakes with a prey in the stomach) were spared. The analyses of long-term recapture data on the two most intensively monitored populations (nearly 4500 individually marked snakes) provided a powerful opportunity to assess the effect of a regurgitation event on body condition and survival. We also examined the influence of the most commonly used field technique on free ranging snakes: the effect of capture and marking. Marked snakes need a short period of healing (i.e. scale clipping, branding or PIT tags injection provoke superficial skin damages); handling also entails a significant stress revealed by increased corticosterone levels (Langkilde and Shine, 2006). Having yielded 10 years of data, we addressed the effect of the first capture event and marking on body condition one year after the initial capture. We predicted that body condition index and survival should remain constant if the snakes tolerated our field procedures (i.e. marking, regurgitation) but should decrease if we inflicted detrimental effects.

Although classified as "least concern" on IUCN red list (2010), sea kraits show dramatic population declines in many parts of their distribution range, like many other snake species (including other sea snakes) and reptiles (Gibbons et al., 2000; Reading et al., 2010; Rasmussen, 2011; Anonymous, 2012). Since the field methods we employed on amphibious sea kraits reproduce the typical protocol used elsewhere to monitor reptiles, assessing the impact of some of the potentially more stressful techniques is timely.

Materials and methods

Study species and field methods

Sea kraits are amphibious marine snakes widespread in the Eastern Indian and the Western Pacific coral reefs (Heatwole, 1999). Two species occur in great densities in New Caledonia, the yellow (or common) sea krait (*L. saintgironsi*) and the blue sea krait (*L. laticaudata*) (Saint-Girons, 1964; Brischoux and Bonnet, 2009). They forage at sea on a community of over 50 species of cryptic anguilliform fish, and consequently they are considered as useful bio-indicators (Ineich et al., 2007; Brischoux and Bonnet, 2008; Brischoux, Bonnet and Legagneux, 2009). On land, sea kraits are faithful to their site, usually a small coralline islet (Brischoux, Bonnet and Pinaud, 2009).

Most sea kraits were caught by hand when resting on land (e.g. basking in the sun, beneath rocks, logs or roots), or when commuting between the land and the sea. The snakes were kept in calico bags until processed and released 1 to 24 hours later. They were measured (e.g. body size, body mass, head morphology), their colour pattern was described in details (e.g., number of black bands), feeding and reproductive status was assessed and the presence of injuries, scares, and ecto-parasites were also recorded. The snakes were marked by scale clipping coupled with iron branding in order to induce permanent changes in scale colouration (Brischoux and Bonnet, 2009). Apparently, these procedures did not harm the snakes as individuals recaptured within 1-7 days displayed superficial lesions (very light scabs); although in some cases the marks facilitated tick parasitism (Bonnet, 2012). Overall, during 2002-2012, 12 900 individuals have been permanently marked by scale clipping and iron branding (Bonnet, 2012); in addition, more than 2000 snakes have been forced to regurgitate their meal for dietary analyses.

The abdomen of each snake was palpated to check for the presence of prey. Some snakes were forced to regurgitate by gentle pressure applied to the rear of the stomach. Sea kraits feed essentially on non-spiny scaleless fish (conger and moray eels) that are easily pushed out of the digestive tract. However, emaciated individuals and reproductive females were systematically spared from forced regurgitation; and no individual was forced to regurgitate more than once.

Although we studied sea-kraits in more than 30 sites spread out in the lagoon of New Caledonia (see fig. 1 in Bonnet, 2012), the current study focuses on the two populations of Signal islet (22°17′45S, 166°17′34E) which attracted most of our long-term field effort. Since 2002, over 27 different field sessions, 2407 blue sea kraits and 1985 yellow sea kraits have been individually marked; forced regurgitation was performed on 237 (Ls) and 293 (Ll) snakes respectively.

Short term effects of manipulation

Basal and stress-induced corticosterone plasma levels were assayed on blood samples (100-500 μl) collected via intracardiac punctures using 30G-needles (Bonnet et al., 2001). The blood was immediately centrifuged (3 min × 10 000g) and the plasma stored at −25°C. We followed a standardized capture/handling protocol (Wingfield, 1994). We sampled snakes at three different time intervals: shortly after handing (<10 min after capture in the field) for basal level, and then 30-45 min, and 60-70 min later in order to obtain the stress response (the snakes were held in calico bags). We used radioimmunoassay (RIA) to determine corticosterone plasma concentrations (performed at the CEBC). The mean extraction rate of the steroids from the plasma was of 97.3 ± 5.2%; intra- and inter-assays coefficients of variation remained lower than 4%; the sensivity of the assay was of 1.9 pg/tube. Cross-reactions with other steroids were as follow: androstenedione ($<0.1\%$), compound S (7%), cortisol (0.1%), 11-deoxy-corticosterone (0.1%), progesterone (7%), testosterone ($<0.1\%$).

Both species were pooled for the analysis, sample sizes for the three time intervals were respectively 17 (6 *L.l.*, 11 *L.s.*), 6 (all *L.s.*) and 5 (all *L.s.*) individuals.

Long term effect of marking and regurgitation on body condition

The body condition index was calculated as the residual of the linear regression of log body mass against log snout vent length (SVL) on all adults collected on Signal islet. Among each sex, the values of BCI were divided by their standard deviation in order to standardize the values between the sexes. We excluded individuals with prey in the stomach as well as reproductive females (i.e., with vitellogenic follicles or oviductal eggs) from our calculations.

We examined the impact of marking (capture + measurements + marking) by selecting individuals recaptured approximately one year later (365 ± 60 days). We then compared the variation of body condition between the initial capture and one year later using paired sample t-tests. The same procedure was used to examine long-term variations in body condition following forced regurgitation. A decrease in body condition over this period should reveal a detrimental effect; on the contrary, a lack of variation suggests an absence of long-term impact. The selected time-period elapsed between capture and recapture (∼1 year) enabled us to control for spurious seasonal effects. For instance, during austral spring (mating period) males and females reduce or cease feeding (Brischoux, Bonnet and Shine, 2011); additionally, egg laying induces a considerable mass loss. Capturing, marking a snake in spring and assessing possible change in body condition few months later only (e.g. <2 months) would lead to the deceptive result that field procedure provoked a negative impact. Conversely, following the reproductive season, feeding rate and body condition increase.

Long term effect of regurgitation on survival

We used a multistate extension of the Cormack Jolly Seber model with two states (two age classes: immature and mature) and two groups (males and females). The best fitting model for survival in sea kraits was Φ (sex × age class + transience), p (time + sex × age class), Ψ (sex + age class) for *L. laticaudata* and Φ (sex × age class + transience), p (time + sex + age class), Ψ (sex + age class) for *L. saintgironsi* (Fauvel et al., unpublished). To test the effect of regurgitation on survival, these models were compared by their Akaike Information Criterion (AIC, Akaike, 1974) to the models including an effect of "regurgitation" as an individual covariate ("1" if the animal has been forced to regurgitate *versus* "0" if not).

Results

Stress response

Handling (capture + measurements) provoked a strong elevation of corticosterone plasma levels (fig. 1). We obtained a typical stress response with low basal levels (<10 min), high values 30-45 min later and a slow decrease more than 60 min later.

Effect of marking and regurgitation on body condition

In *L. saingironsi*, we found no effect of marking on body condition one year later ($N = 101$ snakes; paired t-test, $t_{198.55} = 1.026$, $P = 0.31$) (fig. 2). Surprisingly, in *L. laticaudata* we found a positive effect ($N = 303$ snakes, paired t-test, $t_{601.75} = -3.93$, $P < 0.05$). We found no effect of regurgitation on body condition one year later in both *L. saintgironsi* ($N = 15$, paired t-test, $t_{26.07} = 0.85$, $P = 0.40$) and *L. laticaudata* ($N = 17$, paired t-test, $t_{31.38} = 0.15$, $P = 0.89$). We note however that sample sizes were modest for some of the tests above.

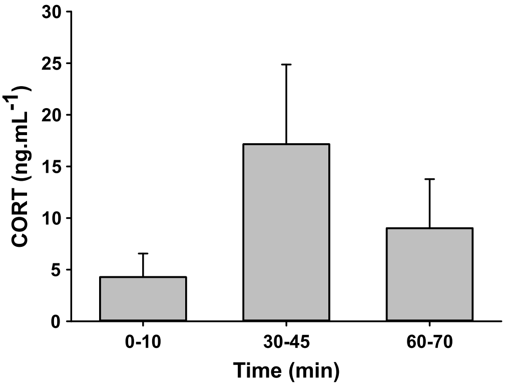


Figure 1. Mean values (±SD) of corticosterone plasma concentration obtained in sea kraits sampled in the field. The snakes were blood sampled shortly after capture (0-10 min), or later (30-45 min, 60-70 min). The stress-induced increase of corticosterone plasma concentration (0-10 *versus* 30-45 min) was significant ($W = 1$, $P < 0.001$). The decrease observed more than hour later (60-70 min) was not significant ($W = 25$, $P = 0.08$; perhaps due to the small sample size), and the mean value remained significantly higher compared to the basal level ($W = 14$, $P = 0.03$).

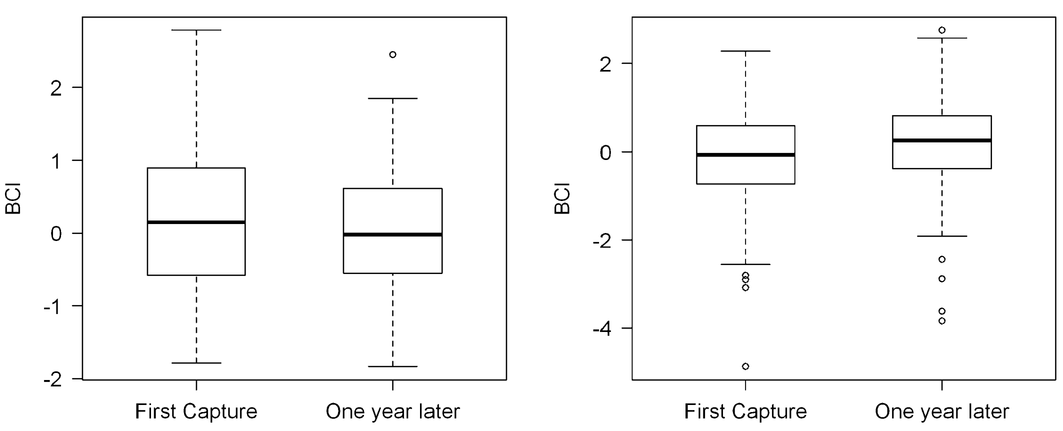
Effect of regurgitation on survival

Models accounting for an effect of regurgitation on survival had consistently lower AIC value than the default models (table 1). We therefore conclude that in both species, regurgitating did not significantly affect survival.

Discussion

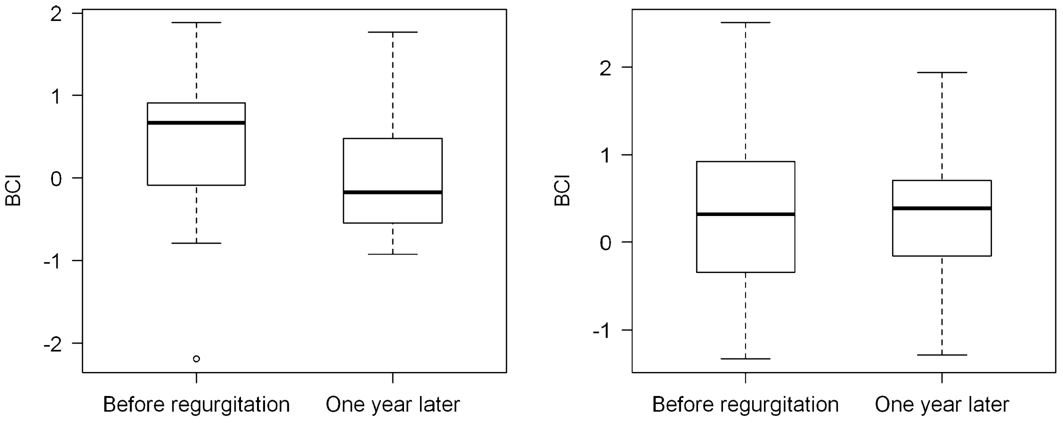
Our long-term study enabled us to accumulate a considerable data set (>22 000 observations over 10 years). On one hand, this research yielded substantial results regarding sea snake foraging ecology (Brischoux, Bonnet and Shine, 2007; Brischoux, Bonnet and Shine, 2009), physiology (Brischoux et al., 2012), prey community (Ineich et al., 2007; Brischoux and Bonnet, 2008), conservation issues (Bonnet et al., 2009; Brischoux, Bonnet and Pinaud, 2009; Bonnet, 2012), and others (Brischoux and Bonnet, 2009). On the other hand, we inevitably perturbed a very large number of individuals with a potential impact on the populations. Apparently, the short-term stress due to handling and/or forced regurgitation did not entail a negative population effect.

Our relatively large sample sizes, the use of two species, and the long-term monitoring provided appropriate statistical power to examine the impact of marking and forced regurgitation. The main indexes we retained in the analyses, body condition and survival, are key parameters with a strong fitness value. For instance, individuals in low body condition exhibit low survival and low reproductive rates (Bonnet et al., 2002a). By comparison, short-term indexes (e.g. increase of stress hormone levels) offer limited



a) Marking effect: *L. saintgironsi*

b) Marking effect: *L. laticaudata*



c) Regurgitation effect: *L. saintgironsi*

d) Regurgitation effect: *L. laticaudata*

Figure 2. Boxplots showing the changes in body condition following first handling and marking in a) *L. saintgironsi* and b) *L. laticaudata*, and following forced regurgitation in c) *L. saintgironsi* and d) *L. laticaudata*. The middle band in the box represents the median, the bottom and top of the box are the lower and upper quartiles, the ends of the whiskers are the extremes data points still within 1.5 interquartile range from the box and the points are outliners.

Table 1. Model selection table for the capture mark recapture analysis. In both species the models that did not account for regurgitation effect were better supported by the data.

Species	Model survival	AIC	dAIC	AIC weight
L. laticaudata	no regurgitation effect	15 508.71	0	0.881
	with regurgitation effect	15 512.71	4	0.119
L. saintgironsi	no regurgitation effect	13 477.21	0	0.704
	with regurgitation effect	13 478.94	1.73	0.296

information for population monitoring. Indeed, on both sea krait species, our analyses revealed an absence of long-term impact of field techniques on individuals (i.e. no change in body condition) and populations (i.e. no change in survival rates) despite a strong short-term stress effect of handling.

The transitory stress inflicted to the snakes during marking (raise of corticosterone, fig. 1) associated to the superficial skin lesions were thus well tolerated by the snakes on the long run. Ectoparasites (ticks) are occasionally observed attached with the lesion caused by marking but they are eliminated during subsequent skin shedding and/or foraging trips at sea. By comparison, sea kraits regularly display deep wounds (inflicted by retaliating prey, Bonnet, Brischoux and Lang, 2010) which are massively colonized by ticks (Bonnet, 2012). Over time, sea kraits accumulate injuries and as a result, the larger (i.e. older) sea kraits monitored in New Caledonia generally wear more and larger natural scars (e.g., fish bites) than artificial scars (marks). Importantly, climatic conditions are mild all year round in New Caledonia so that cicatrisation is never prevented by low temperatures. Consequently, we emphasize that our conclusions cannot be generalized to all reptile species. For instance scale clipping or branding might entail local infection if performed on reptiles during prolonged periods with low ambient temperatures (e.g. early spring or late fall in temperate climates, XB pers. obs.).

The increase in body condition observed in the blue sea kraits one year after making was unexpected. Blue sea kraits are extremely philopatric, therefore most individuals captured (and marked) for the first time might be new (hence inexperienced) recruits whose body condition would later increase with improved local familiarity. In support of this assumption, newly captured snakes were on average smaller (presumably younger) than marked individuals (mean SVL, $M = 79.6$ cm in new males *versus* $M = 86.0$ cm in marked males; $M = 81.1$ cm in new females *versus* $M = 100.9$ cm in marked females; $P < 0.01$ in all comparisons). Future analyses are required to assess this issue more precisely.

Regurgitation is a natural behaviour in snakes, however spontaneous or forced regurgitation could be detrimental as sea kraits invest considerable amount of time and energy capturing prey, and they also must engage in risky combats to subdue their prey (Bonnet, Brischoux and Lang, 2010). Unfortunately, on one occasion the sharp teeth of the prey pushed forward in the digestive gut and provoked a fatal haemorrhage (Brischoux and Bonnet, 2009; note that we observed a single accident on more than 2000 forced regurgitations). Our results nonetheless suggest that losing one meal has no long-term impact on body condition and survival. Trophic resources are likely to be abundant in the New Caledonian lagoon (Brischoux and Bonnet, 2008), and favourable climatic conditions enable sea kraits to feed all year round at a relatively high frequency, once every two weeks on average (Brischoux, Bonnet and Shine, 2007). Depriving a snake form one meal was likely rapidly compensated without detectable effect on survival or body condition one year later. Although not tested yet, similar moderate population impact (if any) of forced regurgitation should apply in tropical snakes that feed frequently such as *Causus* spp. (Ineich et al., 2006), *Emydocephalus annulatus* (Shine et al., 2004), or *Tropidonophis mairii* (Brown and Shine, 2002). However, we stress that in other snake species that feed on relative large prey and where foraging opportunities are limited to a few foraging events per year (e.g. low frequent feeders such as pythons, vipers from temperate climates) forced regurgitation might entail detrimental effects.

The absence of negative impact on the two sea krait populations (e.g. populations of Signal islet are still prosperous despite ten year of intensive field research) mirrors the stability recorded in other systems that have been monitored using similar techniques (e.g. tiger snakes in Australia, Bonnet et al., 2002b). More generally, population declines of snakes have been observed in degraded habitats whereas stability was recorded in well-protected areas (Reading et al., 2010). It should be noted however, that population collapses also occurred in some well-protected areas for unknown reasons (Reading et al., 2010). Overall, many species of reptile are tolerant to stressful procedures (handling, iron branding, toe clipping) and long term population monitoring are unlikely to represent a major threat – at least compared to other perturbations such as habitat loss or direct killing. Researchers are devoted to their study systems and tend to minimize their impact on wild populations; however, even classical and widely used field procedures can be detrimental (Gauthier-Clerc et al., 2004). Further studies are thus required, notably to test the notion proposed above that foraging strategies (e.g. relative prey size, feeding frequency) and climatic constraints are key factors in determining the impact of field research on snake populations. Such assessment might contribute to the improvement of field procedures (e.g. counter-intuitively, pit tags are more stressful compared to toe clipping in some lizards; Langkilde and Shine, 2006) and thus might be useful to encourage field research. In fact, long-term monitoring can have beneficial outcomes for the study species. For instance, our research on sea kraits improved local knowledge (e.g. strong media coverage) and promoted the conservation status of the species and of their terrestrial habitat (i.e. beach rocks on Signal islet, Bonnet et al., 2009). However, evaluating the balance between the benefits and costs of scientific studies on populations needs rigorous assessments.

Herpetologists have tested their impact on the welfare of their study animals by measuring handling stress (Langkilde and Shine, 2006; see also our results). Our study adds another dimension by addressing the effect of field research at the population scale. As our results show that a significant short-term stress does not translate into detrimental population consequences, we advocate that more attention should be devoted on the impact of long-term monitoring and stressful field procedures. It is indeed essential to minimize the stress induced by field procedures (welfare issue), but it is vital to control for possible impact on the populations (conservation issue). For instance, field management, translocations, or reintroduction programs may provoke stressful short-term effects on individuals that may nonetheless generate population benefits. Assessments are thus required to provide robust analyses to ethic committees in order to better prioritize and organize field studies.

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References

Akaike, H. (1974): A new look at the statistical model identification. IEEE Trans. Autom. Control **19**: 719-723.

Anonymous (2012): Dwindling sea snakes. (News of the week). Science **335**: 150.

Bonnet, X. (2012): Long-term field study of sea kraits in New Caledonia: fundamental issues and conservation. Integr. Comp. Biol. **52**: 1-15.

Bonnet, X., Naulleau, G., Bradshaw, D., Shine, R. (2001): Changes in plasma progesterone in relation to vitellogenesis and gestation in the viviparous snake *Vipera aspis*. Gen. Comp. Endocr. **121**: 84-94.

Bonnet, X., Lourdais, O., Shine, R., Naulleau, G. (2002a): Reproduction in a typical capital breeder: costs, currencies, and complications in the aspic viper. Ecology **83**: 2124-2135.

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O., Bradshaw, D. (2002b): Heaven for serpents? A mark-recapture study of Tiger Snakes (Notechis scutatus) on Carnac Island, Western Australia. Austral. Ecol. **27**: 442-450.

Bonnet, X., Brischoux, F., Pearson, D., Rivalan, P. (2009): Beach-rock as a keystone habitat for amphibious sea snakes. Environ. Conserv. **36**: 62-70.

Bonnet, X., Brischoux, F., Lang, R. (2010): Highly venomous sea kraits must fight to get their prey. Coral Reefs. **29**: 379.

Brischoux, F., Bonnet, X. (2008): Estimating the impact of sea kraits on the anguilliform fish community (Congridae, Muraenidae, Ophichthidae) of New Caledonia. Aquat. Living Resour. **21**: 395-399.

Brischoux, F., Bonnet, X. (2009): Life history of sea kraits in New Caledonia. Mémoir. Mus. Natl. His. **198**: 133-147.

Brischoux, F., Bonnet, X., Shine, R. (2007): Foraging ecology of sea kraits Laticauda spp. in the Neo-Caledonian Lagoon. Mar. Ecol. Progr. Ser. **350**: 147-151.

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

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

Brischoux, F., Bonnet, X., Pinaud, D. (2009): Fine scale fidelity in sea kraits: implications for conservation. Biodivers. Conserv. **18**: 2473-2481.

Brischoux, F., Bonnet, X., Shine, R. (2011): Conflicts between feeding and reproduction in amphibious snakes (sea kraits, Laticauda spp.). Austral Ecol. **36**: 46-52.

Brischoux, F., Rolland, V., Bonnet, X., Caillaud, M., Shine, R. (2012): Effects of oceanic salinity on body condition in sea snakes. Integr. Comp. Biol., in press.

Brown, G.P., Shine, R. (2002): Reproductive ecology of a tropical natricine snake, *Tropidonophis mairii* (Colubridae). J. Zool. **258**: 63-72.

Carpenter, C.C. (1952): Comparative ecology of the common garter snake (*Thamnophis sirtalis*), the ribbon snake (*Thamnophis s. sauritus*), and Butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecol. Monogr. **22**: 235-258.

Gauthier-Clerc, M., Gendner, J.P., Ribic, C.A., Fraser, W.R., Woehler, E.J., Descamps, S., Gilly, C., Le Bohec, C., Le Maho, Y. (2004): Long-term effects of flipper bands on penguins. P. Roy. Soc. Lond. B Bio. **271**: S423-S426.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T. (2000): The global decline of reptiles, déjà vu amphibians. Bioscience **50**: 653-666.

Heatwole, H. (1999): Sea Snakes, Aust. Nat. Hist. Ser. Univ. of New South Wales, Sydney.

Ineich, I., Bonnet, X., Shine, R., Brischoux, F., Lebreton, M., Chirio, L. (2006): What, if anything, is a 'typical' viper? Biological attributes of basal viperid snakes (genus Causus Wagler, 1830). Biol. J. Linn. Soc. **89**: 575-588.

Ineich, I., Bonnet, X., Brischoux, F., Kulbicki, M., Séret, B., Shine, R. (2007): Anguilliform fishes and sea kraits: neglected predators in coral-reef ecosystems. Mar. Biol. **151**: 793-802.

IUCN (2010): IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland and Cambridge, UK.

Keck, M.B. et al. (1994): Test for detrimental effects of PIT tags in neonatal snakes. Copeia **1994**: 226-228.

Lagarde, F., Guillon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., Slimani, T., El Mouden, H.E. (2008): Slowness and acceleration: a new method to quantify the activity budget of chelonians. Anim. Behav. **75**: 319-329.

Langkilde, T., Shine, R. (2006): How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. J. Exp. Biol. **209**: 1035-1043.

Lorioux, S., Bonnet, X., Brischoux, F., De Crignis, M. (2008): Is melanism adaptive in sea kraits? Amphibia-Reptilia **29**: 1-5.

McCarthy, M.A., Parris, K.M. (2004): Clarifying the effect of toe clipping on frogs with Bayesian statistics. J. Appl. Ecol. **41**: 780-786.

Monestiez, P., Dubroca, L., Bonnin, E., Durbec, J.P., Guinet, C. (2006): Geostatistical modelling of spatial distribution of *Balenoptera physalus* in the northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. Ecol. Model. **193**: 615-628.

Rasmussen, A.R., Murphy, J.C., Ompi, M., Gibbons, J.W., Uetz, P. (2011): Marine reptiles. Plos Biol. **6**: e27373.

Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D., Rugiero, L. (2010): Are snake populations in widespread decline? Biology Letters **6**: 777-780.

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

Secor, S.M., Diamond, J. (1997): Determinants of the postfeeding metabolic response of Burmese pythons, *Python molurus*. Physiol. Zool. **70**: 202-212.

Shine, R., Bonnet, X., Elphick, M.J., Barrott, E.G. (2004): A novel foraging mode in snakes: browsing by the sea snake Emydocephalus annulatus (Serpentes, Hydrophiidae). Funct. Ecol. **18**: 16-24.

Taberlet, P., Waits, L.P., Luikart, G. (1999): Noninvasive genetic sampling: look before you leap. Trends Ecol. Evol. **14**: 321-325.

Wingfield, J.C. (1994): Modulation of the adrenocortical response to stress in birds. In: Perspectives in Comparative Endocrinology, p. 520-528. Davey, K.G., Peter, R.E., Tobe, S.S., Eds, National Research Council of Canada, Ottawa.

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