Thirsty sea snakes forsake refuge during rainfall

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Abstract   Vertebrates living in dry or salty habitats spend significant amounts of time and energy maintaining their hydro-mineral balance; any opportunity to drink fresh water should reduce such expenses. However, to find fresh water, individuals are generally forced to leave the safe and buffered conditions that prevail in their refuges. Therefore, they must face harsh environmental conditions and increased predation risks. We examined this trade-off in the field, using a very large dataset gathered on amphibious sea snakes that confront periodic droughts. The study was carried out on different islets in the lagoon of New Caledonia. As expected, sea kraits remain concealed most of the time under rocks or within burrows during dry weather. They select precise time windows to move rapidly between the sea and the land, thereby minimizing the time spent in the open. Rainfall triggered massive disruptions of this rhythm: many snakes quickly forsook their shelter to drink in the open, and remained almost motionless until satiety. Interestingly, they adopted specific and unusual postures to drink. They perched on the top of rocks that were benefiting from running and less salty water during downpours. They also drank the droplets attached to vegetation during drizzle.

Key words: drinking, *Laticauda*, sea snakes, water balance.

INTRODUCTION

At any time, the activity of animals is regulated by complex interactions between physiological and environmental factors (Abrahams 2002; Kotler *et al.* 2004). For instance, although hunger promotes foraging behaviours, unfavourable thermal conditions and/or predator-threats strongly restrict the possibilities for food searching (Anderson 1986; Metcalfe *et al.* 1987; Lima & Dill 1990; Gotceitas & Godin 1991; Robin *et al.* 1998). More generally, the outcomes of behavioural decisions have major impacts on survival, foraging or reproductive success, and thus are assumed to influence individual fitness. Therefore, life history theory postulates the existence of optimal regulations between alternative behaviours (Emlen 1966, 1968; Stephens & Krebs 1986; Houston & MacNamara 1999). Both theoretical and experimental published reports support the existence of selective pressures favouring optimal decisions (Pyke *et al.* 1977; Sih 1992; Brown *et al.* 1999; Kay 2002; Gordon & Saint-Amour 2004). However, the complexity and the diversity of natural situations are immense; empirical field observations of poorly documented behaviours are required to better identify and understand the main trade-offs that regulate the day-to-day activity of most animal species. Indeed, encompassing a wide array of organisms has proven to be critical to frame life history

theories within a realistically context (Bonnet *et al.* 1998; Zera & Harshma 2001), including optimal behaviours (Spaethe *et al.* 2001; Reinhardt 2002).

For the vast majority of animal species, retreating in a safe and thermally buffered refuge (e.g. burrow) is a key attitude around which revolve a number of important alternative decisions. For example, leaving a shelter to forage generally increases predation risks and exposes individuals to harsh thermal and hydric conditions (e.g. Wehner *et al.* 1992; Schwarzkopf & Alford 1996; Williams *et al.* 1999; Bulova 2002; Seebacher & Alford 2002; Beck & Jennings 2003; Goldsbrough *et al.* 2004). Consequently, the availability of retreat sites is of extreme importance for survival, reproduction and energy budget (Iribarne 1990; Lorenzo & Lazzari 1999; Steele 1999; Armstrong & Griffiths 2001). Unfortunately, hidden animals are not easily accessible to the observer. Investigations of the trade-off between incompatible decisions, remaining sheltered versus leaving a refuge, have been essentially carried out under experimental conditions, notably in fish (Eggleston *et al.* 1992; Griffiths *et al.* 2004; Orpwood *et al.* 2004; Millidine *et al.* 2006). Therefore, several potential conflicts between safety and resources gathering remain virtually unexplored in natural situations. Leaving a retreat site to drink provides such a typical example of almost undocumented sets of behaviours.

Indeed, although drinking is vital for most terrestrial and marine species (Bennett *et al.* 1986; Schmidt-Nielsen 1990), relevant ecological studies are rare. A

broad review using four key words (water intake, thirst, drinking, and drinking behaviour; Google Scholar & PubMed) provided more than one million references (≈1 191 500). The examination of the first 100 references of each sub-search (total 800 articles screened) showed that only 1% concerned ecological studies; the rest (98%) was published in medicine and cell biology journals (1% unclassified). A similar search using four different key words relating to other randomly selected behaviours (i.e. parturition, mating, sleeping, and grooming) provided >682 000 references; 21% were published in ecological journals (the difference between the two proportions was significant, $\chi^2 = 411.4$, d.f. = 4, $P < 0.001$). A more focused search on three leading behavioural journals (*Animal Behaviour*, *Behavioral Ecology*, and *Behavioural Ecology & Sociobiology*), using eight key words, drinking plus seven other contrasted behaviours (grooming, mating, hunting, vigilance, scent marking, foraging and fighting; $n > 4300$ articles) showed that the studies about drinking represented only 1.1%. The mean percentage for the other behaviours was ten times greater (14.1 ± 15.8% on average). A meticulous analysis of >200 articles published in the three journals cited above revealed another important phenomenon: drinking was rarely directly observed and quantified in the field (1%: Laurenson 1995); whereas for instance grooming was often measured in the field (38% of the studies). Clearly, ecological studies that investigated drinking behaviour *per se* are very scarce, limited to a few species of birds (Cade 1965; Fisher *et al.* 1972; Ferns & Hinsley 1995), and mammals (Laurenson 1995; Starin 2002), and restricted to few descriptive parameters isolated from the general activity of the studied organisms (Cade *et al.* 1966; Rode *et al.* 2003). However, in many species, the maintenance of the hydro-mineral balance imposes strong behavioural constraints (Bradshaw 1986, 1997). Animals that face hot and dry conditions remain sheltered within burrows over long time periods, thereby trading water saving against other activities such as foraging. Any opportunity to drink fresh water should relax such constraints. Unfortunately, drinking is rarely a simple task; individuals must leave their refuge and sometimes undertake long-trips (Shepherd 1981; Klaassen 1996; Bergström & Skarpe 1999; Georgiadis *et al.* 2003; Scholz & Kappeler 2004). Even for animals living close to fresh-water bodies, drinking can be problematical as many predators wait in ambush positions around ponds, riverbanks and under the water surface (Cade 1965; Beck *et al.* 1973; Dill 1977; Shepherd 1981; Ferns & Hinsley 1995; Shine *et al.* 2004). Dry and/or salty habitats pose such types of behavioural challenge with force to a wide array of organisms (Schmidt-Nielsen 1990).

In the current study, we took advantage of an ecological situation faced by two species of amphibious sea snakes (sea kraits). Snakes are very cryptic organisms, they remain well sheltered over very long time periods, and therefore they constitute appropriate models to investigate ecological causes likely to stimulate emergence from refuge (i.e. trade-off between safety and drinking). Sea kraits use both marine and terrestrial environments, the sea to forage and the sandy shore of many coral islets in the Pacific Ocean the rest of the time (Heatwole 1999). In most coral islands there are no water bodies or rivers and rainfall is scarce and the sandy substratum cannot hold the rain. Nonetheless, sea snakes have been observed drinking from rainwater (Guinea 1991; Lillywhite & Ellis 1994). This suggests that sea kraits rely, at least partly, on the absorption of freshwater to preserve their hydro mineral equilibrium. More generally, for air-breathing species that live in dry/salty habitats, the maintenance of the hydro-mineral balance entails significant energy expenditure (Schmidt-Nielsen 1990). Likely, ephemeral freshwater represents a valuable resource. Therefore, weather events during which water becomes available (e.g. rainfall) should markedly influence activity budget and behaviours. In this context, several predictions can be proposed.

1 Hidden animals should quickly emerge from their shelter to drink freshwater as soon as available.
2 Most individuals should rapidly return under shelter after completion of drinking.
3 Individuals should select the best quality water. For instance, a preference for freshwater instead of brackish water would reduce the time and physiological efforts necessary to restore their water balance.

Our long-term study on free-ranging sea snakes enabled us to address these issues.

METHODS

Study species

Sea kraits (sea snakes) forage in the ocean, but return to land to digest their prey, slough their skins, rest and reproduce (Heatwole 1999; Brischoux & Bonnet 2008; Brischoux *et al.* 2007). We studied two species, *Laticauda saintgironsi* (yellow or common sea krait) and *Laticauda laticaudata* (blue sea krait). Sexual maturity is reached at a body mass of approximately 100 g (corresponding to a body size of 70 cm snout vent length (SVL)); neonates or very young snakes usually weigh less than 50 g (SVL < 50 cm); snakes in between these two body sizes were considered as juveniles. Sea kraits exhibit a marked tolerance to slow moving human observers; this feature greatly facilitated behavioural observations. However, they show a

typical anti-predator response when threatened: they hide under rocks, or flee in the sea (Shine *et al.* 2003).

Study sites and general survey procedures

Signal island

The main study site, Signal Island, is a 6-ha, flat, rectangular islet situated in the south-western lagoon of New Caledonia (22°17′47″S; 166°17′34″E). Signal Island is characterized by irregular summer rainfall and the absence of water bodies (natural or artificial), and thus is covered by a sclerophylic forest. Strong trade winds generate substantial spray most of the time.

Since 2002, we spent 140 days on Signal Island. Over that period, we carried out 408 standardized successful surveys (i.e. 'survey during which at least one snake was observed', henceforth referred as 'survey' for simplicity); essentially along 450 m of west shore protected from the main trade winds. Each survey lasted 30 min to 1 h, depending on the number of observers and on the number of snakes encountered. The zone monitored was composed essentially of flat beach rocks (≈80%) alternating with small sandy beaches (≈20%). Two block fields (roughly L-20, W-5 m, H-2 m) made of large coral boulders accumulated decades ago for lime production span between the shore and the sandy bank. Behind the beach, very large numbers of petrel burrows can be observed. Crevices, flat rocks, block fields and burrows provide many shelters for the snakes as assessed by direct observations and radio tracking. During each survey, one to five persons walked along the shore, searching for snakes. The number of observers accelerated the process (e.g. data recording) and shortened each survey, our walking speed varying from 0.5 to 1.0 km h^{-1}. Sea kraits were easily located (owing to their banded colour pattern) and captured (due to their tolerance to handling). Our searching effort was lower at night (23.00 hours to 05.00 hours, using head torches). By contrast, because our campsite and field-lab were located within the study site, a few meters from the shore, daytime corresponded to the most intensive period of monitoring of the study area: we surveyed at least one quarter of the shore (≈100 m) almost every day from 06.00 hours to 17.00 hours. During the hottest phases of the day the snakes remained invisible most of the time. We did not include such unsuccessful surveys ($n > 1200$) as correcting factors in the analyses because the patterns were clear (see results), thereby avoiding unnecessary complications in the calculations and figures, irrelevant in terms of biological information. Broadly, during the day-phase, searching was facilitated because our vision was not limited to the spotlight provided by the torches. This means that all else being equal, the maximal numbers of observations should have occurred during this time slot, but most of the observations were instead collected during the dark-phases. Overall, the patterns observed (see results) were conservative relative to differential searching efforts.

For almost every snake found, the time and the behaviour were recorded. When a snake was seen crossing the beach, basking in the sun, mating, or immobile on the substrate, it was considered as visible. When the snake was found under a rock (or a log), it was considered as concealed. For simplicity, we classified the snakes as inactive when concealed (=sheltered), and active in the other cases (=exposed in the open). The sex was determined by inspection of the tail. Body mass (±1 g) and body size (±1 cm) were measured using an electronic scale and a flexible ruler (see Bonnet *et al.* 2005 for details). For most snake species, including sea kraits, drinking is easily identifiable: the tip of the mouth is placed in direct contact with the water and slow and rhythmic movements animate the jaws in order to pump the water (Berkhoudt *et al.* 1994; Cundall 2000). During behavioural observations, the snakes were not systematically captured. This procedure produced the least interference with behaviours. From distance, the age and the sex of the snake can often be determined. Snake's size (hence age) can be crudely estimated by sight with a precision of 5–10 cm (5 cm on small snakes, 10 cm on large snakes). A test (visual estimates followed by captures and measurements) on 50 snakes showed that visual estimates correctly assigned snakes to age classes in 90% of the cases. Neonatal snakes are easily identifiable owing to their very small size; similarly most of the adults are large (>70 cm, >100 g) and easily classified; incorrectly classified snakes represent a small proportion (12%) of the total (e.g. large juveniles and small adults). Similarly, the sex of the adults was obtained by visual examination of the shape of the tail without capture (misclassification 4%).

Within a given survey, the risk of counting an individual twice was almost nil because the observers were moving along the shore far more rapidly than the snakes did. Among surveys, we could not fully eliminate the possibility that unidentified snakes (e.g. individuals not captured during behavioural observations) were counted more than once, thereby generating pseudo-replicates in the dataset. However, most of the snakes observed on Signal Island have been individually and permanently marked ($n = 2672$ snakes marked by scale-clipping plus 3855 recaptures); a relatively small proportion of animals remained unidentified ($n = 362$, 5.2%). Therefore, snake identity was available for 94.7% of the observations. This means that it was possible to remove almost all potential pseudo-replicates from the analyses. In practice,
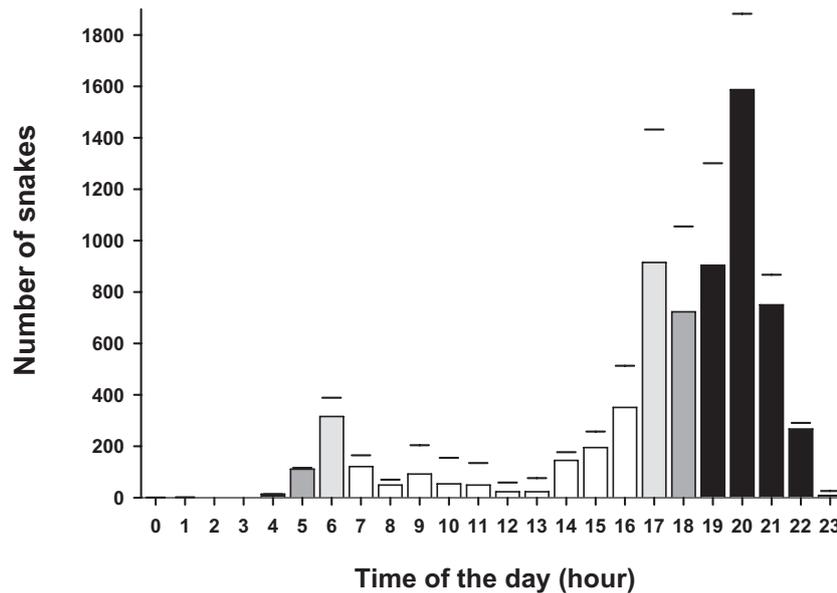
Fig. 1. Numbers of sea snakes (two species pooled: *Laticauda saintgironsi* and *Laticauda laticaudata*) observed over 140 days on Signal Island, New Caledonia. The total number of observations was 6889 (2672 captures + 3855 recaptures + 362 unidentified). Each bar represents the total number of snakes counted per hour (note that the searching effort was more intense from 06.00 to 17.00 hours, see text). The grey-black colouration provides a rough scale for sunlight, from full day (white), partial darkness (grey) to full darkness (black). The line above each bar indicates additional data from eight other islets (=additional numbers in excess of the bars; see text).

pooling captures and recaptures versus excluding potential pseudo-replicates (e.g. removing all recaptures) did not change the outcome of any of the results. Therefore, we retained the entire dataset for several figures to provide pictures gathered on very large datasets that are directly representative of the field observations, but we deleted them from all of the analyses to meet current statistical conventions. Consequently, unless clearly stated, the statistics presented are free from pseudo-replicates.

Other islands

From 2002 to 2006, during 93 days, regular surveys were carried out on eight other islands of the New Caledonian lagoon: îlots Brosse, Amédée, Nouaré, Bayonnaise, Larégnère, Mba, Ténia and Porc Epic (Brischoux & Bonnet 2008). The protocol used to monitor the different populations of snakes was broadly similar for all of the sites (i.e. adjusted to the peculiarities (size) of each islet). These additional data (n = 2544 observations, split as follows: 2043 marked snakes + 377 recaptures + 124 unidentified animals) provided an opportunity to assess the generality of the patterns observed on Signal Island. Overall, combining all study sites (nine islets), we collected data on 9433 snakes; among them 8947 were captured, marked, measured and sometimes re-captured, 486

other snakes were not captured and remained unidentified. As above, we removed pseudo-replicates from the statistical analyses.

On several instances, some data were missing (e.g. exact time at capture, SVL, attitude of the snake etc.) or were not available (e.g. the actual mass of a snake with a prey in the stomach remained undetermined). Therefore, the sample sizes varied depending on the question addressed (but most analyses were nonetheless based on large sample sizes).

RESULTS

General activity patterns of the snakes

In the course of the 140 days monitoring Signal Island, we observed 6889 snakes (2672 marked + 3855 recaptures + 362 not-captured). Hourly counts of the total numbers of snakes observed revealed clear activity patterns with marked peaks of displacements (Fig. 1). The snakes crossed the beach mainly at dusk and at the beginning of the night. Despite intensive searching, we observed few snakes crawling on the beach from 07.00 hours to 15.00 hours. After removing the time period of lower searching effort (23.00 hours to 05.00 hours) and comparing the actual distribution against a theoretical homogeneous time-distribution of
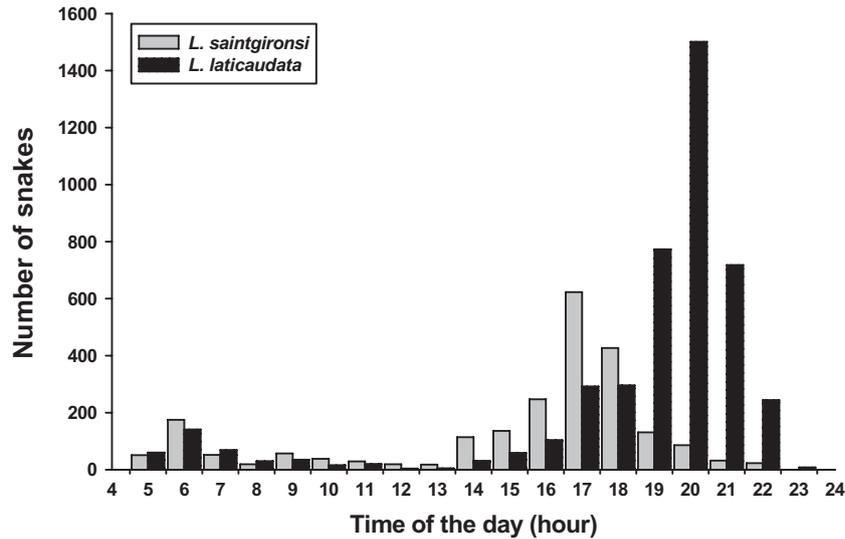
Fig. 2. Comparison of the total numbers of snakes counted per hour for each species of sea snake: *Laticauda saintgironsi* (grey bars) *versus Laticauda laticaudata* (black bars). This figure is limited to Signal Island (140 days) and it encompasses solely the time period of higher searching effort, from 05.00 to 23.00 hours.

observations, the peaks of activity led to a significantly non-random distribution of observations (using only captures to eliminate pseudo-replicates; contingency table, $\chi^2 = 2410.8$, $n = 2552$, d.f. = 16, $P < 0.001$). Performing similar analyses with the data gathered on the other islets did not change the results (using only captures; $\chi^2 = 2124.8$, $n = 1991$, d.f. = 16, $P < 0.001$, Fig. 1). We carried out various selections on the dataset to explore the robustness of the patterns. For instance, we tested if the recaptured snakes exhibited a peculiar activity pattern (e.g. reacted to first capture and consequently avoided moving at dusk) relative to the snakes not previously captured, thereby revealing a potential anti-predator behaviour. On Signal Island the number of snakes observed per hour at first capture was closely correlated with the number of snakes recaptured later ($r = 0.88$, $P < 0.001$), leading to very similar temporal patterns. There was no support for a trap-shyness effect. In practice, whatever the selection or the analyses (e.g. using mean numbers of snakes observed per survey instead of numbers of snakes per hour), our conclusions remained unchanged. Overall, the bi-modal activity of the snakes with a minor peak early in the morning and a marked peak at dusk separated by a strong decrease of movements during the day was a robust pattern.

The two snake species, however, exhibited significant differences. Most of the yellow sea kraits (*L. saintgironsi*) started to move half an hour before the sun set; most of the blue sea kraits (*L. laticaudata*) crossed the beach later, after sunset (Fig. 2; comparing the two species, restricting analyses to Signal island, to the time period of intensive searching, and to a single capture per marked individual: contingency table,

$\chi^2 = 840.2$, d.f. = 16, $n = 1187$ *L. s.* and $n = 1365$ *L. l.*, $P < 0.001$). Overall, the activity pattern of the snakes was strongly affected by a combination of at least two factors, essentially the time of the day and to a lesser extent by the species.

Occurrence of rainfall

Rainfall occurred rarely in the study site: over a total of 221 days of fieldwork during which precipitation events were recorded (all study sites included), we observed one strong downpour, 6 rainy days, and 11 days with a fine drizzle, all occurring on Signal Island (hence this study site was exclusively used for the analyses about the effect of rain). Table 1 provides further information on the time-slots for the occurrence of the precipitations. The strong downpour, and to a lesser extent the rains, quickly produced puddles and little streams running on hard substrates (rocks, logs). By contrast the drizzle generated only droplets on the vegetation, notably on the purslanes (*Sesuvium portulacastrum*). For all these events, the preceding days were dry by definition; and owing to the combination of high summer temperatures with permanent trade winds we never observed the formation of dew. For instance, from 21 January to the 3 February 2005, no rain at all occurred and the vegetation was very dry. Therefore, during at least 2 weeks, no fresh water at all was available before the downpours of 3 February at 17.08 hours. Similarly, a sudden rain starting at 17.05 hours on 18 January 2006 interrupted a 30-day drought. Each precipitation event lasted less than 30 min on average (≈5 min to 1 h). However, for the

Table 1.   Number of sea snakes (no. *Laticauda sp.*) observed during rainy versus dry weather on Signal Island (percentages in brackets are calculated within a column)

Time period	N	D-R-dz	No. snakes rainy-days	No. snakes dry-days	Mean no. dry-day	R/D
Daylight (13.00–17.00 hours)	12	1-5-6	451 (90.4%)	183 (33.6%)	3	80.25
Dusk (18.00 hours)	3	0-1-2	37 (7.4%)	66 (12.2%)	3	40.05
Night (19.00–20.00 hours)	3	0-0-3	11 (2.2%)	294 (54.2%)	14	0.26

N indicates the number of rain events (total = 18: one downpour (D), six rain (R), 11 drizzle (dz)). Sampling period under dry climate was limited to 7 days (6.2 × N on average) prior to the rain and to the time-slots during which precipitations occurred. R/D represents the ratio between the number of snakes observed during a given time slot of 1 h during a rainy-day divided by the mean number of snakes observed during the same time-slot over the preceding dry-days (mean no. dry-days).

following analyses we used a time-span of 1 h for simplicity and consistency; in addition such a procedure was conservative with respect to the results presented below, notably by avoiding any artificial inflation of the rain effects on the snake's behaviours.

Influence of rainfall on activity patterns

During rainfall, many snakes rapidly left their shelter and became visible in the open (Table 1). For the following analyses, we limited the investigations to a maximum of 7 days of drought prior to rainfall (mean = 6.2 ± 1.6 days; range 1–7 days), and to the precise time slots during which the rain occurred. For example, we used the data gathered between 17.00 and 18.00 hours over the 7 dry-days (27 January 2005 to 2 February 2005) preceding the 17.00–18.00 hours downpour of the 3 February 2005. Overall, we obtained a total of 499 snakes observed during the rain versus 543 snakes pooling all the preceding dry-days. Based on such sub-sample, we compared the numbers of snakes observed (no. snakes per survey per day) respectively before and during the rain. Most of rains occurred during daylight, and on average the rain multiplied by 54 the number of snakes observed per survey (Table 1). This effect was particularly visible when comparisons were restricted to the time slots of low activity under dry conditions (daylight phases); but no clear effect was observed at night, perhaps because at that time only drizzle occurred and many snakes had already emerged (Table 1). Indeed, the type of precipitation was important too; on average the visibility of the snakes increased by 126.3 during strong rain ($n = 7$) and by 8.4 during drizzle ($n = 11$; Mann-Whitney, adjusted-Z = −3.03, $P < 0.01$).

Comparing the proportion of snakes visible in the open *versus* those hidden during the 13.00–18.00 hours time slot when most of the rain occurred, we found a strong effect of the weather: under dry conditions 51% of the snakes ($n = 1353$, including all dry days) were hidden under rocks. In stark contrast,

during the rain, 98% of the snakes ($n = 490$) were visible in the open (contingency table, $\chi^2 = 334.2$, d.f. = 1, $P < 0.001$).

Difference between the species

We limited the investigation to the time slot (13.00–18.00 hours) when most of the rain occurred (15/18 = 83%), and that also corresponded to the peak of activity of *L. saintgironsi*, but not yet to the peak of activity of *L. laticaudata* (Fig. 2). The rain provoked an early emergence of *L. laticaudata*: we found 452 blue sea kraits, essentially sheltered ($n = 336$, 74% hidden *versus* $n = 116$, 26% visible) under dry conditions but 163 individuals ($n = 9$, 6% hidden *versus* $n = 154$, 94% visible) during the same time slot under wet conditions (contingency table, $\chi^2 = 230.3$, d.f. = 1, $P < 0.001$). By comparison, 901 *L. saintgironsi* were found during the dry days and only 36% were hidden, *versus* 327 snakes (1% hidden) during the rainy days ($\chi^2 = 151.5$, d.f. = 1, $P < 0.001$). Thus, in the afternoon, precipitations had a broad similar effect on the two snake species, but specific peculiarities were clearly recorded. Almost all blue sea kraits were concealed and inactive under daylight phases, and they emerged in the open during the rain. Several yellow sea kraits were already active at the same time during dry periods, but many sheltered individuals became visible under wet conditions.

Why do snakes emerge from their shelter during the rain?

The following analyses are limited to cases where the behaviour (e.g. drinking, exploring the substrate etc.) was recorded without disturbance due to capture. Clearly, the snakes emerged massively from their shelter to drink (Fig. 3). During the rain, the snakes were not moving to, or from the sea, as usually observed; they were relatively immobile instead. The vast majority of them, 87%, were drinking (143 snakes
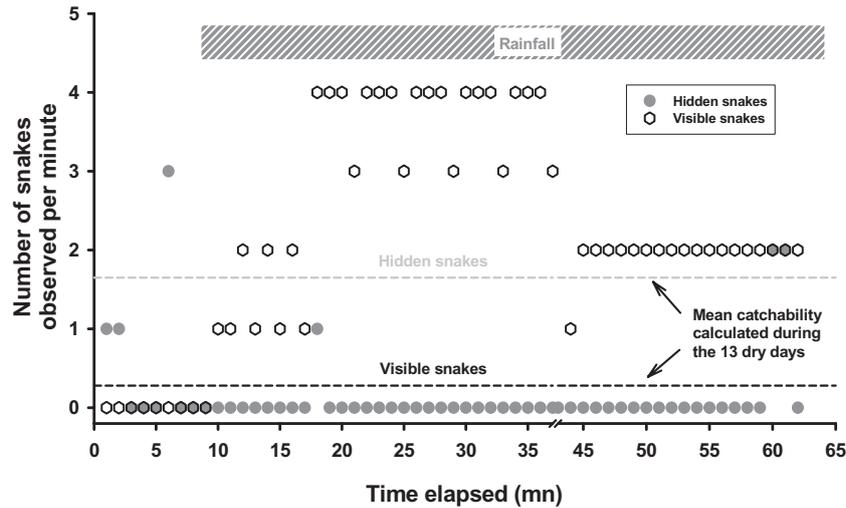
Fig. 3. Precise time-pattern of visibility of sea kraits shortly before (10 min) and during a strong downpour starting at 17.00 hours and that finished at 18.00 hours (rainfall are indicated by the hatched box). The two species, *Laticauda saintgironsi* and *Laticauda laticaudata*, were pooled together. Each circle provides the number of snakes observed per minute, ranging from zero to four (the maximal value owing to the capacity to observe individuals and to record the data). The open circles refer to the visible snakes (e.g. observed drinking in the open); the grey circles refer to the hidden snakes (e.g. found under flat rocks). The 'x' axis indicates the exact timing during the survey, starting at 17.00 hours and lasting roughly 1 h (the break indicates a short interruption of monitoring). The dashed lines indicate the average catchability of the snakes (no. snakes min^{-1}) during the time slot (17.00–18.00 hours) under dry conditions over the 13 previous days. The grey line provides the mean value for the snakes found hidden, and the black line provides the mean value for the snakes found visible.

observed drinking *vs.* 21 not). Fifty snakes have also been observed drinking droplets or from puddles during the first 30 min after the rain stopped. Obviously, during the dry days, we never observed any snake drinking ($n = 1084$; $\chi^2 = 1737.0$, d.f. $= 1$, $P < 0.001$, Fig. 3). The type of precipitation (rain, drizzle) influenced the proportion of drinking snakes. During rainfall, 97% ($n = 122$) of the snakes were drinking; such percentage dropped to 66% ($n = 76$) following the 30 min after the rain stopped, and to 60% during the drizzle ($n = 42$; $\chi^2 = 1074.3$, d.f. $= 3$ $P < 0.001$).

Do individuals select the best quality water?

To address this question we focused on the surveys during which the exact postures of each snake, and the time at observation were systematically recorded. Under wet conditions the different situations, rainfall, drizzle and the post-rain humidity of the vegetation triggered peculiar drinking behaviours.

During rainfall, the first snakes drinking were essentially situated on top of the rocks or logs. For that, they climbed quickly (i.e. as soon as they emerged) onto the nearest relief, positioned their head very close to the top and drank the water. In comparison to the water running to the base of the rocks, the water that collected on the top did not run over the salty substrate (the salt is deposited by the spray and by the tide that

covers a large proportion of the shore twice a day). In support of this, after several minutes of strong rain, the snakes went down and almost all individuals were observed drinking from puddles. A logistic regression with the position of the drinking snakes, on the top versus on the ground, as the discrete dependent variable and the exact time of the observation as the continuous independent variable revealed a significant effect of time ($\chi^2 = 19.80$, d.f. $= 1$, $P < 0.0001$). At the beginning of the surveys carried out in the rain, 64% of the snakes were observed perched on rocks or logs; 30 min later this proportion dropped to 24%. Although we had no means to measure the salinity of the water, the strong and continuous rainfall probably washed the salt rapidly from the substrate. The willingness of the snakes to climb rapidly after the beginning of the rain is further illustrated by an inter-specific comparison. During the strong downpour, within the first 30 min of rain, 28 *L. laticaudata* and 30 *L. saintgironsi* managed to reach the top of the rocks to drink. This proportion was very different from that observed during the next half-hour: 38 *L. laticaudata versus* 12 *L. saintgironsi* were drinking from puddles ($\chi^2 = 8.7$, d.f. $= 1$, $P < 0.01$). The best climbing species (see Bonnet *et al.* (2005) for a comparison of the climbing abilities) exploited more rapidly the fresh water available on top on the relief, whereas the poor climbers relied more heavily on the accumulating water after a delay. Similarly, *L. saintgironsi* represented 96% of all of the snakes observed perched on the top

of the large boulders in the block field. The only snakes that climbed trees were adult *L. saintgironsi*.

During drizzle and after rainfall, many droplets remained attached to the vegetation. The snakes drunk directly from these droplets, and as a result, many were observed in the thick purslanes that border the shore of our study area (58%, *n* = 126).

Overall, the proportion of snakes perched on top of the rocks (*n* = 77) compared to the number of snakes observed on the ground (*n* = 99) or in the purslanes (*n* = 74) was greater during rainfall (51%, *n* = 114) compared with drizzle (26%, *n* = 43), and such proportion decreased after the end of the rain (9%, *n* 93; χ^2 = 106.1, d.f. = 2, *P* < 0.001). The different percentages of snakes drinking the droplets attached to the purslane leafs mirror this trend: 0% during rainfall, 35% during drizzle, and 64% after the rain stopped.

DISCUSSION

Risks associated with the decision to leave a refuge have been widely examined in various taxa (Lima 1998). However, there is little field data revealing clearly ecological circumstances likely to stimulate individuals to emerge from shelter. Indeed, the influence of environmental fluctuations on emergence behaviour rates has been documented on very few occasions, and always in response to food availability and/or predator abundance (Dill & Fraser 1997; Sih 1997; Berryman & Hawkins 2006). Refuges certainly provide safety against predators, but they also offer crucial protection against extreme temperatures, dehydration and various sources of disturbance. In addition, animals leave their shelter not only to forage, but for many other reasons; for instance for reproduction, social interactions, emigration, defecation, etc. Therefore, the trade-offs between the conflicting behaviours linked to the decision to emerge from refuge have been incompletely explored. In this context, our results add fluctuations in freshwater availability as a strong stimulus for emergence. In addition, our results suggest that individuals adjust their behaviour in relation to the type of precipitation, and hence are somehow able to combine complex local information (time of the day, luminosity, strength of the rain, characteristics of substrates etc.) to estimate water availability.

To our knowledge, our study provides the first quantitative information gathered on large numbers of individuals monitored in the field, about the direct effects of precipitation on drinking behaviour associated with major disruption of activity patterns. The alternation of drought and wet conditions had strong effects on the two species of sea kraits examined; and such effects were probably representative of many animal species that, like snakes, spend significant amounts of time hidden in their refuge. Indeed, only strong motivations

such as mate searching, for example, have been identified as factors likely to force snakes to abandon their cryptic habits (Bonnet *et al.* 1999; Shine 2005). Why should fluctuations of freshwater be considered as another major factor for sea krait emergence?

The high skin surface/body volume ratio of sea kraits generates significant movements of Na^+Cl^- through body walls, especially during foraging trips (>10 days, Brischoux *et al.* 2007). To cope with the salinity of the sea, or prolonged droughts when on land, sea snakes can expel salt overload through active physiological mechanisms (Dunson & Robinson 1976; Heatwole 1999). This happens via the activity of sublingual salt glands, a process that requires energy expenditure and entails physiological costs (Potts 1954; Dunson 1968; Dunson & Dunson 1975; Pequeux & Gilles 1978; Shuttleworth & Thompson 1987; Shuttleworth & Hildebrandt 1999; Reina *et al.* 2002). The benefits associated with fresh water intake likely overwhelmed the potential risks associated with emergence from refuges. In addition, a recent study suggests 'that sea snakes do not drink sea water and require fresh water to replenish water stores that are depleted by dehydration in air or water' (Harvey B. Lillywhite *et al.*, unpubl. data, 2007). Taken together, these ecophysiological data show that drinking freshwater was important for sea kraits because they potentially suffer from dehydration in their natural habitat (Harvey B. Lillywhite *et al.*, unpubl. data, 2007). As expected, such physiological requirements entailed marked behavioural responses.

The well-defined general activity patterns of two species of snakes monitored over several years, on various sites, and on large samples led to robust patterns. Sea kraits exhibited precise timing to undertake displacements between their terrestrial shelter and the sea (Figs 1,2). The non-random timing of displacements suggests that important benefits are associated with the observed patterns. The snakes undertake displacements on land (going to, or coming back from the sea) once a week on average, the typical duration of a foraging trip or of a digestive episode (Shetty & Shine 2002; Brischoux *et al.* 2007; Ineich *et al.* 2007). In the absence of rain, the majority of individuals remained concealed. They selected precise time periods, around dusk, to cross the beach and to cover the open distance between the sea and their refuge. This reinforces the notion that the snakes are very secretive, and behave carefully with regards to the environmental conditions during displacements in the open that last only a few minutes (often less than 1 min, Xavier Bonnet, François Brischoux, unpubl. data, 2006) per week. Perhaps the sea kraits decided to move at dusk and at night, after the sunlight decreased, to limit their visibility (on land and/or at sea) and predation by birds or fish? Alternatively, they may have also avoided the hot temperatures of the substrates

during the day; we note however that the patterns held true under dry and cloudy days and that the snakes remained sheltered in the early morning when the substrate was still cool.

By contrast, during rainfall and drizzle the two snake species adopted very conspicuous behaviours. Indeed, the stochastic availability of freshwater systematically disrupted very quickly the usual pattern of activity. To drink, concealed snakes rapidly left shelter, remained motionless and highly visible in the open, and exhibited different types of behaviours, including unusual climbing postures.

One of the most surprising behaviours was the eagerness shown by large numbers of individuals to perch on top of rocks and logs as soon as the first drops touched the soil. Sea kraits have the ability to climb steep cliffs; such aptitude is well developed in *L. saintgironsi* but less expressed in *L. laticaudata* (Bonnet *et al.* 2005). Therefore, it was not surprising to see that many *L. saintgironsi* quickly exploited their climbing talent likely to reach the best quality water. Nonetheless, despite lower abilities, many blue sea kraits managed to perch on the rocks with the head oriented to the top to drink. Such willingness to climb suggests that the snakes somehow estimated that the availability of freshwater was potentially limited in time. After a time delay, the downpours and the strong rainfall supposedly washed the salt from the surface, and many blue sea kraits came out of their shelter to drink from puddles. By contrast, few yellow sea kraits were observed drinking from puddles, probably because their climbing abilities enabled them to access easily and rapidly freshwater as soon as it was available.

Drinking behaviours during drizzle or after the rainfall stopped brought further evidence that the sea kraits adjust their behaviour with regard to water availability. When droplets attached to the vegetation was the only accessible form of water, many snakes were observed sucking up patiently one droplet after the next. This was a time-consuming task compared to drinking directly from puddles or running water. Because sea kraits can ingest large amounts of water when drinking (Xavier Bonnet, François Brischoux, unpubl. data, 2005), it was not surprising to observe that drinking from droplets was abandoned when puddles and streams were available.

Overall, when on land, sea kraits remained concealed under large rocks or within burrows most of the time, probably to avoid overheating, disturbance and to minimise evaporative water loss (Lillywhite in press), and/or to escape predation. The strong motivation of the snakes to drink intermittent fresh water suggests that they may save sufficient amounts of energy (Nagy & Medica 1986). Such effects combined with irregular precipitations both in their occurrence and form (rainfall, drizzle) constitute the substrate for natural selection to favour the development of ephemeral, albeit spectacular, drinking behaviours.

ACKNOWLEDGEMENTS

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