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Conflicts between feeding and reproduction in amphibious snakes (sea kraits, *Laticauda* spp.)

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Abstract If reproduction impairs an organism's ability to perform other fitness-related activities, natural selection may favour behavioural adjustments to minimize these conflicts. This is presumably the reason why many animals are anorexic during the breeding season. We studied amphibious sea snakes, a group whose ecology facilitates teasing apart the causal links between reproduction and feeding. In both *Laticauda laticaudata* and *L. saintgironsi* in New Caledonia, adult females cease feeding as their eggs develop. The advantages of foregoing feeding do not relate to thermoregulation (because foraging does not entail lower body temperatures), nor are they attributable to physical constraints on abdominal volume (because in a snake's linear body, there is little overlap between the stomach and the oviducts). Instead, female sea kraits appear to cease feeding because their bodily distension impedes locomotor ability, rendering them less effective at foraging and more vulnerable to aquatic predators.

Key words: anorexia, bodily distension, reproduction, sea snake.

INTRODUCTION

In many species, reproduction entails major changes to morphology (e.g. antlers in male deer; bodily distension in pregnant mammals), behaviour (activity levels, rates of display) and ecology (habitat use, movement patterns) (Beier & McCullough 1990; Andersson 1994; Rodewald & Foster 1998; Shaffer *et al.* 2003). Some of those changes (e.g. antlers) clearly reflect adaptations that enhance reproductive success, but others (e.g. bodily distension) are direct consequences of reproductive investment. Life history theory suggests that the form and magnitude of the costs of reproduction (i.e. the fitness consequences of reproduction-enforced changes) can substantially affect selection on optimal reproductive tactics (Shine 1980; Stearns 1992). One common result of such selection may be a temporal displacement in activities incompatible with reproduction; and one widespread example of this phenomenon is anorexia in reproducing animals (Mrosovsky & Sherry 1980; Sherry *et al.* 1980). For example, male elephant seals do not feed during their mating season, because the sites that allow feeding do not provide access to females (Le Bouef 1974; Anderson & Fedak 1985).

Temporal dissociation between foraging and reproduction (capital breeding) is widespread in ectotherms, because their low metabolic rates allow them to persist for long periods on stored reserves (Pough 1980; Shine 1988; Bonnet *et al.* 1998). For example, gravid females of many snakes species feed rarely or not at all (reviewed in Table 1). Previous studies generally have interpreted the anorexia of gravid snakes as an adaptation to avoid predators and/or to carefully thermoregulate (Shine *et al.* 1997; Gregory *et al.* 1999; Lourdais *et al.* 2002). Although this anorexia is widespread, its causal basis is unclear. Reproductive females might forego feeding because of physical constraints (eggs take up abdominal space that would otherwise allow gut distension: see Weeks 1996; Gregory *et al.* 1999) or adaptation (if the presence of eggs conflicts with foraging, either through impaired locomotor ability or unfavourable thermal regimes enforced by foraging habitats).

Distinguishing among potential causal factors for reproduction-induced anorexia is difficult in most species, but some taxa provide excellent opportunities for such an analysis. We focus on amphibious sea snakes (sea kraits, Laticaudinae), that forage entirely in the ocean (for fish) but return to small islets to bask, slough, digest their prey, mate and oviposit (Heatwole 1999; Shetty & Shine 2002; Brischoux & Bonnet 2009). Sea kraits are well suited to such an analysis because: (i) as ectotherms, they can survive long periods without feeding and hence potentially can dissociate foraging from reproduction; (ii) as snakes, their linear body plan facilitates quantification of the degree

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Table 1. Effect of reproduction on food intake in female snakes

Family	Species	Mode of reproduction	Food intake reduced	Source
Boidae	*Acrantophis madagascariensis*	Viviparous	Yes[†]	Branch and Erasmus 1976
	Antaresia childreni	Oviparous	Yes[†]	Lourdais *et al*. 2008
	Liasis fuscus	Oviparous	Yes	Madsen and Shine 2000
	Morelia spilota	Oviparous	Yes[†]	Shine 1980
	Lichanura roseofusca	Viviparous	Yes[†]	Kurfess 1967
	Python molurus	Oviparous	Yes[†]	Van Mierop and Barnard 1978
	P. regius	Oviparous	Yes[†]	Ellis and Chappell 1987
	P. sebae	Oviparous	Yes	Fitzsimons 1930
Colubridae	*Coluber hippocrepis*	Oviparous	Yes	Pleguezuelos and Feriche 1999
	Cylindrophis rufus	Viviparous	Yes	Brooks *et al*. 2009
	Elaphe obsoleta	Oviparous	Yes	Blouin-Demers and Weatherhead 2001
	Grayia smithii	Oviparous	Yes	Akani and Luiselli 2001
	Lampropeltis triangulum	Oviparous	Yes[†]	Tryon and Hulsey 1976
	Natrix natrix	Oviparous	Yes	Gregory and Isaac 2004
	Nerodia sipedon	Viviparous	No[†]	Brown and Weatherhead 1997
	Oxyrhopus guibei	Oviparous	Yes[†]	Pizzatto and Marques 2002
	Psammophis phillipsi	Oviparous	Yes	Akani *et al*. 2003
	Seminatrix pygaea	Viviparous	No	Winne *et al*. 2006
	Thamnophis elegans	Viviparous	Yes	Gregory *et al*. 1999
	T. ordinoides	Viviparous	Yes	Brodie 1989
	T. sirtalis	Viviparous	Yes	Gregory and Stewart 1975
	Tropidoclonion lineatum	Viviparous	Yes[†]	Ramsey 1946
	Tropidonophis mairii	Oviparous	Yes	Brown and Shine 2004
	Xenochrophis piscator	Oviparous	No	Brooks *et al*. 2009
Elapidae	*Acantophis antarticus*	Viviparous	Yes	Mirtschin 1976
	A. praelongus	Viviparous	Yes	Schultz *et al*. 2008
	Austrelaps labialis	Viviparous	Yes	Shine 1987
	A. ramsayi	Viviparous	Yes	Shine 1987
	A. superbus	Viviparous	Yes	Shine 1987
	Drysdalia coronata	Viviparous	Yes	Shine 1981
	D. coronoides	Viviparous	No	Shine 1981
	Laticauda laticaudata	Oviparous	Yes	This study
	L. saintgironsi	Oviparous	Yes	This study
	Notechis scutatus	Viviparous	Yes	Shine 1979
	Ophiophagus hannah	Oviparous	Yes	Leakey 1969
	Pseudechis porphyriacus	Viviparous	Yes	Shine 1979
Homalopsidae	*Enhydris bocourti*	Viviparous	No	Brooks *et al*. 2009
	E. enhydris	Viviparous	Yes	Brooks *et al*. 2009
	E. longicauda	Viviparous	No	Brooks *et al*. 2009
	Erpeton tentaculatus	Viviparous	No	Brooks *et al*. 2009
	Homalopsis buccata	Viviparous	No	Brooks *et al*. 2009
Viperidae	*Agkistrodon contortrix*	Viviparous	Yes	Fitch & Shirer 1971
	A. piscivorus	Viviparous	Yes[†]	Crane & Greene 2008
	Calloselasma rhodostoma	Oviparous	Yes	Daltry *et al*. 1998
	Causus lichtensteinii	Oviparous	No	Ineich *et al*. 2006
	C. maculatus	Oviparous	No	Ineich *et al*. 2006
	C. resimus	Oviparous	No	Ineich *et al*. 2006
	C. sp.	Oviparous	No	Ineich *et al*. 2006
	Crotalus enyo	Viviparous	No[†]	Tryon & Radcliffe 1977
	C. horridus	Viviparous	Yes	Keenlyne 1972
	C. unicolor	Viviparous	Yes[†]	Kauffeld & Gloyd 1939
	C. viridis	Viviparous	Yes	Fitch & Glading 1947
	Sisturus catenatus	Viviparous	Yes	Keenlyne & Beer 1973
	Vipera aspis	Viviparous	Yes	Lourdais *et al*. 2002
	V. berus	Viviparous	Yes	Prestt 1971
	V. ursinii	Viviparous	No	Baron *et al*. 1996

[†]indicates records based on captive specimens.

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to which food-induced bodily distension would conflict with egg-induced bodily distension; and (iii) as amphibious animals, the cessation of foraging entails a shift from aquatic to terrestrial activity, rendering it straightforward to evaluate potential costs (such as exposure to predation or suboptimal thermal regimes). Based on a 6-year mark–recapture study, the aim of this paper was to quantify if reproduction induces a decrease of feeding in female sea kraits (as it does in many snake species, Table 1). Additionally, we set out to compare the different factors potentially responsible for reproductive anorexia, such as reduced mobility (quantified in Shine & Shetty 2001), available thermal regimes at sea and on land (measured in Brischoux *et al.* 2007b,c, 2009b; Bonnet *et al.* 2009) and conflicts between food-induced and egg-induced bodily distension (this study).

METHODS

Study species

Laticaudine sea kraits are front-fanged (proteroglyphous) venomous elapid snakes, common through much of the Indo–Pacific region (Heatwole 1999). We studied two species, *Laticauda laticaudata* and *L. saintgironsi*, that are broadly sympatric on small islets in the Lagoon of New Caledonia (see Brischoux & Bonnet 2009 for details). Both species grow to approximately 1.2 m in length, and feed exclusively on marine fishes (mostly anguilliforms, sometimes almost as large as the snakes that consume them: Brischoux *et al.* 2007b, 2009a). Locomotor trials have shown that the presence of a prey item in the stomach reduces swimming speeds (Shine & Shetty 2001), and phylogenetic shifts in the volume and anatomical position of oviductal eggs in aquatic snakes argue that reproduction imposes a locomotor cost also (Shine 1988). The major predators of sea snakes likely are sharks and other large fishes (see Ineich & Laboute 2002). In contrast, adult snakes appear to be relatively invulnerable to predation while on land; our study sites do not contain any large terrestrial or avian predators known to feed on these snakes (Brischoux & Bonnet 2009).

Feeding frequency and reproductive status

Data for the present analysis were gathered during a 6-year mark–recapture study on these animals. Prey items, vitellogenic ovarian follicles and oviductal eggs are easily palpated in these slender-bodied animals, and we routinely recorded the presence and sizes of such items when we processed snakes (see Brischoux & Bonnet 2009 for details of the procedures).

Fine-scale body measurements

In order to locate and quantify prey-induced and egg-induced bodily distensions, we made precise morphological measurements. To quantify the typical shape of a female sea krait, we measured the snout–vent length (SVL, ±0.5 cm) and total length (TL, ±0.5 cm) of six adult females of each species, as well as body diameter at intervals along the snake's length (every 4.6 ± 0.7% of SVL, ±0.5 mm). The distension induced by an ingested prey item was quantified from data on body diameters of 21 females with food in the stomach ($n = 13$ *L. laticaudata* and $n = 8$ *L. saintgironsi*). Mean prey length was calculated from 88 regurgitated prey items ($n = 19$ *L. laticaudata* and $n = 69$ *L. saintgironsi*; see Brischoux *et al.* 2007a) and mean pylorus position was calculated from the posteriormost position of 16 prey items palpated inside females ($n = 8$ *L. laticaudata* and $n = 8$ *L. saintgironsi*) and 9 specimens dissected at the Australian Museum ($n = 3$ *L. laticaudata* and $n = 6$ *L. saintgironsi*). The two methods (palpation and dissection) yielded similar results.

Reproduction-induced distension was quantified for *L. laticaudata* only, as it was the only species reproducing at the time we took these data (Brischoux & Bonnet 2009). We measured the linear position of vitellogenic follicles and eggs (by palpation) on five females, and measured body diameters at regular intervals along the body (as above) of four of these animals.

RESULTS

Cessation of feeding by gravid snakes

Based on a sample of more than 1300 snakes ($n = 367$ and $n = 194$, respectively, for non-reproductive and reproductive *L. laticaudata* and $n = 617$ and $n = 208$, respectively, for non-reproductive and reproductive *L. saintgironsi*; restricted to reproductive periods, see Brischoux & Bonnet 2009), reproduction entailed a reduction of feeding rates in both *Laticauda* species (comparing reproductive and non-reproductive females for *L. laticaudata* and *L. saintgironsi*, respectively, $\chi^2 = 14.50$, d.f. = 1, $P < 0.001$ and $\chi^2 = 10.24$, d.f. = 1, $P < 0.01$), and ultimately, a total cessation of feeding (Fig. 1). On average, 76% of non-reproductive *L. laticaudata* and 79% of non-reproductive *L. saintgironsi* contained food, but this proportion fell consistently as ovarian follicles increased in size (Fig. 1; logistic regressions, $\chi^2 = 8.64$, d.f. = 1, $P < 0.01$ for *L. laticaudata* and $\chi^2 = 21.71$, d.f. = 1, $P < 0.001$ for *L. saintgironsi*).

Bodily distension and linear overlap between prey items and eggs

Both prey ingestion and pregnancy distend snake body shape but there is little overlap (<5% of the SVL in almost every case) between the distensions created by prey *versus* eggs, because the stomach lies anterior to the ovaries and oviducts (Fig. 2). If this minor overlap

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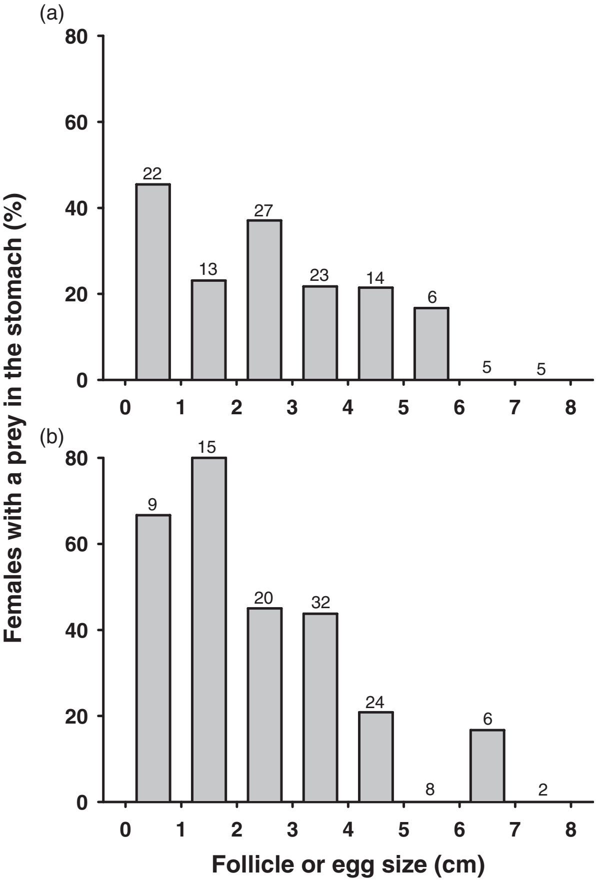

Fig. 1. Proportion of reproductive females with a prey item in the stomach in the sea kraits (a) *Laticauda laticaudata* and (b) *L. saintgironsi* relative to follicle/egg size. This proportion fell consistently as ovarian follicles increased in size. The numbers above the bars represent the sample sizes for each follicle/egg size category. For comparison, 76% of non-reproductive *L. laticaudata* and 79% of non-reproductive *L. saintgironsi* contained food.

was significant, we might expect to see a progressive decrease in prey length as the ovarian follicles enlarge (i.e. the prey need to fit into the shrinking proportion of body not distended by developing ova). Our data do not support this scenario: the linear space occupied by eggs (egg number * egg size) was not significantly correlated with prey size (Spearman rank correlations between linear space occupied by the eggs and prey diameter (a robust predictor of prey length: Brischoux *et al.* 2007a), $r_s = -0.36$, $P > 0.05$ for *L. laticaudata* and $r_s = -0.26$, $P > 0.05$ for *L. saintgironsi*). Hence, the presence (and growth) of follicles or oviductal eggs seems to have little effect on the snake's capacity to ingest a large prey item.

DISCUSSION

Reproduction reduces feeding rates of female sea kraits, as it does in many snake species (Table 1). However, gravid females continue to feed through pregnancy in some snake taxa, including some aquatic homalopsines and natricines (Table 1). Previous studies generally have interpreted the anorexia of gravid snakes as an adaptation to facilitate careful behavioural thermoregulation at temperatures that optimize offspring development (e.g. Gregory *et al.* 1999). Although this explanation is compelling for cool-climate species that must sun-bask to maintain high temperatures, it is not applicable to sea kraits. Most terrestrial retreat sites offer thermal regimes similar to those experienced when snakes are foraging at sea (difference in mean body temperatures on land *vs.* at sea <3°C for *L. laticaudata*, <1°C for *L. colubrina*: Brischoux *et al.* 2007b,c, 2009b; Bonnet *et al.* 2009). Why, then, do female sea kraits cease feeding?

Our morphological data do not support the interpretation of physical constraint. Distension caused by a full stomach involves the anterior part of a snake, whereas distension caused by oviductal eggs involves the posterior part (Fig. 2). Thus, even a fully gravid snake would be physically capable of ingesting a large prey item. Other body plans may create greater conflicts and enforce stronger trade-offs (Weeks 1996), but the linear arrangement of internal organs in a snake generally minimizes those effects (Pizzatto *et al.* 2007; but see Daltry *et al.* 1998 for an example of severe reproductive burden).

If gravid sea kraits could physically accommodate a large meal, and would suffer no thermal penalty for foraging, why do they stop feeding? The likely answer is that the bodily distension imposed by oviductal eggs impairs swimming ability (Webb 2004; Winne & Hopkins 2006) as has been shown for prey-induced distension (Shine & Shetty 2001). That inference is supported by a consistent trend for the invasion of aquatic habitats to be accompanied by a reduction in the size of the clutch, and a shift in the position of the clutch within the female's body in a way that reduces the negative impact of bodily distension on swimming performance (Shine 1988). A wider body also may impair a snake's ability to penetrate small coral interstices in search of anguilliform prey (Brischoux *et al.* 2009a).

Under this scenario, a gravid female snake faces higher costs during foraging (slower and less efficient travel to foraging areas; reduced foraging ability; reduced ability to evade predators). By remaining on land (i.e. foregoing feeding), such a snake loses relatively little (as foraging would likely be energetically expensive and/or unproductive) and gains in terms of safety (because she is safer on land than in the water). Reduced foraging ability and risk aversion thus seem the likeliest reasons for cessation of feeding by reproductive female sea kraits. In addition, female sea kraits are characterized by low breeding frequency:

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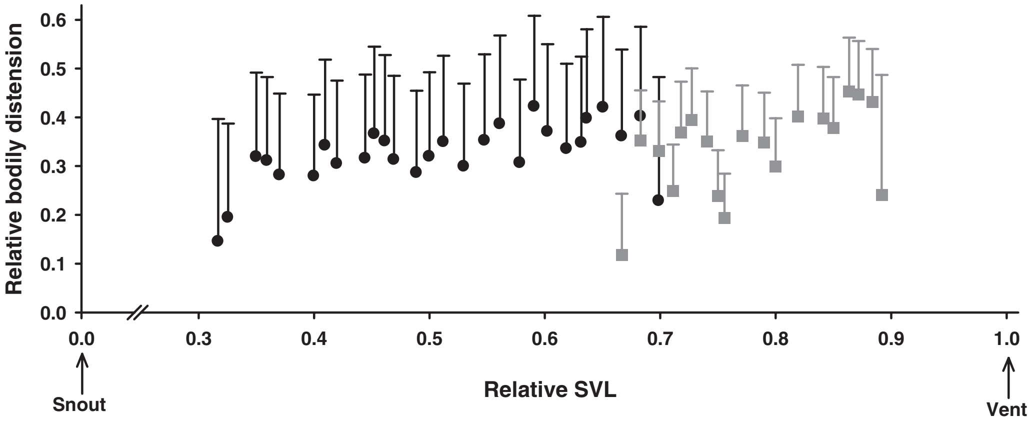

Fig. 2. Bodily distensions caused by the presence of a prey in the stomach (black circles, mean ± SD) or growing follicles eggs in the ovaries/oviducts (grey squares, mean ± SD) along the body length of females *Laticauda laticaudata*. The bodily distensions (increase in body diameter) are given as a proportion of the body diameter of a typical (unfed and non-reproductive) adult female *L. laticaudata*. Note that the overlap between a prey and the follicles/eggs is very low (<5% of the SVL). SVL, snout–vent length.

each clutch represents a considerable reproductive asset (Brischoux & Bonnet 2009; François Brischoux, Xavier Bonnet and Richard Shine 2009). Therefore, female sea kraits should minimize any additional costs when oviposition is near (Clark 1994; Gordon & Saint-Amour 2004). Why, then, are some females with advanced follicles still found with food in the stomach (Fig. 1)? A simple explanation could involve the duration of foraging trips. The time elapsed between the capture of a prey item and the snake's return to its home-islet could be long enough (up to 5 days: Brischoux *et al.* 2007b) for ovarian follicles to increase in size.

The progressive decrease in feeding rate with increasing follicle size (Fig. 1) suggests that this anorexia is not a threshold effect, but instead relates to increasing degrees of female burdening that render foraging less productive and increasingly risky. Further research to evaluate the locomotor consequences of bodily distension (both by eggs and by prey; and both on land and in the water) could help to test our interpretation. In particular, the wide ranges of distensions induced both by ova and by prey, and the frequent combination of the two early in the female reproductive cycle, provide robust opportunities to examine the performance consequences of simultaneous feeding and ovarian growth.

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