

# Adaptive maternal cannibalism in snakes (*Epicrates cenchria maurus*, Boidae)

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In many animal species, mothers that produce stillborn offspring or undeveloped ova immediately ingest them. This cannibalism has been interpreted in two ways: (1) as a form of parental care (to prevent disease spreading to healthy littermates, and eliminate predator-attracting scent cues); or (2) to recycle otherwise wasted energy, thus facilitating maternal recovery. Our experimental study on captive Colombian rainbow boas (*Epicrates cenchria maurus*) provides the first quantitative support for this latter hypothesis. We show that by eating their non-viable offspring and undeveloped eggs, female boas can rapidly recycle a significant component of their otherwise wasted reproductive investment. Female boas that ingested non-viable progeny equivalent to half their litter mass exhibited rapid recovery of dorsal musculature and hence were able to constrict prey items more forcefully than were unfed females when tested 2 weeks after parturition. The consequent enhancement of constricting ability may influence maternal survival and foraging success. Thus, maternal cannibalism may be an effective tactic to avoid wasting reproductive resources, and to shorten the period required for recovery from pregnancy. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 84, 767–774.

ADDITIONAL KEYWORDS: eggs – filial cannibalism – musculature – stillborn.

## INTRODUCTION

Although early studies in animal behaviour generally regarded cannibalism (consumption of conspecifics) as an infrequent and maladaptive trait, more recent research has shown that cannibalism occurs commonly under natural conditions in a diversity of animal species (Lorenz, 1966; Wilson, 1975; Polis, 1981). One superficially perplexing form of cannibalism involves the consumption of offspring by their own parents. Intuition suggests that a parent would be likely to reduce rather than enhance its own fitness by consuming its offspring. Surprisingly, however, filial cannibalism is common, suggesting that it has an adaptive basis (Polis, 1981). For example, filial cannibalism occurs in many species in which males guard developing eggs, but occasionally consume some of the

clutch they are 'protecting' (Rohwer, 1978; Petersen & Marchetti, 1989; Thomas & Manica, 2003). One possible resolution to this paradox is that fitness benefits to the parents (and possibly, other offspring) may outweigh the reduction in effective reproductive output, especially during periods of food scarcity (Polis, 1981).

Clearly, we would expect filial cannibalism to enhance parental fitness most directly if the offspring that are consumed are already dead. In keeping with this prediction, females of many animal species have been reported to selectively ingest non-viable offspring (undeveloped eggs and stillborn neonates: Lorenz, 1955; Kevles, 1986; Mitchell & Groves, 1993; Somma, 2003). Scientific discussion of this phenomenon broadly agrees on the idea that such filial cannibalism does not confer fitness costs (because the offspring have no possibility of reproductive success) and hence should evolve so long as there are significant fitness benefits. However, the nature of these benefits has

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been a source of debate, with two main hypotheses proposed.

The first is that filial cannibalism is a form of parental care, with the primary fitness benefit accruing to this behaviour involving siblings of the dead neonates (Polis, 1981). For example, by eating dead or decaying offspring, the female can prevent the spread of disease or fungal infection to the entire clutch (Polis, 1981; Somma, 1989, 1990, 2003). This behaviour may also erase chemical clues that otherwise could attract predators (Groves, 1981; Polis, 1981; Shine, 1988; Somma, 1990).

Alternatively, the fitness benefit to selective cannibalism may accrue to the parent rather than to the siblings: a female that eats her stillborn neonates may thereby recoup some of the resources that she has expended during pregnancy, and can do so without the potentially risky and energy-expensive activities required for normal foraging (Fitch, 1954). Eggs and newborns typically are rich in nutrients (Polis, 1981; White, 1991; Speake *et al.*, 2003) and may provide a substantial energy resource as well as raw materials for tissue synthesis. By ingesting such items, a female might substantially accelerate her recovery from pregnancy.

Despite the formulation of clear alternative hypotheses on the adaptive significance of selective maternal cannibalism (above), these possibilities remain largely untested. Part of the reason for this neglect involves logistical problems, especially with species (such as most endothermic vertebrates) where parents care for the offspring over a long period during which cannibalism can occur at any time. In such cases, any energy consequences of filial cannibalism must be interpreted within a complex framework of the parents' rates of energy acquisition and expenditure during the period of parental care. Squamate reptiles (lizards and snakes) offer simpler and more logistically feasible systems in which to quantify the potential nutritional benefits of cannibalism to a reproducing female. Parental care (if present) typically ceases at parturition or hatching (Shine, 1988; Somma, 2003) and thus the nutritional effects of cannibalism can be measured at a time (postpartum) when the female is not continuing to invest in the surviving offspring. In many squamate species, the litters of some females contain stillborn neonates and/or undeveloped ova (Ross & Marzec, 1990; Mitchell & Groves, 1993). While the proximate mechanisms are poorly known, records of partial or even complete reproductive failures have been obtained in natural conditions (Bonnet *et al.*, 2003; Lourdais *et al.*, 2002, 2004b; Taylor and DeNardo, pers. comm.). Ingestion of these non-viable offspring by the mother has been reported in several squamate taxa (Ross & Marzec, 1990; Mitchell & Groves, 1993; Somma, 2003).

One lineage in which mothers frequently ingest their undeveloped ova and/or stillborn neonates comprises tropical boas of the genus *Epicrates* (Groves, 1981; Mitchell & Groves, 1993 and references therein). We set out to quantify the energetic consequences of maternal cannibalism in a colony of captive rainbow boas (*Epicrates cenchria maurus* Gray, 1849). In another study on the same colony, we have shown that gestation imposes substantial costs not only in terms of depleted energy stores, but also in reduction of the female's dorsal musculature (and thus, her ability to constrict prey) due to mobilization of protein reserves during pregnancy (Lourdais *et al.*, 2004a). Thus postparturient females are weak as well as emaciated, and take several weeks to recover from this condition. In this context, ingestion of non-viable neonates may allow a female not only to recoup energy, but also to restore her body musculature. Because these are separate and biologically significant aspects of maternal physiology, we attempted to assess the effects of filial cannibalism on rates of maternal recovery in muscular strength as well as energy stores.

## MATERIAL AND METHODS

### MODEL SPECIES AND MAINTENANCE

Colombian rainbow boas (*Epicrates cenchria maurus*) are medium-sized (up to 1500 mm snout–vent length) non-venomous constricting snakes from South and Central America (Ross & Marzec, 1990; Matz, 2001). The snakes in our study (22 females, plus 20 males used for matings) were maintained in the laboratory in separate enclosures (50 × 50 × 20 cm), each providing access to a heat source (temperature range in the cage: 28–33 °C). Water was available *ad libitum*.

Mating occurred after a 1.5-month wintering period (Ross & Marzec, 1990) in an open enclosure (2.5 × 1.5 m) with a heat source and water, with each female exposed to numerous males over a three-week period. Copulation was frequently observed. After mating, we used ultrasonography to assess reproductive status and determine litter characteristics before parturition.

The components of the litter were characterized (undeveloped ova, stillborns, healthy offspring), counted, and weighed ( $\pm 0.1$  g). Additionally, young and stillborns were measured ( $\pm 0.5$  cm) and sexed. Because we could not distinguish unfertilized ova from ova that had been fertilized but had died early in embryogenesis, these were grouped in the same category (undeveloped ova). Stillborn offspring are easy to recognize in snakes. Pigmentation occurs only at the latest stages of embryonic development, and late embryonic death typically results in dull skin coloration. Also, stillborns often showed axial deformation

and/or significantly smaller body size. Litters were removed shortly after parturition as postparturient females often ingest their stillborns and undeveloped eggs. When this happened, we used gentle stomach flushing to retrieve the ingested elements of the litter. For three females, we were unable to obtain complete stomach contents; in these cases the ingested ova were identified by palpation.

#### EVIDENCE OF MATERNAL CANNIBALISM

We recorded parturition of 14 litters in the first year of our study, and ten in the second (total of 18 different females). The production of non-viable elements, stillborns, and undeveloped eggs was common (occurrence: 19 of 24 litters). The number of non-viable elements varied significantly among litters (see Table 1). The average number of non-viable elements produced was  $5.47 \pm 3.54$ , representing an average mass of  $95.96 \pm 66.6$  g. Of 12 females that gave birth at night (and thus were not disturbed during parturition), all ingested these non-viable elements. Abdominal palpation and stomach-flushing of these animals confirmed that all had consumed stillborns or undeveloped ova, and none had ingested live neonates. Females that were disturbed during parturition often did not eat their non-viable offspring; the latter were stored at  $-25$  °C prior to use in the experiment described below.

#### EXPERIMENTAL DESIGN

In the second year of the study, we examined the effects of females consuming their non-viable progeny.

**Table 1.** Production of non-viable elements (NVE = stillborn and/or undeveloped ova) during the two years of the study. For three females (ND), complete stomach contents could not be obtained and the mass of undeveloped eggs was not available

No. NVE produced/litter	No. litters	Mass NVE (g)
0	5	0
1	2	$27.70 \pm 6.8$
2	4	$44.18 \pm 9.57$
3	2	$61.45 \pm 10.81$
4	1	ND
5	1	78.15
6	1	ND
7	1	125.4
8	2	$127.68$ (1 ND)
9	2	$184.17 \pm 107.8$
10	2	$142.90 \pm 14.0$
12	1	195

During this year, both reproducing ( $N = 10$ ) and non-reproducing females ( $N = 12$ ) experienced a prolonged fast (3 months) before the first parturition occurred. In a sister study (Lourdais *et al.*, 2004a) we found that this extended anorexia translated into a significant mass loss and a decrease in musculature in both groups. Additionally, we found that postparturient females were weaker and less muscular than the 12 non-reproducing females, reflecting the high energy requirements of reproduction. The latter group was also used in the present study as a control and was kept under the same conditions; it was not fed and thus faced an additional 2 weeks of fasting.

Because our sample size in the current study was limited, we fed all the postparturient females ( $N = 10$ ) to test whether cannibalism facilitated recovery in musculature and performance (see details below). Each postparturient female was gently force-fed undeveloped eggs and stillborns (2–3 eggs + 2–3 stillborns, average total mass:  $100.32 \pm 15.9$  g = 51.3% of the litter mass). Importantly, this treatment represented an average level of reproductive failure and litter ingestion. It was thus realistic, as some females actually produced up to 260 g of non-viable elements.

We measured musculature and strength (see below) for each female 1 day before force-feeding and 2 weeks afterwards. The same measurements were made in the control group of (unfed) non-reproductive females. Our experimental design thus confounds reproductive status with feeding status (i.e. all non-reproductive females were unfed, and all postparturient females were fed), but in this respect it exactly mimics the situation in nature (i.e. non-reproductive females would never normally feed on neonates).

Importantly, the two groups of females (postparturient and non-reproductive) are comparable as both previously faced an extended and similar fasting period (3 months; these results are described in Lourdais *et al.*, 2004a). Additionally, the comparison for each individual measured before and after feeding provides direct evidence on the changes that occurred at this time.

#### VARIABLES EXAMINED

##### *Changes in epaxial musculature*

In snakes, the complex epaxial muscles lying beside the vertebral column are of primary importance for locomotion (Cundall, 1987) and constriction (Moon, 2000). Magnetic resonance imaging (MRI) of epaxial musculature in rainbow boa shows that external measurements of muscle width with callipers provide accurate estimates of actual muscle dimensions (Lourdais *et al.*, 2005). On each snake, we measured the width of the epaxial muscles at four equally spaced points between the head and the vent.

### Performance measures

Boid snakes rely upon muscular contraction to generate the forces needed to subdue and kill prey by constriction, as well as to escape from predators (Cundall, 1987). We measured muscular strength of postparturient snakes (and non-reproductive females, tested at the same time) in three contexts designed to mimic these biologically important situations. The relevance of those estimators is established in the sister study (Lourdais *et al.*, 2005).

(1) *Escape from predator*: These snakes react to handling, especially attempts to stretch out their bodies, by vigorous and extended body contraction. We quantified the strength of these contractions using a dynamometer (Pesola, Baar, Switzerland) connected to the snake's tail. Whole body contraction was stimulated by gentle palpation of the back and resulted in a displacement of a cursor on the dynamometer. The highest tension value obtained during 5 minutes of stimulation was recorded.

(2) *Prey handling*: We measured the intensity of muscular contraction during prey constriction using a compressible lure (10 cm long  $\times$  2 cm diameter water-filled rubber balloon surrounded by mouse-scented cloth; Lourdais *et al.*, 2004a). The lure was connected to an open water column via a rigid plastic tube (5 mm in diameter). Snakes readily bit and coiled around the lure, which was then wiggled for 10 s to simulate normal prey reactions; this movement stimulated continued constriction. Displacements of the water column were videotaped so that maximal displacement could be measured (cm) at a later time.

(3) *Climbing ability*: When held by the tail, these snakes orientate the head upwards and climb up their own body towards the hand of the operator. We measured the length of time it took for the snakes' heads to reach the operator's hand (three consecutive trials) as an index of arboreal manoeuvrability.

### STATISTICS

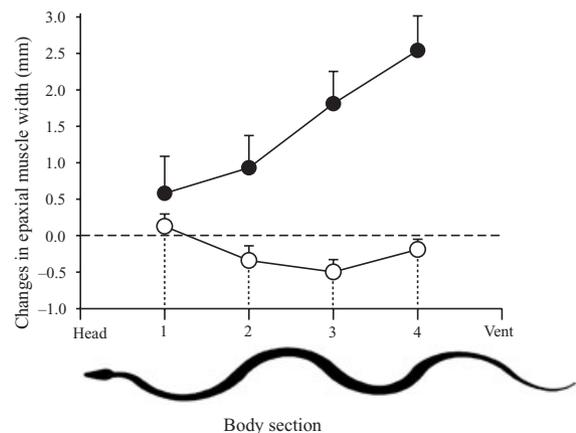
All statistics were performed with Statistica 6.0. To evaluate changes in musculature width we performed repeated-measures analysis of variance (ANOVA) with epaxial muscle width as the dependent variable, body section as a fixed factor and individual identity as a random factor. We also conducted separate repeated-measures ANOVA analyses (with epaxial muscle width as the dependent variable) for each body section. We used paired *t*-tests to assess changes in locomotor, predation and antipredator performance, comparing the values obtained before and 2 weeks after feeding. To compare musculature profiles of non-reproducing and postparturient females after treat-

ment, we conducted a mixed model ANCOVA (using treatment and body section as factors, snout-vent length as covariate, and individual identity as a random factor). Finally, differences in performance between the two groups were assessed using *t*-tests for independent samples. Unless otherwise stated, values in the text are reported as means  $\pm$  standard deviation and statistical significance was considered to be  $< 0.05$ .

## RESULTS

### CHANGES IN EPAXIAL MUSCULATURE

At the beginning of the experiment, postparturient females were less muscular than the non-reproductive females, particularly in the posterior body (sections 3 and 4: see initial measurements, Table 2; Lourdais *et al.*, 2004a; for statistics). Females that ate undeveloped eggs and non-viable offspring exhibited a significant increase in muscle width (mean values  $15.54 \pm 2.89$  vs.  $17.01 \pm 2.47$  mm, before and after, respectively; time effect:  $F_{(1,9)} = 15.91$ ;  $P < 0.0032$ ; Table 2). Interestingly, the gain in muscle thickness differed among body sections (time by body section interaction effect:  $F_{(3,27)} = 10.03$ ;  $P < 0.0001$ ) with the greatest increase in sections 3 and 4 (Table 2 and Fig. 1). No such increase was seen in the unfed females; instead, mean muscle width tended to decrease in those animals (mean values =  $17.01 \pm 1.84$  vs.  $16.78 \pm 1.60$  mm before and after, respectively; time effect:  $F_{(1,11)} = 3.29$ ;  $P < 0.09$ ). Comparison of body section revealed that the muscle width decrease was concentrated in the posterior sections (time by body section interaction effect:  $F_{(3,33)} = 3.29$ ;  $P < 0.03$ , see Table (2). As a consequence, musculature profiles of



**Figure 1.** Absolute changes in epaxial muscle width in the four body sections in unfed non-reproducing females (○) and fed postparturient females (●). Error bars represent SE.

**Table 2.** Mean epaxial muscle width (mm) before ('Initial') and 2 weeks after treatment ('Final') for (A) ten fed post-parturient females and (B) 12 unfed non-reproducing females. The former were initially less muscular than the latter, notably in the posterior body (body sections 3 and 4; bold values). After feeding, emaciated females from this group exhibited significant gains in muscle width in those two sections (respectively +12.06 and +19.51%). No such increase was detected among the non-reproductive females, where the animals exhibited a small decrease in section 3 (-2.88%). *P*-values were obtained from separate repeated-measures ANOVA. Values are reported as means  $\pm$  standard deviation

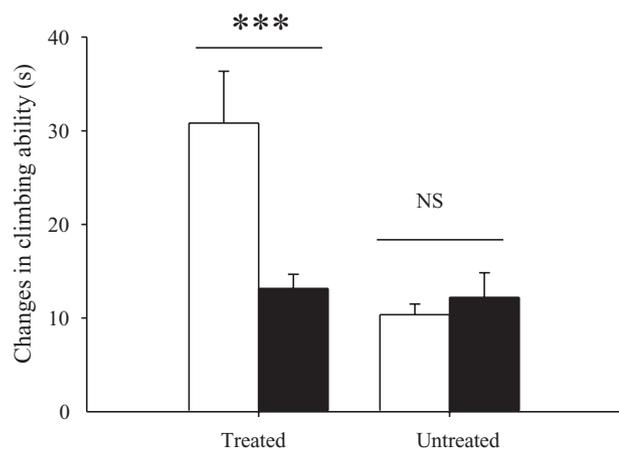
Body section	Initial muscle width (mm)	Final muscle width (mm)	Relative change	<i>P</i> -value
<b>A</b>				
1	16.94 $\pm$ 2.98	17.20 $\pm$ 2.67	+3.41%	0.54
2	17.31 $\pm$ 2.28	18.46 $\pm$ 2.65	+5.32%	0.054
3	<b>14.90 <math>\pm</math> 2.23</b>	<b>16.80 <math>\pm</math> 2.00</b>	<b>+12.06%</b>	<b>0.002</b>
4	<b>13.00 <math>\pm</math> 1.96</b>	<b>15.58 <math>\pm</math> 1.89</b>	<b>+19.51%</b>	<b>0.0003</b>
<b>B</b>				
1	16.77 $\pm$ 1.47	16.90 $\pm$ 1.25	+0.77%	0.52
2	18.56 $\pm$ 1.72	18.22 $\pm$ 1.27	-1.84%	0.13
3	<b>17.27 <math>\pm</math> 1.53</b>	<b>16.77 <math>\pm</math> 1.53</b>	<b>-2.88%</b>	<b>0.01</b>
4	15.43 $\pm$ 1.19	15.23 $\pm$ 1.17	-1.27%	0.18

the two groups became indistinguishable only 2 weeks after treatment (mixed model ANCOVA:  $F_{(1,19)} = 0.001$ ;  $P = 0.96$ ). This conclusion also holds true when comparing postfeeding musculature profiles of post-parturient females to prefeeding musculature profiles of the non-reproducing females (mixed model ANCOVA:  $F_{(1,19)} = 0.09$ ;  $P = 0.76$ ).

#### CHANGES IN PHYSICAL PERFORMANCE

(1) *Climbing ability*: The ingestion of stillborn neonates and undeveloped eggs caused a significant increase in maternal climbing ability. When held by the tail, females that had eaten neonates reached the operator's hand more rapidly than before treatment (mean values 7.92  $\pm$  5.15 s vs. 25.47  $\pm$  12.66 s, *t*-test for dependent samples,  $t_{(1,9)} = 3.98$ ,  $P < 0.0032$ , Fig. 2). Conversely, no change between trials was observed in unfed non-reproductive females (10.95  $\pm$  5.88 vs. 10.76  $\pm$  8.34 s;  $P = 0.90$ , Fig. 2).

(2) *Escape from predator*: Traction performance increased in the fed females (*t*-test for dependent samples,  $t_{(1,9)} = -9.25$ ,  $P < 0.0001$ ), whereas no change was detected among unfed animals ( $t_{(1,11)} = -0.53$ ,  $P = 0.60$ , Fig. 3). As a result, the two groups were similar after treatment (*t*-test for independent samples,  $t_{(1,20)} = -0.52$ ,  $P < 0.60$ , Fig. 3). Among fed females, individuals that gained the most in strength were those that increased the most in muscle thickness; this correlation with strength increase was evident for width variations in sections 3 and 4 but not sections 1 and 2 (see Table 3). No such correlation was detected for the non-reproductive females.

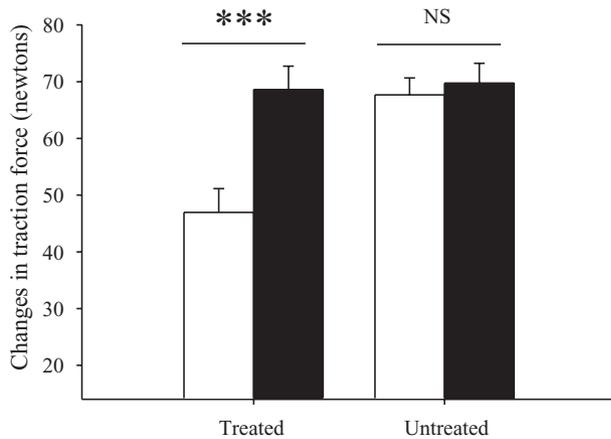


**Figure 2.** Changes in climbing ability over the 2 weeks of the experiment in untreated and treated females. We measured the amount of time (s) that snakes required for their head to reach the operator's hand. White bars: initial conditions; black bars: 2 weeks after feeding. Error bars represent SE.

(3) *Prey handling*: Feeding enhanced constriction capacity and resulted in a significant gain in the maximal force exerted (4.65  $\pm$  2.57 cm vs. 5.77  $\pm$  2.16,  $t_{(1,9)} = -7.44$ ,  $P < 0.0003$ ) as well as the duration of constriction (334  $\pm$  145 s vs. 273  $\pm$  125, *t*-test for dependent samples,  $t_{(1,9)} = -2.94$ ,  $P < 0.018$ , Fig. 4).

#### DISCUSSION

Female boas that ate their stillborn neonates and undeveloped eggs rapidly regained both body

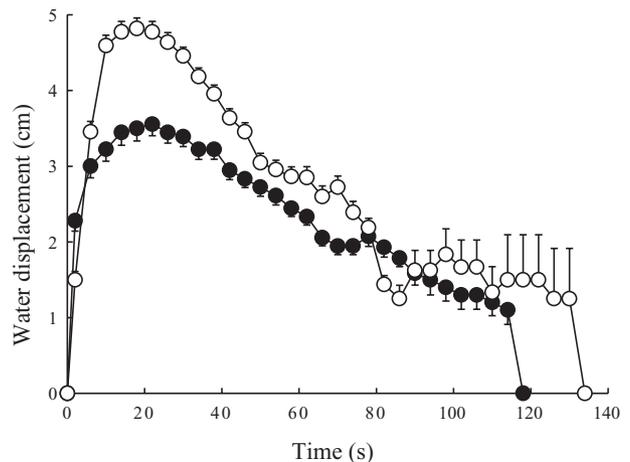


**Figure 3.** Changes in traction force over the 2 weeks of the experiment in untreated and treated females. White bars: initial conditions; black bars: 2 weeks after feeding. Error bars represent SE (10 Newtons = 1 kg).

**Table 3.** Relationship between the magnitude of changes in mean epaxial muscle width (mm) and changes in traction forces (Newtons) for each body section, in (A) ten fed postparturient females and (B) 12 unfed non-reproducing females. The changes were measured over a 2-week period, beginning at the time of parturition. The table shows correlation coefficients and associated *F*-ratios and probabilities

Body section	<i>r</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>P</i>
<b>A</b>				
1	0.46	0.21	1.66	0.24
2	0.25	0.06	0.4	0.55
3	0.83	0.70	16.66	0.004
4	0.68	0.44	6.14	0.04
<b>B</b>				
1	0.35	0.12	1.45	0.25
2	0.24	0.06	0.65	0.43
3	0.46	0.22	0.12	0.12
4	0.15	0.02	0.23	0.64

musculature and physical performance. The recovery in epaxial muscles was concentrated in the posterior part of the body (Table 2, Fig. 1), where the emaciation was initially most severe. Consistent with this result, the females also recovered in all of the performance measures that we scored: climbing abilities, traction and constriction capacities. Females that increased more in muscle width also increased more in strength, further supporting a functional relationship between these two measures. Conversely, among the control group, we saw a minor decrease in musculature in the



**Figure 4.** Changes in constriction strength of postparturient females over the 2 weeks of the experiment. Initial conditions (○); 2 weeks after feeding (●). Error bars represent SE.

posterior part of the body and no significant variation in physical performance.

Due to the small initial sample size, all postparturient females were fed, and compared with the group of unfed non-reproductive females. Thus, our experimental data may not directly reveal effects of feeding; one could argue that we simply have documented the rate of recovery of females after pregnancy, and cannot specifically attribute that recovery to the ingestion of neonates and undeveloped eggs. Nonetheless, the inference of causation due to feeding is strong. Unfed females did not increase in muscle thickness or strength over the 2-week study period, whereas the postparturient females that ate non-viable offspring recovered dramatically (Fig. 1). Importantly, previous work has shown that postparturient female boas remain emaciated and weak for weeks after giving birth (Matz, 2001; O. Lourdaï, pers. observ.). Published data indicate that this situation is widespread among viviparous snakes. Emaciation can be so pronounced as to directly affect survival (Bonnet *et al.*, 1999) or delay further reproduction (Bonnet *et al.*, 2002). More generally, it is difficult to imagine how organisms that have already expended a large proportion of their body reserves (i.e. postparturient females) can spontaneously build new tissues such as locomotor muscles without a substantial input of resources (energy + materials). Thus, the rapid recovery of the fed females in the present study provides compelling evidence that eating non-viable progeny was a critical factor in allowing the females to recover so rapidly.

Unfed, non-reproductive females faced a 2-week fast combined with repeated musculature and per-

formance measurements. They displayed a slight but nonetheless significant loss in musculature over this period. This result may reflect the energetic costs of repeated physical exercise without any energy intake. Thus, the increase in musculature and performance in our postparturient females is likely to be even higher in nature, where cannibalistic behaviour does not entail any foraging costs. Recovery should be especially rapid for a female that fails to reproduce and instead produces a large quantity of unviable elements.

Our results suggest that the recycling of undeveloped eggs and stillborn neonates not only provided an energy source to the postparturient females, but also provided the raw materials needed for a functional restoration of skeletal musculature. The synthesis of contractile proteins (myofibrils) requires a substantial amount of both dietary protein and energy content (Bos *et al.*, 2000). Importantly, this restoration of muscle mass and performance was achieved over a very short period of time (14 days), illustrating the potentially high benefits of cannibalistic behaviour. Eggs and neonates are particularly rich in energy (notably lipids) but also contain a diversity of proteins and essential nutrients such as minerals and proteins (Polis, 1981; White, 1991; Houston, Donnan & Jones, 1995; Thompson & Speake, 2002; Speake *et al.*, 2003). This rich chemical composition probably accounted for the rapidity and magnitude of musculature restoration seen in our study.

Reproduction imposes high energetic costs in female snakes, especially in viviparous species (Shine, 1980; Madsen & Shine, 1993; Bonnet *et al.*, 1999). For example, females of many boa species undergo extended fasting during reproduction, sometimes for several months prior to parturition (Rivas, 1999). During prolonged fasting, skeletal muscles represent an important source of protein (Goodman *et al.*, 1984). Gestation in rainbow boas induces a high level of protein catabolism that translates into a reduction in musculature and performance of reproductive animals (Lourdais *et al.*, 2004a), as seen in the postparturient females at the beginning of the present study (see initial measurements in Table 2). In this context, the present findings suggest that recycling stillborn neonates and undeveloped eggs allows the emaciated mother to cease protein catabolism (Nagasawa *et al.*, 1998) and thus to begin to recover from the structural and functional loss induced by reproduction. Importantly, while postparturient females were initially less muscular than non-reproductive females (Table 2, Lourdais *et al.*, 2004a), this difference was removed 2 weeks after treatment.

Overall, the hypothesis that maternal cannibalism is adaptive (Polis, 1981) is supported by results from our study, notably (1) only non-viable progeny were

consumed; and (2) females that consumed non-viable offspring recovered very rapidly from pregnancy (in terms of both musculature and performance). These data support the idea that nutrient recycling is an important advantage of maternal cannibalism. The alternative hypothesis, that mothers eat non-viable offspring as a form of parental care, seems unlikely to be applicable to this system. Neonatal boas disperse soon after birth (Ross & Marzec, 1990), so that cross-infection or attraction of predators to the parturition site are unlikely to constitute realistic risks for neonates of this species.

Finally, this work reveals an impressive degree of structural 'plasticity' for muscle tissues. Not only do rainbow boas break down skeletal muscles during prolonged fasting (Lourdais *et al.*, 2004a), but these snakes also can rapidly reconstitute those muscles after feeding recommences (present study). Available data on muscle atrophy and regrowth in endothermic vertebrates typically reveal much longer timescales for both of these processes, suggesting that further studies on muscle physiology in boas might be of great interest.

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