Cannibalism of nonviable offspring by postparturient Mexican lance-headed rattlesnakes, *Crotalus polystictus*

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Female vertebrates frequently ingest undeveloped ova and stillborn offspring. Two hypotheses have been proposed to interpret this behaviour: (1) it is a form of parental care, and (2) it recycles otherwise wasted energy, facilitating maternal recovery. Our study of Mexican lance-headed rattlesnakes provides the first quantitative description of cannibalism by postparturient rattlesnakes. We collected gravid females during June–July of 2004–2007 in central México, recording 239 litters from 190 females. Production of nonviable offspring was common (48% of litters). Most females (68%) ate some or all nonviable offspring, consuming an average of 11% of postpartum mass. Females consumed undeveloped ova and stillborn neonates in similar proportions. To evaluate factors that influenced the decision to cannibalize we used logistic regression. The best model included four predictive variables: (1) parturition date; (2) proportion of nonviable offspring mass per litter; (3) maternal investment index; and (4) snout–vent length (SVL). All variables exerted a positive effect on maternal cannibalism, although SVL was only a marginally significant predictor. Consumption of nonviable offspring confers energetic benefits to emaciated postparturient females. Energetic benefits are greatest when a large proportion of a litter is nonviable, while the pressure to cannibalize is greatest when late parturition shortens the time available to forage before the next reproductive event. Our results demonstrate the importance of maternal cannibalism in rattlesnakes, and suggest stronger support for the maternal care hypothesis than for the parental care hypothesis.

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of the nonviable offspring. A second hypothesis proposes that maternal cannibalism functions to recycle otherwise wasted energy, facilitating maternal recovery (Fitch 1954; Lourdais et al. 2005). A cannibalistic female snake can recoup some of the energy spent in reproduction without the dangerous, time-consuming and energetically expensive activities demanded by normal foraging (Arnold 2001; Lourdais et al. 2005). In this case, the fitness benefit of maternal cannibalism accrues to the parent rather than to the living offspring.

These hypotheses are not mutually exclusive, and both may be important factors driving the development of maternal cannibalism. Furthermore, neither hypothesis posits a fitness cost to females engaging in maternal cannibalism. In the absence of a cost, viviparous snakes should maximize fitness by engaging in maternal cannibalism whenever afforded the opportunity to do so. If, however, maternal cannibalism does present some cost to snakes, we can hypothesize the following. (1) If parental care is a stronger selective force, then maternal cannibalism should be most prevalent when a high proportion of the litter is viable (multiplying fitness benefits among more living neonates). (2) In contrast, if maternal recovery is a more important driver of maternal cannibalism, the impetus to cannibalize should be strongest when more offspring are nonviable (resulting in more energy available to the parent). If maternal snakes are in poor condition following parturition, and when snakes have less time available to forage prior to subsequent reproductive events.

The most dramatic fitness cost associated with maternal cannibalism is the possibility of accidental ingestion of viable offspring. This possibility may be considered most acute when female snakes are confronted with the decision to consume full-term, stillborn offspring soon after birth. Stillborn neonates are superficially similar to recently born live offspring. Live neonates may remain nearly motionless, and partially within placental membranes, for some time (exceptionally, up to 4 h) following parturition. Accordingly, we can hypothesize that if ingestion of living neonates imposes a fitness cost to maternal cannibalism, then females should attempt to minimize this risk by preferring to cannibalize undeveloped ova over stillborn neonates, and by allowing more time to pass before cannibalizing stillborn neonates than ova.

We investigated the importance and frequency of cannibalistic behaviour among postparturient female Mexican lance-headed rattlesnakes, *Crotalus polystictus*. We tested the existence of a fitness cost by examining how long female snakes wait following parturition before consuming nonviable neonates, and whether snakes preferentially consume some nonviable offspring (ova) over others that more closely resemble living neonates (stillborn neonates). We evaluated the relative importance of parental care and maternal recovery as drivers of maternal cannibalism, using logistic regression to identify predictive variables that influence a female rattlesnake’s decision to consume nonviable offspring.

**METHODS**

**Study Species**

*Crotalus polystictus* is a medium-sized rattlesnake (total length 50–90 cm) endemic to central México. This species primarily inhabits mid-elevation humid and subhumid grasslands and open woodlands. Published information concerning the natural history and biology of this little-studied species is scarce (Campbell & Lamar 2004); however, *C. polystictus* has been reported to consume small mammals and birds (Klauber 1972; Bryson et al. 2003), and animals from our study population feed almost exclusively on small mammals (E. Mocíño-Deloya & K. Setser, unpublished data).

Females frequently reproduce annually, and may have large litters relative to their size (Table 1). Females in this population give birth from late May to mid-August (Bryson et al. 2003; K. Setser & E. Mocíño-Deloya, unpublished data).

**Data Collection**

As part of an ongoing, long-term, mark–recapture study, we captured snakes from the valley plains along the Rio Lerma at ca. 2500 m above sea level in the state of México. Most natural vegetation in this area has been converted to agricultural use, and remnant populations of *C. polystictus* persist in pastures and hayfields and along margins of crop fields. Gravid female snakes were captured during June–July 2004–2007. Snakes were captured using a funnel, measured from snout to vent (SVL; ±1 mm) and weighed (±0.1 g) on an electronic balance. Measurements were taken while snakes were anaesthetized to improve precision and reduce the risk of snakebite (Setser 2007). Snakes were anaesthetized by the open method, using an approximate dosage of 0.8 ml/litre (1 ml of isoflurane within a 1.2-litre plastic tube; Setser 2007). All snakes were placed in warmed cages (ca. 30 °C) following isoflurane inhalation to facilitate rapid recovery. Most snakes recovered quickly, typically within 5–15 min of removal from the isoflurane tubes. We did not observe any adverse effects of isoflurane use among adult snakes; some neonates (fewer than 2%) recovered slowly from isoflurane exposure, sometimes requiring artificial respiration prior to resuming normal breathing. These neonates did not show further, long-term effects following recovery. We permanently marked snakes with subcutaneously injected passive integrated transponders (PIT tags; models TX1400L, 11.0 × 2.1 mm, 0.1 g, 125.0 kHz and TX148511B, 8.5 × 2.1 mm, 0.1 g, 134.2 kHz; Destron-Fearing, St Paul, MN, U.S.A.). PIT tags were implanted dorsolaterally at the midbody, and have been shown not to impact the growth, movement or survival of snakes (Keck 1994; Jemison et al. 1995).

Gravid females were retained in captivity in individual plastic tubes (30 × 43 cm and 18 cm high) until parturition. Cages were outfitted with a heat source situated under one end of the enclosure, allowing snakes to thermoregulate within a thermal gradient with a range of ca. 18–30 °C during the day (14 h). Heating elements were turned off and temperatures allowed to drop to ambient levels (ca. 12–18 °C) at night. Both day and night-time temperatures approximate body temperatures of free-living *C. polystictus* (K. Setser & E. Mocíño-Deloya, unpublished data). Because gravid females rarely feed, we did not offer captive females food, but provided water ad libitum.

After parturition, we counted and weighed (±0.1 g) both nonviable and live offspring, as well as postparturient females. We returned females along with their viable and nonviable offspring to natal cages, detaining them together up to 48 h to allow females the opportunity to cannibalize offspring. Some snakes (*N = 20*) cannibalized offspring before we could weigh them. To include these snakes in our analyses, we calculated their litter masses by multiplying the number of neonates and ova eaten (determined by palpation) by mean stillborn neonate (*N = 75*) and ova (*N = 111*) masses. The resulting sums were added to the summed mass of each female’s uneaten nonviable and live offspring. Litter masses of all other females (*N = 73*) were calculated by summing masses of all viable and nonviable offspring. All females and their live offspring were released at the female’s site of capture 3–7 days following parturition.

To prevent unnecessary stress, we did not regularly reweigh gravid snakes. However, 117 snakes were reweighed at least once during gestation. Of these snakes, 69 lost mass (*X ± SD = 7.2 ± 5.5 g, range 0.1–26.8 g) between weighing events (*X ± SD = 16 ± 10 days, range 3–48 days), while 48 snakes gained mass (*X ± SD = 5.7 ± 5.1 g, range 0.1–26.2 g) between weighing events (*X ± SD = 18 ± 12 days, range 3–49 days). Changes in mass largely reflected defecation events and changes in hydration level. In all instances, we
used the mass most recently recorded prior to parturition in calculations.

All research activities were authorized by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) of México in permits issued to D. Lazcano and E. Mociño-Deloya.

Statistical Analysis

We excluded three snakes with obvious health problems, and three additional snakes that spontaneously aborted entire litters of partially developed embryos, from all analyses of cannibalism. To avoid pseudoreplication, we randomly removed 1 year of data from each of six snakes that gave birth to litters including nonviable offspring in 2 different years. Because we were not interested in interannual differences in the rate of cannibalism, and because year of capture was not a significant variable in preliminary analyses, we pooled data from all 4 years in all analyses. We calculated indices of postpartum (initial) body condition (iBCI), postpartum body condition (pBCI), and maternal investment (MII) by regressing ln prepartum (initial) body condition (iBCI), postpartum body condition (pBCI) and ln maternal body mass per litter; (3) pBCI; (4) MII; and (5) SVL. Next, we tested models including first-order interactions between the five predictive variables. Only the interaction between pBCI and SVL was significant at \( P < 0.05 \), and hence included in the explanatory model (Quinn & Keough 2002). We evaluated the resulting six-variable model for best model subsets based on Akaike Information Criterion (AIC) scores, resulting in the selection of an explanatory model consisting of four predictive variables.

RESULTS

We recorded 239 litters from 190 females: 48 litters in 2004, 59 in 2005, 81 in 2006 and 51 in 2007. The production of at least a single ovum or stillborn neonate was common (48% of litters; 115 of 239). The percentage of nonviable offspring in such litters varied from 7% to 100% (\( \bar{X} \pm SD = 30.0 \pm 22% \)).

Sixty-three of 93 (68%) postparturient females ate some or all of the nonviable offspring available to them. These females consumed an average of 9.5 g (range 3.0–25.5 g), representing an average of 11% of their postpartum mass (3–39%). Most snakes (52 of 63; 83%) consumed all nonviable offspring available; snakes consumed a mean of 92% (range 28–100%) of the available mass. A single female consumed live neonates. This snake (540 mm, 119.5 g prepartum) gave birth to two live and three stillborn neonates, consuming one stillborn neonate and both live neonates.

Females did not show a preference to cannibalize either ovum or stillborn neonates (2 × 2 contingency table: \( \chi^2 = 0.84, P = 0.36 \)). Similarly, cannibalistic females did not wait longer to cannibalize litters containing stillborn neonates (\( \bar{X} \pm SD = 21.5 \pm 16.4 \) h, \( N = 26 \)) than litters without (\( \bar{X} \pm SD = 18.7 \pm 17.8 \) h, \( N = 35 \))
Considerable variation existed in the time to cannibalism. Some females ate nonviable neonates almost immediately after giving birth, whereas other snakes did not feed until days later. We note that our data tend to overestimate the time between birth and cannibalism as, to avoid stressing snakes, we typically inspected snake cages only twice per day.

The best explanatory logistic regression model included four predictive variables useful in predicting cannibalism: (1) parturition date; (2) proportion of nonviable offspring mass per litter; (3) MII; and (4) SVL. It correctly categorized the behaviour of 55 of 63 (87%) females that cannibalized offspring, but was less accurate in predicting noncannibals (correctly categorizing 12 of 30, 40% of females). Three variables significantly impacted a female snake’s decision to cannibalize offspring, while the effect of SVL was marginally significant (Table 2). All variables had a positive relationship with maternal cannibalism (Fig. 1, Table 2).

**DISCUSSION**

Production of nonviable offspring was a common occurrence among female *C. polystictus*. Ingestion of nonviable offspring by postparturient females has been reported in several squamate taxa (Huff 1980; Groves 1981; Shine 1988; Ross & Marzec 1990; Mitchell & Groves 1993; Somma 2003); however, previous reports have not detailed the extent and frequency of maternal cannibalism in snake populations. Maternal cannibalism was consistent and widespread among female *C. polystictus* collected during late gestation in central Mexico. To our knowledge, this behaviour has not yet been reported from other *Crotalus* species; however, we suggest that this probably reflects the difficulty of observing parturition by wild snakes rather than any peculiarity of *C. polystictus* biology with respect to its congeners. The consumption of nonviable offspring by female rattlesnakes may be important in allowing a rapid recuperation of some of the considerable energetic and physiological costs of reproduction (Lourdais et al. 2005).

The consumption of nonviable offspring may be a simple evolutionary outgrowth of normal rattlesnake feeding behaviour, as prey are ordinarily killed prior to consumption and may die for some time before ingestion by the snake. After envenomation, prey animals sometimes move considerable distances before dying. To find envenomated prey, rattlesnakes depend on olfactory stimuli which are probably enhanced by putrefaction (Lillywhite 1982). Rattlesnakes, and vipers in general, may thus be considered to be ‘preadapted’ to the consumption of carrion (Lillywhite 1982); accordingly, little additional dietary plasticity may be needed for rattlesnakes to consume stillborn neonates and ova when available.

None the less, our results mirror previous observations of maternal cannibalism that detail consumption of only part of the total mass of nonviable offspring available (Groves 1981; Mitchell & Groves 1993). Additionally, some females with the opportunity to consume nonviable offspring did not do so, suggesting that maternal cannibalism either carries some cost that offsets hypothesized benefits, or is beyond the plasticity of normal foraging behaviour. Alternatively, captive conditions and research activities may have inhibited cannibalistic behaviour. Anorexia is a common response in newly captured rattlesnakes (Klauber 1972; Murphy & Armstrong 1978). Similarly, Aubret et al. (2007) observed that the feeding response of tiger snakes, *Notechis scutatus*, was mediated by the perception of predation risk. Accordingly, maternal cannibalism may be more ubiquitous among free-living snakes than our study indicates.

Our results provide little support for the hypothesis that some females abtain from cannibalism to reduce the risk of mistakenly consuming live neonates. Although a single snake consumed two live neonates, no other snake showed any predatory interest in live neonates, nor any difficulty in distinguishing live neonates from nonviable offspring. Contrary to our prediction, females did not have a preference for ova, nor did they wait longer to consume stillborn neonates. While the inconsistency of maternal cannibalism in *C. polystictus* suggests the existence of some cost balancing the hypothesized fitness benefits, we detected little evidence that females trade off benefits of maternal cannibalism against the risk of cannibalizing live neonates. We did not test for another potential cost of cannibalism, pathogen transmission (Pfenng et al. 1998). Transmission of pathogens may be less prevalent in cases of maternal cannibalism than it is in other forms of cannibalism. Unlike live conspecifics, recently born nonviable offspring are unlikely to carry any host-specific pathogens not already shared with their female parent.

Female rattlesnakes frequently remain with newly born litters following parturition, often until the neonates’ first ecdysis (Greene et al. 2002; Holycross & Fawcett 2002; Clark 2004), making the parental care hypothesis particularly applicable to maternal cannibalism in rattlesnakes. We have observed postparturient female *C. polystictus* with litters of fresh neonates, as well as apparently entire litters of pre-ecdysis neonates unaccompanied by females, inhabiting the same sites over successive days. If we assume that these aggregations of neonates remain near birth sites, then the elimination of stillborn neonates and ova prior to decomposition should act to reduce the probability of predators investigating parturition sites. Despite the appeal of this hypothesis, we detected little evidence to support it. We predicted that if parental care was a strong driver of maternal cannibalism, females with litters containing higher proportions of live neonates should be more likely to cannibalize nonviable offspring, multiplying fitness benefits among a larger number of neonates. Instead, we encountered the opposite effect. Females were more likely to cannibalize when they gave birth to litters containing more nonviable offspring. The number of live neonates in a given litter is a function of litter size and the proportion of live offspring. Females with proportionally large litters (e.g. high MII scores) had a slightly increased tendency towards cannibalism. However, MII scores correlated poorly with the number of live neonates in litters, partly because litter size (MII score) was negatively correlated with the proportion of nonviable neonates in a litter (r = −0.56). In fact, there was little difference between the number of live neonates born to cannibals (X ± SD = 5.5 ± 2.6, N = 63) and those born to noncannibals (X ± SD = 5.6 ± 2.3, N = 30).

Our results provide stronger support for the primacy of the maternal recovery hypothesis. Reproduction imposes high energetic costs on female snakes, especially in viviparous species (Seigel & Ford 1987; Madsen & Shine 1993; Bonnet et al. 1999; Lourdais

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**Table 2**

Logistic regression analysis of the effects of predictive variables on the decision to consume nonviable offspring by postparturient female *Crotalus polystictus*

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>95% confidence intervals</th>
<th>Wald statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−20.892</td>
<td>−33.539—−8.245</td>
<td>10.483</td>
<td>0.001</td>
</tr>
<tr>
<td>Parturition date</td>
<td>0.059</td>
<td>0.019—0.098</td>
<td>8.443</td>
<td>0.004</td>
</tr>
<tr>
<td>% Litter mass nonviable</td>
<td>0.064</td>
<td>0.017—0.111</td>
<td>7.205</td>
<td>0.007</td>
</tr>
<tr>
<td>Maternal investment index</td>
<td>3.072</td>
<td>0.673—5.471</td>
<td>6.299</td>
<td>0.012</td>
</tr>
<tr>
<td>Snout–vent length</td>
<td>0.012</td>
<td>−0.0001—0.023</td>
<td>3.833</td>
<td>0.050</td>
</tr>
</tbody>
</table>
et al. 2002b, 2005). Rapid replenishment of energy stores may be particularly important to annually reproducing snakes (Seigel & Ford 1987). Furthermore, recycling energy invested in nonviable offspring allows females to accelerate recovery from the structural and functional losses induced by reproduction (Lourdais et al. 2005). Snakes were most likely to cannibalize when litters contained large proportions of nonviable offspring, as predicted. In addition, snakes that gave birth later in the year were more likely to cannibalize offspring than were snakes that gave birth earlier. *Crotalus polystictus* feed heavily during the summer rainy season (June–September) when rodents reproduce, and populations increase in density (Choate & Jones 1970; Vázquez et al. 2000; K. Setser, personal observation). As gravid *C. polystictus* feed infrequently, snakes giving birth later forgo summer foraging opportunities (E. Mocin˜o-Deloya & K. Setser, unpublished data), and hence experience greater pressure to regenerate energetic reserves necessary to sustain reproduction the following year. A third prediction, that postparturient snakes in poor condition (pBCI) would be more likely to cannibalize nonviable offspring, was not supported by our results.

Two variables that emerged as useful predictors of maternal cannibalism are less clearly related to either the parental care or maternal recovery hypotheses. Cannibalistic female *C. polystictus* had greater MII scores than did noncannibalistic females. Factors unrelated to either hypothesis may explain the importance of MII as a predictive variable. Snakes gestating large litters may have been more efficient, or more versatile, foragers. Such females may also be better able to take advantage of uncommon and atypical food sources, such as nonviable offspring. In a similar vein, such snakes may be more likely to feed during stressful conditions (e.g. captivity) than snakes with low MII scores. It is also possible that females gestating larger litters were less able, or less inclined, to forage during gestation, and may have been anorexic for longer periods of time. However, this hypothetical relationship between anorexia and cannibalism was not supported by any relationship between postparturient condition (pBCI) and cannibalism. Female SVL was also a useful predictive variable, although marginally significant in the final model. As with MII, large size may correlate with a greater willingness to feed under stressful conditions or indicate a greater ability to forage.

Our results lend support to the maternal recovery hypothesis as a driving force behind cannibalism of nonviable offspring by *C. polystictus*. We failed to detect strong evidence that the risk of consuming live offspring reduces the benefits of maternal cannibalism. As such, the failure of snakes to consume all or most offspring available consistently is surprising. We suggest that free-living snakes may show more consistent behaviour, and that maternal cannibalism is more widespread among viviparous snakes than has been reported.

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References


Caldwell, New Jersey: Blackburn Press.


