

Do Sidewinder Rattlesnakes (*Crotalus cerastes*, Viperidae) Cease Feeding During the Breeding Season?

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Seasonal aphagia (a lack of feeding) can occur if foraging and reproduction occasionally result in conflicting demands on an individual, such that one activity takes precedence over the other. We tested the hypothesis that female and male *Crotalus cerastes* (Sidewinders) exhibit seasonal aphagia during the reproductive season. We examined the stomach contents of preserved specimens to assess variation in the feeding rates of *C. cerastes*. Non-reproductive females fed during the early and late stages of the active season, but reproductive females only ate during the first half of the active season. Female Sidewinders fed throughout the early vitellogenic phases of the reproductive cycle, but exhibited a tendency to reduce or cease feeding during the later stages of the cycle (gestation). Prey consumption during early reproductive stages can provide valuable energetic resources for sustaining a female's subsequent breeding activities. However, the physical burden of offspring mass and the concomitant decrease in locomotor efficiency can reduce a female's foraging efficiency in the later phases of the reproductive cycle. Male *C. cerastes* displayed a trend to feed more frequently during the reproductive season, perhaps because enhancing their energy reserves allows males to travel longer distances and maximize encounter rates with females. The discovery of this intersexual variation in feeding patterns of *C. cerastes* underscores the importance of descriptive ecological studies to elucidate distinct patterns of life history evolution.

LIFE history tradeoffs are prevalent in nature because organisms, which are often resource-limited, need to allocate time and energy to different components of fitness, such as foraging, growth, maintenance, and reproduction (Pianka, 2000). Feeding is a necessary activity, for it provides the energetic resources that are expended in daily activities, as well as in growth and reproduction. Therefore, individuals may spend considerable amounts of time foraging. Reproductive activities (e.g., gamete production, mate searching, courtship, copulation, gestation) can impose significant time and energy demands on animals (Shine, 1980; Aldridge and Brown, 1995; Hunt et al., 2002), and as a result there may be a temporal displacement of activities that are incompatible with reproduction (Brischoux et al., 2011). Conflicts in the time and energy allocated to foraging and reproduction during the breeding season can result in seasonal aphagia (a lack of feeding) in reproductive individuals (Mrosovsky and Sherry, 1980; Sherry et al., 1980; Rivas and Burghardt, 2005). The low metabolic rates of ectotherms, coupled with relatively infrequent reproductive bouts, may allow for long-term energy storage to sustain reproductive activities in the absence of feeding (Bonnet et al., 1998; Warner et al., 2008), a strategy referred to as capital breeding.

Reproduction elicits changes in the body morphology of organisms, with females exhibiting significant increases in body mass during gestation, which can result in decreased locomotor ability (Seigel et al., 1987; Cooper et al., 1990; Shaffer and Formanowicz, 1996). Impaired locomotion can reduce a female's foraging efficiency (Lourdais et al., 2004a) and also lead to increased predation risk (Bauwens and Thoen, 1981; Brodie, 1989; Brischoux et al., 2011). Therefore, by ceasing foraging behavior (i.e., exhibiting aphagia), reproductive females can reduce the costs of reproduction. Aphagia may also result from physical constraints caused by developing offspring within the body cavity, which may limit the size that a female's body can expand to accommodate prey (Weeks, 1996), particularly in elongated animals (e.g., caecilians, amphisbaenians, snakes).

Males can also exhibit seasonal aphagia (Aleksiuk and Stewart, 1971; Daltry et al., 1998). During the reproductive season, males can exhibit shifts in behavior and forgo foraging activities in order to engage in reproduction (O'Donnell et al., 2004). As a result, males can experience significant decreases in body condition during the reproductive season (Bonnet and Naulleau, 1996; Madsen and Shine, 2000). Males of various species of snakes invest a considerable amount of time and effort into mating activities such as mate searching, combat, courtship, and copulation (Waldron et al., 2006; Jellen et al., 2007; Glaudas and Rodríguez-Robles, 2011). Increased time invested in reproduction may decrease the foraging effort of males, and thus lead to aphagia during the reproductive season.

Crotalus cerastes (Sidewinder) is a small-bodied rattlesnake with a reported maximum snout–vent length of ca. 82 cm, although most adults are 50–60 cm long (Ernst and Ernst, 2003). The species inhabits sandy washes, dunes, and flatlands of the deserts of southwestern North America. Female *C. cerastes* are viviparous and give birth to 1–20 young (average 9.2, $n = 57$ litters) during late summer to early fall (Ernst and Ernst, 2003) after a 2.5–3 month gestation period (Reiserer, 2001). Herein we tested the hypothesis that reproductive Sidewinders exhibit seasonal aphagia during the breeding season. Specifically, we predicted that reproductive females consume prey less often than non-reproductive females. We also predicted that a lower proportion of mature male *C. cerastes* feeds during the reproductive season, compared to the non-reproductive season.

MATERIALS AND METHODS

An indirect way of assessing feeding rates in studies of snake foraging ecology is to examine museum specimens, for the proportion of animals found to contain prey in their stomachs is an indication of how often they fed (Shine, 1986). Accordingly, we relied on preserved specimens to determine variation in the feeding patterns of male and

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female *Crotalus cerastes*. We checked the stomach contents of adult snakes by making a mid-ventral incision in 586 specimens from the following institutions: CAS ($n = 109$), LACM ($n = 272$), MBM ($n = 23$), and MVZ ($n = 182$). Whenever possible, for each snake we recorded the following variables: locality data, date of collection, body size (SVL ± 1 cm), body mass (± 0.1 g), sex and reproductive status (determined by inspection of the reproductive tract), and presence or absence of prey in the stomach. Because prey can be stored for an indefinite length of time within the intestinal tracts of snakes (Lillywhite et al., 2002), we only examined stomach contents, for they more accurately reflect a relatively recent feeding event.

We divided 253 adult females (SVL ≥ 38 cm; Reiserer, 2001) into three categories: non-reproductive (follicle diameter < 8 mm; Goldberg, 2004), vitellogenic (follicle diameter ≥ 8 mm; Goldberg, 2004), and gravid (determined by the presence of embryos in the oviduct). Follicle diameters were measured using a digital caliper (± 0.01 mm). We compared the frequency of females with prey in their stomachs and females with empty stomachs using chi-square contingency tests. For reproductive (i.e., vitellogenic and gravid) females, we compared follicle sizes between snakes with empty stomachs and those that contained prey using a single-factor ANOVA. We also used a single-factor ANOVA to compare variation in dates of feeding events in reproductive and non-reproductive females.

We relied on published and unpublished behavioral observations of breeding activities (courtship and mating) of *C. cerastes* from California (Kern, San Bernardino, and Riverside counties) and Nevada (Esmeralda County), USA, to define the males' reproductive season (Lowe, 1942; Klauber, 1972; S. M. Secor, University of Alabama, Tuscaloosa, pers. comm.). Field observations indicated that Sidewinders have two distinct mating periods, one in spring (Mating season 1) and another one in fall (Mating season 2). Therefore, we assigned 333 adult males (SVL ≥ 34 cm; Reiserer, 2001) to one of three groups, according to their collection date: Mating season 1 (22 March–4 June), Mating season 2 (20 September–22 October), and the non-reproductive season (all intervening dates). None of the specimens we examined was collected between October 22 and March 22 of the following year, and therefore male feeding frequency during this time remains undetermined. We performed chi-square tests to make pairwise comparisons of the frequencies of males that had consumed prey and those that had empty stomachs in the first and second mating season, and in the non-reproductive season. All statistical tests were conducted using StatView (version 5.0.1; SAS Institute, 1998; StatView 5.0.1, Cary, North Carolina).

RESULTS

We examined 253 adult female *C. cerastes*, 60 (23.7%) of which contained prey. One hundred and seventy-four (174) females were non-reproductive, 70 were vitellogenic, and nine were gravid. Twenty-three percent (23%) of non-reproductive females contained prey, compared to 27.1% of vitellogenic females and 11.1% of gravid females. Pairwise comparisons between the three groups indicated that there were no significant differences in the proportion of females that had consumed prey and those that had empty stomachs (Table 1). Non-reproductive females had consumed 21 (52.5%) mammals and 19 (47.5%) lizards, whereas vitellogenic females had consumed 10 (45.5%) mammals, 11 (50%)

Table 1. Frequencies of Vitellogenic, Gravid, and Non-reproductive Female *Crotalus cerastes* with Prey in the Stomach and with an Empty Stomach.

Reproductive status	Prey in stomach	Empty stomach
Vitellogenic	19	51
Gravid	1	8
Non-reproductive	40	134
Vitellogenic versus Gravid: $\chi^2 = 1.08$, $df = 1$, $P = 0.30$		
Vitellogenic and Gravid (combined) versus Non-reproductive: $\chi^2 = 0.12$, $df = 1$, $P = 0.73$		
Vitellogenic versus Non-reproductive: $\chi^2 = 0.47$, $df = 1$, $P = 0.49$		
Gravid versus Non-reproductive: $\chi^2 = 0.69$, $df = 1$, $P = 0.40$		
Global contingency test: $\chi^2 = 1.3$, $df = 2$, $P = 0.52$		

lizards, and one (4.5%) bird. The single gravid female with prey its stomach had consumed a mammal.

We observed temporal variation in follicle diameter (Fig. 1), with all but two vitellogenic females (follicle diameter ≥ 8 mm) occurring between mid-March and late June. Gravid females were recorded from early May to mid-August, whereas non-reproductive females occurred year-round. No significant difference was found in the follicle sizes of reproductive (i.e., vitellogenic and gravid) females that had consumed prey (follicle diameter: 13.8 ± 4.2 mm, range 8.3–21.5 mm, $n = 20$) and those that had empty stomachs (follicle diameter: 16.9 ± 7.6 mm, range 8.1–43.0 mm, $n = 59$; single-factor ANOVA, $F_{1,77} = 3.0$, $P = 0.09$). Still, females with follicles larger than 21.5 mm in diameter did not contain prey (Fig. 2), and only one of nine gravid females had consumed food. Non-reproductive females fed during the early and late stages of the active season, but reproductive females only ate during the first

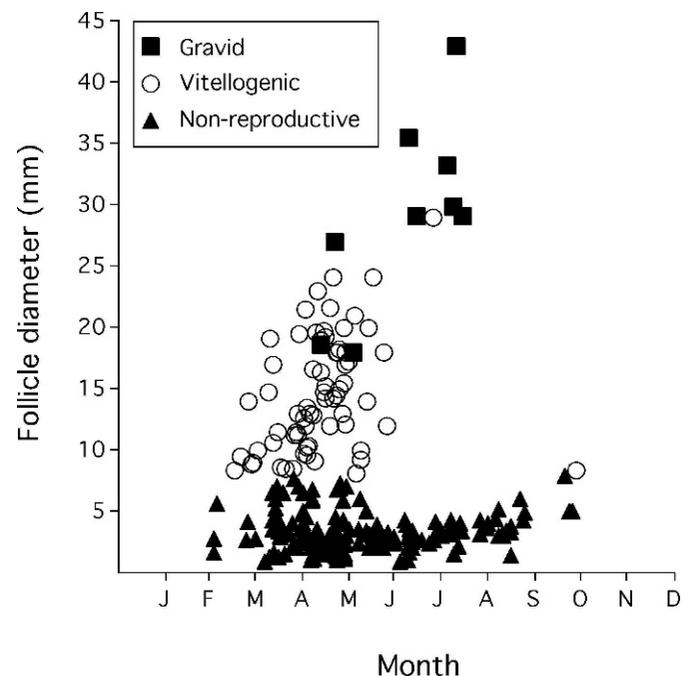


Fig. 1. Temporal variation in follicle diameter in non-reproductive ($n = 167$), vitellogenic ($n = 67$), and gravid ($n = 9$) female *Crotalus cerastes*. On the x-axis, the position of each letter indicates the last day of the month.

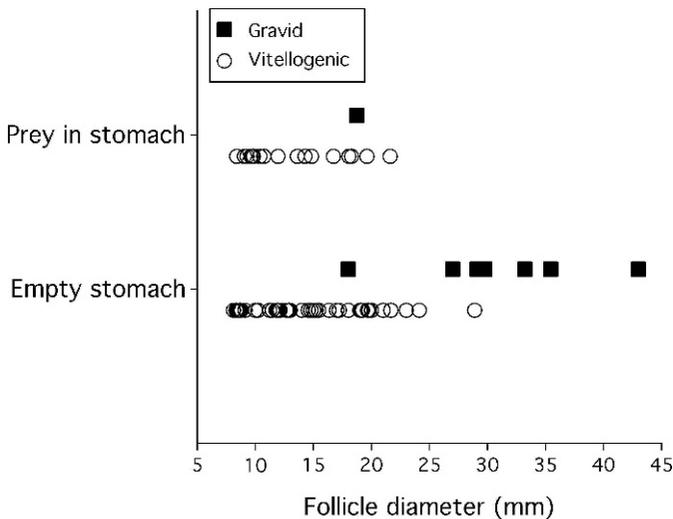


Fig. 2. Relationship between follicle diameter and presence ($n = 20$ [19 vitellogenic, 1 gravid]) or absence ($n = 59$ [51 vitellogenic, 8 gravid]) of prey in the stomach of reproductive female *Crotalus cerastes*.

half of the breeding season (single-factor ANOVA, $F_{1,39} = 10.97$, $P = 0.002$; Fig. 3).

Seventy-four of the 333 (22.2%) adult male *C. cerastes* examined contained prey. There was no difference in the proportion of males that contained prey and those that did not between the first (longer) and second (shorter) mating seasons. There was a statistical trend for males collected during the first mating season, and during the two mating seasons combined, to consume prey at a higher frequency than males collected during the non-reproductive season (Table 2).

DISCUSSION

Do reproductive *Crotalus cerastes* experience seasonal aphaagia during the breeding season? Our findings indicate that female Sidewinders continue to feed throughout the early stages of the reproductive cycle (vitellogenesis), but exhibit a tendency to reduce or cease feeding during gestation. What

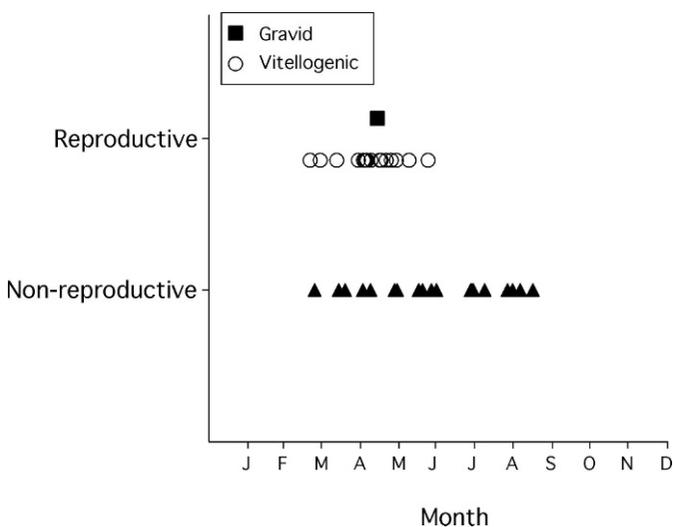


Fig. 3. Temporal variation in feeding events in non-reproductive ($n = 22$) and reproductive (vitellogenic [$n = 18$] and gravid [$n = 1$]) female *Crotalus cerastes*. On the x-axis, the position of each letter indicates the last day of the month.

Table 2. Frequencies of Adult (SVL ≥ 34 cm) Male *Crotalus cerastes* with Prey in the Stomach and with an Empty Stomach in the First and Second Mating Seasons, and in the Non-reproductive Season.

Season	Prey in stomach	Empty stomach
Mating season 1 (22 March–4 June)	58	177
Mating season 2 (20 September–22 October)	2	8
Non-reproductive season (all intervening dates)	14	74
Mating season 1 versus Non-reproductive season: $\chi^2 = 2.84$, $df = 1$, $P = 0.09$		
Mating season 2 versus Non-reproductive season: $\chi^2 = 0.11$, $df = 1$, $P = 0.74$		
Mating seasons 1 and 2 (combined) versus Non-reproductive season: $\chi^2 = 2.76$, $df = 1$, $P = 0.097$		
Mating season 1 versus Mating season 2: $\chi^2 = 0.11$, $df = 1$, $P = 0.74$		
Global contingency test: $\chi^2 = 2.88$, $df = 2$, $P = 0.24$		

factors may allow vitellogenic *C. cerastes* to continue feeding? During the initial phase of the breeding cycle, vitellogenic females likely are as mobile as non-reproductive females (Brown and Weatherhead, 1997), implying that the former probably maintain their ability to forage and evade predators efficiently. Throughout the year, Sidewinders can be found near or within rodent burrows (Secor, 1994a, 1994b), which may increase the likelihood of opportunistic feeding on mammalian prey. Further, *C. cerastes* is a sit-and-wait forager (i.e., an ambush predator; Secor and Nagy, 1994), and predators that use this strategy predominantly eat mobile prey (Huey and Pianka, 1981; Greene, 1986; Reilly et al., 2007). Indeed, during cooler months in spring and fall, Sidewinders can remain active on the surface during the daytime (Brown and Lillywhite, 1992), and vitellogenic females prey upon diurnal, wide-foraging lizards (M. M. Webber, unpubl. data), such as *Aspidoscelis tigris* (Tiger Whiptail; Anderson and Karasov, 1981) and *Dipsosaurus dorsalis* (Desert Iguana; Cooper and Alberts, 1990). Predation on active animals probably increases the chances that vitellogenic *C. cerastes* will encounter and consume this type of prey while remaining relatively immobile. Finally, unlike other viperid snakes, Sidewinders feed, mate, and hibernate in the same relative location (Secor, 1992), which could allow females to feed opportunistically while engaged in reproductive activities. In conclusion, prey consumption by *C. cerastes* during early reproductive stages is a likely event that can provide valuable energetic resources for fueling a female's subsequent breeding activities (gestation, parturition, maternal care).

On the contrary, why may gravid female *C. cerastes* cease feeding? At least three, non-mutually exclusive hypotheses could account for aphaagia in reproductive female snakes during the gestation period. First, gravid snakes move less often than non-gravid individuals (Charland and Gregory, 1995; Gardner-Santana and Beaupre, 2009), possibly because they experience reductions in locomotor ability due to the physical burden of offspring mass (Seigel et al., 1987; Cooper et al., 1990; Shaffer and Formanowicz, 1996). Impaired locomotion can reduce a female's foraging efficiency (Lourdais et al., 2004a) and also lead to increased predation risk (Bauwens and Thoen, 1981). Despite the fact that Sidewinders are sit-and-wait foragers, individuals engage

in intermittent periods of continuous locomotion during spring, summer, and fall (Brown and Lillywhite, 1992). Although decreased locomotor ability may not significantly reduce the foraging efficiency of an ambush forager per se, it can lead to an increase in predation risk. Therefore, aphagia could enable gravid Sidewinders to reduce activity levels, lessening their susceptibility to predation (Brodie, 1989). Second, viviparous species in temperate zones are expected to maximize the developmental rate of their embryos by selecting high body temperatures to ensure parturition before winter (Beuchat and Ellner, 1987). In fact, gravid females of various snake species (e.g., *Charina bottae* [Northern Rubber Boas], *Crotalus horridus* [Timber Rattlesnakes], *Crotalus oreganus* [Western Rattlesnakes], *Nerodia rhombifer* [Diamond-backed Watersnakes], *Thamnophis elegans* [Terrestrial Gartersnakes]) exhibit higher and/or less variable body temperatures than non-gravid females (Gardner-Santana and Beaupre, 2009, and references therein). Gravid females may be under strong selection to prioritize gestation over foraging, and to optimize embryonic thermal conditions, perhaps to maximize offspring quality (Lourdais et al., 2004b). If so, the specific microhabitats selected by gravid females to meet their thermal requirements may not be suitable foraging locations, leading to decreased predator-prey encounter rates and a lesser likelihood that the snakes will consume food (Gregory et al., 1999). Third, developing offspring may create space constraints within the body cavity, thus limiting the size that a female snake can expand to accommodate prey (Weeks, 1996). This explanation may be less likely, however, because the linear arrangement of body organs in a snake allows for distention of the anterior part of the body when prey is ingested, and of the posterior part of the body due to developing offspring (Brischoux et al., 2011), suggesting that gravid females may still be physically capable of consuming prey.

Alternatively, temporal variation in the feeding rates of females may be caused by changes in foraging behavior and prey availability that are independent of reproductive status. For instance, if during the spring and fall snakes forage during the day and at night, then they could feed upon diurnal and nocturnal prey (e.g., lizards and mammals, respectively), and hence may have greater foraging success, which would be reflected in a higher frequency of specimens containing food. In contrast, if during the summer individuals mainly or exclusively forage nocturnally, the unavailability of diurnal taxa as potential prey may lead to a decrease in the snakes' foraging success. Our data revealed that non-reproductive females fed throughout the active season, but that reproductive females only consumed prey during the first part of the breeding season. This pattern suggests that any temporal change in the foraging behavior of female Sidewinders does not decrease foraging success, and that reproductive condition negatively affects the feeding rates of female *C. cerastes*. Laboratory studies of *Thamnophis elegans* showed that gravid snakes, even when presented with food *ad libitum*, ate less than non-gravid individuals, suggesting that the former exhibit aphagia while pregnant (Gregory et al., 1999).

For male snakes, time spent searching for mates (Aldridge and Brown, 1995), competition for access to females (Madsen, 1998), and courtship and copulation (Daly, 1978) are hypothesized to result in aphagia during the mating season. For instance, adult male *Crotalus viridis* (Prairie Rattlesnake) abandon foraging activities in mid-

summer in favor of episodic mate searching behavior (King and Duvall, 1990). In contrast, adult male *C. cerastes* exhibited a tendency to feed more frequently during the first (longer) mating season than during the non-reproductive season. Male *C. cerastes* significantly increase the distances traveled during the reproductive season in search for mates (Secor, 1994a). Males that feed during the breeding season likely enhance their energy reserves, which may increase their mating opportunities by enabling them to travel longer distances, and thus to maximize their encounter rates with females, which may in turn enhance the males' mating success (Duvall and Schuett, 1997).

A possible limitation of our study is that the inference that individual male *C. cerastes* have two distinct mating seasons was based on field observations of breeding activities in spring and fall. However, it is possible that this conclusion is the result of combining all those behavioral observations, and that individual males engage in mating activities only once per year, during either spring or fall. If the latter scenario is correct, males could potentially exhibit seasonal aphagia when they are engaged in reproductive activities, but the available data do not allow us to evaluate this possibility. Field studies that follow individual male *C. cerastes* during their entire active season and that compare prey availability to feeding frequency may clarify whether males ignore feeding opportunities in order to engage in reproductive activities (mate searching, courtship, and copulation).

Our findings have implications for two additional aspects of the reproductive biology of *C. cerastes*. First, as previously mentioned, Sidewinders seem to have two distinct mating periods, one in spring and another one in fall (Reiserer, 2001; Ernst and Ernst, 2003). The reproductive phenology of female *C. cerastes* (Fig. 1) indicates that the vitellogenic cycle is not necessarily linked temporally to mating activities. Female Sidewinders may use sperm from spring matings immediately, but may also be capable of long-term sperm storage (Schuett, 1992), in which case sperm from fall matings is stored in the reproductive tract until fertilization in spring of the following year. At least three other rattlesnake species, *Crotalus atrox* (Western Diamond-backed Rattlesnake; Schuett et al., 2004), *C. molossus* (Black-tailed Rattlesnake; Greene et al., 2002), and *C. oreganus* (Aldridge, 2002), also have dissociated reproductive cycles in which there is a time lapse between copulation and vitellogenesis.

Second, females of most North American rattlesnakes exhibit a prolonged vitellogenic cycle, which is typically initiated in late summer or fall and completed in the spring of the following year (Aldridge and Duvall, 2002; Gludas et al., 2009). On the contrary, female *C. cerastes* undergo a relatively short period of vitellogenesis predominantly in the spring, although occasionally some individuals may develop enlarged follicles in late fall (Fig. 1; Goldberg, 2004). A rapid vitellogenic cycle has also been documented in *C. atrox* (Taylor and DeNardo, 2005) and *C. mitchellii* (Speckled Rattlesnake; X. Gludas, unpubl. data), suggesting that this pattern may be more common in rattlesnakes than previously thought.

Conflicting time and energy demands between reproduction and feeding can result in seasonal aphagia during the breeding season. Females of many ectothermic organisms seem to be predisposed to a capital breeding strategy (Bonnet et al., 1998), because their low rates of energy intake and expenditure, coupled with infrequent reproduction, allow long-term energy storage for reproductive activities. However, our findings do not support this

contention. Instead, they illustrate intersexual differences in the manner in which *C. cerastes* acquires energy to sustain reproduction. Female Sidewinders do not reduce their feeding frequency during the vitellogenic stages of their reproductive cycle, but tend to consume fewer prey during gestation. On the contrary, male *C. cerastes* continue feeding throughout the reproductive season. The discovery of this intersexual variation in feeding patterns of *C. cerastes* underscores the importance of descriptive ecological studies to elucidate distinctive patterns of life history evolution.

ACKNOWLEDGMENTS

We thank J. Vindum and R. Drewes (CAS), J. Seigel (LACM), and C. Spencer and J. McGuire (MVZ) for allowing us to examine specimens, M. Irick and G. Webber, Jr. for assisting with data collection, and R. Bryson, Jr. for valuable comments on an earlier version of this manuscript. This work was partially funded by grants from the Graduate and Professional Student Association of the University of Nevada, Las Vegas to MMW, and by grants from the National Science Foundation (DBI-0001975, DEB-0327415) to JAR-R.

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