

Ambient Temperature Activity of Horned Adders, *Bitis caudalis*: How Cold Is Too Cold?

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Most physiological processes are greatly affected by temperature; therefore animals thermoregulate to maintain a body temperature (T_b) that approximates that which is optimal for physiological performance (reviews by Avery, 1982; Huey, 1982; but see Webb and Shine, 1998). As an ectotherm, a snake relies on external heat sources to maintain its preferred T_b . Although heat sources are readily available during the day, the nocturnal environment has few, if any, heat sources. Even though the nocturnal environment poses a significant thermal handicap, numerous snakes species are nocturnal (Greene, 1997). Because of the lack of heat sources, activity of nocturnal species should be sensitive to ambient temperature (T_a).

The physiological and behavioral means by which snakes adapt to thermal challenges associated with nocturnality has not received extensive study. Many performance measures including locomotion, digestion rate, tongue flick, and strike velocity are maximized at relatively high T_b (e.g., Stevenson et al., 1985; Ayers and Shine, 1997; Dorcas et al., 1997; Webb and Shine, 1998). These body functions are near maximum levels during the day but are significantly reduced at night (Stevenson et al., 1985). Activity at night would not only require a snake to use physiological processes associated with foraging (e.g., locomotion, tongue-flick rate, strike velocity) when they are suboptimal but could also negatively impact temperature-sensitive physiological processes, which are not associated with activity (e.g., digestion). Nocturnal activity of rubber boas, *Charina bottae*, led to a T_b below that which would occur if the snake remained in a nighttime refugium (an inverted T_b pattern; Dorcas and Peterson, 1998).

A nocturnally active snake typically has a T_b that approximates T_a (Dorcas and Peterson, 1998); therefore, T_a may be more critical to performance of nocturnal species than of diurnal species, where radiation and conductance can lead to a T_b much greater than T_a (Peterson, 1987). Because of the thermosensitivity of processes critical to foraging, thermal factors might constrain the timing, place, and duration of predatory bouts (Ayers and Shine, 1997). Such constraints can lead to seasonal differences in activity period. For example, copperheads, *Agkistrodon contortrix*, are diurnal during cool seasons (spring and fall) but are nocturnal during the warm summer months (Sanders and Jacob, 1981). Thermal constraints can also lead to ontogenetic differences in activity period. Adult diamond pythons, *Morelia spilota spilota*, forage nocturnally, whereas juveniles are diurnal (Ayers and Shine, 1997). We used a controlled laboratory environment to test the

thermosensitivity of activity in a small nocturnal snake. We hypothesize that activity by a nocturnal snake will decrease as nocturnal T_a decreases.

Four male horned adders, *Bitis caudalis*, were collected in October, 1996, in the vicinity of Keetmanshoop, Namibia. *Bitis caudalis* is a small viper distributed throughout southern Africa. Snout-vent length of males ranges from 190 to 400 mm (Shine et al., 1998). Males used in this study ranged in mass from 40 to 77 g. *Bitis caudalis* feeds on small mammals and lizards, using a sit-and-wait foraging mode by day but actively foraging at night. In more xeric environments, such as the Keetmanshoop area, *B. caudalis* is considered nocturnal and saurophagous (Shine et al., 1998).

Snakes were housed individually in standard 40-liter glass aquaria containing a substrate of utility sand, a water bowl, and a refuge. Mylar heat tape (Flex Watt, West Wareham, MA) was placed under one end of each aquarium to provide subsurface heat and therefore a thermogradient. Room lighting and supplemental heat were set to a 12:12 cycle. Room temperature was a constant 25°C. The snakes were offered a diet of lizards or small mice approximately every two weeks. At this frequency, meals were routinely consumed unless the animal was in preecdysis.

Behavioral testing was conducted in an environmental chamber set at the desired test temperature (5, 10, 15, 20, or 25°C). The test arena consisted of an approximately 76 cm × 92 cm fiberglass tub containing utility sand at a depth of approximately 1.5 cm. Four equal-sized quadrants were created by stringing yarn across the top of the arena, connecting the midpoints of opposite walls. Supplemental heat sources (subsurface mylar heat strip and one or more flood lamps) were provided at one end of the arena (quadrants 1 and 2). The wattage of the bulbs in the lamps varied with varying experimental room temperature, so as to attain a surface temperature of $38 \pm 1^\circ\text{C}$ when the lights were on. The lights and the mylar heat strip were on a 12:12 cycle (lights and heat on from 0600–1800 h). When the heat sources went off, surface temperature under the lamps gradually cooled to test temperature. Test runs using temperature dataloggers (Stowaway XTL, Onset Computer Corporation, Bourne, MA) verified that the rate of cooling increased with lower test temperatures. The time it took for surface temperature to decrease from 38°C to 2°C above room temperature ranged from 95 min at 5°C to 147 min at 25°C. A red light was suspended high above the arena to allow for videotaping during the scotophase but made a negligible heat contribution to the arena. A piece of driftwood was placed in the center of the arena to serve as a potential refuge.

Experimental trials were conducted from March to December 1998. A snake that had not been offered food for two weeks was placed in the test arena at least 24 h prior to the experimental trial to allow it to adjust to the new environment. Twenty minutes prior to the time the lights and subsurface heating went off on the day of the trial, a circular tray was placed in the middle of each quadrant. Trays in quadrants 1 and 2 (those associated with the supplemental heat sources) were empty. The third tray contained fresh artificial bedding material (CareFRESH, International Absorbents, Inc., Bellingham, WA), whereas the fourth tray contained artificial bedding which had been soiled with feces, urine, and pieces of shed skin from a gecko (*Coleonyx variegates* or *Diplodactylus stenodactylus*). The quadrant location of each of the latter two

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trays alternated between quadrants 3 and 4. A video camera secured directly above the arena recorded activity for two hours starting just prior to the onset of the scotophase. This time period was chosen because, based on previous observations, this is the time of peak activity in captive *B. caudalis*.

Each snake was tested in four trials at each of five environmental temperatures (5, 10, 15, 20, and 25°C). At the end of the final run at each temperature, a live gecko (*C. variegatus* or *D. sphenodactylus*) was introduced into the arena. Although neither of these species is African, they are terrestrial and of a size similar to that of the most common geckos we observed in the Keetmanshoop area (e.g., *Ptenopus garrulous* and *Pachydactylus mariquensis*). After presentation of a gecko, snakes were observed via the video monitor for 30 min. If the gecko was eaten, the time of consumption was recorded. If not eaten during the observation period, the gecko was left in the arena with the snake for the remainder of the night. If not consumed by the following morning, the gecko was removed from the arena. The sand in the arena was replaced with new sand before the introduction of a new snake.

Video tapes were analyzed using a slow motion video cassette recorder. Onset of activity, termination of activity, and total activity time were determined for all trials. The first hour of two randomly selected trials for each snake at each temperature were further analyzed to detail the animal's activity. Six parameters were assessed: (1) frequency entering each quadrant; (2) time spent in each quadrant; (3) time spent in close proximity to each tray and head oriented toward the tray; (4) time spent in close proximity to a tray but not with the head oriented toward the tray; (5) time spent not in close proximity of a tray but with head oriented toward a tray; (6) time that the head was in contact with each tray. An animal was recorded as entering or leaving a quadrant when its entire head passed into or out of the quadrant. The head of the snake was considered oriented to a tray when the animal's rostrum was pointed toward ($\pm 10^\circ$) the tray in the quadrant occupied. Close proximity is defined as being within two head lengths from a tray.

We used a two-factor (subject, temperature) repeated measures analysis of variance (ANOVA) to determine the effect of temperature on measures of activity. The model also included the interaction temperature \times lizard ID number to determine whether individuals responded differently to temperature. Where significant effects were detected, we used Tukey's Honestly Significant Difference to determine which means were different from each other. Differences were deemed significant if $P < 0.05$.

For analysis of foraging parameters, data from each run were combined for each animal and results analyzed using repeated measures ANOVA. The model used temperature and quadrant (quad) as nominal variables. We used Fisher Protected Least Significant Difference to determine the source of any differences obtained. Statistical calculations were made using StatView (SAS Institute, Inc., Cary, NC).

Environmental temperature had a significant effect on activity duration of *B. caudalis* (Fig. 1; $F_{4,3} = 26.2$; $P < 0.0001$). Activity duration at 5 and 10°C was significantly shorter than activity at 15°C ($P = 0.007$ and $P = 0.027$ for 5 and 10°C, respectively), which was

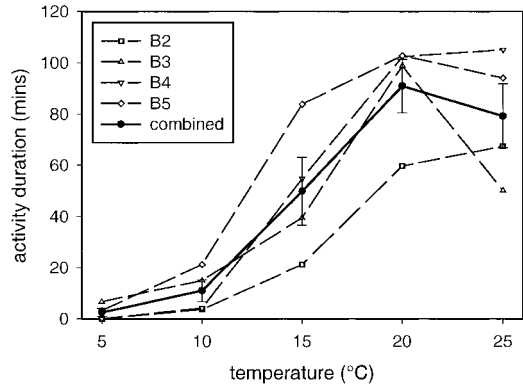


FIG. 1. Effect of temperature on the duration of activity of *Bitis caudalis*. Each broken line represents the average of four trials for a given animal (error bars omitted for simplicity), whereas the bold solid line represents a mean of the means (\pm standard error). Temperature had a significant effect on activity (5°C = 10°C < 15°C < 20°C = 25°C). Notice that while there was variation in the absolute activity among individuals, relative responses to temperature were similar.

significantly shorter than that at 20°C ($P = 0.019$). Although there was some variation among animals ($F_{3,3} = 4.39$; $P = 0.007$), animals responded similarly to temperature differences ($F_{12,9} = 1.17$, $P = 0.33$).

At temperatures of 15°C and above, animals were active for at least some time in all trials. At lower temperatures, animals showed no activity in a large proportion of trials (75% and 50% of trials with no activity at 5°C and 10°C, respectively). When activity did occur, onset was closely associated with the time when the lights went out (onset of activity occurred at an average of 3.80 min after lights out). Onset of activity was not influenced by ambient temperature ($F_{4,3} = 0.990$; $P = 0.443$), but, rather, differences in activity duration were related to differences in the time that activity ended (Fig. 2; $F_{4,3} = 12.03$; $P = 0.0001$). Activity was usually continuous until terminated for the remainder of the observation period. Occasionally, snakes would initiate a second activity session after a short break.

Active snakes did not show a preference for the quadrant containing the lizard-soiled tray ($F_{3,9} = 0.03$; $P = 0.86$ for times entering the quadrant; $F_{3,9} = 0.015$; $P = 0.90$ for time spent in the quadrant) nor did the snakes orient preferentially toward the lizard-soiled tray ($F_{3,9} = 0.46$; $P = 0.50$ for direct orientation in close proximity; $F_{3,9} = 1.53$; $P = 0.23$ for direct orientation from a distance). Temperature had a significant effect on feeding ($F_{4,3} = 3.83$; $P = 0.024$), in that feeding was completely inhibited at 5°C ($P < 0.02$). Snakes fed frequently at higher T_a (i.e., three snakes ate at all other temperatures, whereas one snake consumed its prey only at 10°C). There was no significant effect of temperature on time from offering of prey to consumption of prey ($F_{4,3} = 0.26$; $P = 0.86$).

Bitis caudalis showed a nonlinear sensitivity to ambient temperature. Snakes showed similar activity at higher ambient temperatures (20°C, 25°C), but activity

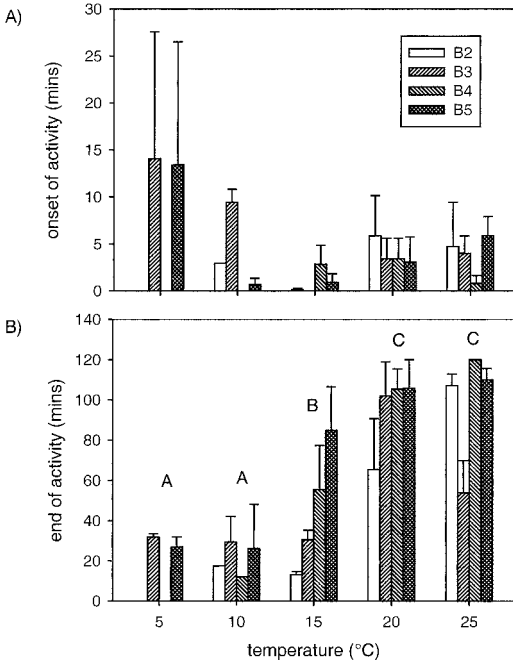


FIG. 2. Effect of environmental temperature on the (A) onset and (B) end of activity. Individual *Bitis caudalis* are denoted in the legend. The absence of data or standard error bars denotes activity by that animal in no or only one trial, respectively, at that temperature. There was no significant difference in the onset of activity, but the end of activity was temperature-sensitive as denoted by capital letters.

was significantly reduced at an intermediate temperature (15°C). At low temperatures (5°C, 10°C), activity was even further reduced, and oftentimes snakes chose not to be active (Fig. 1). The reduced activity at decreasing T_a is probably reflective of the thermosensitivity of most physiological processes, because reduced body temperatures have a negative effect on performance measures vital to foraging, including locomotion, tongue flick rate, and strike velocity (Greenwald, 1974; Stevenson et al., 1985; Ayers and Shine, 1997; Webb and Shine, 1998).

At all environmental temperatures tested, onset of activity in *B. caudalis* began shortly after the onset of the scotophase. Initiating activity at this time would enable snakes to use the thermoregulatory benefits of the just terminated photophase. Prior to testing, snakes routinely basked under the lights while submerged to varying degrees in the sand. Similar activity patterns have been documented in the field with the broad-headed snake, *Hoplocephalus bungaroides*, which uses protected thermoregulation during the latter parts of the day to maintain preferred T_b and then commences foraging activity shortly after dusk (Webb and Shine, 1998).

Although we did not measure T_b during our trials because of the impact the disturbance would have on activity, it can be assumed (because the majority of snakes were basking just prior to the onset of the sco-

tophase) that T_b was, in most instances, significantly higher than ambient temperature during the initial moments of the scotophase. Because the rate of cooling of the snakes should approximate the rate of surface temperature cooling, it is not surprising that the rate of surface temperature cooling showed an inverse relationship to the duration of snake activity. Larger snakes can use coiled postures to reduce the rate at which they cool; however such postures do not influence cooling rate in snakes of a size similar to *B. caudalis* (Ayers and Shine, 1998). These results are consistent with field observations. Hoffman (1988) noted a spate of activity of *B. caudalis* over a three-day period in August and suspected this activity was in response to the relatively high air temperatures during those days (average temperature for those three days was 3.9°C greater than the average August temperature).

The frequent lack of activity at low temperatures (75% and 50% of trials with no activity at 5 and 10°C, respectively) may reflect a decision by the snake that the costs of activity outweigh the likelihood of foraging success. As ectotherms, snakes do not need to forage daily and may forego foraging activity or days when the likelihood of success is reduced as a result of decreased performance capacity. Dorcas and Peterson (1998) discovered that *C. bottae* shows an inverted activity pattern (an indication of nocturnal activity) about once every eight days. Unfortunately, thermal conditions of active versus inactive days were not compared.

Even though activity of *B. caudalis* was moderately reduced at 15°C and dramatically reduced at 10°C, snakes consumed prey introduced into the test arena at those temperatures. This suggests that snakes may abandon foraging activity as the likelihood of prey capture is reduced, but the physiological capability remains. Although geckos are known to be active at temperatures below 15°C (e.g., Brain, 1962; Henle, 1990; Autumn et al., 1994), the relative activity of geckos at various temperatures is unknown. No snake consumed prey at 5°C, which may be a temperature at which prey capture or digestion is severely compromised. Although a distinctly different species, it is worth noting that digestion rate in grass snakes, *Natrix natrix*, is reduced at 15°C and completely arrested at 5°C (Skoczylas, 1970).

Although prey scent has been shown to influence foraging behavior in viperids (Theodoratus and Chiszar, 2000), we were unable to detect such an effect. We detected no significant differences for either time spent in the quadrant that contained prey scent or in orientation relative to the prey scent. Whether prey scent does not influence *B. caudalis* activity or the scent stimulus provided was inappropriate or insufficient is unknown without further investigation.

Our results demonstrate that temperature can have a significant effect on activity, but inferences to the natural setting must be made with caution. No field study has substantially addressed the effect of daily temperature variation on activity. Such studies would be of extreme interest if conducted at the community level where predator-prey relationships could be assessed. Remaining virtually unexplored is the possibility of adaptive physiology, akin to the reduced cost of locomotion in geckos (Autumn et al., 1999), which would enable nocturnal snakes to perform at lower T_b

more effectively than diurnal species. Evolutionary theory suggests that such adaptations would occur to at least partially offset the handicap associated with the nocturnal environment (Autumn et al., 1999).

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Reproduction in a Group-Living Lizard, *Cordylus cataphractus* (Cordylidae), from South Africa

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Both oviparous and viviparous clades occur within the Cordylidae, a scincomorph family of lizards endemic to sub-Saharan Africa (Mouton and Van Wyk, 1997; Frost et al., 2001). A single origin of viviparity in the family is suggested by the recent phylogeny of Frost et al. (2001), the oviparous genus *Platysaurus* forming the most basal cordylid clade. Viviparous cordylids were formerly partitioned into three genera, but Frost et al. (2001) transferred both *Chamaesaura* and *Pseudocordylus* to the genus *Cordylus* to render a monophyletic taxonomy.

In the *Cordylus*-*Pseudocordylus*-*Chamaesaura* clade, viviparity evolved as an adaptation to cold climates, apparent in the highland or temperate distribution of extant species (Mouton and Van Wyk, 1997). This was probably facilitated by a preceding transition to a sit-and-wait foraging mode, lack of prey chemical discrimination ability, and a rupicolous lifestyle in the ancestor of the Cordylidae, but the adaptive significance of these transitions remains unknown (Mouton and Van Wyk, 1997).

Available information suggests that the reproductive cycles of members of this viviparous clade are conservative (for review, see Van Wyk and Mouton, 1998). Females typically deposit yolk into growing follicles during winter months, followed by ovulation in

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spring, and parturition during late summer to early autumn. Males follow one of two reproductive cycling patterns. In the more common pre-nuptial cycle, spermatogenesis occurs over autumn-winter. Maximum spermatogenic activity is present during spring, coinciding with ovulation in females. In postnuptial spermatogenic cycling, males produce sperm maximally toward late summer. Spermatogenic activity is minimal during winter months when males store sperm in epididymides or vasa deferentia until the mating season in spring (intrauterine sperm storage has not been illustrated in any cordylid thus far). Too little information is available to understand the significance of pre- versus postnuptial cycling in the family, despite the fact that a molecular phylogeny (Frost et al., 2001) is now in place. Information on reproductive cycling of many more cordylids, specifically basal members of the viviparous clade, is needed before this issue can be addressed appropriately.

The phylogeny of Frost et al. (2001) indicates *Cordylus cataphractus* as one of the basal species within the *Cordylus-Pseudocordylus-Chamaesaura* clade. It is heavily armored with osteodermate scales and a thickest body, rather sluggish in its movements and is almost never encountered far from crevices (Peers, 1930; Branch, 1998). It is endemic to the arid and semiarid areas along the west coast of South Africa (Mouton, 1988; Branch, 1998) and displays the clearest manifestation of permanent grouping behavior recorded for any lizard to date (Mouton et al., 1999; Visagie, 2001). Recent studies on *C. cataphractus* showed that it has a particularly low metabolism (Mouton et al., 2000a), feeding activity may be reduced for long periods or even interrupted because of its grouping habit (Visagie, 2001). At specific times of the year, energy availability may be extremely low (Visagie, 2001) and may seriously constrain reproductive activity.

The aim of the present study was to determine the annual reproductive cycle in a basal viviparous cordylid, *Cordylus cataphractus*. Fecundity and seasonal variation in fat body cycles were also examined.

Lizards were collected over several years (1983–2000) in the Graafwater district (32°10'S; 18°35'E; 100–800 m elevation), located on the west coast of South Africa. These are now housed as preserved specimens in the Ellerman Collection, Stellenbosch University, Stellenbosch. Accession numbers are USEC/H-403, 759, 770, 773, 779, 854, 904, 1089, 1101, 1189, 1197, 1234, 1242, 1281, 1292, 1302, 1692–3, 1707–8, 1726, 1743, 1783, 1785, 1787, 1789–90, 1804–6, 1982–3, 2035, 2283, 2285–6, 2383, 2408–9, 2412, 2414–5, 2418–9, 2422–3, 2453, 3070–2, 3074–5, 3077–81, 3083, 3085–6, 3090, 3092–6, 3098–3100, 3103–7, 3110, 3112–3, 3115, 3118, 3129, 3131–2, 3134–5, 3138, 3145, 3148–51, 3156–9, 3161–2, 3166–8, 3173–4, 3177, 3179–83, 3187, 3191, 3199, 3201–2, 3240, 3244–5, 3250–1, 3477–81. On coastal plains, dense colonies of *C. cataphractus* inhabit scattered rocky outcrops. The climate is arid with an annual rainfall below 200 mm, consisting mainly of winter rains. Vegetation is classified as Namaqualand Coastal Belt, a subdivision of Succulent Karoo (Acocks, 1988) and is characteristic of low altitude, arid areas. Frequent sea mists reduce aridity along the western coastline.

Snout-vent length (SVL) was measured to the nearest millimeter using vernier callipers, and reproduc-

tive organs and fat bodies were excised from all preserved specimens. Fat bodies, of both males and females, were dried to constant mass (60°C), and these values were recorded to the nearest 0.1 mg. In females, both ovaries were examined with an ocular micrometer to determine the diameter of the largest follicle (nearest 0.01 mm). Reproductive condition was assessed using the following criteria: diameter of the largest ovarian follicle, presence of oviductal eggs, presence of corpora lutea or corpora albicantia, and condition of the oviducts. Eggs (embryos + yolk) were excised and dried to constant mass (60°C) which was recorded to the nearest 0.1 mg. The number of embryos in utero and their developmental stages (Dufaure and Hubert, 1961) were determined for all gravid females. In males, the longest and shortest axes of the left testes were measured to the nearest 0.1 mm. Testis volume was calculated using the formula for the volume of an ellipsoid. Paraffin sections (10 µm) were cut from the middle of the right testis and stained with Harris hematoxylin and eosin. Spermatogenic activity was assessed qualitatively by using a slightly modified version of the classification system of Licht (1967).

Data were tested for normality and homogeneity of variances using the Kolmogorov-Smirnov and Bartlett's tests, respectively (Sokal and Rohlf, 1981). Data on ovarian follicle diameter, testis volume, and fat body dry mass met the assumptions of normality. Analysis of covariance (ANCOVA) with SVL as independent variable was used to determine whether ovarian follicle diameter, testis volume and fat body dry mass were significantly affected by body size. In cases where they were affected by SVL, one-way analysis of variance (ANOVA) was used to indicate significant seasonal variation in the parameters, followed by the Fisher LSD test for comparisons among pairs of means. Where SVL explained a significant percentage of monthly variation in a parameter, ANCOVA was used. ANCOVAs were followed by Scheffé's multiple comparison procedure. Probability values (P) less than 0.05 were recognized as significant. All means are reported \pm 1 SE.

Sexual maturity was attained at about 95 mm SVL in both sexes. The smallest female with enlarged follicles measured 93 mm SVL; therefore, only females with SVL > 93 mm were used in the present study. Mean SVL of females used in the present study was 106 mm ($N = 52$). Regression analysis indicated that the diameters of the largest follicles were not significantly affected by variation in female SVL ($r = 0.273$, $P > 0.05$). Mean follicle diameter values showed significant monthly variation (ANOVA, $F = 20.36$, $df = 6$, $P < 0.0001$; Fig. 1). Females with mean ovarian follicle diameter < 3 mm were either postpartum/previtellogenic or postovulatory/gravid. Previtellogenic (nonreproductive) females were present during February through April, and all females during May and September were vitellogenic (ovarian follicle diameter > 3.5 mm; Figs. 1–2). Females with mean ovarian follicle diameter > 6 mm (i.e., late vitellogenic) were found during July through December. Postovulatory/gravid females were present during October through April, but ovulation may have occurred as late as December in some females in different years. Parturition may have occurred as early as February, as indicated

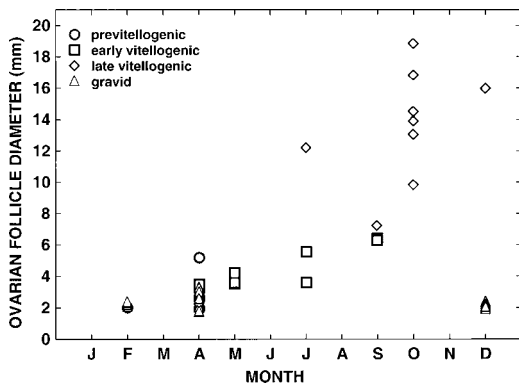


FIG. 1. Relationship of mean diameter of largest ovarian follicles to month of the year in *Cordylus cataphractus*. Each symbol represents one lizard and four female reproductive groups are indicated.

by the presence of conspicuous remnants of corpora lutea (corpora albicantia) and stretched oviducts, but more than 70% of females investigated were still gravid in April (Fig. 2). The few females collected in May were all postpartum. All gravid females examined ($N = 29$) contained a single large embryo in utero. In 27 of 29 (93%) gravid females, the embryo was found in the right oviduct. Significant increases in wet mass of eggs (embryo + yolk) were observed toward the end of gestation, as compared to newly ovulated eggs (mean 3.3–5.2 g, constituting an increase of up to 58%). Dry mass of eggs, however, decreased significantly during gestation with late-term embryos at –42% of newly ovulated egg mass. The mean dry mass recorded for newly ovulated eggs was 2.14 g ($N = 5$).

The smallest male with enlarged testes measured 90 mm SVL; therefore, only males with SVL > 90 mm were used in the present study. Mean SVL of males used in the present study was 107 mm ($N = 70$). Regression analysis indicated that testis volume was not significantly affected by variation in male SVL ($r =$

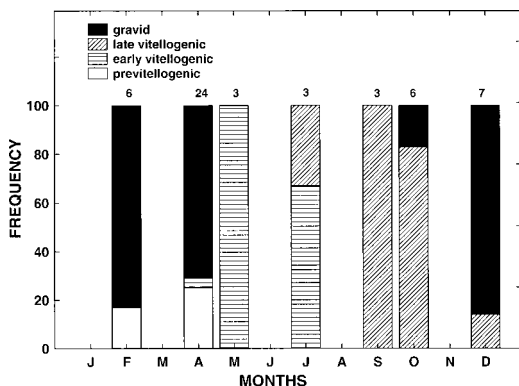


FIG. 2. Stacked bar diagram showing percentage of female *Cordylus cataphractus* in various reproductive stages at different months of the year. Sample sizes are given above the bars.

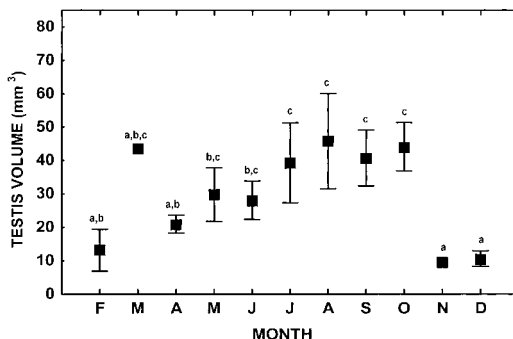


FIG. 3. Variation (mean \pm 1 SE) in testis volume during the annual reproductive cycle of male *Cordylus cataphractus*. Monthly sample sizes are reported in Table 1. Values with different superscripts are significantly different (Fisher LSD Test; $P < 0.05$ per comparison).

0.263, $P > 0.05$). Mean testis volume showed significant monthly variation (ANOVA; $F = 3.29$, $df = 10$, $P < 0.005$; Fig. 3), with increased values evident during late autumn through winter, and a peak being reached during late winter-spring. During summer, testes volumes were at their lowest values.

Histological examination indicated that most males had testes in a regressed state during November through April, with seminiferous tubules mostly occluded by spermatogonia and a Sertoli syncytium (Table 1, stage 1). Testis volume was small during this time (Fig. 3). Proliferation of spermatogonia with appearance of primary spermatocytes (stage 2) com-

TABLE 1. Seasonal changes in male spermatogenic activity of *Cordylus cataphractus*. Classification of spermatogenic stages are as follows: (1) seminiferous tubules involuted with spermatogonia only; (2) primary spermatocytes appearing; (3) secondary spermatocytes abundant and early spermatids appearing; (4) transforming spermatids with few spermatozoa; (5) spermatids and spermatozoa abundant; (6) spermatozoa abundant (maximal level of spermiogenesis); and (7) spermatozoa abundant, but spermatids and spermatocytes greatly reduced.

Month	N	Spermatogenic stages with numbers of lizards in each stage						
		1	2	3	4	5	6	7
Feb	3	2	1					
Mar	1			1				
Apr	18	2	15		1			
May	6		1	2	2	1		
Jun	8		2	3	3			
Jul	6			2	1	3		
Aug	2			1		1		
Sep	4			2		2		
Oct	11	1		1	1	3	4	1
Nov	1	1						
Dec	10	10						

menced in February (late summer) and this stage dominated until April (midautumn). Lumina were formed and the seminiferous epithelia consisted of 1–3 layers of cells and testis volume remained relatively small. The occurrence of secondary spermatocytes and early spermatids from March onward (stage 3) coincided with a gradual increase in testis volume. Transforming spermatids were abundant with spermatozoa present in small numbers (stage 4) in some males from April onward (marking onset of spermiogenesis). Spermiogenic activity peaked toward October (stages 5 and 6), during which time testes volumes reached maximum values. In one male spermatogenic activity was declining during October, despite an abundance of spermatozoa (stage 7), whereas the testes of another male were in a regressed state.

Highest fat body dry mass (10.3 g) was recorded in a male of 122 mm SVL. The female with the largest fat bodies (7.2 g in dry mass) measured 101 mm SVL. ANCOVA revealed that fat body dry mass was significantly affected by variation in female SVL ($F_{1,37} = 14.4$; $P < 0.001$), the latter accounting for 28% of the variation in fat body size. In males, SVL similarly explained a significant amount (13.7%) of variation in fat body size ($F_{1,60} = 10.7$; $P < 0.01$). By removing the effect of overall body size (SVL), fat bodies of both sexes showed a significant variation in mean dry mass in monthly samples (females, ANCOVA; $F = 8.56$; $df = 6$; $P < 0.0001$; males, ANCOVA; $F = 6.63$; $df = 10$; $P < 0.0001$; Fig. 4). Fat bodies in both sexes were small during autumn and winter months, with marked size increases evident during midspring, followed by a gradual decline toward late summer. Fat body size in adult females was thus at its greatest during gravidity (summer and autumn); in males peak fat body sizes coincided with the later stages of spermiogenesis or testicular regression during summer (see Table 1).

Cordylus cataphractus conforms to the basic pattern of conservatism in reproductive cyclicity that has been reported for cordylids in general (see recent review of Van Wyk and Mouton, 1998). Females exhibit autumn to winter vitellogenic activity. Ovulation occurs during late spring, which is later than in other cordylids in which ovulation is a late winter to early spring phenomenon. As in other cordylids, parturition in *C. cataphractus* occurs in early to midautumn. Autumn/winter reproductive activity is considered atypical for temperate zone lizards, among which most species reproduce during spring and summer (Fitch, 1970; Duvall et al., 1982; Licht, 1984; James and Shine, 1985). Autumn/winter reproductive activity was originally thought to be associated with the evolution of viviparity in certain squamate genera (Guillette and Mendez-de la Cruz, 1993), but such activity seems not always to lead to the evolution of viviparity as it has now been described in a few oviparous lizards (Ramirez-Pinilla, 1991, 1994; Van Wyk and Mouton, 1996). Although anecdotal reproductive information suggests many lizards from the southern African subcontinent comply with the characteristic spring-summer cycle of temperate zone lizards in general (Fitch, 1970), all cordylids, and a few oviparous and viviparous representatives of other families from this region, display autumn/winter reproductive activity (Flemming, 1994; Flemming and Bates, 1995). More studies are required on reproductive cycling of lizards from

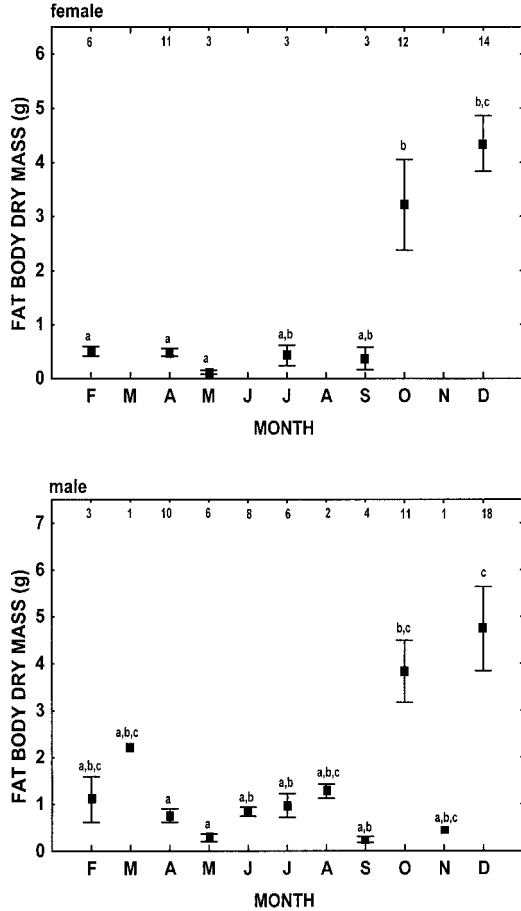


FIG. 4. Variation (mean \pm 1 SE) in fat body dry mass during the annual reproductive cycle of *Cordylus cataphractus*. Monthly sample sizes are reported above the error bars. Values with different superscripts are significantly different (Sheffé; $P < 0.05$ per comparison).

this subregion, before the significance of such atypical reproductive activity can become clear.

Cordylus cataphractus males follow a prenuptial spermatogenic cycle, with peak spermatogenesis coinciding with spring ovulation in females. A prenuptial cycle has also been recorded for *Platysaurus* species studied to date (Van Wyk and Mouton, 1996) and the basal position of *C. cataphractus* in the *Cordylus-Pseudocordylus-Chamaesaura* clade suggests that this cycling strategy is the ancestral one for this clade.

Cordylus cataphractus females produce a single large offspring each year. In the formerly recognized viviparous genera *Cordylus* and *Pseudocordylus*, the maximum number of young produced per female in any particular species ranges from 2–7, increasing to 8–17 in *Chamaesaura* (Branch, 1998; Du Toit, 2001). In contrast, oviparous *Platysaurus* species produce only two eggs per clutch, although more than one clutch may be deposited from summer to autumn (Branch, 1998; Van Wyk and Mouton, 1996). Gerrhosaurids, consid-

ered the sister taxon to cordylids, produce a maximum of 2–12 eggs per clutch (Branch, 1998). Low fecundity in *C. cataphractus* seems unusual for cordyliform lizards and may relate to its group-living behavior.

It is possible that increased resource limitations experienced under group-living conditions may influence life-history characteristics, such as timing and duration of reproductive events, and fecundity. *Cordylus cataphractus* is one of three girdled lizards known to display permanent grouping behavior in its natural habitat (Mouton et al., 1999; Visagie, 2001). Groups of up to 40 individuals coinhabiting a rock crevice are regularly encountered (Peers, 1930; Mouton et al., 1999; Visagie, 2001). It is a sit-and-wait forager (Cooper et al., 1997; Mouton et al., 2000b) that undergoes an extensive period of inactivity. Visagie (2001) studied seasonal activity patterns and noted that there was a high rate of activity during the mating season (September). Activity declined sharply at the onset of warm, dry conditions (February). Virtually no activity occurred just prior to the first winter rains (July), after which the lizards emerge to forage and replenish energy stores before onset of the mating season.

Resource limitations have indeed been implicated as the reason for low fecundity in another cordylid, *Cordylus giganteus* (Van Wyk, 1991, 1994). *Cordylus giganteus* is the largest member of the family and has a terrestrial lifestyle. It produces two offspring at a time but only biennially. The magnitude of energy reserves at the onset of vitellogenesis in autumn apparently determines whether an individual female reproduces in a specific year or not. Van Wyk (1991) proposed that no winter feeding together with large body size and relatively large preovulatory egg size, and meaningful placental energy transfer toward developing young, are possible reasons for females not being able to build enough fat reserves for annual reproduction. *Cordylus cataphractus* does not exhibit placentotrophy or winter hibernation, but extremely low activity levels throughout the drier, warmer months. Mouton et al. (2000b) reported that a significant number of lizards had empty stomachs during this time. Two possibilities may explain why *C. cataphractus* is able to reproduce annually. One is that low fecundity is accompanied by lower energy investment into reproduction by the female. The other is that the animal has sufficient capacity to replenish energy reserves during the wetter months, with no lowered energy investment by the female.

The energy investment hypothesis seems implausible as *C. cataphractus* produces an embryo of about the same absolute dry mass (just over 2.0 g) than that of the total clutch in other cordylids. *Pseudocordylus melanotus* females (mean SVL of 107 mm), for instance, produces up to six embryos and they weigh 0.31 g each just before birth. *Cordylus polyzonus* females (mean SVL of 106 mm) deliver up to three young, and late-term embryos weigh 0.65 g each. *Cordylus giganteus*, in contrast, produces two young and total clutch mass is just over 4 g (Van Wyk, 1994), but females have a mean SVL of 185 mm; there is also evidence of substantial nutrient transfer from mother to embryo during late gravidity in this species (Van Wyk, 1994). The question remains as to the significance of low fecundity in *C. cataphractus*. This probably reflects the

fact that neonates do not have to disperse under group-living conditions, and females can thus invest in a single offspring.

Cordylus cataphractus has a remarkable ability to replenish energy reserves. It builds very large fat bodies—well over 5 g in dry mass for an animal growing to about 125 mm in SVL. The only other cordylid studied thus far with comparable absolute fat body dry mass, is *C. giganteus* (highest value recorded in a male of SVL = 185 mm was 8 g; J. H. Van Wyk, pers. comm.), but SVL in this species is almost double that of *C. cataphractus*. Highest absolute fat body masses recorded in *Pseudocordylus melanotus* and *Cordylus polyzonus* are 1.24 and 1.34 g, respectively (values are all for males, with respective SVLs of 124 and 101 mm; (unpubl. data). Further, *C. cataphractus* builds energy reserves over a relatively short time, despite its low metabolic rate (see Mouton et al., 2000a). Fat body cycling reflects the feeding activity pattern noted by Visagie (2001). Mass increases in fat body size during the late spring/summer months follow the period of heightened feeding efforts during winter/spring. Apparently *C. cataphractus* can find enough food during winter/spring for general metabolism and reproductive purposes (vitellogenesis/spermatogenesis, mating, etc.), and build fat reserves at the same time. A similar pattern has been noted in most other cordylids (see Van Wyk and Mouton 1998), although fat accumulation occurs slightly later in *C. cataphractus*.

Apart from later vitellogenesis and ovulation, low fecundity and exceptionally large fat body sizes as compared to other cordylids, *C. cataphractus* displays several unique physiological and behavioral characters, which may be associated with energy constraints brought about by the permanent group-living lifestyle. These characters include an extremely low resting metabolic rate, a degree of thermally independent metabolism (Mouton et al., 2000a), and extremely low activity levels during dry summer months (Visagie, 2001), whereas other cordylids remain active. It is difficult to assess whether the unique characteristics of *C. cataphractus* are the cause of its group-living behavior or a consequence thereof, and further investigations on the biology of the species are needed.

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