

Dynamic aggregations of newborn sibling rattlesnakes exhibit stable thermoregulatory properties

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Abstract

Information on behavioural and physiological processes of newborn reptiles is often difficult to obtain under natural conditions, especially in lizards and snakes. Consequently, we lack information on a wide range of biological phenomena (e.g. thermoregulation, digestion, circadian activity rhythms) in neonates of these taxa. Here, we report novel behaviour in newborn sibling sidewinder rattlesnakes *Crotalus cerastes*, a desert-inhabiting species of south-western North America. At the entrances of their natal burrows, neonates formed aggregations ('balls') during daylight hours, which involved frequent movements of individuals within these balls. Through the study of two radio-telemetered females and their litters ($n = 20$ offspring), we obtained temperature data from the mothers, centre of the snake balls, and from multiple sites in the immediate environment for 10 days post-birth, the period that is coincident with maternal attendance and the first cycle of ecdysis. The core temperatures of the snake balls showed significant stability over the extreme thermal ranges of the environment. Although other functions are possible, such as those related to water conservation and antipredator defence, we suggest that frequent movements of individuals within the balls involved selection of a thermal optimum to enhance ecdysis. Based on other studies of aggregation in animals, dynamic aggregative behaviour in newborn sibling *C. cerastes* implicates self-assembly and suggests that individuals benefit from behavioural interactions with their siblings. One plausible scenario for the evolution of this type of dynamic aggregation involves thermal selection among sibling neonates for optimal basking sites within natal refugia in extreme environments such as desert landscapes. Moreover, it is possibly limited to species of vipers (and other snakes) that are viviparous and where maternal care is present up to the time of shedding in neonates.

Introduction

Owing primarily to a variety of logistical issues, behavioural and physiological processes of newborn reptiles have been challenging to obtain under natural conditions, particularly in lizards and snakes (Peterson, Gibson & Dorcas, 1993; Shine, 2005). We have therefore a relatively poor understanding of a wide range of biological phenomena in neonates of these taxa (Blouin-Demers, Weatherhead & McCracken, 2003; Lutterschmidt, Lutterschmidt & Hutchinson, 2003). Information on thermal relations in newborn snakes in nature, for instance, is sparse, yet its importance is fundamental to a comprehensive synthesis of their behavioural and physiological ecology (Bartholomew, 1982; Lillywhite, 1987, 2006; Beaupre, 2002; Shine, 2005; Lillywhite & Navas, 2006). A robust understanding of proximate control of thermoregulation in reptiles and other ectothermic vertebrates will lend insights to the evolution and

maintenance of thermal responses and properties of endotherms (Seebacher, Grigg & Beard, 1999; Geiser, Goodship & Pavey, 2002; Seebacher & Franklin, 2005). Accordingly, by widening our phylogenetic perspective, thermoregulatory research should reveal not only evolutionary conservatism of traits among distant taxa but also those that are novel (Else & Hulbert, 1981, 1985; Seebacher & Franklin, 2005). Hence, unconventional types of mechanisms related to activities such as thermoregulation should not be unexpected in reptiles and other ectothermic vertebrates (Seebacher & Franklin, 2005; Shine, 2005).

Here, we report a novel type of aggregative behaviour in newborn sibling Mohave Desert sidewinder rattlesnakes *Crotalus cerastes cerastes*, a desert-inhabiting species of south-western North America (Klauber, 1972). By forming tight 'balls' at the entrances of their natal burrows, sometimes to the extent of plugging them, and frequently shutting in and out of them, we show that core temperatures of

these structures were thermally stable over a broad range of extreme temperatures in the immediate environment. The siblings achieved this level of thermal stability during daylight hours of their first 10 days of life, which is concomitant with maternal attendance and the first cycle of ecdysis. Following ecdysis, neonates dispersed from the natal burrows and did not exhibit similar aggregations while under our observations (see Klauber, 1972; Greene *et al.*, 2002). The type of aggregative behaviour we discuss in newborn *Crotalus cerastes* possibly has functions outside of thermoregulation, such as those related to water conservation (Duvall, King & Gutzwiller, 1985; Graves *et al.*, 1986; Graves & Duvall, 1987, 1995; Lillywhite & Navas, 2006) and antipredator behaviour (Greene, 1988). Finally, based on studies of aggregation in other species, the phenomenon we discuss in this study implicates self-assembly and suggests that individuals benefit from behavioural interactions with their siblings (e.g. Parrish & Edelman-Keshet, 1999; Anderson, Theriault & Deneubourg, 2002).

Methods

Behaviour and thermal measurements

All observations and experiments were conducted in Johnson Valley, San Bernardino County, California, USA. In this low-lying region of the Mohave Desert, availability of water is severely restricted and daily temperatures are frequently extreme (Reiserer, 2001). Two female sidewinder rattlesnakes *C. c. cerastes* were fitted with temperature-sensitive radiotransmitters (AVM Instruments, model G3, AVM Instruments Company, Ltd., Colfax, CA, USA) via intraperitoneal implantation (Reiserer, 2001). The activities of both females were monitored daily throughout pregnancy, and thereafter multiple times each day following parturition. On 16 September 1998, an additional female (non-telemetered) and eight of her progeny were located, observed for 1.5 h as her neonates formed an aggregation at the entrance of a small rodent burrow that was used as a birth site, and collected for measurement. Temperature data, however, were not obtained from this individual nor her progeny.

Thermal profiles of the two females fitted with radiotelemetry, their newborn progeny in aggregations, and immediate environs were recorded during the period of surface activity (\approx 09:30–16:30 h), on 13–14, 18 and 23–24 September 1998. Daily observations of the mothers and their neonates confirmed that the behaviour occurred recurrently throughout the pre-shed period (10 days post-birth) of the siblings. On the above dates (spanning 5 days), durations of the temperature profiles were 5.4, 0.5, 6, 3 and 5.5, respectively. We obtained the following temperature data: (1) ambient air 1 m above ground in shade near natal burrows (Miller & Weber fast-acting mercury thermometer, Miller & Weber, Inc., Ridgewood, NY, USA); (2) substrate in a shady location beneath a bush (Raytek Raynger ST2L infrared non-contact thermometer, Raytek Corporation, Santa Cruz, CA, USA); (3) females (data derived from temperature-sensitive radiotransmitters); (4) core of aggregation (mass or

ball) of sibling neonates at the entrance of the natal burrow (Barnant thermistor thermometer – model no. 600-8525, Barnant Company, Barrington, IL, USA, with a general-purpose probe – YSI 402, YSI Temperature, Dayton, OH, USA); (5) control burrow entrance at 1 mm below the surface of the substrate (Barnant DualogR thermocouple thermometer with K type probe); (6) substrate in a sunny location near natal burrows (Raytek Raynger ST2L infrared non-contact thermometer). Thermistors and thermometers were calibrated frequently and tested for accuracy and precision. When sibling neonates formed ‘balls’ at the entrances of their natal burrows, temperatures were recorded at their core at 5-min intervals. Other temperature data were obtained during these observation periods.

Short fences (25 cm tall \times 8 m diameter) were constructed around the burrows of the telemetered females to confine the neonates after their first shed. When the neonates dispersed from their burrows after shedding (10 days post-birth), they were captured for processing and subsequently released near their natal burrows. Body mass to the nearest ± 0.1 g was obtained with an O’haus triple-beam balance and body length (total length) was measured to the nearest ± 1 mm using a standard laboratory millimetre ruler. To achieve a high level of accuracy, all measurements on newborn snakes were made while they were under light vapour anaesthesia (isoflurane).

Statistical analysis

Design and statistical procedures followed Zar (1996) and Quinn & Keough (2002), and all tests were performed using the statistical software SAS v. 9.0 (1999, SAS Institute, Cary, NC, USA). Before statistical analysis, data were inspected for outliers, normality (skewness and kurtosis) and homogeneity of variance; all conditions were satisfied. We performed a mixed-model two-factor repeated measures analysis of variance, with ‘natal burrow’ (burrow 1 and burrow 2) as the repeated unit (subject) and six temperature sources (air, shade, female, aggregate, burrow, sun) and time (10:00–15:00 h) as the main effects. The mixed procedure in SAS requires fitting the best covariance structure to the data by comparisons of the Akaike and Schwarz Bayesian information criteria (Wolfinger & Chang, 1995). Of 11 covariance structures, the compound symmetry-type best fit the data. Least-squares means differences (LSMD) contrasts with sequential Dunn–Sidak adjustments were used to ascertain differences among levels of the source \times time interaction and to account for compounding of type I error, respectively. Although temperature data were $y^{0.25}$ -transformed to achieve normality, only non-transformed data (± 1 SE) are presented in the graphs.

Results

Behaviour of mothers and sibling neonates

All three females of this study gave birth inside small mammal burrows, and burrows were not communal with other female *C. cerastes* or other species. These birth sites

were ≈ 5 cm in diameter, probably constructed by rodents (e.g. *Dipodomys merriami*), and directed to the east; thus, they were positioned to directly face sunrise. Within 24 h post-birth, newborn siblings of three litters formed tight aggregations ('balls') at the entrances of their natal burrows. There were a total of 30 living neonates in the three litters. Litter size ranged from 8 to 12 offspring (mean total length: 177 ± 8 mm; mean body mass: 4.8 ± 0.6 g).

Following parturition (c. 12 and 22 September in the case of the two females with radiotelemetry), the mothers typically emerged from their burrows shortly after sunrise and basked directly adjacent to them, and then returned to the burrows when substrate temperatures were >35 °C. The newborn *C. cerastes* would begin to aggregate at the burrow entrance ≈ 30 min before their mother withdrew, and they remained there for 5–6 h during the hottest part of the day. They entwined to form a tight ball that at times completely obstructed the entrance of the burrow. Throughout the day, individual siblings slowly shifted their coils around and through the mass, but by accelerating these movements rapid positional turnover was achieved. The formation of these balls occurred for c. 10 days post-birth in both litters. The largest groups and longest durations occurred on days that were hot and cloudless. On days that were cool and cloudy, as well as at the end of hot days, neonates thermo-regulated individually or in smaller groups.

Thermal profiles

Thermal profiles of the two radio-telemetered mothers and their aggregating newborns, as well as temperatures of the immediate environment, were recorded on five different days, two of which encompassed the entire surface activity period of large groups of neonates from the two litters (Figs 1 and 2).

Statistical analysis

The mixed-model repeated-measures ANOVA revealed significant main effects (source: $F_{5, 36} = 2403.8$, $P < 0.0001$; time: $F_{5, 36} = 84.5$, $P < 0.0001$) and a significant source \times time interaction ($F_{25, 36} = 30.7$, $P < 0.0001$), which indicates that the sources exhibited different patterns of temperature change from 10:00 to 15:00 h. Substrate temperatures (shade, sun and control burrow substrate) showed similar patterns, with progressive elevations in temperature to a peak at 12:00–13:00 h and then a progressive decline to 15:00 h (Fig. 2). Air temperature increased from 10:00 to 12:00 h, and remained elevated through 15:00 h. The mother snakes showed shallow increases in body temperature throughout the day, with a peak at $\approx 15:00$ h (Fig. 2). The core temperature of the neonatal aggregations remained static, with no qualitative or quantitative differences among time points (Fig. 2).

Substrate temperature near the aggregation burrow (sun) and the control burrow (burrow) was significantly higher than all other temperature sources at all time points (Fig. 2). Air (1 m above ground in shade) and shaded substrate

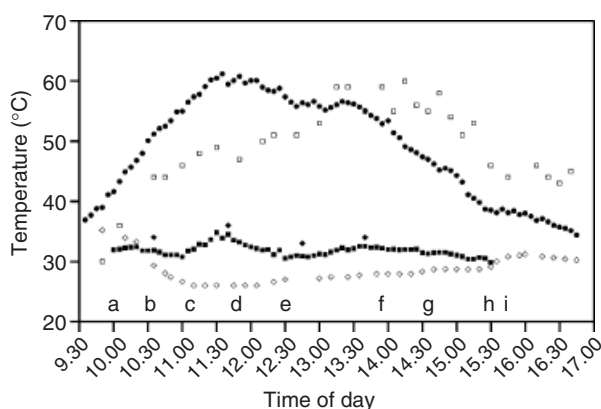


Figure 1 Temperature profile (24 September 1998) of newborn sibling Mohave sidewinder rattlesnakes *Crotalus cerastes cerastes* when undergoing dynamic aggregation. The symbols denote temperatures of (1) ball (aggregate of siblings) core (solid squares), (2) mass surface (solid diamonds), (3) female core body temperature (open diamonds), (4) control burrow substrate (solid circles) and (5) substrate in full sunlight (open squares). Air and shaded substrate temperatures (not shown) peaked at 14:15 h, and typically remained below the temperature of the neonatal aggregate. Lowercase letters indicate the occurrence of the following events: (a) mother slowly entering burrow after basking; thermistor probe inserted into forming ball of neonates at burrow entrance; (b) mother completely inside burrow; large mass of young present; (c–d) rapid shifting of newborn snakes in ball; (e) burrow entrance becoming shaded with sun dappled by a bush; (f) mother moving forward in burrow, resting her head atop the aggregate of newborn offspring; (g) mother rapidly emerging from burrow until half exposed; newborn snakes beneath or crowded to her side; (h) newborn snakes retreating into burrow; and (i) mother's body is 75% visible, resting on thermistor probe, with none of her young visible.

temperatures were significantly lower than all other sources at 10:00 and 11:00 h, and were indistinguishable from female body temperature at 12:00 and 14:00 h. At 13:00 and 15:00 h, temperature in the shade was significantly higher and lower than the body temperatures of the two mothers, respectively. The core temperature of the neonatal aggregations was significantly higher than air, shaded substrate and mother temperatures at all time points except 13:00 h (significantly higher than air and mothers' body temperatures but statistically indistinguishable from shaded substrate) and 15:00 h (significantly higher than air and shaded substrate temperatures but statistically indistinguishable from mothers' body temperatures). The core temperature of the aggregation was significantly lower than substrate temperatures at the aggregation den (sun) and control burrow (burrow) at all time points (Fig. 2).

Discussion

Here, we document a novel type of social behaviour in newborn siblings of the Mojave Desert sidewinder rattlesnake *C. c. cerastes* that involved the formation of dynamic aggregations ('balls') in natal burrows. Although

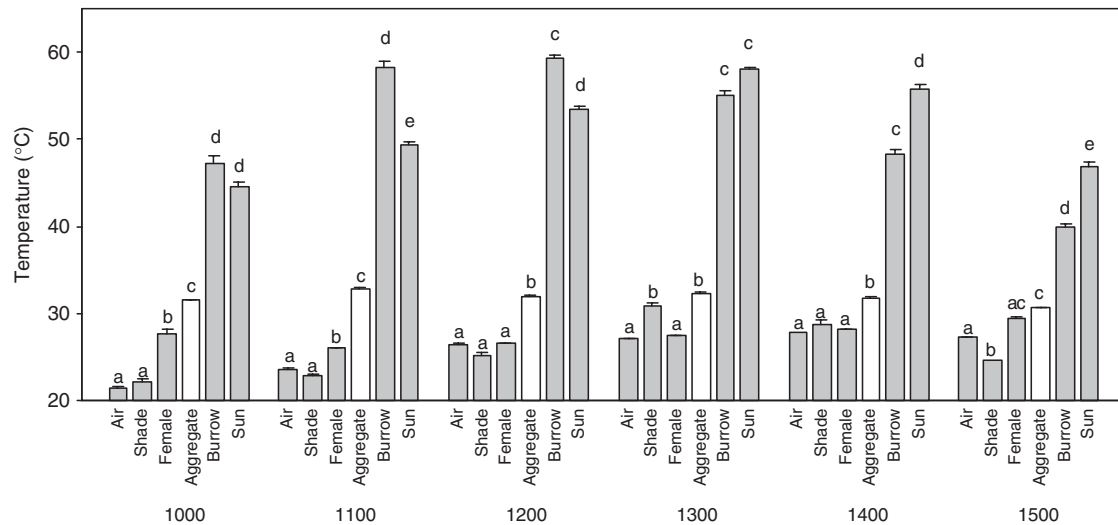


Figure 2 Mean temperature ($^{\circ}\text{C}$) profiles of *Crotalus cerastes* (mothers and newborns) and environmental sources at each hourly period. Bars with different letters within each time point are significantly different ($P < 0.05$ after sequential Dunn–Sidak adjustments). No comparisons were made across time points on this graph. Open bars (mass) denote newborn aggregation temperature. With the exception of one time point (1500 h), the temperatures of the aggregations of the newborn were significantly greater than air, shade and female (mother) and significantly less than burrow and sun temperatures.

aggregations of newborn rattlesnakes have been documented (e.g. Duvall *et al.*, 1985; Graves *et al.*, 1986), none have described the frequent movements of individuals within the balls, nor have temperature data of the balls and immediate surroundings been supplied. Despite a growing number of ecological studies on this species (Brown & Lillywhite, 1992; Secor, 1994), some involving telemetry (Brown & Lillywhite, 1992; Secor, 1994), the activities of newborns with their mothers have not been reported. Also in this study, we document for the first time maternal attendance at the birth sites (reviewed in Greene *et al.*, 2002).

While the function of dynamic aggregation in neonatal *C. cerastes* remains to be fully elucidated, we showed that core temperatures of these dynamic structures showed significant temperature stability over extreme thermal ranges during specific daylight hours for 10 days post-birth. Interestingly, variation in core temperatures was maintained within the narrow and arbitrary limits ($\pm 2^{\circ}\text{C}$) that have been used to define homeothermy (Refinetti, 1999; Mzilikazi & Lovegrove, 2006). Nonetheless, because we were unable to collect body temperatures of neonates outside of the core, whether or not individuals maintained this high degree of thermal stability remains to be investigated.

Unlike other types of thermoregulatory behaviour in snakes, aggregation in newborn sibling *C. cerastes* was highly localized and occurred only at the interface of two microhabitats: the burrow entrance and the immediate environment outside, both of which differed substantially in thermal characteristics over the course of the 5-h period of daylight in days tested (Figs 1 and 2). The sharpness of the thermal gradient at the burrow interior and outside environment appeared to be modified by the presence of a sufficient number of sibling neonates that blocked sunlight

at the burrow entrance and prevented heating of the substrate. Temperature data derived from the substrate of the entrance of a control burrow (neonates and mother not present) showed that temperatures attained levels $>42^{\circ}\text{C}$, which are lethal (critical thermal maximum) to individual *C. cerastes* (Lillywhite, 1987). The steep rise in temperature in unoccupied burrows also indicated that there was a limited period during which individual snakes could be present at the entrance of the burrow before temperatures exceeded their thermal tolerance. Size limitations of the natal burrows did not permit all littermates to simultaneously occupy an optimal location along the presumed thermal gradient at the entrance, and selection among individuals for optimal or preferred temperatures possibly drives the behavioural component of the aggregation. Body size and shape appear to be important in the thermoregulatory mechanics of these types of aggregations.

Rates of change in body temperatures are rapid in small-bodied vertebrates that are ectothermic, and behavioural control of heat exchange often takes precedence over physiological control (Bartholomew, 1982). Organisms with elongate body forms have high surface area to volume ratios which permit rapid heat exchange, but most snakes can also assume positions that closely approximate a sphere that minimizes thermal exchanges with the environment (Lillywhite, 1987). In the present case, aggregation functionally makes each individual part of a spheroid that is $\approx 50\text{ g}$ (e.g. litter size of 10), which is a 10-fold increase of the average mass of a single neonate ($\approx 4.8\text{ g}$). Furthermore, the spheroidal configuration is predicted to minimize thermal exchange with the environment, yet individuals maximize the potential for heat exchange by remaining extended and woven throughout the aggregate. Under conditions where

burrow size does not limit access to favourable thermoregulation sites, aggregation by siblings may not occur. Furthermore, under uniform thermal conditions in the laboratory, newborn *C. cerastes* disperse shortly after birth and appear to have no affinity for their mother and/or littermates (R. Reiserer, unpubl. data).

To our knowledge, dynamic aggregative behaviour in newborn sibling *C. cerastes* occurred only during the first 10 days of life. During this time, sibling neonates restricted their movements to the natal burrow (mother present) and prepared to undergo their first ecdysis. In addition to concerns of thermal biology, these tight aggregations would likely minimize exposure of individual body surfaces to the environment and presumably reduce water loss through the integument (see Graves *et al.*, 1986; Lillywhite, 1987). Importantly, the first cycle of ecdysis of life controls excessive trans-epidermal water loss by reducing permeability through lipid barrier structures (Duvall *et al.*, 1985; Graves *et al.*, 1986; Tu *et al.*, 2002; Lillywhite & Navas, 2006), and any corruption of the sloughing process has potentially negative consequences to survival and fitness (Aubret & Bonnet, 2005; Lillywhite & Navas, 2006). Furthermore, before ecdysis, physiological preparation includes opacity of the eyes, possibly due to zip splitting of the two epidermal generations (L. Alibardi, pers. comm.). Consequently, this process presumably impairs vision and movements, and vulnerability to predation and the environment is increased (Greene *et al.*, 2002; Agugliaro & Reinert, 2005; Aubret & Bonnet, 2005). Nonetheless, skin sloughing in snakes may require elevation of metabolism, typically through increasing body temperatures via solar basking (e.g. King & Turmo, 1997), and in neonatal snakes this carries potential risks such as predation (Aubret & Bonnet, 2005; Webb & Whiting, 2005). If solitary basking is indeed risky in neonatal *C. cerastes* as a result of increased predation, aggregative behaviour might offset such dangers (Graves & Duvall, 1995; Greene *et al.*, 2002; Agugliaro & Reinert, 2005).

Other types of thermoregulatory behaviour in snakes that involves the formation of aggregations function in heat retention during cooling phases (Myers & Eells, 1968; Aleksiuik, 1977). In the present study, however, low environmental temperatures did not induce aggregations in newborn *C. cerastes*. Aggregation occurred, moreover, during the heating and plateau phases of the daily thermal cycle, and falling temperatures were associated with the disintegration of the aggregate and retreat of the neonates into their natal burrows. The core temperatures of sibling *C. cerastes* in tight aggregations (mean = 31.94 ± 0.80 °C) were at the upper limit of the preferred range for the species (26–32 °C) (Lillywhite, 1987), an observation consistent with temperature preferences of other snakes undergoing the ecdysis cycle (Peterson *et al.*, 1993).

Recent advances in the thermal biology of organisms have exposed a continuum where a dichotomy was once perceived (Pough & Gans, 1982; Varghese & Pati, 1996; Angilletta, Niewiarowski & Navas, 2002; Seebacher & Franklin, 2005). Diverse taxa have arrived at both common and novel solutions to achieving thermal stability, particu-

larly in extreme environments, through various mechanisms ranging from avoidance to evolutionary changes in genomic structure (Seebacher & Franklin, 2005; Lillywhite & Navas, 2006). Importantly, unusual mechanisms continue to be identified, such as in this study. Here, we provide evidence that newborn sidewinder rattlesnakes responded to thermal conditions related to excessive high temperatures by exhibiting an unusual type of dynamic aggregation. This social phenomenon implicates self-assembly (Sendova-Franks & Franks, 1999; Anderson *et al.*, 2002) and suggests that individuals benefit from the behavioural activities of same-aged siblings (Parrish & Edelman-Keshet, 1999). In addition to further analyses of thermal relations, other hypotheses (e.g. prevention of water loss, antipredator behaviour, social facilitation) concerning the function of dynamic aggregations in *C. cerastes* need to be tested (e.g. Duvall *et al.*, 1985; Graves *et al.*, 1986), including the role of maternal attendance (Duvall *et al.*, 1985; Greene *et al.*, 2002).

One plausible scenario for the evolution of dynamic aggregative behaviour in newborn sibling *C. cerastes* involves thermal selection for optimal basking sites within natal refugia in extreme environments such as desert landscapes. This behaviour, moreover, is possibly limited to species of vipers (and other snakes) that are viviparous and where maternal care is present to the first ecdysis of the neonates. Accordingly, we predict that newborn siblings of other taxa of snakes will exhibit dynamic aggregation under these conditions.

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