Diurnal aggregation in banded geckos (*Coleonyx variegatus*): Socially mediated or the result of rare retreats?

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Background

The formation of social aggregations is widespread in animals and is known to have important social, ecological, and fitness implications (Boersma 1982; Cohen and Alford 1996; Caro 1998). Some species aggregate as an adaptive response to abiotic variables in their environment, such as low moisture availability (e.g., Cohen and Alford 1996). Others aggregate because of social factors such as conspecific attraction. Attracting conspecifics can be important to finding mates, defending resources, and avoiding predators. The ability to recognize individual conspecifics has been documented in many species, including squamate reptiles (e.g., Yeager and Burghardt 1991). Among lizards, several species of nocturnal geckos are reported to form diurnal aggregations (Greenberg 1943; Cooper et al. 1985; Burke 1994; Kearney et al. 2001); however, few studies have attempted to determine the mechanistic basis of these aggregations.

Diurnal aggregation was first reported in the western banded gecko (*Coleonyx variegatus*) 60 years ago (Greenberg 1943). Subsequent studies have shown that patterns of grouping, both in the field and under laboratory conditions, differ significantly from that expected if individuals were distributed randomly (Cooper et al. 1985; Burke 1994). Researchers have suggested that grouping behavior is influenced by a number of biotic (e.g., attraction between conspecifics, reducing predation risk) and abiotic factors (e.g., temperature, moisture, physical dimensions of retreat site) (Kearney et al. 2001). Temperature and moisture preferences are expected to be important to *Coleonyx* because they live in the hot, dry deserts of southwestern North America, yet have high rates of evaporative water loss relative to most desert reptiles (Mautz 1982; Dial and Grismer 1992). Banded geckos avoid environmental extremes by restricting their activity to nighttime and seeking refuge in insulated retreats such as in rock crevices or under large boulders by day (Stebbins 2003). These geckos likely select retreat sites based on their needs for specific combinations of conditions, thus suitable retreat sites may be rare. Consequently, aggregation may be an incidental result of attraction to rarely occurring retreat sites rather than for conspecific attraction.

In laboratory studies, *Coleonyx variegatus* show a greater tendency to aggregate when a group is given a choice between aggregating in a constructed burrow vs. a burrow that must be constructed on their own (Cooper et al. 1985). However, the tendency to aggregate when retreat sites were relatively abundant was also found to be higher than expected if retreat sites were being selected at random (Cooper et al. 1985). These researchers also found that geckos were frequently in physical contact with each other in the retreat site even when there was ample space for them to avoid touching. This suggests a possible mechanism to reduce effective surface area:volume ratios, and thus minimize evaporative water loss for members of the aggregation. For example, cane toads (*Bufo marinus*), a species whose activity is limited by moisture availability, reduce rates of water loss by aggregating when environmental moisture levels are low (Cohen and Alford 1996). If this is also true for banded geckos, I would expect these lizards to increase aggregative behavior when relative humidity is low.

It is not known whether aggregating geckos assort differentially between the sexes or during different times of the year. Kingsbury (1989) reports that male geckos in the field display a wider range of body temperatures and are active for longer periods of time than the females. He attributes this to the possibility that males are searching for females as well as for prey. Thus, if aggregative behavior is socially mediated, geckos could become more gregarious in the breeding season when males may be actively searching for females. It is also unknown whether, or to what extent, other abiotic or biotic factors influence these aggregations.

Objectives

The objectives of my study are to (1) identify and determine the relative importance of the abiotic and biotic variables used by western banded geckos (*Coleonyx variegatus*) in diurnal retreat-site selection, and (2) isolate the potential causes (abiotic vs. biotic) of aggregative behavior during periods of inactivity in this species. I will first explore the retreat-site conditions that are favored by *C. variegatus*. Because this species is unlike other desert reptiles in terms of its moderate thermal preferences (Vance 1973; Kingsbury 1989) and relatively high evaporative water loss (Mautz 1982; Dial and Grismer 1992), the selection of appropriate diurnal retreat sites should be crucial to even short-term survival. My investigation will include assessments of abiotic variables such as temperature and humidity preferences. Geckos are expected to select diurnal retreats with a narrow range of temperature and humidity conditions because of their small body size and high rates of evaporative water loss.

The assessment of biotic factors will include the influence of predator and conspecific chemical cues on retreat-site selection. Banded geckos use chemical cues to detect conspecifics and predators (Dial et al. 1989). If retreat-site selection includes assessments of chemical stimuli, geckos are expected to avoid predator cues and seek out conspecific cues. After the factors that create a “preferred” retreat site are identified, groups of geckos will be presented with a surplus of preferred shelters to determine if diurnal aggregation is socially mediated or merely the result of a rarity of suitable shelters in their natural habitat. To investigate whether grouping provides a predator-avoidance benefit, groups of geckos will be introduced to arenas with a surplus of suitable retreats that either have predator scent or no predator scent. If predator avoidance is a factor in diurnal aggregation, geckos should group more when a predator's presence is detected. This series of experiments will be conducted in both the breeding and nonbreeding seasons to determine whether the tendency to aggregate is associated with reproduction.

Methods

Animal Husbandry.—Thirty banded geckos (15 adults of each sex) were collected in California and Arizona during 2002–03. Lizards are housed individually in plastic containers (29.8 x 19.0 x 20.3 cm) that are covered with paper so they cannot view other individuals, thereby avoiding the potentially confounding effect of visual familiarity. Cages have a sand substratum with one retreat consisting of an inverted terra cotta dish (10 cm diameter x 1.5 cm high) with an opening cut out on one side. Each cage also has an inverted plastic deli cup (11.5 cm diameter x 4.5 cm high) with an opening cut out and damp moss inside to provide a humid retreat to aid in shedding. Geckos are kept on a 10L:14D photocycle October–March and a 14L:10D photocycle April–September, which roughly corresponds to their natural environment. Lizards are fed crickets (*Acheta domesticus*) and mealworms (larvae of *Tenebrio* sp.) weekly. Water was provided for 2 wk following capture, but thereafter, standing water is available for one day every other month.

Two leaf-nosed snakes (*Phyllorhynchus decurtatus*) were collected in the Mojave Desert in 2003. These snakes are natural predators of *C. variegatus* and both predator and prey occur sympatrically and syntopically over most of their range (Dial et al. 1989; Stebbins 2003). The snakes are housed individually in plastic containers (29.8 x 19.0 x 20.3 cm). They are kept on the same photocycle as the geckos, and standing water is available *ad libitum*. The snakes are fed lizards and lizard eggs including those of *Coleonyx*.

Abiotic Determinants of Retreat-Site Selection.—The influence of temperature on retreat-site selection will be examined by placing individual geckos in a thermal gradient (13.5 x 121.5 x 20 cm) with temperatures ranging 20–40 °C, which includes the range of temperatures (24–34 ºC) measured in retreat sites that are used by banded geckos in nature (Vance 1973). The gradient contains four lanes, allowing four individuals to be tested at once. Each lane has a sand substratum with a screen over the top to prevent geckos from digging into the sand. Lanes are separated by opaque Plexiglas® dividers. The entire gradient will be covered with black shade cloth to provide darkness for the geckos and simulate a retreat. Geckos will be introduced individually to each lane of the gradient in the afternoon (1400) and their body temperatures will be recorded every 15 min the following day from 0900–1600. This allows the geckos to explore the range of available temperatures overnight, and it also allows for identification of the range of temperatures selected by individual geckos diurnally (Dial and Grismer 1992). Body temperature will be determined by the gecko’s position in the gradient. To calibrate lizard body temperatures as a function of position in the gradient, a gecko will be placed in the gradient with a thermocouple inserted ~1 cm into its cloaca, to record its body temperature. The corresponding body temperature will be recorded for every marked position along the gradient (1-cm apart) for each lane. Once body temperature at every position is determined, individual geckos will be introduced to each lane of the gradient. Their positions can then be noted as described above, and the corresponding body temperature will be noted. This indirect means of body temperature measurement will be used so that geckos will not be disturbed by the more invasive methods of temperature data collection such as use of cloacally implanted thermocouples. If geckos are frequently disturbed, their thermoregulatory behavior may be disrupted. Also, to directly measure each gecko's temperature would require a possible "chase" and subsequent handling that may result in a change in the gecko's body temperature that would add a an unknown margin of error. The consistency of the gradient's temperature will be monitored by small dataloggers (iButton Thermochrons, Maxim/Dallas Semiconductor, Dallas, TX). Four dataloggers will be evenly spaced per lane, and temperature will be recorded every 5 min for the duration of the experiment.

I expect to find geckos selecting temperatures within the range reported for their natural retreat sites, but they are likely to select more precise temperatures than the entire 10 ºC range reported by Vance (1973) (i.e., Pianka [1986] reports 28.4 ± 3.4 °C as the field body temperature).

Preferred relative humidity (RH) will be measured by placing geckos in a humidity gradient. The details of the gradient are still under consideration, as a previous prototype failed to provide an adequate range of humidity levels. Time of introduction to the gradient and the observation period will be the same as that for the thermal preference experiment, but the position of the geckos and the corresponding RH will be determined hourly to allow the gradient time to stabilize after each measurement. Offering a wide range of humidity levels will allow me to determine humidity preferences in these lizards, which has not been recorded in the lab or from natural retreats. I expect that humidity and temperature will be important aspects of retreat-site selection because of the relatively high rates of evaporative water loss experienced by these geckos (Mautz 1982; Dial and Grismer 1992).

Biotic Determinants of Retreat-Site Selection.—I will present individual geckos with shelters that have been scent marked by (1) conspecific males, (2) females, (3) the resident gecko's own scent, (4) a known snake predator (*Phyllorhynchus decurtatus*; Dial et al. 1989), and (5) a control shelter (washed).

Shelters used in these experiments will consist of inverted clay dishes (10 cm diameter and 1.5 cm high). The shelter height is such that the reptiles will make dorsal contact with the retreat shelter surface (Downes and Shine 1998a,b). Shelters will be conditioned with scent from the treatment animals by placing the shelters with the scent donator for ≥24 h (S. Downes, pers. comm.). Because shelters will be reused it is imperative that chemical cues from previous trials are removed. A study will be conducted to determine the effectiveness of the method used to wash the shelters between trials. This will be assessed by offering individual geckos a choice between never-used + washed shelters and those used by *P. decurtatus* + washed. Western banded geckos can detect and identify this snake predator's scent (Dial et al. 1989). If the geckos show a significant avoidance of shelters that were washed after conditioning with predator scent, this would suggest that the method of washing is inadequate. If this is the case, shelters will be used only once.

I will conduct pair-wise comparisons between a control (clay retreat left in an aquarium with identical conditions except the predator or conspecific) and each experimentally treated shelter to identify which treatments are selected or avoided by banded geckos. Geckos will be introduced individually to a 45.5-L (490 x 330 x 250 cm) aquarium with sand substratum and one shelter randomly assigned to each end. Lizards will be left in the enclosure overnight (1900–0900), videotaped to observe behavior, and checked in the morning to determine the shelter that they have chosen for their diurnal retreat (following Downes and Shine 1998a,b). This time interval incorporates their normal active period (Kingsbury 1989) and allows them to explore and choose retreat sites as they might in nature. Treatments that differ significantly in use from controls will be used in the subsequent experiments. The video data will be used to quantify the number of agonistic behaviors, matings, number of times in and out of each shelter, and other relevant interactions. These data are expected to complement patterns of aggregation (should any be detected) with mechanistic behavioral interactions.

Next, I will identify the relative importance of the various treatments in retreat-site selection. The same experimental procedure described above will be repeated with two different treatments instead of a treatment and a control. This will identify the relative importance of the various biotic treatments in habitat selection. If aggregation facilitates mate location, male geckos should choose shelters marked by female conspecifics during the mating season (Parker [1972] reports peak testes sizes during April–May). Males should also avoid male conspecifics at this time to minimize competition for mates. However, if aggregation is a predator-avoidance strategy, I do not expect to see significant differences in aggregative tendencies between the sexes or seasons. Geckos, regardless of sex or breeding condition, should be more attracted to shelters marked with their own scent because of its familiarity and associated safety. I predict that both female and male geckos will actively avoid predator chemical cues during both seasons (Dial et al. 1989).

Choice data will be analyzed using the G-test of independence and the exact sign test, correcting for small sample sizes if necessary. *Isolating Aggregation Behavior from other*

Variables.—After the abiotic and biotic variables that make a retreat site “preferred” by the geckos are identified, I will present groups of six geckos (3 males and 3 females) with high and low densities of these favored retreats. The shelters will be identical to the ones used previously, except they will have a diameter of 15.5 cm to allow room for multiple geckos to enter. Ten shelters will be equally spaced in a large circular arena (122-cm diameter; plastic “kiddy pool”) with a sand substratum. Experiments will be conducted overnight, the arenas will be videotaped to observe movements and interactions (as described above), and the location of the geckos will be recorded at 0900 the following morning (Schlesinger and Shine 1994, Downes and Shine 1998a,b). Six treatments will be evaluated: control (all shelters unscented/identical), predator scent in arena (see below for description), female gecko-scented shelters, male gecko-scented shelters, preferred-temperature shelters, and preferred-humidity shelters. For the treatments in which conspecific scent is used, the geckos used to scent the shelters will not be present in the experimental group for that trial. For each treatment, 3-6 randomly chosen shelter positions will contain treated shelters and remaining shelters will be controls with the number of treated shelters in each trial randomly determined. Each treatment will be tested in five trials, allowing each of the 30 geckos to participate in every treatment experiment once. Individual geckos will be randomly assigned to groups for each trial and individuals will be used only once for each treatment, thus each night and number of treatment shelters will have different geckos. This will prevent the geckos from becoming familiar with each other and their surroundings, which could confound this experiment.

If diurnal aggregation has a social component, I expect to find a significantly nonrandom aggregative pattern in retreat-site selection when a surplus (≥1 shelter per lizard) of suitable habitats is available. If there is no difference in tendencies to aggregate when excess shelters are provided, and if geckos only aggregate when their density is high relative to the number of favorable retreat sites, this would suggest that geckos tolerate each other in retreat sites because of their limited availability. If the latter result is supported, the adaptive explanations posited for the occurrence of aggregation in this species will have to be reevaluated.

I will also investigate the influence of perceived predator presence on grouping behavior. I will set up one large arena as above. The arena will contain ten equally spaced, unscented retreat sites with the same temperature and humidity, but the arena will have snake predator scent on the substratum. I will allow snakes to occupy the arena for at least 24 h prior to the introduction of the neutral retreat sites and the geckos. This will allow snakes to deposit integumentary chemicals onto the substratum of the arena. Snakes will then be removed and groups of geckos will be introduced to the arena as described above for the other variables. A control arena will also be tested. The control will be set up identical to the predator-scented arena, but a non-predatory snake will be used. Geckos will be presented with the non-predatory snake’s scent in advance to assure no response. The second arena will serve to control for the disturbance of sand, etc. done by the snakes. If geckos aggregate in the presence of snake pheromones more than when this predator was not present, then diurnal aggregation may serve be partially attributable to predator avoidance.

Aggregation for each treatment will be detected by comparing data obtained in the arena experiments to the Poisson distribution using the G test.

Significance

My study is the first to comprehensively examine the mechanistic basis of diurnal aggregative behavior in nocturnal lizards as it pertains to retreat-site selection. My goal is to determine the variables that geckos use to select among retreat sites and test whether it is these factors that lead to aggregation or, alternatively, if aggregation provides an as-yet-unidentified adaptive benefit to geckos.

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