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Factors Influencing Activity in *Coleonyx variegatus*

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Abstract.—The activities of the banded gecko, *Coleonyx variegatus*, were observed in the field and in an outdoor enclosure. Fieldwork supported previous studies suggesting eurythermy in the species, but it was predominantly the males that exhibited this tendency. The males were also active over a broader range of time. These differences may have been because the males were searching for females with which to mate, as well as for food. In an enclosure, the banded geckos moved about 15 m/hr while foraging, with individuals frequently changing position ($\bar{x}$ = 34 moves/hr). Banded geckos search for food in a manner which is intermediate between classical sit-and-wait foragers and active foragers.

Studies on the behavioral ecology of squamate reptiles have focused predominantly on diurnal, heliothermic species (Anderson and Karasov, 1981; Huey and Pianka, 1981; Bennett et al., 1984; Huey et al., 1984; Nagy et al., 1984). This bias in our information potentially limits comparative interpretations, as many of the world's species are secretive or nocturnal in habit, and active at reduced body temperatures. Nocturnal and secretive forms may differ physiologically and behaviorally from diurnal heliotherms. Nocturnality not only exposes an animal to low-light conditions, but also frequently to lower ambient temperatures. Nocturnal forms are typically eurythermic (Licht et al., 1966; Bustard, 1967*a*, 1968; Vance, 1973; Marcellini, 1976; Dial, 1978*a*). Since performance of many whole-animal processes such as endurance or digestive rate are strongly temperature-dependent (Harwood, 1979; Bennett, 1980*a*; Huey, 1982), reduced body temperatures may strongly influence the behavior of nocturnal species.

The banded gecko, *Coleonyx variegatus*, is a nocturnal lizard inhabiting the arid regions of southwestern North America. Several studies on its ecology suggest that the species is eurythermic, thermoconforming while foraging (Klauber, 1945; Parker, 1972; Vance, 1973). Vance (1973) and Dial (1978*a*) (for the congeners *C. brevis* and *C. reticulatus*) demonstrated active thermoregulation during the inactive (daytime) period. Although some work has been conducted on the diet of the species, microhabitat use and foraging behavior have not been studied quantitatively. The purpose of the following study was to observe *Coleonyx variegatus* in the field and laboratory to ascertain correlates of activity and to quantify patterns of movement during activity.

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Materials and Methods

Fieldwork was conducted on private property in Hellhole Canyon, 10 km west of Borrego Springs, San Diego Co., California, during April–June of 1983 and 1984. Spring was selected as the survey period because it is the peak activity period for this species (Klauber, 1945). Repeated sweeping searches between 1900 and 2400 hr were made of the study site using a Coleman lantern after preliminary work with a wide variety of searching and trapping methods showed this technique to be best for finding the lizards. Upon sighting a lizard, its location was noted, then it was captured by hand. All lizards were toe-clipped for future identification and the snout–vent length (SVL) and sex recorded. During 1984 sampling, body temperature was taken immediately upon capture. This was done using an Electromedics ITS 600 telothermometer with a substrate thermocouple placed firmly against the abdomen of the lizard. This technique was used to minimize heating during handling of these small lizards (3–6 g). A substrate temperature and an ambient temperature approximately 10 cm above the surface were then taken, and the animal released at site of capture.

Efforts to observe the behavior of the banded gecko in the field were unsuccessful because the presence of the observer disturbed normal behavior. An outdoor enclosure was therefore used to observe the activities of the banded gecko in greater detail. The enclosure was located in Escondido, California, 40 km W of Borrego Springs. Ambient temperatures in the enclosure (22–32°C) were on average lower than those found at the field site during the summer, yet within the range of activity temperatures for the species. Preliminary observations demonstrated that the lizards maintained high levels of activity in the enclosure and appeared to be in excellent health throughout the summer.

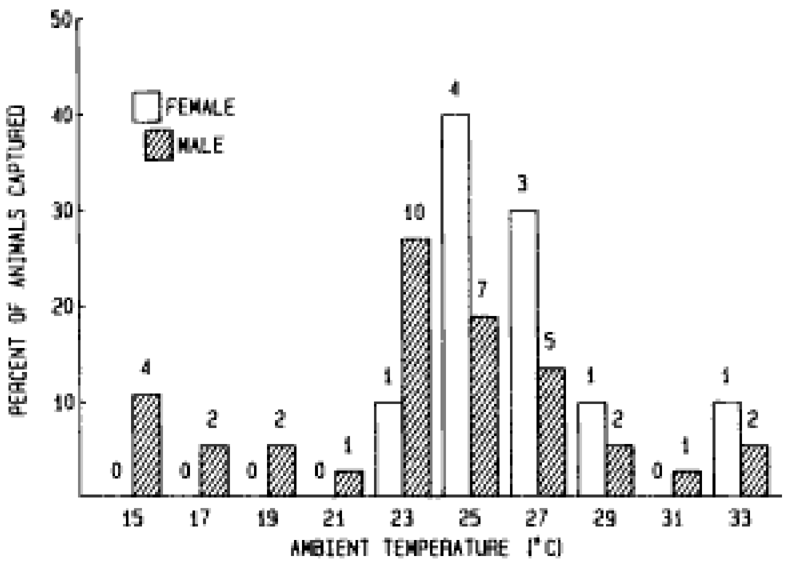

FIG. 1. Ambient temperatures at time of capture for *Coleonyx variegatus*. The percentage of animals captured within each temperature range is given for each sex. The number above each bar is the actual sample size within each temperature category. Each temperature range is 2°C wide and is represented by its central value.

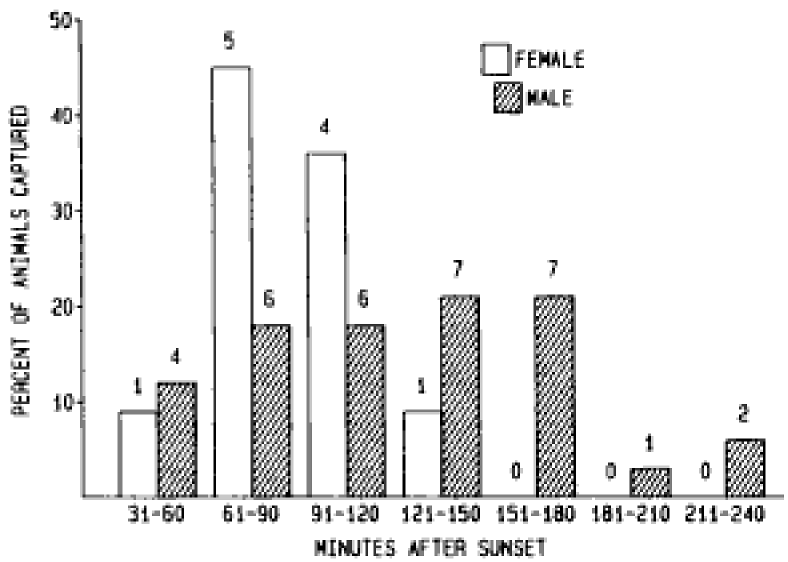

FIG. 2. Time of capture in minutes after sunset. The number above each bar is the actual sample size within each time category.

The enclosure was constructed on well-drained soil and was 5 m in diameter. A circular design was used to eliminate corners and encourage use of the entire enclosure. The walls of the enclosure were constructed of particle board and were about 1 m high, except on the southeastern side, where they were 2.5 m high to capture more heat from the afternoon sun. A blind was installed in the center of the enclosure to allow inconspicuous observation of the lizards. Cement tiles and three large branches were placed in the enclosure to provide shelter and foraging sites. A 20 cm strip of paint was applied around the upper inner edge of the walls to prevent escape.

Three groups of lizards, each composed of two males and two females, were used in the enclosure. One group was placed in the enclosure at a time to limit intraspecific interaction. Each group was given 5–7 days to explore and become accustomed to the enclosure before any data were recorded. Small crickets and mealworms were added to the enclosure on an infrequent basis to supplement the insect life already inside. Geckos not being used in the enclosure were housed outside in terraria in groups of three or four (one male, two or three females), and were fed regularly on a diet of crickets and mealworms. All individuals were housed outside for at least one month before being used in the enclosure.

Observations were aided by the use of red light from four 25 W Westinghouse Colortone light bulbs, which provided just enough light for identification of individuals. Data were collected using focal animal sampling from July to August 1984, between 2000–2400 hr. The distance and frequency of movements, the location and duration of stops, and general behavior of the lizards were recorded. Nine animals were observed six or more times in this manner, while one was observed only four times, for a total of 64 observation periods (20 min/period). Data for two lizards (from group 3) were excluded from analyses because one of the animals became inactive and died and the other escaped from the enclosure.

RESULTS

Environmental correlates to activity differed between the sexes (Figs. 1–3). The mean observation time (in minutes after sunset) for females (94 min) was significantly earlier in the evening than the mean observation time for males (117 min, $t = 2.4$, $P < 0.05$, df $= 50$). Males were also active over a broader range of times (variance ratio test, $F = 4.2$, $P < 0.05$). Females were also found at lower air temperatures ($t = 1.2$, $P < 0.05$, df $= 50$).

Air temperature (10 cm above ground) and surface temperature were closely correlated ($r^2 = 0.85$, N $= 42$). The mean field body temperature (FBT) of the geckos was 27°C (SE $= 0.59$). Mean male FBTs ($\bar{x} = 27.2$°C) were not significantly different from female FBTs ($\bar{x} = 26.2$°C) (Mann-Whitney $U = 55.5$, $P > 0.05$). Body temperature was most closely correlated with air temperature ($r^2 = 0.79$, N $= 24$). However, body temperatures below 24°C were rare, and did not follow environmental temperatures at lower values (Fig. 4). Use of a polynomial model for correlation of body temperature to ambient temperature significantly reduced model sums of squares to the addition of the cubic term ($F = 4.75$, $P < 0.05$).

Behavioral observations of animals in the field were limited. Individuals did not seem to be restricting activities only to bushy areas, as they were frequently found in the open. Individuals also did not seem to regularly use perches or

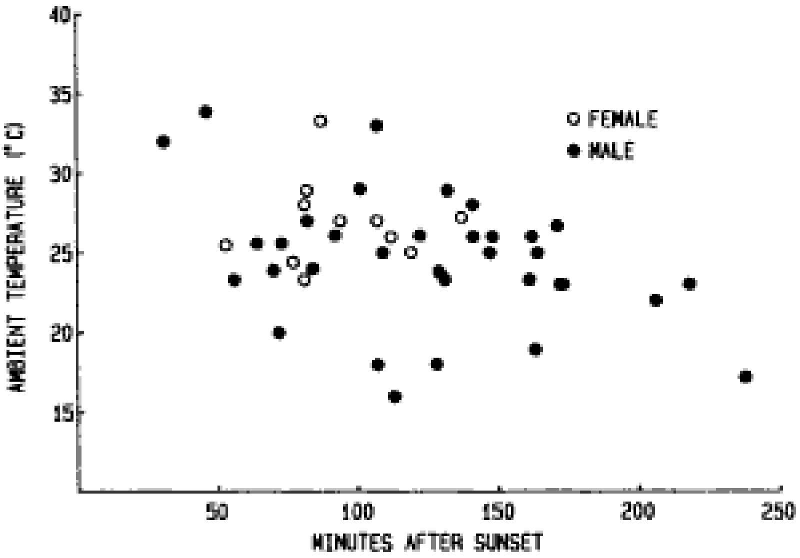

FIG. 3. Ambient temperatures at time of capture. Note that female data points fall centrally on the graph.

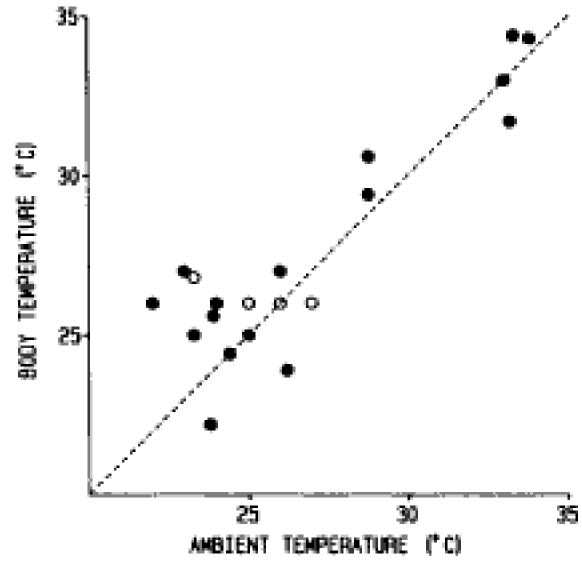

FIG. 4. Body temperature relative to air temperature. The data for both sexes are presented together. The dashed line shows where body temperature would equal ambient temperature. Open circles indicate multiple measures of the same value. Similar results are observed for substrate temperature.

other vantage points: only one lizard was found in a bush.

An analysis of enclosure data showed differences in patterns of movement between the sexes. The mean total distance moved per hour by males (17.6 m/hr) was significantly greater than the mean for females (9.4 m/hr; $t = 3.29$, $P < 0.05$). These differences in rates of movement were not due to differences in frequency of moves (both sexes averaged 34 moves/hr), but were a result of differences in the distance moved each time. Males averaged 0.53 (± 0.07) m/move, while females only averaged 0.31 (± 0.04) m/move.

The effect of temperature on rates of movement was varied. During enclosure observations, no correlation was found between ambient temperature and number of moves (Pearson's $r^2 = 0.01$, $P > 0.05$, N = 52). Ambient temperature did, however, affect the total distance moved per observation period for males ($r^2 = 0.34$, $P < 0.05$, N = 27), but not for females ($r^2 = 0.06$, $P > 0.05$, N = 25).

The basic pattern of movement by lizards observed in the enclosure was to move about 0.25 to 0.5 m every minute or so while foraging. During observations, males spent about 38% of their time moving, while females were moving an average of 30% of the time. This difference was not significant ($t = 1.08$, $P > 0.05$), but was in agreement with the longer distance/move by males. As a gecko moved about it would lick the substrate and investigate objects it encountered along the way, crawling beneath objects briefly when possible. Perches were rarely used, even though they were readily available.

DISCUSSION

Body temperature data from this study confirm previous work indicating that this species is eurythermic and active at reduced temperatures (Klauber, 1945; Mayhew, 1968; Parker, 1972; Vance, 1973). These features are typical of nocturnal and crepuscular lizards (Licht et al., 1966; Bustard, 1968; Marcellini, 1976; Dial, 1978*a*; Putnam and Murphy, 1982), and reclusive lizards (Mautz, 1979).

However, the eurythermy exhibited by the species is predominantly a male feature: females were found only during a short period about one and a half hours after sunset, and over a much narrower range of environmental temperatures (Fig. 3). Since the field data for this study were collected in the spring, the differences observed might be due to males spending activity time searching for females as well as for food. Bustard (1967*b*) found that banded geckos could ingest enough food in four days to allow survival for 6–9 months in the laboratory without further feeding. An individual not searching for mates might therefore be more selective about when it came out. This might

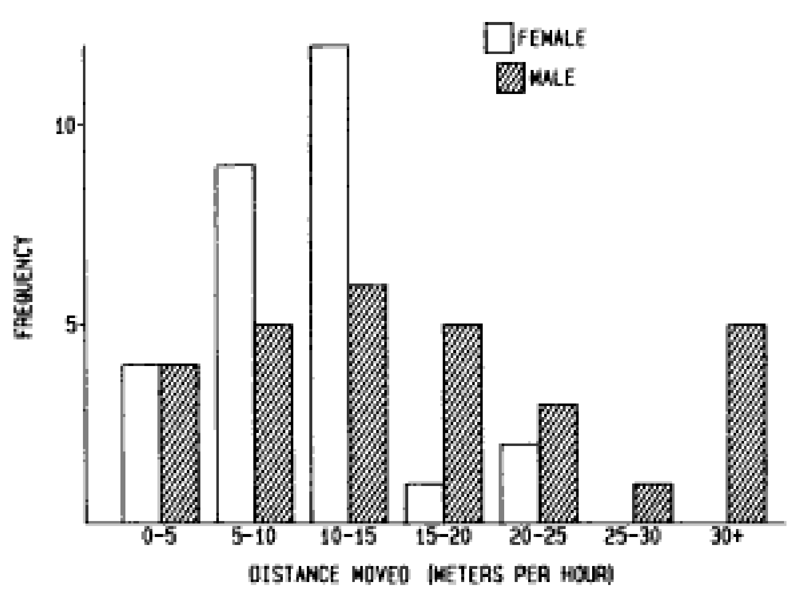

FIG. 5. The frequency distribution of total distance moved per hour, based on enclosure observations. The distance moved by females rarely exceeded 15 m/hr, while several males moved over twice this far.

also explain the capture of three times as many males as females. In the enclosure, males were moving about twice as far as were females per unit time. This might also be due to their searching for mates, although no courtship or mating was observed.

Body temperatures (T_b) of *Coleonyx* during activity correlate highly with ambient temperatures (this study; Parker and Pianka, 1974; Dial, 1978*a*). This is because the sun is not available as a radiant heat source. However, the data from the present study suggest the *Coleonyx variegatus* may be thermoregulating at lower environmental temperatures during activity. This conclusion is supported by the loss of a linear correlation between T_b and ambient temperature at lower ambient temperatures. Few lizards were found with body temperatures below 24°C, producing a lower body temperature "plateau" in the mid-20s.

Banded geckos may warm up while foraging below ground, or they may be intermittently utilizing the soil as a heat source for foraging above ground. Substrate temperatures tended to be slightly warmer than ambient temperatures, suggesting the potential for thigmothermy. Dial's (1978*a*) laboratory observations on *C. brevis* and *C. reticulatus* in diurnal retreats show that these congeners thermoregulate during daytime periods of inactivity. Thermoregulating while foraging also seems likely, provided that the opportunity is available. Heat gain tends to improve locomotor capacity (Licht, 1964, 1967; Bennett, 1980*a*), and has also been implicated in enhancing digestive efficiency (Harwood, 1979; Waldschmidt et al., 1986), auditory capacity (Campbell, 1969) and learning ability (Krekorian et al., 1968; Brattstrom 1978). Utilizing the warmth of the soil to maintain a higher body temperature while foraging might therefore be advantageous. However, it also increases metabolic expenditures in a temperature-dependent fashion (Bennett, 1980*a*, *b*).

Nightfall appears to be the most important determinant for the onset of activity. In the field, lizards were never found earlier than thirty minutes after sunset. Activity peaked around two hours after sunset, then decreased dramatically at 2300–2400, although activity continued all night in both the field and in the enclosure (pers. obs.; Klauber, 1945). My field observations, the fieldwork of Klauber (1945), and laboratory work by Evans (1966) suggest that this species is strictly nocturnal. However, in the enclosure, where closer observations could be made, animals were also active just prior to nightfall, suggesting that the species may also be crepuscular.

Based on enclosure observations, *Coleonyx variegatus* forage over about 15 m/hr, and is in motion about 30–40% of the time they are active. A gecko will change position every minute or two, moving about 0.25–0.5 m before stopping again. As it moves, it inspects any debris it encounters, and goes underneath it if possible. However, perches or other vantage points were almost never used in the foraging process.

In many ways, the foraging pattern of banded geckos described above does not fit into either the classic sit-and-wait or active forager category, but is intermediate between the two. On the one hand, these geckos spend more time moving than do most sit-and-wait foragers, yet they do not move nearly as far as active foragers (Anderson and Karasov, 1981; Huey and Pianka, 1981; Huey et al., 1984; Van Berkum et al., 1986). Furthermore, while vision is the most important sense used while foraging, chemosensory information is also used. Enclosure observations in this study, as well as other laboratory work (Dial, 1978*b*; Kingsbury, 1986), show that banded geckos constantly lick the substrate and objects that they are investigating, and can identify motionless prey in this manner. Sit-and-wait foragers characteristically cannot rely on chemical cues to identify motionless or hidden prey (Simon, 1983; but see Goodman, 1971).

Studies on species with intermediate foraging strategies are lacking. Most researchers, while focusing theoretical discussion on foraging strategy extremes, acknowledge a continuum between active and sit-and-wait foragers. Toft (1985) and others, while accepting this continuum, have stressed the dichotomy of foraging patterns, suggesting that coevolution between three trophic levels (lizard prey, lizard, lizard predator) has led to the suites of characters that now define active and sit-and-wait foragers seen in lizards studied to date.

Why then does *Coleonyx variegatus* have an intermediate foraging strategy? Banded geckos are nocturnal. To an animal occurring in a temperate environment, this has two obvious consequences. First, ambient light levels are dramatically reduced. Vision may be compromised by lack of light, while chemosensitivity is not. We might therefore expect the incorporation of chemoreception into the foraging strategy.

Second, these lizards are frequently active at reduced environmental temperatures. The effects of temperature have yet to be quantified for this species, but the locomotory performance of eurytherms at reduced temperatures generally do not approach the levels of performance exhibited by diurnal, thermophilic foragers (Bennett, 1980*b*). Furthermore, declines in body temperature severely limit a reptile's already poor ability to repay an oxygen debt (Bennett and Licht, 1972; Bennett, 1978). Nocturnal foragers may therefore frequently be physiological constrained from too "active" a foraging strategy. The present study does not address this issue quantitatively, beyond the observation that rates of movement by enclosure males was positively correlated with increasing temperature. Further work investigating the interaction of physiology and behavior in "low temperature" species would help to resolve this issue.

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Activity Patterns and Thermoregulatory Behavior of the Egyptian Tortoise *Testudo kleinmanni* in Israel

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ABSTRACT.—**In Israel, *Testudo kleinmanni* is active during winter. In summer the tortoises retreat to rodent burrows and their activity decreases. Decline of populations resulting from commercial collecting has resulted in its status as an endangered species. The behavior, activity, and thermal requirements of the species are examined.**

The Egyptian tortoise *Testudo kleinmanni* has a very limited distribution ranging from north central Libya eastward to Israel and to the south to about 200 km inland from the Mediterranean coast (Flower, 1933; Iverson, 1986). Loveridge and Williams (1957) reported that this tortoise inhabits desert areas in northwestern Egypt and that in the northern Sinai it is found among bushes near brackish lagoons. In Israel this tortoise inhabits areas of sandy soils and dunes with some cover of bushes and shrubs (Mendelssohn, 1982).

In Egypt, *Testudo kleinmanni* is active throughout the winter (Lortet, 1887). Mendelssohn (1982) reported that the main activity period in Israel is from December to March, first-active individuals being observed as early as October. Rodent burrows were used as cover sites during the activity period if ambient temperature became unsuitable (Mendelssohn, 1982).

The Egyptian tortoise is an endangered species, whose decline is the apparent result of commercial collecting in Egypt (Buskirk, 1985) and destruction of habitat in Israel (Mendelssohn, 1982). This paper describes the annual activity, thermal habits, and behavior associated with aestivation in the Egyptian tortoise; these data are essential to an understanding of the ecology of the species in Israel.

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METHODS

The study was carried out at Holot Agur, about 15 km north of Beer-Milka (63375, 42435; U.T.M. Grid), in the northwestern Negev Desert, on an area of 3 km^2. This area is characterized by east-west trending sand ridges separated by deep valleys. Mean annual air temperature is 20°C (Israel Meteorological Service, unpubl. data) with mean maximum temperature of 30°C in the hottest month (July) and a mean minimum of 12°C in the coldest month (January). Subzero temperatures are rare. Large fluctuations in air temperature (10–15°C) are common during the day. Most precipitation (100–200 mm) occurs between October and March.

Vegetation cover averages 20–30% and consists primarily of the *Artemisia monosperma* plant association (Waisel et al., 1982). Other common plants are *Retama raetam, Panicum turgidum, Stipagrostis scoparia, Lycium europaeum, Echiochilon fruticosum, Neurada procumbens,* and *Moltkiopsis ciliata*.

Data were obtained from nine radio-tagged adult tortoises (five males and four females), and from randomly collected individuals. Activity-sensing transmitters were glued with dental acrylic to the posterior carapace. The weight of transmitter and glue totalled 15–17 g, roughly 5–10% of body weight (males and females were about 150 and 300 g, respectively). Males carried transmitters for 18, 16, 10, 9, and 5 months; females for 16, 14, 5, and 4 months. Tortoises were monitored with AVM LA12-DS