ECOLOGICAL ASPECTS OF FORAGING MODE FOR THE SNAKES *CROTALUS CERASTES* AND *MASTICOPHIS FLAGELLUM*

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ABSTRACT: This study demonstrates the correlation of an array of ecological characteristics with foraging mode in sit-and-wait foraging *Crotalus cerastes* and widely foraging *Masticophis flagellum*. *Crotalus cerastes* are chiefly nocturnal and spend most of their time on the surface either coiled on or partially buried in the sand waiting to ambush prey. *Masticophis flagellum* are strictly diurnal predators and cruise through the habitat searching for active and sedentary prey. In this study, *C. cerastes* averaged 7.2 ± 0.7 (SE) h/day on the surface, almost twice the time of *M. flagellum* (3.9 ± 0.9 h/day). Body temperatures (T_b's) of active *M. flagellum*, determined from surgically implanted radio transmitters, were significantly greater than those of active *C. cerastes*. *Crotalus cerastes*, whose T_b's conform to changing environmental temperatures, appear to possess a broad "thermal performance breadth," enabling them to move and to acquire prey over a relatively wide range of T_b's (16–38 C). Active *M. flagellum* typically possessed a narrower range of T_b's (30–35 C), suggesting that they operate with a narrow "thermal performance breadth." *Masticophis flagellum* traveled greater distances (241 ± 38 m) and more frequently ($76 \pm 4\%$ of days monitored) than *C. cerastes* (111 ± 12 m and $32 \pm 2\%$ of days monitored, respectively). Thus, *M. flagellum* averaged more than five times the distance traveled per day (186 ± 37 m/day) than *C. cerastes* (35 ± 4 m/day). Consequently, *M. flagellum* possessed activity ranges (53.4 ± 13.3 ha) that were significantly larger than those of *C. cerastes* (20.1 ± 3.3 ha). Additional correlates of widely foraging for *M. flagellum* include higher predation risks, streamlined body shape, and greater rates of energy expenditure and acquisition. Correlated with their sit-and-wait foraging tactics, *C. cerastes* are stocky in body shape, rely on crypsis and immobility to escape detection from predators, and balance low foraging success with low energy requirements.

Key words: Activity; Activity range; Colubridae; *Crotalus cerastes*; Foraging behavior; Foraging mode; *Masticophis flagellum*; Movement; Predation; Snake; Thermal biology; Viperidae

PREDATORS generally exhibit one of two generalized modes of foraging behavior: sit-and-wait (=ambush) or widely (=active) foraging (Gerritsen and Strickler, 1977; Pianka, 1966; Schoener, 1971). Past studies have concluded that foraging modes reflect specific sets of ecological, physiological, behavioral, and morphological characteristics (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984; Secor and Nagy, 1994; Vitt and Price, 1982). For example, widely foraging lizards typically forage for shorter periods, have higher body temperatures, possess greater field metabolic and energy intake rates, have a lower relative clutch mass, and are more streamlined in body shape

than sit-and-wait foraging species (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984; Vitt and Price, 1982).

Snakes also conform to these broadly defined classes (Mushinsky, 1987; Seigel and Fitch, 1984), although only a handful have been investigated for possible correlates of their foraging tactics. Closely related, widely foraging *Coluber constrictor* and *Masticophis flagellum* possess greater aerobic and anaerobic metabolic capacities than distantly related sit-and-wait foraging *Crotalus viridus* and *Lichanura roseofusca* (Ruben, 1976). Field metabolic rates and water influx rates of *M. flagellum* are significantly greater than those of sympatric sit-and-wait foraging *Crotalus cerastes* (Secor and Nagy, 1994). Hailey and Davis (1986) noted differences in prey capture rate and prey size between sit-and-wait foraging *Natrix maura* and widely

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foraging *Natrix natrix*. Seigel and Fitch (1984) found no significant relation between foraging mode and relative clutch mass for either oviparous or viviparous snakes. The paucity of comparative field studies on snakes is due largely to snakes' secretive nature and low population densities. Recently, researchers have used radiotelemetry (Reinert, 1992) to monitor movements, activities, and body temperatures of free-ranging species (Duvall et al., 1990; Peterson et al., 1993). Radiotelemetry has thus provided the means by which correlates of foraging mode can be investigated for free-ranging snakes (Secor and Nagy, 1994).

In this study, I explored ecological aspects of foraging mode in snakes by investigating the activities, thermal biology, and spatial patterns of two sympatric free-ranging species that differ in foraging behavior: the sit-and-wait foraging sidewinder (*Crotalus cerastes*; family Viperidae) and the widely foraging coachwhip (*Masticophis flagellum*; family Colubridae). In my investigation, I specifically addressed: (1) What influence does foraging mode have on the timing and duration of daily activities? (2) Are body temperatures of these snakes strongly correlated with their respective foraging behavior? (3) How do these snakes differ quantitatively in movements and spatial patterns as a consequence of foraging mode?

MATERIALS AND METHODS
Study Organisms

Crotalus cerastes (Fig. 1A) chiefly inhabit the sandier regions of the Sonoran and Mojave deserts of North America and are most noted for their sidewinding means of locomotion (Ernst, 1992; Klauber, 1972). They are a relatively small species of rattlesnake, ranging from 16.5 to 61.5 cm in snout–vent length (SVL) and 5 to 304 g in body mass (Secor, 1994a). *Masticophis flagellum* (Fig. 1B) exist in a variety of arid to mesic habitats throughout the southern United States and northern Mexico (Wilson, 1970). In the southwestern United States, Wilson (1970) noted that *M. flagellum* (subspecies *piceus*) range from 29.4 to 129 cm in SVL and 39.3 to 166.8 cm in total length (TL).

During the 3-yr study (April 1988–March 1991), I captured 181 *C. cerastes* and 25 *M. flagellum* (all age-classes) on the study site and measured (SVL and TL), weighed, sexed, and permanently marked (by clipping portions of their subcaudal scales) each individual (Fitch, 1987). I used 21 adult *C. cerastes* and 9 *M. flagellum* to assess ecological aspects of foraging mode. The 9 male and 12 nongravid female *C. cerastes* ranged from 47.5 to 61.2 cm ($\bar{x} \pm 1$ SE = 53.5 $\pm$ 0.8 cm) in SVL and 92 to 190 g ($\bar{x}$ = 130 $\pm$ 6 g) in body mass. The six male and three nongravid female *M. flagellum* ranged from 67.7 to 106.3 cm ($\bar{x}$ = 93.9 $\pm$ 2.7 cm) in SVL and 115 to 256 g ($\bar{x}$ = 173 $\pm$ 16 g) in body mass.

Study Site

I conducted this field study at the northeastern edge of the Kelso Dunes (Devil's Playground) in the eastern Mojave Desert, San Bernardino County, California. The 120-ha site has primarily a fine-sand substrate and is crossed by several dry washes. The gravel and rocky substrate of a surrounding alluvial fan blends with the loose sand along the site's southern, eastern, and northern borders. The perennial vegetation is dominated (96% composition) by *Hilaria rigida, Ambrosia dumosa, Larrea tridentata,* and *Krameria parvifolia,* with approximately 32% coverage (Secor and Nagy, 1994). Elevation of the site rises gently from the northwest corner (650 m) to the southeast edge (700 m). From 1988 to 1990, annual rainfall on the site ranged from 6 to 20 cm. Daily shaded air and exposed surface temperatures during the summer averaged 28–32 C (range = 15–45 C) and 35–40 C (range = 15–65 C), respectively. Wintertime air and surface temperatures averaged 10–12 C (range = −3–30 C) and 12–16 C (range = −3–35 C), respectively. I marked the study site with surveyor's tape at 100-m intervals (north–south and east–west transects) to facilitate mapping locations and measuring movements of individual snakes.
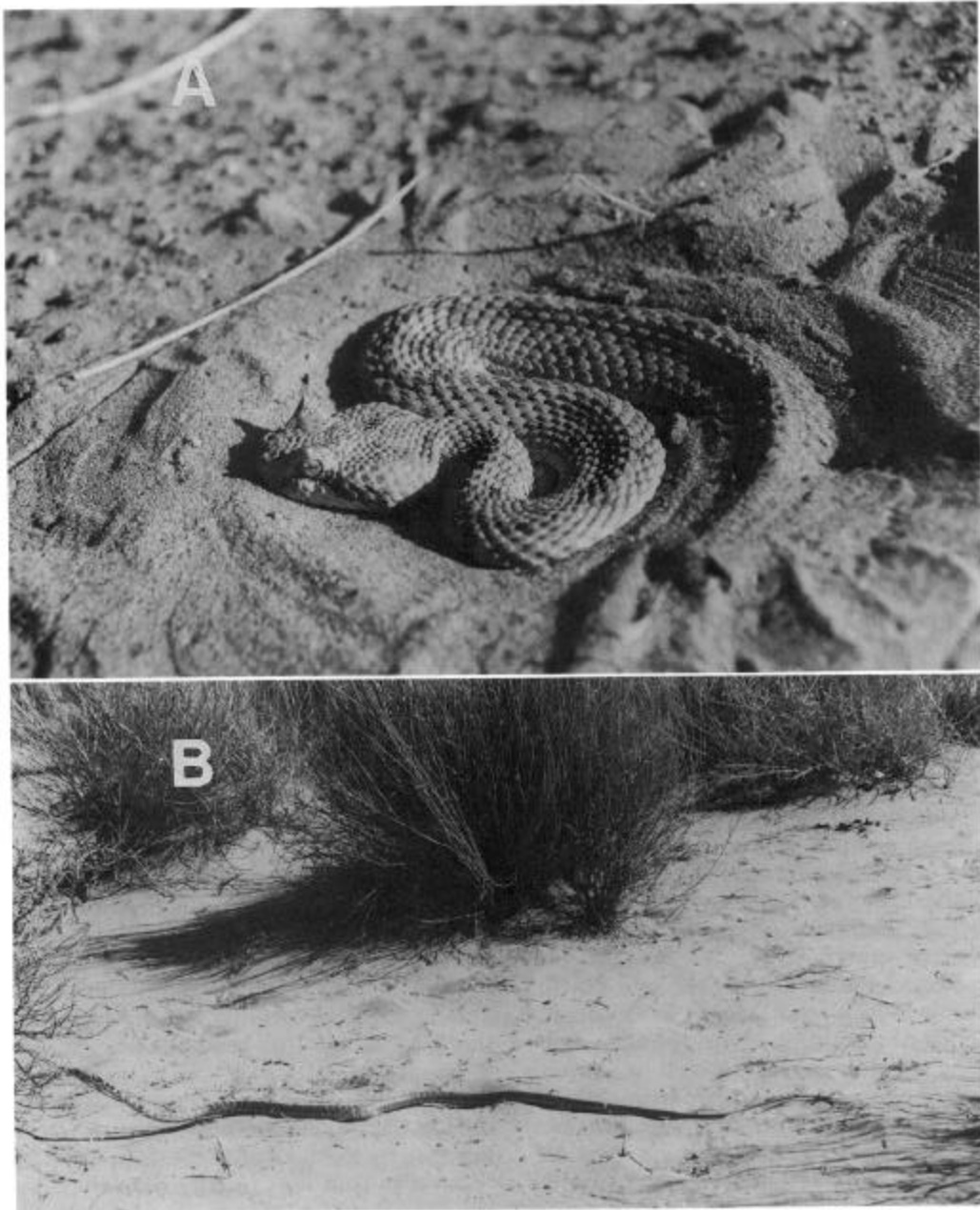
FIG. 1.—(A) An adult *Crotalus cerastes* in the characteristic "cratered" foraging position during the early morning. (B) An adult *Masticophis flagellum* searching the site for prey during midday.

Radiotelemetry

To assist in relocating snakes and determining body temperatures (T_b), I surgically implanted (by a modification of the technique of Reinert and Cundall, 1982) temperature-sensitive radio transmitters (Telonics Inc.; CHP-2P or CHP-3P) into 20 *C. cerastes* ($\bar{x}$ SVL = 53.6 ± 0.8 cm; $\bar{x}$ body mass = 132 ± 6 g) and all 9 *M.*

flagellum. Prior to implantation, each transmitter was calibrated in a water bath (10–40 C) to produce a calibration equation (temperature = f(pulse rate); Reinert, 1992). Transmitter mass (CHP-2P, mass = 6.1 ± 0.1 g; CHP-3P, mass = 10.4 ± 0.1 g) averaged 4.7 ± 0.2% and 4.0 ± 0.3% of the body masses of implanted *C. cerastes* and *M. flagellum*, respectively. Transmitters were equipped with whip antennas (25–30 cm), had a reception range of 250–850 m, and operated continuously for 5–7 mo (CHP-2P) or 8–11 mo (CHP-3P). I replaced implanted transmitters with fresh units approximately every 5 (CHP-2P) or 8 (CHP-3P) mo. I intermittently monitored transmitter-implanted *C. cerastes* for 41–743 days ($\bar{x}$ = 225 ± 35 days) and *M. flagellum* for 36–403 days ($\bar{x}$ = 192 ± 45 days).

Activity and Body Temperatures

Throughout the study, I visited the site almost daily from April to October and for several days every other week during the other months. Each day in the field I located individual snakes by radiotelemetry and monitored their activities and body temperatures during the day and evening. Individuals were observed from a distance of 10–15 m for 5–30 min to record activities and foraging behaviors. Activities were recorded as: inactive (within burrow), moving, stationary (pause in movement), coiled or cratered (only *C. cerastes* cratered), and eating. During the mid-portion of each month from March to October, I calculated durations of surface activity by noting the time of the day that individuals of each species emerged from underground shelters (typically rodent burrows) and when they re-entered them. The frequency of daily activity was calculated by dividing the number of days that an individual was active on the surface by the total number of days monitored.

I timed transmitters' pulse rates, made audible by a tracking receiver (Telonics Inc.; TR2), opportunistically over the course of the day and systematically at ½-h intervals for 30–36 h during the middle of each month (March 1990–February 1991). Following the timing of pulse rates, I re-

corded air (T_a, measured ≈3 cm above the surface and shaded during the day) and surface (T_s, measured on sun-exposed sand during the day) temperatures with a hand-held digital thermometer (Omega Engineering Co.; HH-99A-T2). Body temperatures of snakes were calculated by applying the timing of audible signals to the calibration equations. I first divided T_b's into two general categories: (1) those recorded from snakes inactive within burrows (T_b burrow) and (2) those recorded from snakes active on the surface (T_b surface). This latter category included T_b's from individuals either on the surface (moving or stationary) or actively moving through a burrow system. Body temperatures recorded during the activity season (mid-March to mid-November) were also partitioned among the five previously noted activity categories. Individual mean T_b's were used to test for significant differences between the two species for each category. Since body temperatures would predictably correlate with environmental temperatures, I investigated the possible relation that foraging mode had with the relationships between T_b's and air and surface temperatures.

Spatial Patterns

Movements.—I measured the movement of an individual as the distance traveled over a 24-h period (1000–1000 h). *Crotalus cerastes* leave very distinct tracks in the sand (see Mosauer, 1935); thus, I was able to easily determine the direction (by the position of the head mark) and the beginning and end of each movement. *Masticophis flagellum* tracks, all made during the day, were more difficult to follow due to: the lack of shadows formed by the tracks (sun was usually directly overhead), afternoon winds that commonly cleared the sand surface of tracks, and the fact that the snakes occasionally traveled to the rockier alluvium where their tracks were less visible.

I measured each movement by pushing a measuring wheel (Rolotape Corp.; model 394) directly over the set of tracks from its beginning to its end and then mapped that movement on a scaled map of the

study site. The straight-line distance be-
tween the starting and stopping of each
movement was also measured. Over the
course of the study, I measured the dis-
tance of 271 movements by *C. cerastes* and
32 movements by *M. flagellum*. For an
additional 90 movements by *M. flagellum*,
I was only able to measure the straight-
line distance. I estimated the actual dis-
tance of those movements by multiplying
their straight-line distance by the average
ratio of actual distance to straight-line dis-
tance calculated for each individual from
the first set of 32 movements. For com-
parative analysis, I used the average dis-
tance of each individual's movements. I
quantified movement frequency as the
number of days that an individual moved
divided by the total number of complete
days monitored. For each individual, the
mean daily distance of movement (meters
per day) was calculated by multiplying its
frequency of daily movement by its av-
erage movement distance.

Activity range.—I calculated the activ-
ity range of 16 *C. cerastes* ($\bar{x}$ body mass
= 130 ± 6 g) and 6 *M. flagellum* ($\bar{x}$ body
mass = 176 ± 21 g) from mapped coor-
dinates (x, y) of their known localities. Be-
cause the independence of locality coor-
dinates is an assumption of activity range
models (White and Garrott, 1990), I used
the following criteria for recording local-
ities: (1) only one locality coordinate per
day if the snake did not move, (2) the
coordinates of each sighted locality (direct
observation) when it did move, and (3) one
coordinate per month during hibernation.
Based on these criteria, activity ranges were
calculated from an average of 114 ± 20
and 114 ± 29 locality coordinates, respec-
tively, for *C. cerastes* and *M. flagellum*.

Activity ranges were calculated by the
nonparametric harmonic mean method
(Dixon and Chapman, 1980). This tech-
nique provides a fairly accurate measure
of activity range size because the size and
shape of the range are strongly influenced
by the relative distribution of locality co-
ordinates. I used the microcomputer pro-
gram MCPAAL (Micro-computer Pro-
grams for the Analysis of Animal Loca-
tions, National Zoological Park, Smithson-

ian Institution) to calculate activity range
size as the area isopleths that enclosed 95%
of locality coordinates (Secor, 1994a).

Statistical Analysis

Statistical analyses were performed us-
ing SAS (SAS Institute Inc., 1988). Data
with heteroscedastic variances were trans-
formed to logarithms (base 10), and fre-
quency data were arcsine transformed pri-
or to analyses (Zar, 1974). Comparisons
between *C. cerastes* and *M. flagellum* were
made using a two-tailed Student's *t*-test
(Zar, 1974). Data that violated the as-
sumptions of this analysis were subjected
to appropriate nonparametric tests as not-
ed in the text. The Pearson product mo-
ment correlation test was used to identify
possible correlations between T_b's and T_a's
and T_s's. Numerical results are presented
as mean ± one standard error of the mean,
sample size (n) refers to the number of
individuals (unless otherwise noted), and
statistical significance is designated at $P \leq$
0.05.

RESULTS

Activity and Body Temperatures

Daily activity.—During the majority of
their activity season (mid-March to mid-
November), *Crotalus cerastes* and *Mas-
ticophis flagellum* differed in the duration
and timing of their surface activity (Fig.
2). Both species emerged from hibernation
as early as mid-March. For the first several
weeks following emergence, both were ac-
tive on the surface only during the day
and retreated to rodent burrows before
nightfall. During this time, surface activity
of *C. cerastes* spanned the majority of day-
light hours, whereas *M. flagellum* were
active only during midday. In April, side-
winders occasionally remained on the sur-
face throughout the day and night, where-
as coachwhips gradually increased their
span of daytime activities.

Beginning in May, as daytime temper-
atures increased, *C. cerastes* became pre-
dominately nocturnal. During the sum-
mer, a sidewinder would emerge from a
rodent burrow (typically that of *Dipodo-
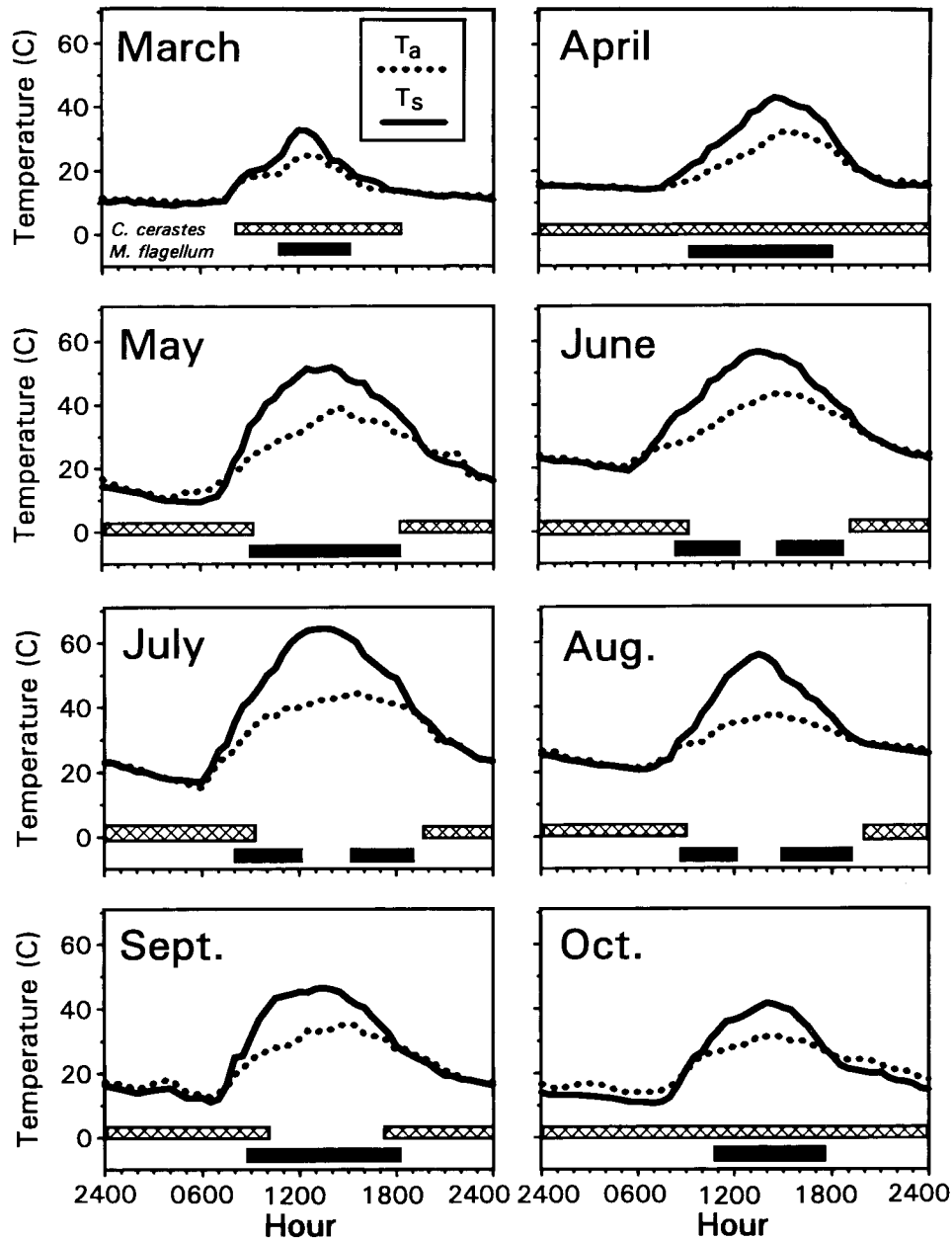mys merriami*) soon after sunset and either

Fig. 2.—Maximum spans of daily surface activity for *Crotalus cerastes* (hatched bars) and *Masticophis flagellum* (solid bars) illustrated with shaded air (T_a, dotted lines) and exposed surface temperatures (T_s, solid lines) for each month, March through October. Activity periods and environmental temperatures were recorded over 24-h periods during the middle of each month.

coil or crater (for description of this behavior see Brown and Lillywhite, 1992) within 10 m of the burrow or travel for up to several hours. A night's travel ended with the snake either entering another burrow or coiling/cratering on the sand surface. In the latter case, once the sun had risen the following morning, the snake's T_b increased at an average rate of 0.095 ± 0.005 C/min (n = 20 observations). Once

T_b's reached 31–35 C ($\bar{x}$ = 32.0 ± 0.4 C, n = 20 observations), sidewinders moved directly into a nearby burrow, one they had emerged from or investigated the previous night (Fig. 3A). Throughout late spring and early summer, *M. flagellum* increased its duration of continuous daytime activity. When environmental temperatures peaked during mid-summer, coachwhips split their surface time between late mornings and late afternoons. Coachwhips active in the morning retreated to burrows at midday (T_s's > 50 C) and usually re-emerged later in the afternoon for several more hours of foraging (Fig. 3A).

As daytime temperatures decreased through the fall, *C. cerastes* became increasingly more diurnal. Beginning in late September and continuing through October, sidewinders commonly remained on the surface throughout the day and night (Fig. 3B). By October, coachwhips had lost the bimodal pattern of their activity, and their spans of surface activity gradually decreased in duration until hibernation. Sidewinders and coachwhips entered hibernation by mid- to late November and overwintered solitarily in abandoned rodent burrows.

Individual *C. cerastes* and *M. flagellum* were never active every day, especially prior to ecdysis and following prey consumption. After excluding known pre-ecdysis and postfeeding periods, *M. flagellum* were active significantly (t = 5.70, df
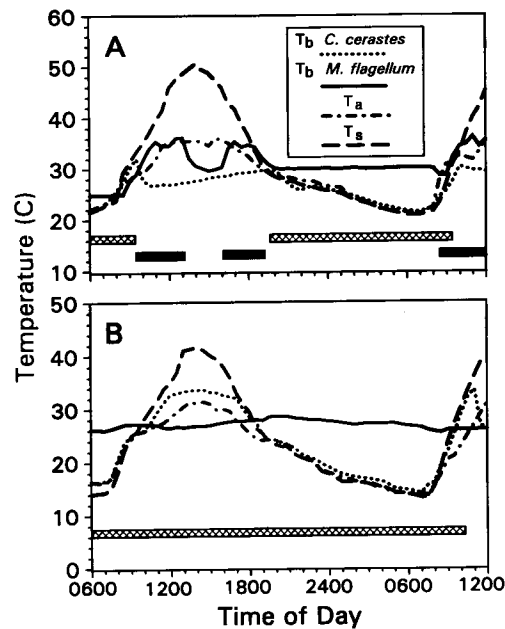

FIG. 3.—Body temperatures of an adult *Crotalus cerastes* (dotted line) and an adult *Masticophis flagellum* (solid line) illustrated with shaded air (T_a, chain dotted line) and exposed surface (T_s, dashed line) temperatures. Temperatures were recorded at ½-h intervals over a 30-h period during (A) 15–16 August 1990 and (B) 18–19 October 1990. The hatched bars and solid bars designate the period of time that the *C. cerastes* and *M. flagellum*, respectively, were on the surface. In (B), the T_b's of the *C. cerastes* are characteristic of the "plateau pattern," whereas the T_b's of the *M. flagellum* (which spent the whole time in a burrow) are characteristic of the "smooth pattern" as described by Peterson et al. (1993).

TABLE 1.—Comparison of activities and spatial patterns of sit-and-wait foraging *Crotalus cerastes* and widely foraging *Masticophis flagellum* in the eastern Mojave Desert. Refer to text for explanation of each variable. Values are expressed as means ± 1 SE, and numbers in parentheses represent the sample size of individuals. A two-tailed t-test was used to test for interspecific differences unless otherwise noted; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

| Variable	C. cerastes	M. flagellum	t-test
Activity duration (h)	13.1 ± 0.4 (7)	4.9 ± 1.1 (5)	***
Activity frequency (days active/days monitored)	0.49 ± 0.03 (21)	0.79 ± 0.03 (9)	***
Daily activity duration (h/day)	7.2 ± 0.7 (7)	3.9 ± 0.9 (5)	*
Movement distance (m)	111 ± 12 (21)	241 ± 38 (9)	***
Straight-line distance (m)	64 ± 8 (18)	146 ± 13 (7)	***
Movement distance to straight-line distance ratio	1.8 ± 0.1 (18)	1.4 ± 0.02 (7)	*a
Movement frequency (days moved/days monitored)	0.32 ± 0.02 (21)	0.76 ± 0.04 (9)	***
Daily distance of movement (m/day)	35 ± 4 (20)	186 ± 37 (8)	***
Activity range (ha)	20.1 ± 3.3 (16)	53.4 ± 13.3 (6)	**

a Wilcoxon two-sample test.
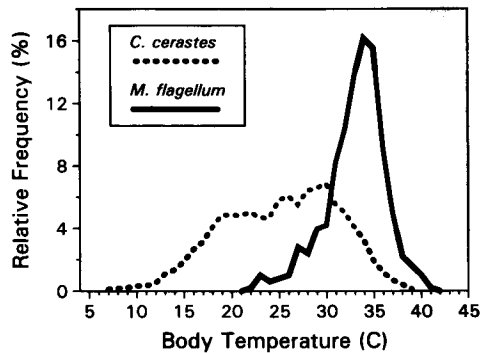
FIG. 4.—The relative (% of total recorded) distribution of T_b's of Crotalus cerastes (dotted line) and Masticophis flagellum (solid line) recorded from snakes on the surface. Note that T_b's of surface-active C. cerastes were evenly spread over a wide range, whereas those of surface-active M. flagellum were concentrated within a narrower range that was centered at a higher temperature.

TABLE 2.—Comparison of individual mean body temperatures (T_b in C) of Crotalus cerastes and Masticophis flagellum recorded from snakes in various positions from mid-March to mid-November. Values are expressed as means ± 1 SE, and numbers in parentheses represent the sample size of individuals. Below each mean value is the range of recorded T_b's. A two-tailed t-test was used to test for interspecific differences; NS = not significant, $*$ = $P \leq 0.05$, $***$ = $P \leq 0.001$.

Position	C. cerastes	M. flagellum	t-test
T_b burrow	28.1 ± 0.5 (18) 12.7–36.6	28.8 ± 0.6 (8) 13.9–40.1	NS
T_b moving	27.2 ± 0.8 (16) 15.7–38.1	33.0 ± 1.0 (8) 28.6–40.8	***
T_b stationary on surface	28.3 ± 1.6 (7) 18.1–37.8	32.7 ± 0.9 (8) 22.4–40.3	*
T_b coiled/ cratered	26.7 ± 0.6 (17) 8.2–37.7	32.8 ± 0.6 (3) 29.1–37.5	***
T_b eating	26.3 ± 1.7 (7) 20.7–32.5	33.3 ± 1.1 (4) 30.4–35.3	*

= 28, $P < 0.001$) more frequently than C. cerastes (Table 1). Active C. cerastes, on the other hand, remained on the surface for significantly ($t = 8.38$, df = 10, $P \leq 0.0001$) longer durations over 24-h periods than active M. flagellum (Table 1). The duration of daily activity (hours/day), a product of activity frequency and mean duration of activity, of C. cerastes averaged twice that of M. flagellum (Table 1).

Foraging behavior.—Crotalus cerastes always struck and envenomated prey from a coiled position either on or partially buried in (cratered; Fig. 1A) the sand. While on the surface, sidewinders spent 97.3 ± 0.8% (n = 7) of the time in one or the other of these two foraging positions. On my study site, sidewinders preyed upon diurnal lizards (Cnemidophorus tigris, Uma scoparia, and Uta stansburiana) and nocturnal rodents (Dipodomys merriami and Perognathus longimembris). Envenomated lizards were held until they died and then swallowed head-first. Rodents were released immediately after being envenomated and were eventually located by the use of chemoreception (Secor, 1994b). In several foraging episodes, the sidewinder searched for over an hour before locating the envenomated dead rodent.

Coachwhips actively foraged for prey, spending a majority (55.4 ± 7.3%, n = 4)

of their time on the surface moving from one clump of vegetation to another and in and out of burrows (Fig. 1B). Commonly while foraging, a coachwhip would stop beneath a form of vegetation for several minutes to lower its T_b and/or scan the surrounding area for active prey. Occasionally, a coachwhip would move up into a bush and elevate its head and neck above the bush to view the surrounding area. Most observed prey captures by M. flagellum were of surface-active prey (primarily lizards) that were captured following a short dash originating from a moving or stationary position. A lizard occasionally escaped capture by outrunning the snake and fleeing into a burrow. In several instances, coachwhips captured inactive prey within burrows, including two observed captures of adult sidewinders. In one such case, tracks laid in the sand (coachwhip tracks overlapping sidewinder tracks) indicated that the coachwhip had probably used chemoreception to track the sidewinder, which had been active the previous night, to a rodent burrow (Secor, 1994b). The coachwhip entered the burrow, pulled the sidewinder out onto the surface, and then swallowed the sidewinder head-first.

Thermal relationships.—Crotalus ce-

rastes and *M. flagellum* differed noticeably in the distributions of their T_b's recorded while on the surface (Fig. 4). Body temperatures of *C. cerastes* on the surface averaged 25.7 ± 0.1 C ($n = 4726$ T_b's) and were fairly evenly distributed from 18 to 33 C (this range of T_b's encompassed 80% of surface T_b's). Surface-active *M. flagellum* possessed higher T_b's ($\bar{x} = 33.3 \pm 0.1$ C, $n = 571$ T_b's) that were distributed over a narrower range (70% of surface T_b's were between 30 and 36 C). When active, *M. flagellum* T_b's oscillated several degrees as they moved across exposed surfaces, beneath vegetation, and in and out of burrows (Fig. 3A). I seldom observed *M. flagellum* active with T_b's below 28 C (7% of surface T_b's). During the activity season, mean T_b's of sidewinders and coachwhips resting in burrows did not differ statistically (Table 2). For each category of surface activity, mean T_b's of *M. flagellum* were significantly higher than those of *C. cerastes* (Table 2). Monthly mean T_b's of sidewinders and coachwhips recorded while they were in burrows were also statistically equivalent, whereas from April to October, coachwhips on the surface possessed significantly higher T_b's ($P < 0.05$) than surface-active sidewinders (Table 3).

Body temperatures of both species while active on the surface were significantly correlated ($P \le 0.0001$) with T_a's (*C. cerastes*, $r = 0.81$; *M. flagellum*, $r = 0.61$) and T_s's (*C. cerastes*, $r = 0.72$; *M. flagellum*, $r = 0.57$). I found that T_b's of *C. cerastes* closely conformed to T_a's, whereas T_b's of *M. flagellum* were typically higher than corresponding T_a's. For both species, T_b's increased linearly with T_s's, and then leveled off at higher T_s's (Fig. 5A,B). When T_s's exceeded 30 C for *C. cerastes* or 35 C for *M. flagellum*, individuals maintained their T_b's below T_s's by positioning themselves in shadier and cooler locations.

Spatial Patterns

Movements.—*Masticophis flagellum* traveled significantly ($t = 4.41$, df = 26, $P \le 0.0001$) greater distances than *C. cerastes* over 24-h periods (Table 1). I found this also to be true ($P < 0.05$) for each
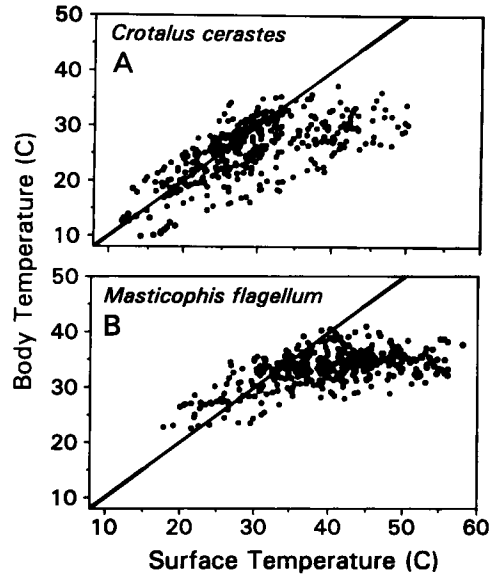

FIG. 5.—Surface temperatures plotted against T_b's of surface-active (A) *Crotalus cerastes* and (B) *Masticophis flagellum* (400 records each). The straight line transecting each plot illustrates a 1:1 relationship between surface and body temperatures.

season (spring, summer, and fall). *Masticophis flagellum* also traveled straighter routes (Fig. 6); the ratios of actual to straight-line distances of their movements were significantly less (Wilcoxon two-sample test; $Z = 2.09$, df = 23, $P = 0.037$) than those of *C. cerastes* movements (Table 1). For the days in which I monitored snakes, *M. flagellum* moved significantly ($t = 10.21$, df = 28, $P \le 0.0001$) more frequently than *C. cerastes* (Table 1). Traveling greater distances and more frequently, *M. flagellum* averaged 5.3 times the distance traveled per day ($t = 7.53$, df = 26, $P \le 0.0001$) by *C. cerastes* (Table 1).

Activity ranges.—Activity ranges of *C. cerastes* and *M. flagellum* overlapped extensively on the study site. I occasionally observed individuals of both species within close proximity (<50 m) to each other. *Crotalus cerastes* typically maintained their activity range within the sandy region of the study site, although during the fall they extended their range onto the alluvium, where they overwintered. Activity ranges of *M. flagellum*, centered in the sandy region of the site, included large

TABLE 3.—Monthly mean (±SE) body temperatures (in C), recorded from *Crotalus cerastes* and *Masticophis flagellum* positioned within burrows (T_b burrow) or on the surface (T_b surface), and air (T_a) and surface (T_s) temperatures. Numbers in parentheses represent the number of individuals for T_b and number of recordings for T_a and T_s. A two-tailed t-test tested for interspecific differences in T_b's; NS = not significant, * = $P \leq$ 0.05, *** = $P \leq$ 0.001.

	C. cerastes	*M. flagellum*	*t*-test	T_a	T_s
January					
T_b burrow	10.1 ± 0.4 (14)	10.7 ± 0.4 (5)	NS	10.4 ± 0.2 (810)	13.9 ± 0.3 (800)
T_b surface	—	—			
February					
T_b burrow	13.9 ± 0.9 (11)	13.5 ± 0.9 (4)	NS	16.1 ± 0.2 (885)	18.7 ± 0.4 (885)
T_b surface	—	—			
March					
T_b burrow	16.4 ± 1.6 (8)	16.8 ± 2.2 (4)	NS	19.9 ± 0.2 (1049)	25.5 ± 0.4 (1044)
T_b surface	23.7 ± 2.1 (7)	29.6 ± 0.2 (2)	NS		
April					
T_b burrow	22.5 ± 0.8 (8)	24.4 ± 1.1 (6)	NS	23.2 ± 0.2 (1161)	31.4 ± 0.4 (1162)
T_b surface	25.8 ± 0.6 (7)	33.0 ± 0.4 (5)	***		
May					
T_b burrow	26.7 ± 0.6 (10)	28.1 ± 0.5 (5)	NS	26.2 ± 0.2 (1791)	34.9 ± 0.3 (1795)
T_b surface	26.9 ± 0.8 (8)	33.1 ± 0.3 (4)	***		
June					
T_b burrow	29.8 ± 0.5 (10)	30.7 ± 0.5 (5)	NS	29.5 ± 0.2 (1412)	35.3 ± 0.3 (1398)
T_b surface	28.5 ± 1.1 (8)	34.1 ± 0.6 (5)	***		
July					
T_b burrow	31.2 ± 0.4 (9)	31.3 ± 0.3 (5)	NS	31.2 ± 0.1 (1510)	35.6 ± 0.3 (1497)
T_b surface	28.1 ± 1.1 (11)	33.6 ± 0.6 (4)	*		
August					
T_b burrow	30.3 ± 0.2 (14)	30.5 ± 0.5 (6)	NS	29.6 ± 0.1 (2922)	34.4 ± 0.2 (2918)
T_b surface	27.8 ± 0.2 (14)	34.4 ± 0.7 (6)	***		
September					
T_b burrow	29.0 ± 0.3 (15)	29.7 ± 0.3 (5)	NS	26.9 ± 0.1 (1946)	31.2 ± 0.3 (1926)
T_b surface	25.0 ± 0.6 (12)	33.2 ± 1.0 (4)	***		
October					
T_b burrow	24.0 ± 0.5 (16)	24.6 ± 1.0 (6)	NS	22.7 ± 0.2 (1261)	25.3 ± 0.3 (1259)
T_b surface	22.5 ± 0.5 (11)	31.2 ± 0.2 (3)	***		
November					
T_b burrow	18.3 ± 0.4 (15)	20.2 ± 1.1 (6)	NS	14.6 ± 0.2 (701)	16.9 ± 0.3 (702)
T_b surface	25.7 ± 1.0 (5)	28.0 ± 6.7 (2)	NS		
December					
T_b burrow	13.1 ± 0.4 (14)	13.9 ± 0.8 (5)	NS	9.3 ± 0.2 (918)	13.7 ± 0.4 (917)
T_b surface	—	—			

areas of the surrounding alluvial fan, where they would forage and also overwinter. Hence, *M. flagellum* possessed significantly ($t = 3.49$, df = 20, $P < 0.005$) larger activity ranges than *C. cerastes*. I found no significant relationships ($P > 0.05$) between sex or body size (SVL and body mass) and activity range size for either species.

DISCUSSION

Crotalus cerastes and *Masticophis flagellum* differ distinctly in their methods of prey acquisition. Previous measures used to quantify predatory behavior include frequency of moves per unit time, average speed of movement, and probability of movement (McLaughlin, 1989). Quanti-
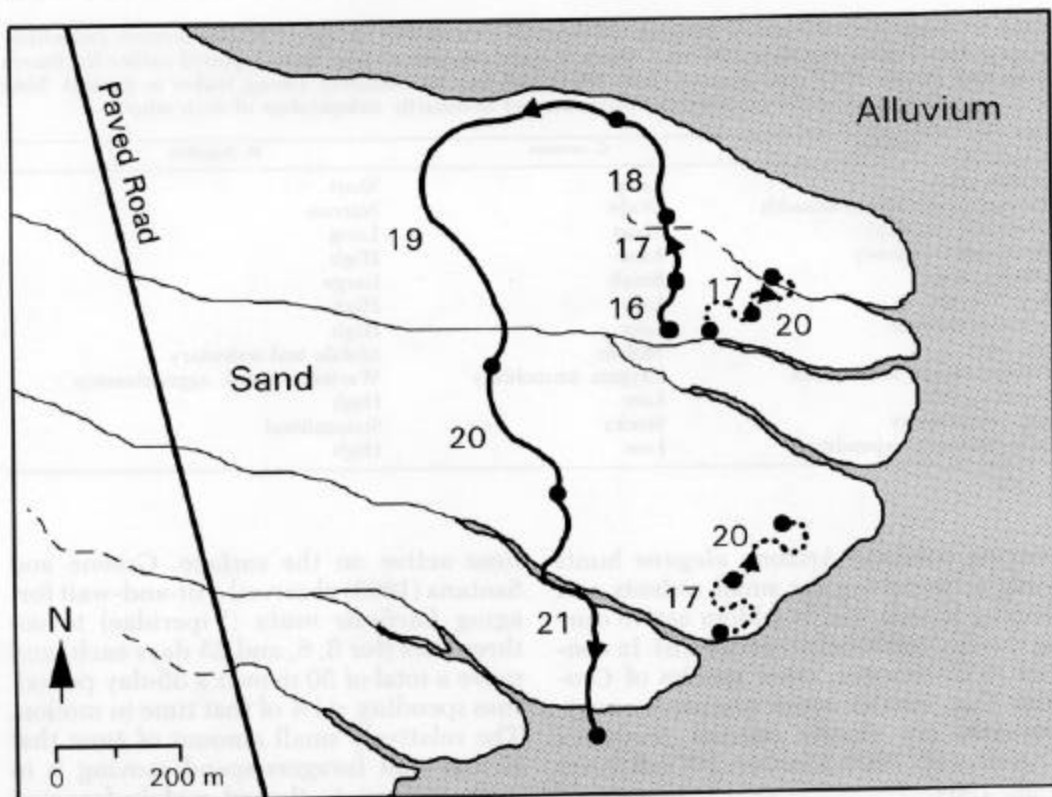
FIG. 6.—Movements of two adult *Crotalus cerastes* (dotted lines) and an adult *Masticophis flagellum* (solid line) during 16–21 May 1989. The solid circles (●) represent rodent burrows that snakes sought refuge in. The numbers represent dates of movement, and the arrows illustrate the direction of travel. During this monitoring period the *M. flagellum* moved every day and the two *C. cerastes* moved during only two of the five nights.

tative evidence of the dichotomy of foraging tactics between *C. cerastes* and *M. flagellum* includes differences in the frequency of movement (32% versus 76%; Table 1) and the relative proportion of the time on the surface that individuals were in motion (2.7% versus 55.4%).

Foraging mode involves a suite ("syndrome") of ecological, physiological, behavioral, and morphological characteristics (Eckhardt, 1979; Huey and Pianka, 1981; Toft, 1981). In the following discussion, I shall explain the observed ecological differences between *C. cerastes* and *M. flagellum* within the realm of activity, thermal relations, and spatial patterns. I shall also present other associated correlates of foraging mode because they have been postulated for lizards and are appli-

cable to these snakes. Table 4 provides a compiled list of suggested correlates, many of which stem from this study.

Activity and Thermal Relationship

Nocturnal during the majority of the activity season, *C. cerastes* seldom overlapped with the strictly diurnal *M. flagellum* in the timing of surface activity. A similar pattern of activity with respect to foraging mode was also observed by Hailey and Davis (1986) for the sit-and-wait foraging *Natrix maura* (nocturnal and diurnal) and the widely foraging *Natrix natrix* (diurnal). Although these associations (sit-and-wait foraging with nocturnality and widely foraging with diurnality) occur among these sets of snakes, they do not exist among snakes in general. The widely

TABLE 4.—Suggested correlates of foraging mode for the sit-and-wait foraging *Crotalus cerastes* and widely foraging *Masticophis flagellum* (see text). Many of these associations have been reported earlier for lizards (Huey and Pianka, 1981) and anurans (Toft, 1981) and may be consistent among snakes in general. Note that many of the proposed correlates are not necessarily independent of each other.

Variable	C. cerastes	M. flagellum
Activity span	Long	Short
Thermal performance breadth	Wide	Narrow
Movement (m/day)	Short	Long
Movement frequency	Low	High
Activity range	Small	Large
Prey diversity	Low	High
Prey capture rate	Low	High
Prey type	Mobile	Mobile and sedentary
Predator escape mechanism	Crypsis, immobility	Wariness, speed, aggressiveness
Predation risk	Low	High
Body morphology	Stocky	Streamlined
Daily energetic expenditure	Low	High

foraging colubrid *Arizona elegans* hunts at night, searching for small rodents and sleeping lizards, and is seldom active during the day (personal observations). In contrast to *C. cerastes,* other species of *Crotalus* that inhabit more temperate environments are chiefly diurnal predators (Duvall et al., 1990; Klauber, 1972; Reinert et al., 1984).

Crotalus cerastes averaged approximately twice the daily duration of surface activity of *M. flagellum.* Similarly, among lizards, sit-and-wait foraging *Callisaurus draconoides* (Phrynosomatidae) were active for twice the daily duration of the widely foraging teiid *Cnemidophorus tigris* (Anderson and Karasov, 1981). Nagy et al. (1984) later noted that sit-and-wait foraging *Eremias lineoocellata* (Lacertidae) were abroad for an average of 10.3 h/day, whereas the congeneric and widely foraging *Eremias lugubris* averaged 2.8 h/day of surface activity.

I commonly observed *C. cerastes* remaining active at one locality for several consecutive days. The snake would move in the early evening from a burrow to a surface foraging position (either coiled or cratered) and then back to the same burrow the following morning (total distance traveled typically <20 m). In several instances, the *C. cerastes* returned to the same foraging spot each night. During these foraging episodes, the time in motion constituted a very small percentage of the time active on the surface. Greene and Santana (1983) observed a sit-and-wait foraging *Lachesis muta* (Viperidae) to use three sites (for 3, 6, and 25 days each) and move a total of 50 m over a 35-day period, thus spending <1% of that time in motion. The relatively small amount of time that sit-and-wait foragers spend moving is in stark contrast to that of widely foraging hunters. *Masticophis flagellum* were in motion almost continuously while foraging. Similarly, widely foraging *Eremias lugubris* and *Eremias namaquensis* were observed in motion four times as often as sit-and-wait foraging *Eremias lineoocellata* and *Meroles suborbitalis* (Huey and Pianka, 1981).

Foraging mode influences the type of prey encountered and the rate of prey acquisition (Gerritsen and Strickler, 1977; Norberg, 1977; Schoener, 1971). Wide foragers encounter prey more frequently and feed upon a wider diversity of both mobile and sedentary prey than their sit-and-wait counterparts, which typically consume a less diverse set of mobile prey. *Crotalus cerastes* preyed only upon several species of diurnal lizards and nocturnal small rodents. In addition to lizards and rodents, *M. flagellum* consumed several species of snakes and possibly small species of birds that nested on the study site.

Actively searching for prey, wide foragers consequently experience a higher frequency of prey capture than sit-and-

wait foragers. From field observations, the prey capture rate of *M. flagellum* (16 prey captures/529 snake-observation days, 3.0%) was twice that of *C. cerastes* (31 prey captures/2006 snake-observation days, 1.5%; Secor and Nagy, 1994). Additionally, daily rates of food consumption, calculated from water influx rates, for *M. flagellum* ($\bar{x}$ = 24.1 ± 5.5 g·kg^{-1}·day^{-1}) were more than twice those for *C. cerastes* ($\bar{x}$ = 9.4 ± 1.4 g·kg^{-1}·day^{-1}; Secor and Nagy, 1994). In agreement with these results, widely foraging *Natrix natrix* were found more frequently to contain prey within their stomachs than sit-and-wait foraging *Natrix maura* (Hailey and Davis, 1986). Similarly, widely foraging lizards demonstrated higher feeding rates (1.2–2.3 times) than sympatric sit-and-wait species (Anderson and Karasov, 1981; Andrews, 1984; Nagy et al., 1984).

Masticophis flagellum are commonly regarded as visual predators, relying on the movement of their prey to direct their attacks (Jones and Whitford, 1989). Interestingly, I also found *M. flagellum* to use chemoreception to locate prey. In the aforementioned capture of the *C. cerastes*, the *M. flagellum* had apparently used chemoreception to track the *C. cerastes* to a burrow. In another instance, I observed for 20 min a *M. flagellum* tongue-flicking an area of sand and then using its head and neck to excavate the sand, in similar fashion to actions performed by the colubrid *Pituophis melanoleucus* and described by Carpenter (1982). I left the snake, and several hours later on my return found it grasping the midbody of a partially buried adult *Arizona elegans*. I can only presume that the *M. flagellum* had detected the *A. elegans* beneath the sand surface and then proceeded to dig it out.

The timing of surface activities of *C. cerastes* and *M. flagellum* was closely attuned to environmental temperatures. *Crotalus cerastes* commonly remained on the surface for as long as possible before retreating to burrows. By repositioning themselves in shifting patches of shade, sidewinders were able to remain on the surface throughout the daylight hours during portions of the spring and fall (Fig.

3B). At such times, their T_b profiles—warming in morning, stable through the day, and cooling at night—were similar to the "plateau pattern" described by Peterson et al. (1993). During the summer and after retreating to burrows in the mid-morning, *C. cerastes* exhibited very stable T_b's, which increased steadily in the afternoon as surface heat descended into the burrows (Fig. 3A).

Masticophis flagellum typically initiated foraging once surface temperatures exceeded 30 C. I occasionally observed coachwhips in the morning with their heads and necks extending from burrow openings. This behavior, also observed by Jones and Whitford (1989), may serve to warm the central nervous system (brain) prior to surface activities (Hammerson, 1977). Once active, they regulated their T_b's below 38–40 C by moving in and out of burrows and the shade of vegetation. When they were unable to consistently maintain their T_b's below 38 C, they sought refuge in burrows and remained there until surface temperatures had decreased. Bimodal patterns of diurnal activity during the summer have also been observed for *M. flagellum* in southwestern New Mexico (Jones and Whitford, 1989) and for *Cnemidophorus tigris* in southern California (Anderson and Karasov, 1988). Body temperatures of *C. cerastes* and *M. flagellum* that remained in burrows throughout the day were relatively stable (Fig. 3B), characteristic of the "smooth pattern" of T_b's described by Peterson et al. (1993).

Differences in mean T_b between surface active *C. cerastes* and *M. flagellum* resulted from differences in their activity patterns (nocturnal versus diurnal) rather from direct differences in foraging mode. The difference in the relative distribution of their T_b's while active (Fig. 4) does appear to be directly linked to foraging behavior. *Crotalus cerastes* remained stationary on the surface for many hours, presumably to increase the chance of capturing prey, and were subjected to a wide range of environmental temperatures, resulting in substantial changes in their own T_b's. On several occasions, I recorded 25 C changes in T_b's over 24-h periods from

foraging sidewinders. Hence, *C. cerastes* would benefit from the ability to envenomate and consume prey over a wide range of T_b's. Over the course of this study, I observed *C. cerastes* traveling with T_b's ranging from 15.7 to 38.1 C and envenomating and consuming prey with T_b's ranging from 20.7 to 32.5 C. *Crotalus cerastes* appear to possess a broad "thermal performance breadth" (Huey and Stevenson, 1979) for movement and prey capture and consequently are "thermal generalists" (Huey and Slatkin, 1976). In support of this hypothesis, the blood-oxygen transport system of *C. cerastes* has been suggested to be adapted to temperature variability because it exhibits increased levels of hemoglobin, oxygen capacity, and oxygen affinity at lower temperatures (MacMahon and Hamer, 1975).

The T_b profile of active *M. flagellum* suggests that they possess a narrow "thermal performance breadth" and are "thermal specialists" (Huey and Slatkin, 1976; Huey and Stevenson, 1979). I observed *M. flagellum* traveling with T_b's ranging 28.6–40.8 C and capturing and consuming prey over a narrower range of T_b's (30.4–35.3 C). This snake may require higher T_b's to achieve the level of performance necessary to chase, capture, and consume active prey (Bennett, 1980; John-Alder and Bennett, 1981). *Thamnophis elegans*, another widely foraging colubrid, attains 80% of maximum crawling performance with T_b's ranging 27.0–38.3 C (Stevenson et al., 1985). For *C. cerastes* and *M. flagellum*, the thermal performance breadth may be a dominant influence in the periodicity of daily activities. Laboratory studies on the thermal dependency of performance of these two species would demonstrate whether their thermal performance profiles match activity T_b's.

Spatial Patterns

Crotalus cerastes occasionally traveled considerable distances (500–800 m) in 24-h periods. I suspect that the majority of their movements were to locate new foraging sites after they had been unsuccessful at earlier sites. Foraging *M. flagellum* repeatedly traveled distances of approximately 1 km as they would cross the width

of the study site in one day and then travel to another distant portion of the site the next day. In addition to foraging or locating new foraging sites, movements could serve to locate mates or oviposition sites (Parker and Brown, 1972; Secor, 1992). Earlier, I reported that adult male *C. cerastes* traveled significantly greater distances than females during the spring and fall mating seasons, presumably because they were searching for females in addition to new foraging sites (Secor, 1994a).

Whereas the large activity ranges of *M. flagellum* reflected their frequent and lengthy foraging bouts, activity ranges of *C. cerastes* were the summation of temporal activity centers (Secor, 1994a). An activity center was an area of the site (typically 1–5 ha) in which a *C. cerastes* concentrated its activities for up to several months. *Crotalus cerastes*, like other sit-and-wait foraging snakes, select new foraging sites based on the detection of prey activity (Duvall et al., 1990). *Crotalus cerastes* shifted their activity centers as they moved to new foraging sites and to overwintering sites (Secor, 1994a).

The activity ranges of *C. cerastes* and *M. flagellum* are among the largest documented for snakes (Macartney et al., 1988). Most earlier studies calculated activity range size by the minimum convex polygon method (Jennrich and Turner, 1969). Activity ranges calculated by this method averaged 23.2 ± 3.8 ha and 57.9 ± 13.2 ha, respectively, for *C. cerastes* and *M. flagellum*. These activity ranges did not differ significantly in size from those calculated by the harmonic mean method. Based upon Macartney et al.'s (1988) tabulation of activity ranges, there is no apparent trend of wide foragers to possess larger activity ranges than sit-and-wait species. The different methodologies and durations of the studies noted in that paper possibly masked any potential trends in spatial patterns that can be attributed to foraging mode.

Associated Correlates of Foraging Mode

Foraging mode has been postulated to have coevolved with predator escape behavior, morphology, and energetics (Huey

and Pianka, 1981; Nagy et al., 1984; Vitt and Price, 1982). Methods employed by *C. cerastes* and *M. flagellum* to escape predators are similar to those of other reptiles with corresponding foraging modes (Vitt and Price, 1982). *Crotalus cerastes* rely upon cryptic coloration and immobility to avoid detection by predators (mammals, birds, and other reptiles). Individuals coiled or cratered matched the surrounding sand in coloration and remained immobile when closely approached (personal observations). *Masticophis flagellum*, reddish in coloration and frequently foraging, are more noticeable to predators and thus depend upon wariness, speed, and aggressiveness to escape capture (Greene, 1988; Stebbins, 1985). When I approached a *M. flagellum* in the field, it was clearly aware of my presence and would follow my movements with its head. If I approached too closely or attempted to capture it, the snake would rapidly move away and escape into a nearby rodent burrow.

Wide foragers predictably experience greater risks of predation due to their higher intensities of surface activity (Andrews, 1979; Gerritsen and Strickler, 1977). Over the 3-yr study, I noted predation on 14 *C. cerastes* (out of 181 marked individuals, 7.7%) and 4 *M. flagellum* (out of 25 marked individuals, 16%). Known predators included coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) (preying upon 6 *C. cerastes* and 2 *M. flagellum*), birds (2 *C. cerastes* and 2 *M. flagellum*), and *M. flagellum* (3 *C. cerastes*). Huey and Pianka (1981) found that widely foraging lizards represented a greater-than-expected proportion (relative to their abundance) of the stomach contents of the sit-and-wait viperid *Bitis caudalis*.

Morphologically, sit-and-wait foraging lizards are generally stocky and possess short tails, whereas wide foragers are streamlined in body shape and have long tails (Vitt and Congdon, 1978). Similarly, *C. cerastes* were significantly ($t = 6.43$, df $= 28$, $P \leq 0.0001$) more heavy-bodied (2.2 versus 1.4 g/cm TL) and possessed significantly (Wilcoxon two-sample test; $Z = 4.25$, df $= 28$, $P \leq 0.0001$) shorter tails relative to body length (7.2% versus 34.4%

of SVL) than *M. flagellum*. Shine (1980) commented that the long, slender morphology of many snakes (e.g., *Coluber, Demansia, Masticophis, Psammophis*) is an adaptation for rapid movement to capture fast-moving diurnal lizards.

Widely foraging lizards possess significantly greater rates of energy expenditure and acquisition than sit-and-wait species (Anderson and Karasov, 1981; Nagy et al., 1984). Likewise, *M. flagellum* (94.7 ± 10.2 kJ·kg^{-1}·day^{-1}) expended more than twice the daily energy of *C. cerastes* (38.6 ± 3.1 kJ·kg^{-1}·day^{-1}) from April to October, determined from doubly labeled water techniques (Secor and Nagy, 1994). During the same period, *M. flagellum* consumed more than twice the amount of energy than did *C. cerastes* (see Discussion: Activity and Thermal Relationships). Widely foraging *M. flagellum* balance high energy expenditure with high food intake, whereas ambushing *C. cerastes* have lower expenditures fueled by lower rates of energy consumption (Secor and Nagy, 1994).

In addition to foraging mode, *C. cerastes* and *M. flagellum* differ phylogenetically (viperid versus colubrid) and in reproductive (viviparous versus oviparous) and locomotory modes (sidewinding versus lateral undulation). These differences, independent of foraging mode, may have contributed to the observed differences in activities, thermoregulatory behaviors, and spatial patterns. The evolution of foraging tactics and associated ecological, morphological, and physiological adaptations in snakes awaits study. Any historical constraints of foraging mode and coevolved features would best be identified from broader studies on species of diverse and known phylogenetic position.

Sit-and-wait and widely foraging are endpoints of a theoretical continuum of foraging behaviors (Pianka, 1973). Foraging behavior of many species may actually lie elsewhere on this continuum. For example, species may forage with repeated series of distinct starts and stops, a tactic referred to as "saltatory search" (Evans and O'Brien, 1988). Species can also shift or combine foraging tactics with age or in response to changes in environmental conditions, predation pressures, and/or food

availability to maximize foraging efficiencies (Huey and Pianka, 1981; Janetos, 1982; Milinski and Heller, 1978). For example, *M. flagellum* inhabiting mesquite (*Prosopis*) stabilized dunes in southwestern New Mexico forage widely during the spring and then switch during the warmer summer to sit-and-wait tactics of ambushing lizards that shuttle in and out of the shade of mesquite trees (Jones and Whitford, 1989).

Crotalus cerastes and *M. flagellum* possess distinctly different tactics of prey acquisition, each involving separate sets of ecological, morphological, and physiological characteristics. *Crotalus cerastes* spend a large majority of their time on the surface waiting cryptically to ambush prey. They appear to possess a broad thermal performance breadth that enables them to capture prey over a wide range of body temperatures. This tactic of prey acquisition results in balancing a low rate of prey capture with a low rate of energy expenditure. *Masticophis flagellum* appear to be thermal specialists, regulating their T_b's as they actively search for active and sedentary prey. Their high T_b's and streamlined body shape facilitate the rapid pursuit of prey. Foraging over a large activity range, *M. flagellum* balance elevated energetic expenditures with many prey captures. The foraging success of both of these species throughout this study appeared to be relatively equivalent. As one indication, they experienced similar yearly energetic profits (energy consumed minus energy expended): 177 kJ and 212 kJ, respectively, for *C. cerastes* and *M. flagellum* (Secor and Nagy, 1994). The relative success of these foraging modes may diverge with a change in prey availability. For example, *C. cerastes* may fare better during low prey availability because of their relatively small initial investment in foraging. I hope this study will provide the foundation and incentive for future investigations of correlates of foraging mode among snakes and lead to an understanding of the links between food availability, foraging strategies, and foraging success.

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