Foraging behavior and predation success of the sand viper (*Cerastes vipera*)

Aziz Subach, Inon Scharf, and Ofer Ovadia

Abstract: Activity levels and foraging success of ectotherms are dependent both on extrinsic factors (e.g., ambient temperature) and intrinsic factors (e.g., hunger level). We focus here on activity and foraging of sand vipers (*Cerastes vipera* (L., 1758)) (Squamata: Viperidae) in the northwestern Negev desert of Israel. Viper activity is bounded by a specific thermal range, but within this range, temperature does not affect the distance moved. Movement distances are, however, positively correlated with relative humidity. The capture success of lizards, the main prey of this viper, is strongly related both to movement distances of the snake and to the number of the lizard burrows scanned. Body size and shape have a direct effect on the number of burrows scanned and on the number of lizards captured. The increase in capture success with size is probably due to the consequent increase in the range of prey items the sand viper can subdue or handle. Vipers are larger and have a higher mass to length ratio in one of the three study sites, characterized by higher mean annual rainfall and vegetation cover. Finally, females tend to have a higher mass to length ratio than males, which may provide some space within the female body for reproductive materials such as eggs.

Résumé : Les niveaux d'activité et de recherche de nourriture des ectothermes dépendent à la fois de facteurs extrinsèques (par ex., la température ambiante) et de facteurs intrinsèques (par ex., l'intensité de la faim). Nous nous intéressons ici à l'activité et la recherche de nourriture de la vipère des sables (*Cerastes vipera* (L., 1758)) (Squamata : Viperidae) dans le nord-ouest du désert du Néguev en Israël. L'activité de la vipère est restreinte à une gamme spécifique de températures, mais dans cette gamme, la température n'affecte pas la distance des déplacements. Il y a cependant une corrélation positive entre la distance des déplacements et l'humidité relative. Il existe une forte relation positive entre le succès de la capture de lézards, les proies principales de cette vipère, et à la fois la distance des déplacements du serpent et le nombre de terriers de lézards examinés. La taille et la forme du corps ont un effet direct sur le nombre de terriers examinés et le nombre de lézards capturés. L'accroissement des captures en fonction de la taille s'explique probablement par l'augmentation reliée à la taille de l'entendue des types de proies que la vipère des sables peut maîtriser où manipuler. Les vipères sont plus grandes et possèdent un rapport masse/longueur plus élevé dans l'un des trois sites d'étude, caractérisé par des précipitations moyennes annuelles plus élevées et une couverture végétale plus importante. Enfin, les femelles ont tendance à avoir un rapport masse/longueur plus élevé que celui des mâles, ce qui peut fournir aux femelles de l'espace à l'intérieur du corps pour les produits de la reproduction, tels que les œufs.

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Introduction

All foraging activities of animals are affected by a variety of extrinsic factors (Bell 1990) like prey density and spatial distribution (e.g., Bond 1980), ambient temperature and humidity (e.g., Peterson et al. 1993; Angilletta et al. 2002), and level of illumination, cloudiness, and amount of solar radiation (e.g., Kotler et al. 1994). In ectotherms, abiotic factors like ambient temperature are especially important (Angilletta et al. 2002) at times of searching and foraging during the diel cycle; however, these factors may also play a central role in determining dominant life-history traits such as growth rate and adult body mass (Atkinson and Sibly 1997; Bronikowski 2000). For example, in cool environments, snakes may be less effective in capturing prey and are thus

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expected to spend less time foraging (e.g., Peterson et al. 1993; Vincent and Mori 2008). It is also possible that cold habitats may have an indirect effect on foraging success via habitat selection (i.e., they reduce the suitability of certain places like ambush sites; Shine et al. 2002). Effects of other environmental factors such as humidity, although less well studied, were also shown to influence snake behavior, habitat selection, and foraging success (Daltry et al. 1998; Moore and Gillingham 2006). All foraging activities of animals are also affected by intrinsic factors (Bell 1990) like hunger or satiation level (e.g., Bond 1980) and reproductive state (e.g., Gibbons and Semlitsch 1987). Animals deprived of food may use two alternative behavioral–physiological strategies: (1) either increase activity with the aim to locate new patches or (2) decrease activity to save energy and wait for an increase in food availability (Gutman et al. 2007).

Sand vipers are particularly appropriate animal models for studying foraging behavior, simply because they are easy to follow. Snakes, in general, are found in a diverse range of habitats, where they are highly dependent on their immediate surroundings (e.g., substratum and microclimate; Lilly-white and Henderson 1993), and can therefore be used for studies of local adaptations. Yet, studies of snake foraging

behavior usually relate only to one or two factors that could affect foraging behavior and success (but for more comprehensive studies see Moore and Gillingham 2006; Crnobrnja-Isailovic et al. 2007).

In this study, we used the sand viper (*Cerastes vipera* (L., 1758)) (Squamata: Viperidae) as a model species to study the effects of extrinsic microclimatological factors, such as temperature and humidity, and of intrinsic factors, such as body mass, length, and sex, on foraging activity and capture success of prey. The sand viper is an interesting example of a predator switching from the active foraging mode to the ambush mode. Specifically, it adopts an actively searching foraging mode during most of the night and is inactive during most of the day; however, during the day–night transitions (dawn and dusk), it adopts an ambush mode waiting for lizards to enter its attack radius (A. Subach, personal observations). It is likely that as dawn begins the cost of movement increases with temperature faster than the potential benefit, and therefore a sit-and-wait foraging mode is adopted. When temperature and direct solar radiation increase substantially, the sand viper seeks a shelter inside rodent burrows and ceases its activity. At dusk, both direct solar radiation and temperature decrease considerably allowing the snake to exit its shelter and to wait in an ambush mode until night begins and the active foraging mode becomes preferable again. Most reptiles adopt a distinct foraging mode, but species that switch between foraging modes are not rare. This switch may be related to satiation level, prey density, and habitat structure (e.g., Huey and Pianka 1981; Mullin et al. 1998; Greeff and Whiting 2000; Verwaijen and Van Damme 2008). This plasticity aids reptiles to forage on more than one prey item (Mullin et al. 1998; Greeff and Whiting 2000).

We report here on the relationships between activity of sand vipers, including foraging success and environmental (temperature, humidity, and cloudiness) or intrinsic (body length, body mass, and their ratio) factors. In addition, we test for sexual-size dimorphism, as well as viper size and shape differences among different study sites. More specifically, we hypothesized that viper activity should be correlated with both relative humidity and temperature (i.e., night surface temperature, air temperature, and belowground temperature). Similarly to other ectotherms, we expected that activity will be positively correlated with temperature up to the point that temperature is extremely high and then a sharp decrease in activity should be evident (Huey and Kingsolver 1989; Angilletta et al. 2002). The reason for this thermal reaction shape is that biochemical and physiological systems function better and more efficiently in moderate to high temperature, up to the point where extreme high temperatures become damaging (see Fig. 1 in Huey and Kingsolver 1989). Humidity should have a positive effect on the activity of vipers (Daltry et al. 1998). This should be especially true under desert conditions, often associated with increased water loss and risk of desiccation. Indeed, high humidity levels can enable animals to be active under high temperatures with smaller risk of desiccation, and therefore, vipers would be more active in periods of higher relative humidity. Cloudiness substantially reduces the strength of environmental light and is thus expected to be positively correlated with activity (Kotler et al. 1994). Darkness de-

creases the chances of the vipers being preyed upon and also increases activity of potential widely foraging prey. Furthermore, cloudiness is often positively correlated with temperature and humidity, which in turn should increase activity.

We also expected a strong positive correlation between activity level and capture success of prey items. As the viper moves longer distances, it increases the probability of encountering lizard burrows just by chance. While studying capture success, we also took some intrinsic factors into consideration such as sex and body mass, and thus could test for their effect on activity and capture success. Finally, we predicted that body dimensions should be positively correlated with both activity level and capture success. Larger individuals should consume more prey items, because their larger size allows them to feed on a wider variety of prey (Arnold 1993). They should be also more active (this is true at least for terrestrial mammals under field conditions; Swallow et al. 1999). The mass to length ratio may indicate the physiological state of the viper, i.e., vipers in good condition show higher mass to length ratios (Shine et al. 2003). Consequently, those individuals should invest less in foraging than others with a lower mass to length ratio.

The data collected also enabled us to perform morphological comparisons involving sexual-size dimorphism (SSD), and viper size (length) and shape (mass to length ratio) across different study sites. We predicted that females should be larger and have a higher mass to length ratio than males. We also predicted that vipers in study sites, characterized by higher levels of mean annual rainfall and vegetation cover, should be larger and show a higher mass to length ratio. Indeed, in about two-thirds of studied species, female snakes were larger; the main reason for this size difference is the longer maturation period in females (Shine 1993). Large size at maturity is particularly important in female ectotherms, because reproductive success is tightly and positively correlated with body size in various taxa (Blanckenhorn 2005). Variation in body size can also be related to local environmental conditions. For instance, populations of ectotherms, snakes in particular, were found to be larger in colder environments, at higher altitudes, and in richer environments (e.g., Atkinson and Sibly 1997; Bronikowski 2000).

Materials and methods

Study sites and study species

The study was conducted in the sand dunes of the northwestern Negev desert in Israel (Fig. 1), which are an extension of the vast Saharan dunes of Sinai. Three representative sites were chosen: Agur (30°54′N, 34°28′E; 250 m above sea level (a.s.l.)), Shunra (30°58′N, 34°40′E; 340 m a.s.l.), and Mashabim (31°01′N, 34°45′E; 350 m a.s.l.). These sites, although close to one another (about 10 km from Mashabim to Shunra and 20 km from Shunra to Agur; see Fig. 1), differ in their sand stability and in their annual and perennial vegetation cover (Danin 1978; Abramsky et al. 1985). Shunra has a higher annual rainfall than Agur (94 vs. 71 mm) and has a higher perennial (11% vs. 3%) and annual (42% vs. 11%) plant cover (Abramsky et al. 1985). We have no data on vegetation cover in Mashabim, but the annual

Fig. 1. Map of the southern part of Israel showing the three study sites. Shaded areas represent sand dunes. The three study sites in which vipers were followed are marked with squares.
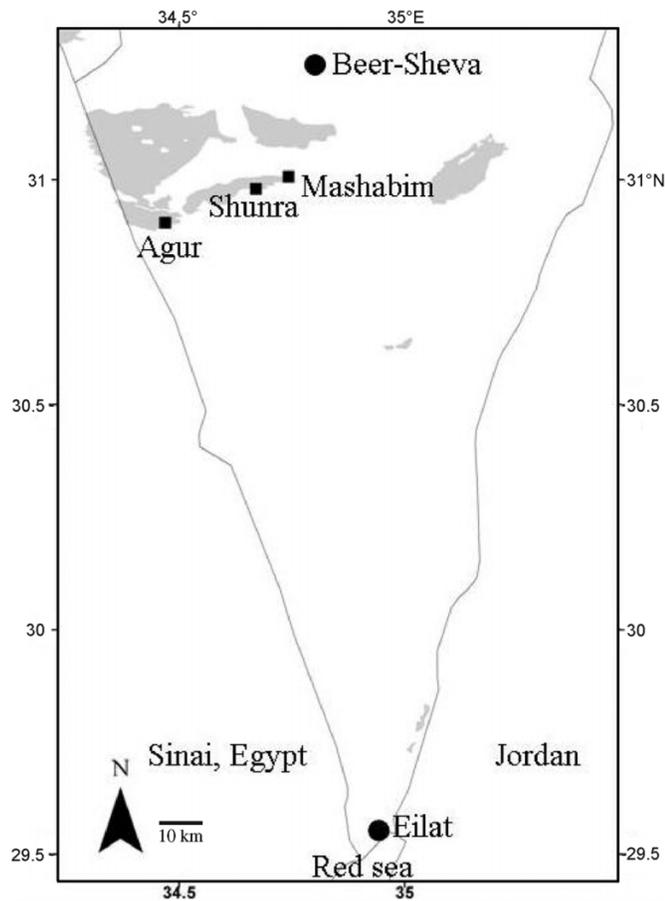
rainfall characterizing this study site is slightly higher than that of the two other sites (108 mm). Productivity and annual plant cover of sandy areas in Israel follow a bell-shaped pattern, which peaks at about 100 mm of rainfall (Abramsky 1988). Therefore, both productivity and annual plant cover are expected to increase from Agur through Shunra to Mashabim (Abramsky et al. 1985). Moreover, gerbils were found to consume more seed biomass as annual plant cover increases (Abramsky 1988). The positive correlation between annual plant cover and prey consumption may be also valid for predators such as *C. vipera*.

The two common shrubs in all three study sites are *Artemisia monosperma* Delile and *Retama raetam* (Forssk.) Webb. Animal burrows are mainly found near or under shrubs, probably because the shrub roots stabilize the sand, and consequently, burrows are less likely to collapse. The desert rodents inhabiting sand-dune habitats in the Negev desert are nocturnal species belonging to the families Gerbillidae and Dipodidae. In addition, two species of lizards are common in these sites: the diurnal Nidua fringe-fingered lizard (*Acanthodactylus scutellatus* Audouin, 1827) (Sauria: Lacertidae) and the nocturnal Anderson's short-fingered gecko (*Stenodactylus petrii* Anderson, 1896 (Sauria: Gekkonidae)). Burrows of both lizard species are found mainly in the vicinity of shrubs. While a single burrow is used by an individual *S. petrii*, many burrows can be found in the territory of an individual *A. scutellatus* (A. Subach, personal observations).

The sand viper (*C. vipera*) is exclusively a desert-dune dweller, commonly found in Israel, the Sinai Peninsula, and North Africa. Similar to related species, *C. vipera* utilizes caudal luring to catch its prey (Heatwole and Davison 1976) and moves by side-winding. The use of caudal luring indicates that this predator uses the ambush foraging mode, at least partially. *Cerastes vipera* is mainly nocturnal and is active over a wide range of temperatures (Schnurrenberger 1959; Heatwole and Davison 1976; Mallow et al. 2003). The sand viper preys upon small lizards such as *Acanthodactylus* spp., which are susceptible to luring (Bar 2003; Mallow et al. 2003), but it does not attack rodents, although it accepts mice in captivity. Juvenile *Acanthodactylus* spp. emerge between June and September. There is a reduction in the abundance of adult lizards from June onwards, with mainly juveniles being found by August. Activity during winter is limited to warm periods (Perry and Dmi'el 1994; Bar 2003). This is one of the reasons why we did not collect our data during winter (December–February).

Sampling and tracking the vipers

The data were collected between April and November 1980. Tracking began around 1600–1700, when vipers renew their activity, and ended between 0600 and 0800 the next day. Random searches were conducted for tracks (i.e., evidence for side-winding), and after tracks had been located, they were followed until the viper was found. When a viper was found, we placed a flag into the sand that indicated the vipers location, identification number, and time of detection. The viper's tracks and location were followed hourly throughout the entire night, from the point where the viper started moving. Viper movement usually included side-winding, unless it moved very close to bushes or either entered or exited a burrow. We still could identify the tracks because sand completely surrounds all bushes. Movement distances were measured using a measuring tape. The vipers were also weighed every hour (Pesola® hanging scale; accuracy of 0.1 g). Vipers were slightly disrupted each hour, when movement distances were measured and vipers weighed. However, between measurements we stood at least 100 m away from the vipers, so they were free to move and search for prey. We determined the number of burrows scanned by documenting the viper tracks at the entrances to and exits from burrows. On some occasions, we saw the vipers in the process of entering or leaving a burrow. The number of lizards captured was determined by weighing the viper every hour and dividing the mass difference by the mean body mass of a lizard (5 g).

Two data sets of viper foraging behavior were collected (both in 1980). The first data set, which encompassed 19 vipers followed at the Mashabim site over 307 h of measurements, included viper individual number, hour (time the data were recorded), distance moved by the viper per hour, the number of burrows scanned, and microclimatological measurements (Table 1). The latter included cloudiness (on a scale of 1 to 8), temperatures below ground (–30 and –15 cm), surface temperature, temperature above ground (10 cm), and relative humidity; all of which were measured hourly starting around 1600–1700 on the first

Table 1. Basic statistics for the data collected on foraging behavior of sand vipers (*Cerastes vipera*).

	Mean	1 SE	*n*	Range
First data set				
Distance moved per hour* (m)	15.27	0.38	124	7–34
Number of burrows scanned per hour*	1.685	0.066	124	0–5
Hours of activity per individual†	7.75	0.80	16	3–11
Second data set				
Distance moved per night‡ (m)	79.31	1.09	429	15–235
Number of burrows scanned per night‡	8.482	0.177	429	1.57–35
Number of lizards captured per night‡	0.169	0.007	429	0–1
Body mass in Agur (g)				
Male	14.2	0.5	86	5.8–23.5
Female	13.7	0.7	57	4.8–25.0
Body mass in Shunra (g)				
Male	14.5	0.5	82	3.1–24.2
Female	13.7	0.6	62	4.2–22.3
Body mass in Mashabim (g)				
Male	14.5	0.4	85	6.9–23.9
Female	14.9	0.5	55	7.4–24.5
Body length in Agur (cm)				
Male	18.8	0.5	86	10.0–28.5
Female	18.8	0.7	57	9.5–26.3
Body length in Shunra (cm)				
Male	17.7	0.6	82	9.5–27.6
Female	18.5	0.6	62	8.8–27.5
Body length in Mashabim (cm)				
Male	20.4	0.4	85	10.1–27.5
Female	21.2	0.6	55	9.4– 26.8

*Only hours when the viper was active were taken into account. Sample size represents hours of activity of the 19 vipers observed.

†Individuals were usually followed starting around 1600–1700 on the first day and ending around 0600–0800 the next morning. Only nights when the vipers were active were taken into account.

‡All observations (e.g., distance moved) were divided by the number of nights that the same viper was observed.

day and ending around 0600–0800 the next day. Temperatures were measured using mercury-in-glass thermometers buried in the sand, placed on the sand surface, or hanged on bushes at different heights. Relative humidity was measured using a psychrometer composed of wet and dry bulb thermometers (Casella, London). Cloudiness level was measured by counting the number of squares covered by clouds of a circular frame subdivided into eight squares that was held up to the sky and aimed towards the north. Three representative tracks are presented in Fig. 2. The second data set was characterized by a larger sample size using a coarser resolution, where the time unit of measurement was night and not hour as was the case in the first data set. This data set included information about 190 vipers, followed usually once but also up to 5 times. Vipers were followed in each session for a period of 4.9 ± 2.5 days (mean ± 1 SD; *n* = 427). This data set included the habitat in which the viper was found, number of nights observed, its sex, length, body mass, total movement distance, cumulative number of burrows scanned, and total number of lizards captured during the observation period. Body mass of the two lizards most commonly found in the study sites was also determined (*S. petrii*: 4.3 ± 1.6 g, *n* = 30; *A. scutellatus*: 7.1 ± 0.8 g; *n* = 33). Observations

indicated that *C. vipera* usually preys on *A. scutellatus* and less often on *S. petrii*.

Statistical analysis

We analyzed the two data sets separately. The analysis of the first data set focused on the effect of microclimatological factors (temperature, humidity, and cloudiness) on the two activity-related variables measured, i.e., distance moved and burrows scanned. For that purpose, we used two stepwise multiple linear regressions (Sokal and Rohlf 1995). In addition, we used a binary variable representing activity (moved versus not moved) and logistic regressions (Sokal and Rohlf 1995; Neter et al. 1996) to relate surface temperature and humidity to general activity rather than to specific movement distances. The results of the logistic regressions are presented in the following equation: $P_{moved} = 1/[1 + e^{-(a + b \cdot ST)}]$, where P_{moved} is the probability of moving and ST is surface temperature (we also used humidity). Additionally, we calculated the odds ratio ($P/(1 - P)$), which shows how variation of one unit in ST affects the probability of moving, i.e., P_{moved}.

For the second data set, we used three multiple linear regressions to study the effect of body characteristics on the distances moved, burrows scanned, and lizards captured per

Fig. 2. Three representative tracks of sand vipers (*Cerastes vipera*) (V1, V2, and V3) in the Mashabim study site. Vipers were followed from around 2000–2100 to around 0500–0700 the next day. Shaded circles and "×"s represent bushes and gerbil burrows, respectively. "LB" and "GB" mark the entrance to a lizard burrow or a gerbil burrow, respectively. "SW" marks short episodes of ambushing for prey while being buried in the sand.
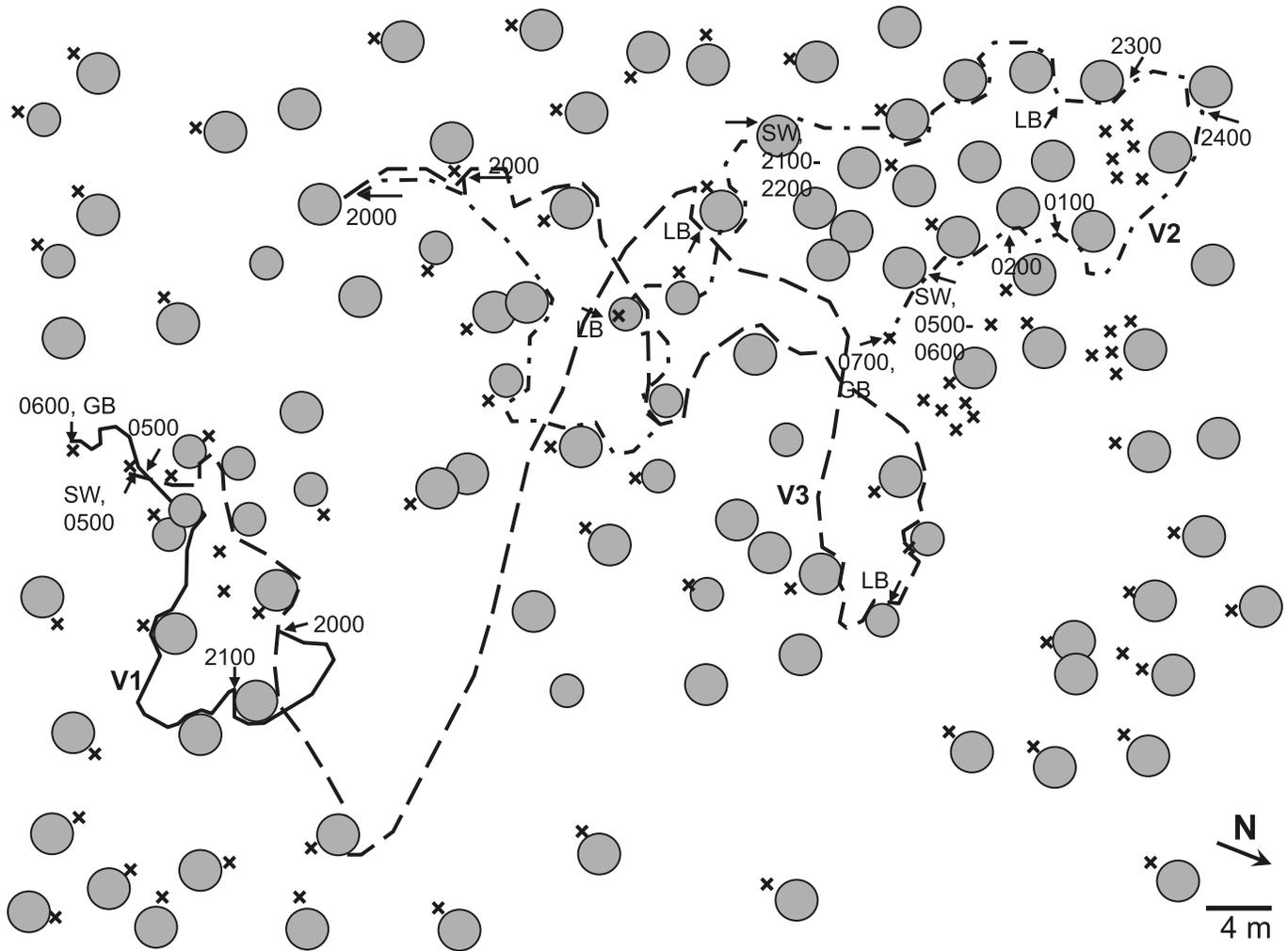
night. We also used two simple linear regressions to test for the effect of movement distances on the burrows scanned and lizards captured per night. We did not use the original measurements of body mass and length, owing to the existing significant correlation between the two factors (R^2 = 0.170); instead, we used principal components analysis (PCA; Zelditch et al. 2004) to create two new composite variables that would be uncorrelated (PCA was performed on log-transformed values using the covariance matrix). Finally, we used two-way ANOVAs to test for the effect of sex, study sites, and the respective interaction term on viper body mass and body length (again, not directly but on the two new composite variables created by the PCA), movement distance, number of burrows scanned, and number of lizards captured.

Results

First data set: effect of temperature, humidity, and cloudiness on viper activity

We used a stepwise multiple linear regression to test for

the important microclimatological factors affecting movement distances and number of burrows scanned. The best model explaining the distance moved included a negative correlation with surface temperature and positive correlations with both temperature 15 cm below the surface (Min15T) and the level of cloudiness (*C*) (R^2 = 0.080, n = 306, $F_{[3,302]}$ = 9.819, P < 0.0001; distance = −1.379 − 0.378·ST + 0.580·Min15T + 2.875·*C*). The best model explaining the number of burrows scanned included a negative correlation with surface temperature (ST) and a positive correlation with temperature 15 cm below the surface (Min15T) (R^2 = 0.057, n = 306, $F_{[3,303]}$ = 10.190, P < 0.0001; burrows = −0.005 − 0.040·ST + 0.061·Min15T). We present in Fig. 3 all significant pathways for both data sets. We also used logistic regression to relate surface temperature and relative humidity to a binary variable representing activity (moved vs. not moved). The propensity to move increased with relative humidity (P = 0.0016 for humidity, P < 0.0001 for the constant). The odds ratio was 1.015, meaning that an increase of 1% in relative humidity increased the probability of the viper moving by 1.5%. The

Fig. 3. A summary of all significant factors affecting activity of sand vipers (*Cerastes vipera*) for the first (A, B) and second (C–E) data sets. Solid and broken arrows indicate positive and negative correlations, respectively. See text for *P* values.
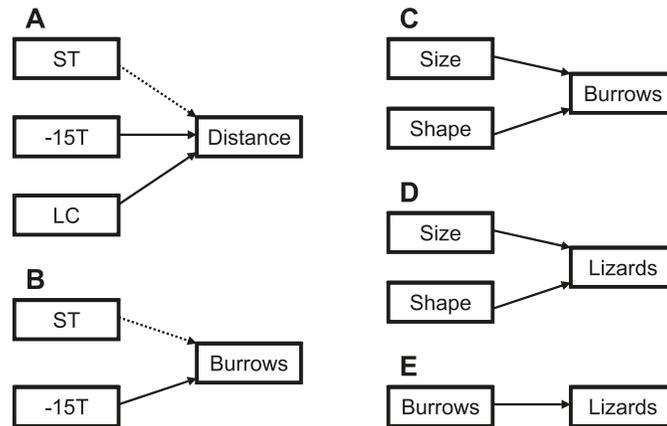
same analysis with surface temperature was not significant ($P = 0.22$ for surface temperature, $P = 0.97$ for the constant). Nevertheless, even though the intensity of activity was not dependent on the temperature, surface temperature did impose a defined limit for viper activity, as no viper was active below 17 °C or above 28–29 °C (Fig. 4). Note that temperatures above or below this range were often measured (80 and 47 times, respectively), so the lack of activity cannot be attributed to the lack of measurement in a broader range of temperatures.

Second data set: effect of body dimensions on activity and foraging behavior

The first principal axis accounted for 74.83% of the total variation and described an overall increase in size (all PC1 loadings were positive; body mass = +0.564; body length = +0.826). The second principal axis accounted for the remaining 25.2% of the variance and described a change in shape (body mass = –0.826; body length = +0.564). An increase along this axis represents a decrease in the ratio between mass and length, meaning that the mass to length ratio decreases. The analysis using these composite variables is more logical, as we can now discuss size and shape separately. Shape can be used to describe the physical conditions of the viper (Shine et al. 2003). Vipers with a smaller mass to length ratio are predicted to be hungrier and at a worse nutritional state.

Body size (PC1) and body shape (PC2) had no effect on the movement distances per night ($R^2 = 0.002$, $n = 426$, $F_{[2,423]} = 0.452$, $P = 0.637$ for the whole model; $t = -0.606$, $P = 0.545$ for body size; and $t = 0.732$, $P = 0.465$ for body shape). However, body size and shape were positively correlated with the number of burrows scanned and the number of lizards captured (burrows scanned — $R^2 = 0.0581$, $n = 426$, $F_{[2,423]} = 14.105$, $P < 0.0001$ for the whole model; $t = 3.755$, $P = 0.0002$ for body size; and $t = 3.761$, $P = 0.0002$ for body shape; lizards captured — $R^2 = 0.258$, $n = 426$, $F_{[2,423]} = 74.802$, $P < 0.0001$ for the whole model; $t = 9.438$, $P < 0.0001$ for body size; and $t = 7.792$, $P < 0.0001$ for body shape). Movement distances were positively correlated with both the number of burrows scanned ($R^2 = 0.222$, $n = 426$, $F_{[1,424]} = 121.933$, $P < 0.0001$) and the number of lizards captured ($R^2 = 0.138$, $n = 426$, $F_{[1,424]} = 69.030$, $P <$

Fig. 4. Relationship between surface temperature and activity of sand vipers (*Cerastes vipera*). Data points represent a range of 3 °C (the temperature specified ±1 °C). Numbers above data points represent sample size.
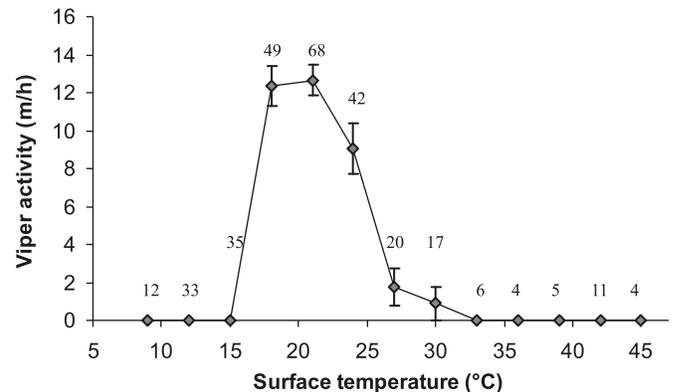
0.0001). Finally, the number of lizards captured was also positively correlated with the number of burrows scanned ($R^2 = 0.457$, $n = 426$, $F_{[1,424]} = 358.097$, $P < 0.0001$).

Second dat aset: dffect of sex and study site on body dimensions and foraging behavior

Body size (PC1) differed among study sites ($F_{[2,421]} = 6.412$, $P = 0.0018$). Specifically, sand vipers from the Mashabim population were larger than vipers from the two other populations (post hoc Tukey–Kramer's test). There was no effect of sex on body size ($F_{[1,421]} = 0.146$, $P = 0.702$), although females tended to be larger, on average. Body shape (PC2) also differed among study sites ($F_{[2,421]} = 6.084$, $P = 0.0025$). Specifically, vipers from the Mashabim population had a higher mass to length ratio than that of the other two populations (post hoc Tukey–Kramer's test). There was a marginal effect of sex on body shape ($F_{[1,421]} = 3.160$, $P = 0.0762$), with females tending to have a higher mass to length ratio than males. The effect of the interaction term sex × study site on both body size and shape was nonsignificant. Both sex and study site had no effect on the number of burrows scanned (sex: $F_{[1,427]} = 0.08$, $P = 0.779$; study site: $F_{[2,426]} = 1.85$, $P = 0.158$) or number of lizards captured (sex: $F_{[1,427]} = 0.19$, $P = 0.661$; study site:

$F_{[2,426]} = 0.7$, $P = 0.497$). Study site had no effect on movement distances, but the effect of sex on movement distances was marginally significant, i.e., females tended to move longer distances (sex: $F_{[1,427]} = 3.34$, $P = 0.0683$; study site: $F_{[2,426]} = 0.59$, $P = 0.557$). A single deviant outlier of extremely long movement distance in the data for females was responsible for this trend; the same analysis without this point showed no effect of sex on movement distances ($F_{[1,426]} = 2.28$, $P = 0.131$).

Discussion

Activity and foraging behavior of snakes, like most ectotherms, are dependent on ambient temperature (Lillywhite 1987; Peterson et al. 1993). Similarly to previous studies (e.g., Lillywhite 1987; Huey and Kingsolver 1989), we found that activity–temperature relationship can be described using a bell-shaped curve bounded by minimal and maximal temperatures. However, in contrast to most studies, temperature did not affect the level of activity within this range limit. It is probable that this bell-shaped relationship between temperature and activity is common in desert environments, because vipers should avoid either too warm or too cold temperatures, which can easily kill even a desert-adapted reptile. Schnurrenberger (1959) observed that desert vipers restrict their activity to hours of maximal humidity. Our study, which showed a positive relationship between activity and relative humidity, supported Schnurrenberger's (1959) observation and provided a rigorous quantitative analysis. The behavioral restriction of activity to hours of maximal humidity seems reasonable in light of the high temperatures and the fact that prey is almost the single source of water for the snakes. Sand vipers were sometimes seen to "lap" water from bushes; these water drops from bushes are in reasonable approach distances for the vipers (vipers were never seen climbing a bush to reach water drops; A. Subach, personal observations). The same relation between activity and humidity was found for the Malayan pit viper, *Calloselasma rhodostoma* (Kuhl, 1824) (Daltry et al. 1998), which is similarly more affected by relative humidity than by temperature; this is in contrast to the majority of the existing literature that regards temperature to be the dominant factor influencing snake activity. In the study of Daltry et al. (1998) on Malayan pit vipers, temperature was usually high and posed no restriction on viper activity, whereas humidity fluctuated, with low activity being positively correlated with low humidity levels, probably to prevent dehydration (Daltry et al. 1998).

The multiple regression analysis showed that two temperature factors were especially important for viper activity: Surface temperature and temperature at 15 cm below the surface. Because *A. scutellatus* lizards hide at night in burrows of about 15 cm deep (A. Subach, personal observations), it is logical that activity patterns of the sand vipers would be positively related to the temperatures of the microhabitat of its common prey (Heatwole and Davison 1976). In other words, warmer temperatures inside the burrows may possibly make it easier for the viper to catch the lizards. This result suggests that the viper quickly equilibrate to the environmental temperature, which is possible due to the viper's relative small size. Viper activity was also positively correlated with the level of cloudiness, which, in turn, may be negatively correlated with the illumination level (night measurements often include both moonlight and cloudiness level (e.g., Taquet et al. 2006)). Many desert predator and prey species behave similarly to sand vipers and decrease activity when exposed to moonlight (e.g., Kotler et al. 1994; Skutelsky 1996; Seligmann et al. 2007; but see no response in Daltry et al. 1998).

One of the important quantitative patterns emerging from this research is the tight positive correlation between movement distance, number of burrows scanned, and number of lizards captured. There was no correlation between the distance moved and the viper's size. Although the absence of a correlation does not necessarily indicate actual differences, we interpret this to mean that larger vipers traveled similar distances to smaller ones, in contrast to our initial prediction that was based on previous field observations in mammals (Swallow et al. 1999). However, larger vipers captured more lizards and also scanned more burrows. Therefore, there is a direct link between viper size and shape (as reflected in PC1 and PC2) and capture success irrespective of the distance traveled. A possible explanation lies in the range of possible prey items that snakes can subdue and handle. Larger snakes can obviously handle larger prey items, but their ability to handle small items is often not affected (this phenomenon is often referred to as "ontogenetic telescope"; Arnold 1993). Therefore, their range of possible prey items also increases. It is possible that smaller vipers simply do not attack all lizards encountered and do not enter all burrows found. Vipers with a higher mass to length ratio scanned fewer burrows and caught fewer lizards. Heavy-bodied vipers may be more cumbersome or satiated and are therefore less successful in capturing prey. It is also plausible that individuals with lower energy reserves (i.e., lower mass to length ratio) are at more risk of starvation and are therefore more prone to attack the prey (e.g., Skutelsky 1996). The factors affecting the distance moved by the viper are still not fully known. All the variables studied, i.e., body mass and length, surface temperature, temperatures at different depths, humidity, and cloudiness, do not explain much of the variance in the movement distances.

The diurnal lizard *A. scutellatus* is the main prey of the sand viper, which actively seeks its prey during the night. Each lizard constructs one or more burrows, but only populates one burrow. It is tempting to speculate that the construction of a number of burrows is an adaptation for coping with the risk of predation. In other words, if the capture success of the viper is dependent on the number of burrows scanned, it might be profitable for the lizards to construct empty burrows to reduce the viper efficiency of searching. The optimal number of burrows that should be constructed by lizards and the intensity of searching activity of the vipers, which can be predicted using game theory (Riechert and Hammerstein 1983), are dependent on the costs and benefits of constructing burrows for the lizards and the costs and benefits of searching for the vipers.

The finding that sand vipers of the Mashabim (the most northern site) population were larger and had a higher mass to length ratio than those of the two southern sites may perhaps be explained in terms of some intrapopulation variation within this species, although the distances between the three

sites are not very large (Shunra is about 10 km southwest of Mashabim and Agur is about 20 km southwest of Shunra). All sites experience a desert climate, but Agur has lower mean annual rainfall and less dense plant cover than Shunra and Mashabim (Abramsky et al. 1985), which could contribute to the smaller size of the sand vipers of the Agur population. The explanation of intrapopulation variation within the species is in agreement with the findings of a previous study focusing on differences in growth rates and body size among different populations of a single species of snake (e.g., Bronikowski 2000).

We could not detect sexual-size dimorphism in the studied species, although females were, on average, larger than males. This trend of larger females is consistent with previous observations on *C. vipera* (Mallow et al. 2003). However, there was a stronger, marginally significant, trend of shape difference between males and females, with the females tending to have a higher mass to length ratio. The same pattern has been seen in other species of snakes, and it is suggested that this heavy-bodied shape may provide more space within the female body for reproductive materials, such as eggs (Shine 1993). This difference in shape may affect activity and movement distances (Shine 1993), but our data do not clearly support this premise.

In conclusion, in this study we provide a quantitative analysis of some extrinsic and intrinsic factors affecting activity and capture success of the sand viper. We show that both temperature and humidity should be taken into consideration, and that capture success of lizards is tightly correlated with both the movement distance of the snake while foraging and the number of lizard burrows that the viper scans. Finally, we show that there are intraspecific differences in size among populations of the same species.

Acknowledgements

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