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AMBUSH SITE SELECTION OF A DESERT SNAKE (*ECHIS COLORATUS*) AT AN OASIS

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Abstract: The selection of an appropriate ambush site by a sit-and-wait predator is necessary for maintaining an adequate energy intake for survival and for future reproduction, especially when events are of long duration. We tested whether the snake *Echis coloratus* (Viperidae), a sit-and-wait predator, selects specific ambush sites in an oasis setting. We characterized the sites used by 22 individuals near a desert spring and compared them to randomly selected available sites. Ambush sites were not random; they were usually located <5 m from water on raised objects. Females, but not males, occurred more frequently under cover than expected by random choice. Field observations did not enable us to determine the cues that lead the snakes to locate their ambush. Thus, we used semi-natural enclosures to test the hypothesis that *E. coloratus* uses prey chemical cues when selecting its ambush sites. Most ambushes were located in sites with cover, whether the odor of gerbils was present or not. Even when odors from additional prey species were presented, there was no preference for sites with odor over control sites. The results suggest that *E. coloratus* at the oasis set ambushes in microhabitats that provide cover, high probability for encounters with prey, and, possibly, a physiologically convenient humid environment. The cues used by *E. coloratus* for predicting future prey availability seem to be the structure of the microhabitat rather than prey odor.

Key words: Habitat use; Prey odor; Sit-and-wait predator; Viperidae

Similar to other predators, snakes can be classified along a gradient of foraging strategies between the two extreme modes of active foragers and ambush predators (sit-and-wait)

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(Perry, 1999). Such a classification for reptiles and amphibians is useful in pointing out the consequences of foraging modes and various correlates associated with them (Cooper, 1994; Huey and Pianka, 1981; Magnusson et al., 1985; Secor and Nagy, 1994; Toft, 1981). One of the fundamental characteristics of predators whose foraging mode nears the sit-and-wait extreme is that they spend long periods in ambush. Some snakes stay in the same ambush site for several days or even weeks (Greene and Santana, 1983; Reinert et al., 1984) and can, thus, serve as model organisms to investigate the implications of ambush site selection.

Predators use different strategies to improve their hunting success. An active forager invests energy in increasing the probability of an encounter with the prey by actively searching for it. When the active search includes the retreats of the prey (e.g., *Walterinnesia aegyptia*, Zinner, 1971), a snake may both increase the probability of an encounter with prey and the probability of prey death given an attack. The strategy of a sit-and-wait predator may also increase the probability of killing the prey, but in different ways. An ambushing snake may increase both the time in which the prey is vulnerable and the rate of encounter with prey by selecting an ambush site that is frequently visited by mobile prey animals. The snake may increase the probability of prey death given an encounter, too, if it selects a site that will enable striking the prey before the prey detects the snake. However, an ambushing site that improves the chances to hunt one prey species may not be beneficial in respect to other prey species. In addition, ambush selection may be constrained by other factors, such as physiological needs. Consequently, the choice of an optimal ambush site may become a severely complicated task.

For snakes that remain in the same ambush site for long periods, the choice of ambush site becomes even more crucial because it may bear a heavy missed opportunities cost and an increase in the risk of starvation if the site is not properly chosen. The selection of an appropriate ambush site by a sit-and-wait snake is thus necessary for maintaining an adequate energy intake for survival and for future reproduction. We tested if the Palestine saw-scaled viper, *Echis coloratus* (Viperidae) selects specific ambush sites in an oasis setting and, if so, what characterize the chosen sites.

Echis coloratus is the most common venomous snake in rocky desert habitats in the Negev and the Judean Deserts (Mendelssohn, 1965). We have indications that these snakes remain in the same ambush site for days; six snakes remained at the same site for 2 d, and two others for 3 d. Two snakes remained in ambush at their respective location for at least 8 d (H. Tsairi and A. Bouskila, unpublished data). Therefore, it appears that, along the gradient of foraging modes (Perry, 1999), *E. coloratus* is closer to the sit-and-wait mode, typical of extreme ambush predators, than to active foraging and, thus, is a convenient model for this study.

Prey animals do not move randomly in a complex habitat, such as an oasis (Barnum et al., 1992). Consequently, ambushing snakes are expected to select locations with a high probability for encountering prey. For example, *Crotalus cerastes* was occasionally seen ambushing on hot days in burrows, facing the entrance where lizards often seek shade (A. Bouskila, unpublished data). In another system, *C. horridus* was found ambushing mostly adjacent to fallen logs, which are often used as runways of small mammals (Reinert et al., 1984). Thus, we hypothesized that *E. coloratus* would not locate its ambush sites randomly, but would select sites that attract potential prey. In an oasis setting, in particular, water is the main attractor. We expected snakes to ambush mostly close to water and that the proximity to water would increase at extremely high temperatures. In the desert, shade also serves as an attractor for prey. However, in an oasis, where shade is abundant, cover may have an important role for prey only on hot days, when the temperature under tree canopies is not low enough. Thus, we expected the proportion of snakes ambushing in the open not to be lower than the occurrence of this microhabitat, with a possible exception on hot days. In the first part of the study, we characterized the ambush sites used by *E. coloratus* in the oasis around the Ein-Gedi Spring and compared them to all available sites. We found that this snake does not choose sites randomly.

Some previous studies of ambush site selection in snakes indicate that rattlesnakes use prey olfactory cues to select their ambush sites (Duvall and Chiszar, 1990; Duvall et al., 1990; Reinert et al., 1984; Theodoratus and Chiszar, 2000). This strategy may allow snakes to locate richer patches and, thus, may be profitable for *E. coloratus*, too. In the second part of the study, we tested the hypothesis that *E. coloratus* uses prey chemical cues when selecting its ambush sites. Because the study of the impact of olfactory cues is difficult to conduct in a natural habitat without eliminating natural prey, we performed these experiments in semi-natural enclosures. We placed snakes in enclosures with four stations with or without cover and with odor of typical prey items (rodent, gecko, bird, or frog) and recorded the ambush sites. The snakes ambushed mostly in sites with cover, whether prey odor was present or not.

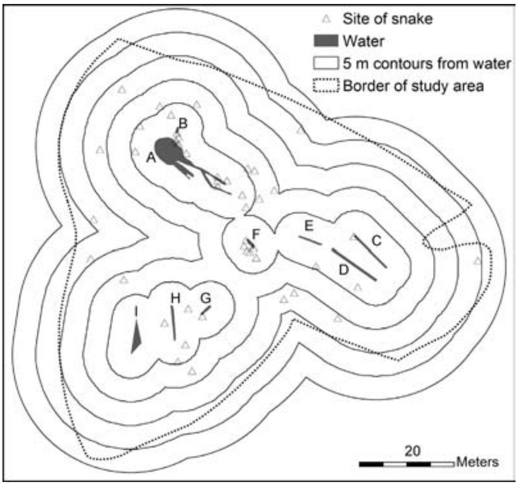

FIG. 1.—Ambush locations of *Echis coloratus* relative to water in the oasis around Ein Gedi Spring. Letters indicate water sources: the main spring (A), the secondary spring (B), and the seven channels that irrigate the slopes (C)–(I).

METHODS

Ambush Sites of E. coloratus *in Ein Gedi Oasis*

Study site.—Our study area was around Ein Gedi Spring, which is part of the Ein Gedi Nature Reserve, Judean Desert, Israel (31° 28 N, 35° 23 E, 100–350 m below sea level). The temperatures are relatively high both in the hottest month of July (average daily maximum and minimum are 39 C and 28 C, respectively) and in the coldest month of January (average daily maximum and minimum are 20 C and 11 C, respectively). The mean annual rainfall is 70 mm (Jaffe, 1988). The 4000-m^2 study site is mostly covered by vegetation and is fairly well isolated from other patches of dense vegetation in the reserve. A large portion of the area is covered by boulders 0.2–5 m in diameter. Two sources of water are found within the site. The main spring originates in a 3-m diameter pool (Fig. 1A), and a second, less defined source of water permeates through the gravel (Fig. 1B). Water from the main spring is captured in a pipe, and some of it is occasionally used to water the slopes by seven channels that are controlled by taps (Fig. 1C–I).

Procedure.—Between February 1996–September 1997, we surveyed the study site and searched for Palestine saw-scaled vipers once or twice a week (depending on the season), resulting in a total of 186 censuses (64 in mornings, 21 in mid-day, 101 during evenings). In addition to the scheduled searches, 55 additional observations were made during random visits to the study site. These visits provided additional information on the natural history of the snakes and their behavior, but this information was not included in the quantitative analysis. In each census, using flashlight and binoculars when needed, we searched in the open, under rocks, and under and on vegetation. Search effort represented the occurrence of microhabitats in the field, and the order in which various parts of the oasis were scanned was randomized.

We tried to minimize disturbance to encountered snakes in order to maintain as much as possible their normal activity. For permanent identification of individual snakes, we photographed them and used their unique individual patterns. In addition, for short-term, quick identification, we wrote with a water-resistant marker a different number on each snake . When we found an *E. coloratus*, we first looked for the marked number or compared its pattern to photographs of previously marked individuals. If the snake was not previously marked, we placed it in a bucket, determined its sex, and photographed it with a scale. The photographs were later used not only for identification but also to measure the total body length of the snake. Snout–vent length (SVL) of snakes was estimated from total length based on measurements made previously of 12 males and 13 females (A. Bouskila, unpublished data). Each captured snake was released at its original location, usually within 15 min of its capture. Snakes with a clear mark were identified with binoculars to minimize disturbance. The following details were recorded from each encountered snake: date, time, identification, description of the posture (whether in ambush or not), description of the microhabitat (substrate: soft soil, soil covered with organic material, or elevated on an object; cover type: vegetation, bolder, or in the open), and environmental conditions (air temperature and illumination as light or dark).

We defined a snake as ambushing when it was coiled with the head raised and leaning either on a body coil, a branch, or another object. Although we could not verify that all the snakes in this posture were alert and ready to strike approaching prey at all times, we decided to follow other authors who used this term under similar circumstances (e.g., Reinert et al., 1984). The location of the snake was marked on a map of the oasis (scale 1:200), and the distance to water was later determined from the map. Water had a visible effect on the microhabitat (wet soil, vegetation, etc.) up to a distance of 5 m. Therefore, we defined proximity to water as any distance <5 m. Due to the small number of observations that were far from water (Fig. 1), we later lumped all distances that were >5 m to water and labeled them as "far from water."

To characterize available sites in the oasis, we marked 100 points, randomly selected by computer, on the map. We then located the random points in the field and recorded the same microhabitat parameters that were recorded from the ambush sites of the snakes.

Statistical analysis.—To compare the characteristics of ambush sites with their availability in the oasis (substrate type, cover type, and distance to water), we compared the distribution of each characteristic at the ambush sites with its distribution at the random points. The analysis was performed with a log-likelihood test, according to the procedures recommended by Manly et al. (1993) specifically for cases in which habitat availability is estimated with random points and habitat use is measured from individually marked animals (Manly et al., 1993:61).

To test what factors affect the characteristics of ambush sites, we used a logistic model; the Generalized Estimating Equation (GEE; Orelien et al., 2002) was calculated with dedicated software, PCGEE (Rational Systems, Inc., v. 1.6, 1991). This analysis is suitable for the analysis of our data because it can handle repeated measures from individuals. The tests of all factors were two-tailed, except those involving temperature, for which we had directional predictions (at high temperatures we expected the snakes to be closer to water, more often under cover, and elevated above ground). After we had identified the factors that significantly affect the characteristics of ambush sites, we preformed another log-likelihood test to compare the distribution of ambush sites at every specific condition with the distribution of the random points. For example, after finding that sex affects the use of cover, we tested whether ambush sites of females or males differ from random.

Preference Experiments in Semi-natural Enclosures

General setting.—We ran the experiments between July–October in 1998 and 1999, in two outdoor circular enclosures (7-m diameter, surrounded by polypropylene fences, 0.7 m above ground, and 0.1 m below it). The enclosures were constructed on the grounds of the Blaustein Desert Research Institute (Midreshet Ben-Gurion, Negev Desert, Israel) where *E. coloratus* occurs naturally. Each enclosure was covered with fishing net to prevent the entrance of predators, and the bottom of the enclosure was left with its naturally occurring loess soil. We divided each enclosure into quarters by marking lines on the enclosure edge; a tray was placed in each quarter. The four trays were at least 2.9 m apart to prevent synergy of multiple odors.

Experiment 1.—Two of the trays contained soil from cages housing gerbils (*Gerbillus dasyurus*), and the other two had natural, unscented soil. In two quarters, we added a pile of rocks near the tray to provide cover for the snake. On every experimental night, we changed the location of the rock piles and scented soil trays while keeping a 2×2 design. Experiments were conducted only on nights with air temperature above 18 C because we noted, during other experiments with this species, that snakes did not attempt to capture prey at lower temperatures (A. Bouskila and H. Tsairi, unpublished data).

Eleven adult Palestine saw-scaled vipers (five males and six females) participated in the experiment; all had been in captivity for at least 1 wk. The snakes for this experiment, as well as those for experiment 2, were collected from various locations in the Negev and Judean Deserts. Only snakes that were large enough to consume an adult gerbil were chosen for this experiment. Between experiments, snakes were kept in individual terraria. Each snake participated on four experimental nights; prior to these nights, it was not fed for 2 wk. To find whether moonlight affected the preference of the snakes, two of the experiments were conducted on new moon nights and two on full moon nights. On experimental nights, we placed a snake in the middle of each enclosure 1 h before sunset. After about 1 h, snakes began behaving naturally and started investigating the trays with tongue flicks. With the aid of a nightscope (Noga Lite Ltd., Katzrin, Israel), we continuously recorded the location of the snake during the first hour following the initiation of this investigative behavior, and then visited the enclosures and recorded the ambush site once every hour throughout the night. In the morning, we returned the snake to its cage, counted the track lines in each quarter, removed the trays and rock piles, and mixed the loess soil in the whole enclosure. We thus ensured that neither prey odors nor the smell of the snake concentrated anywhere in the enclosure.

Experiment 2.—After we found in experiment 1 that snakes reacted only to cover and not to the odor of the gerbils and that this reaction was not modified by moonlight, we repeated the experiment with odors from other prey species known to be captured by *E. coloratus* (Mendelssohn, 1965; H. Tsairi and A. Bouskila, personal observation). We used the same enclosures and protocol from experiment 1 with a few modifications: (1) we placed rock piles in each quarter of the enclosure; (2) we ran the experiment on moonless nights only (each snake on two experimental nights); (3) we monitored the behavior and ambush sites of snakes only during three visits, 1 h and 5 h after sunset and at sunrise. In this experiment, we placed in each of three trays the odors of frogs (a dish filled with water in which *Rana levantina* were maintained), geckos (a stone with fresh feces from cages in which we kept *Ptyodactilus guttatus*), or birds (droppings and feathers that we collected from migratory passerine birds at a bird banding station). One quarter of each enclosure served as control and contained no scented object but did have a tray, a clean stone, and a dish filled with clean water. Of the 10 snakes that participated in this experiment, 6 were also tested in experiment 1.

Statistical analysis.—For the analysis of the number of ambush sites in each treatment, we used the Fisher Exact Test (Zar, 1984). In experiment 1, we performed a separate analysis for full moon nights and new moon nights.

For the number of tracks in each quarter and the time spent in each quarter during the continuous observation (both reflect the interest of the snake in that quarter during the stage of site selection), we used Repeated Measure ANOVA (von Ende, 1993). In experiment 1, the repeated factors were moonlight and treatment (the four combinations of cover × gerbil odor). Post-hoc contrasts between the different treatment combinations separated the effects of cover presence and gerbil odor. In the simplified experiment 2, the repeated factor was the four treatments (the different odors presented).

Results

Ambush Sites of E. coloratus *in Ein Gedi Oasis*

Capture history.—During the regular censuses, we had 136 encounters with 36 marked *E. coloratus* (15 females, 17 males, and 4 individuals whose sex was not determined). In the following sections, we only deal with 69 of these observations that qualified as valid observations of ambushing snakes (22 different individuals, 9 females, and 13 males). In the remaining 67 observations, snakes were detected while moving, and we could not determine confidently whether they were moving actively or leaving an ambush in response to our disturbance. Snakes were detected through most of the year, but only rarely in winter. Most observations occurred during morning and evening censuses; however, in the shaded parts of the oasis, snakes also were found ambushing during daytime.

Association between the different variables that were measured.—We found a strong association between hour of day to season, temperature, SVL, and illumination (Table 1). Assuming that temperature is a more crucial determinant of activity for ectotherms than hour and season, we included in the Generalized Estimating Equation model only SVL, sex, illumination, and temperature as independent variables. We did not find an association between distance of ambushing snakes from water and the cover or substrate types that were used by the snakes (Table 1). However, the substrate type on which a snake ambushed was not independent from its associated cover type (Table 1). Of all ambush sites located in the open, 71% were found on an elevated object, whereas only 36% of the ambushes located under cover were above ground level. Yet, when repeating the same analysis for the random sites, no association was found between substrate and cover types (*Cramer coefficient* = 0.01, $P = 0.87$).

Distance of ambushing snakes from water.—Ambushing snakes were found in locations close to water more often than expected from a random distribution (log-likelihood test, $X_L{}^2 = 24.46$, $P < 10^{-4}$; Fig. 1). While 49.3% of the ambush sites were located 0–5 m from water, only 13.11% of the random sites were in the vicinity of water. We used a cutoff distance of 5 m for our analysis to determine whether a snake was considered near or far from water. Yet, larger cut off distances generated similar results (log-likelihood test, $X_L{}^2 = 30.92$, $P < 10^{-4}$ and $X_L{}^2 = 29.36$, $P < 10^{-4}$, for cut off distances of 10 and 15 m, respectively).

The snake proximity to water was significantly affected by air temperature (Table 2). Of all ambush sites found when temperatures were high (30–39 C), 62.3% were located near water, whereas, during lower temperatures (15–29 C), only 40.5% were close to water. Yet, even when only the sites found during the lower temperatures were considered, more ambush sites were located near water than expected from the random points (log-likelihood test, $X_L{}^2 = 9.00$, $P < 0.01$).

Cover at ambush sites.—We defined three categories for the cover at an ambush site: under cover (boulders, logs, etc.), on or in vegetation (trees, shrubs), and in the open. The ambush sites were located in different proportions compared to the random distribution of available sites (log-likelihood test, $X_L{}^2 = 25.53$, $P < 10^{-4}$; Fig. 2A). Covers were used more frequently than expected, while the number of observations of snakes on trees and in bushes was smaller than expected. The open microhabitat was used in a proportion similar to its availability. Of all factors tested, only sex had a significant effect on the ambush location (Table 2). Females used ambush sites under cover more frequently than expected (log-likelihood test, $X_L{}^2 = 7.87$, $P < 0.05$), but ambush sites of males were not different from random (log-likelihood test, $X_L{}^2 = 0.03$, $P > 0.98$).

Substrate of ambushing sites.—We defined three categories for the description of the substrate: on an elevated object (rocks, logs, branches, etc.); on soft, exposed soil; and on

TABLE 1.—The association between different dependent and independent categorical variables in the field study. Values without parentheses represent the Cramer Coefficient, and values in parentheses represent the significance levels for χ^2 distribution.

Variables	Season	Hour	SVL	Sex	Illumination	Proximity to water†	Cover†
Season	—						
Hour	0.40 (0.003)	—					
SVL	0.06 (0.92)	0.39 (0.02)	—				
Sex	0.15 (0.56)	0.19 (0.37)	0.07 (0.61)	—			
Illumination	0.15 (0.55)	0.39 (0.02)	0.007 (0.96)	0.11 (0.43)	—		
Temperature	0.21 (0.30)	0.72 (0.001)	0.18 (0.43)	0.23 (0.09)	0.22 (0.11)		
Proximity to water†					—	—	
Cover†						0.01 (0.92)	—
Substrate†						0.07 (0.55)	0.35 (0.004)

† Dependent variables.

TABLE 2.—Results of the Generalized Estimating Equation (GEE) testing the effect of SVL, illumination, and temperature on the characteristics of ambush sites in the field study. The statistics Z and the related significant levels are shown.

	Proximity to water		Cover		Substrate	
Variables	Z	P	Z	P	Z	P
Sex	−0.20	0.84	−2.00	0.05	1.23	0.22
SVL	−1.44	0.15	−0.55	0.58	0.47	0.64
Illumination	0.02	0.98	0.51	0.61	−2.21	0.03
Temperature	−1.64	0.05	0.17	0.43	−1.56	0.06

soil covered with fallen leaves, twigs etc. Snakes preferred ambush sites on elevated objects (log-likelihood test, $X_L^2 = 15.16$, $P < 10^{-3}$; Fig. 2B). The ambush location was significantly affected by illumination. Of all ambush sites found at daylight, 63.9% were elevated above ground, whereas at dark only 37.5% were located on an elevated object. Snakes at daylight indeed ambush on elevated objects more frequently than expected (log-likelihood test, $X_L^2 = 9.10$, $P < 0.01$), but ambush sites of snakes at dark were not different from random (log-likelihood test, $X_L^2 = 0.42$, $P = 0.52$).

Preference Experiments in Semi-natural Enclosures

Experiment 1.—The snakes usually entered an ambush posture no later than 3 h after sunset and stayed at the same location until morning. Observations of the behavior of the snakes during the first hour after sunset indicated that they were definitely aware of the odor presented in the manipulation. Only when the snakes encountered trays with scented soil did they advance in a rectilinear movement. When approaching unscented trays or other parts of the enclosure, the snakes used serpentine or sidewinding locomotion. The linear movement was accompanied by pronounced tongue flicking, but tongue flicks were difficult to quantify from the distance and illumination conditions during these observations.

The number of ambush sites in the four treatments was different from random both during the new and full moon (Fisher Exact Test, $FI(X) = 12.34$, df = 3, $P = 0.0042$ and $FI(X) = 16.53$, df = 3, $P = 0.00023$, respectively). The presence of cover had a significant effect in both moon phases (Fisher Exact Test, $FI(X) = 11.81$, df = 1, $P = 0.0015$ and $FI(X) = 18.17$, df = 1, $P = 0.0001$, for new and full moon, respectively). However, the presence of odor did not have a significant effect in both moon phases (Fisher Exact Test, $FI(X) = 0.046$, df = 1, $P = 1$ and $FI(X) = 0.146$, df = 1, $P = 1$, for new and full moon, respectively). The four first P-values were still significant at the table-wide 0.05 level after we applied the sequential Bonferroni correction (Rice, 1989).

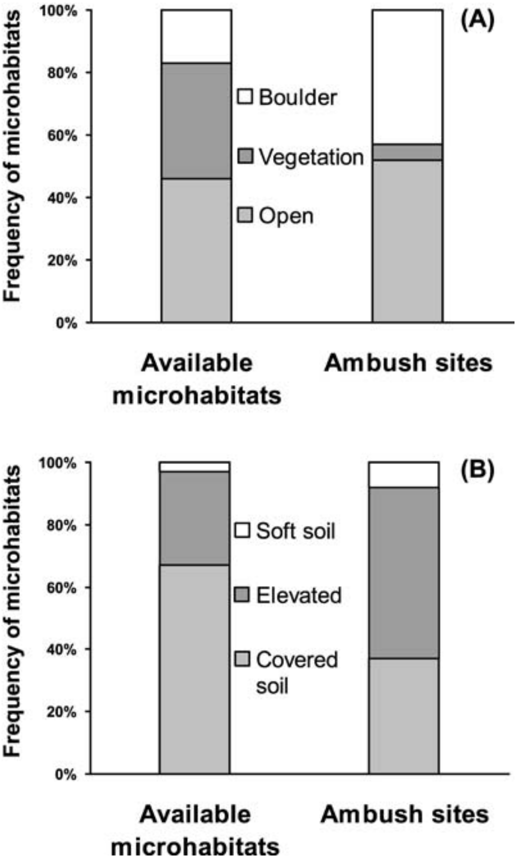

FIG. 2.—Comparison between the available microhabitats: cover (A) and substrate (B) types and the distribution of ambush sites of the snakes in the field study.

The analysis of tracks indicated that snakes sampled the four quarters of the enclosures similarly (Repeated Measures ANOVA, $F = 0.27$, $P = 0.85$), and moonlight did not have a significant effect on the tracks either (Repeated Measures ANOVA, $F = 0.20$, $P =$

0.67). The tracks were equally distributed among treatments even when the variation due to time spent in each quarter was removed with an ANCOVA ($F = 0.00$, $P = 0.97$). Nevertheless, the time spent in each quarter depended on the treatment (Repeated Measures ANOVA, $F = 8.33$, $P < 0.0005$). The snakes preferred the quarters with cover, whether odor of gerbils was present or not (Contrast test, $F = 10.29$, $P = 0.0032$ and $F = 14.66$, $P = 0.0006$, respectively). The snakes did not show any preference for ambush sites located in quarters with odor of rodent, whether cover was present or not ($F = 0.21$, $P = 0.65$ and $F = 0.026$, $P = 0.87$, respectively). Moonlight did not interact with the treatment effect (Repeated Measures ANOVA, $F = 0.41$, $P = 0.74$). Note that the separate effect of moonlight does not have any relevant meaning in this analysis because it averages over all treatments.

Experiment 2.—In this experiment, we only tested the effect of odors from three prey species and an odorless control. Here, too, the distribution of ambush sites among the different odors did not differ from random (Fisher Exact Test, $FI(X) = 0.643$, df = 3, $P = 1$). Similarly, the number of tracks in each quarter did not indicate a preference for any of the odors (Repeated Measures ANOVA, $F = 0.82$, $P = 0.49$).

Discussion

The field study supported our main hypothesis. Ambush sites of *E. coloratus* at the Ein Gedi oasis were not randomly distributed. They occurred <5 m from water and were raised on an object above ground level. In addition, ambush sites of females were common under cover. Shine and Sun (2002) listed some of the characteristics that a successful ambush site must possess: frequently visited by prey, prevents detection of the snake by its prey, must facilitate prey detection and capture, and provides shelter from the predators of the snake and from environmental extremes. Note, however, that ambush sites may possess characteristics that are subject to trade-offs with other needs. For example, a site that is frequently visited by prey may expose the snake to its own predators or to harsh environmental conditions. A snake needs to select those sites in which the maximal benefits are provided while incurring the minimal costs. We will examine our results in light of these considerations.

The diet of *E. coloratus* has not been thoroughly studied, but the scant information available may be useful in understanding the ambushing preference of these snakes. Gasperetti (1988) lists the diet of *E. coloratus* from Arabia as gerbils and *Acomys* spp. Mendelssohn (1965) found that snakes from Ein Gedi regurgitated mainly frogs (*R. levantina*) and toads (*Bufo viridis*); adult specimens in captivity preferred birds and lizards to mice. Our own observations of the diet include birds (three observations of small migratory passerines captured in the Ein Gedi Reserve, and two others in the Negev Desert), geckos (*P. guttatus*, on two occasions, once in the reserve and once in the Negev Desert), and a toad (*B. viridis*, 15 km north of the study site). The rodents of the appropriate size in Ein Gedi are mostly nocturnal (except *Acomys russatus*; Kronfeld et al., 1994), while the birds are active during daytime and the geckos and frogs can be active both during the day and the night.

Distance to Water

The proximity to water could either originate from physiological needs of the snakes or to the attraction of the prey to water. Daltry et al. (1998) found, in a multivariate analysis, that humidity determined the activity of free living Malayan pitvipers. *Echis coloratus*, in most of its range, inhabits extremely dry habitats, with no source of water and with very low relative humidity (Bouskila and Amitai, 2001). Moreover, experiments demonstrated that this species is resistant to dehydration more than other snakes that inhabit the deserts in Israel (Mendelssohn, 1963). However, it is impossible, from our study, to rule out the option that, when snakes have the opportunity, they prefer more humid microclimate.

The tendency to ambush nearer to water in hot times may be explained equally well by the need to balance water or by the higher probability of visits of prey animals near the water at those temperatures; both these explanations may be operating at the same time. Frogs and birds, which are included in the diet of the adult snakes, congregate near water in this dry, arid environment. Frogs (*R. levantina*) are abundant in the vicinity of the spring and are restricted to humid microhabitats. Birds often visit water sources in the oasis to drink during daytime, especially during the hot hours (H. Tsairi, personal observation). Thus, microhabitats in the vicinity of water may attract potential prey and, therefore, increase the chances that a snake will encounter mobile prey.

Cover and Substrate Preferences

We hypothesized that cover would not serve as an important attractor in an oasis setting. However, females were often found ambushing under cover. Snakes may use cover as an important means to reduce risk from their own predators, but we do not know how important this possibility is for *E. coloratus*. No evidence for predation on *E. coloratus* has been collected at the oasis, nor in the whole reserve, by the Ein Gedi Reserve staff for many years. Much of the oasis is covered by tree canopy or by vegetation, and predation from raptors or owls is not likely, particularly due to the sedentary nature of the snakes. Yet, the preference for cover may originate from the general habits of the snakes outside the small oasis. Data collected from six *E. coloratus* that were fitted with radio-transmitters indicated that snakes found in the oasis divided their time between the oasis and the arid environment around it (Bouskila, 2001). The fact that *E. coloratus* from different geographical regions in Israel match (at least to the human eye) extremely well the color of the rocks in their environment (Bouskila and Amitai, 2001) may indicate that they were, or still are, subject to selection by visual predators.

The difference between the sexes in respect to cover is not easy to explain if we assume that the snakes seek cover to minimize predation, because the females used covers more than expected at all times, not only during the reproductive period. Shine et al. (2000) explained the differences in defensive behavior of male and female garter snakes by differences in their locomotory capacity, and this option needs further testing in our system. An alternative explanation, that cover is aimed at concealing snakes from their prey or that ambushing under cover is targeting prey that tend to visit these locations, implies that males and females differ in their diet, their foraging behavior, or the trade-offs that they have to consider. Differences between the diets of males and females are known for the rear fanged *Telescopus dhara* from the Negev Desert (Zinner, 1985); the possibility that the diet of the male and female *E. coloratus* differs needs to be considered, too.

Although cover and substrate types were independently available, ambushing snakes under cover were more frequently found on ground level. Snakes in the open ambushed more often from above ground level. This association between cover and substrate usage may suggest different ambush strategies used by snakes for different prey items. Rodents and geckos often move from one shelter to another (boulders, tree trunks, and fallen logs) and frequently use the shelters as cover (Barnum et al., 1992; Douglass and Reinert, 1982). These animals are highly mobile, and, therefore, a snake that waits for the prey under cover may increase its capture success. Indeed, on one occasion, a snake that ambushed under cover successfully caught, in midair, a gecko that jumped between adjacent rocks (A. Bouskila, personal observation). An ambush site in the open, on a stone or log, above ground level may increase the chances of encountering and surprising birds. Birds tend to land on elevated positions before descending to the ground or water (H. Tsairi, unpublished data). The tendency to ambush from elevated objects during daylight strengthens this suggestion, since passerines are diurnal.

The low proportion of snakes found on vegetation, relative to the occurrence of random points in this habitat, is not likely to be an artifact of our ability to see the snakes or of our search methods. With the same methods, 69.7% of 33 encounters with *E. coloratus* in a different site ('Arava Valley) were recorded on vegetation (A. Bouskila, unpublished data). Relative to other desert habitats, trees and shrubs cover high proportions of both sites but, of the two sites, only in the 'Arava Valley do the snakes seem to use them frequently. The difference between the two sites in microhabitat use may reflect differences in the costs and benefits of ambushing in the open. For instance, ambushing in the open, as we found in the Ein Gedi oasis, may be risky under the more exposed habitat in the 'Arava Valley, where snakes are not protected from raptors and owls by tree canopy. Alternatively, because in the 'Arava Valley there is no specific attractor for birds on the ground (such as the water at the Ein Gedi oasis), ambushing on vegetation may be the best location to intercept birds, as in the case of the pitviper *Gloydius sheadoensis* (Shine and Sun, 2002).

Moonlight

In contrast to *C. cerastes* in the Mojave Desert (Bouskila, 2001), *E. coloratus* did not modify the selection of ambush sites due to moonlight. Data from the shift of *C. cerastes* to the bush habitat on moonlit nights and from the foraging of its nocturnal prey (kangaroo rats) are compatible with a habitat selection game that may be going on between the rodents and snakes (Bouskila, 1995, 2001). A game theoretic model that was designed to explain the microhabitat selection of the rodents and snakes in the Mojave Desert demonstrated that the shift of *C. cerastes* to shrubs can be explained even if the snakes are not subject to risk from their own predators. According to the model, the snakes may have been taking advantage of the expected shift of rodents to the shrubs, a shift that is caused by predation risk from visually oriented owls (Bouskila, 2001). Nevertheless, *E. coloratus* did not react to moonlight, neither in the oasis (maybe due to the canopy) nor in the experimental enclosures. Moreover, the activity of *E. coloratus* in a previous study in the 'Arava Valley, Eastern Negev Desert, was not affected by moonlight either (Bouskila, 1989). The game theoretic model suggested that the microhabitat game between rodents and snakes requires that rodents are exposed to high predation risk from snakes relative to that from owls (Bouskila, 2001); it is possible that this condition is not fulfilled in the current system. In addition, the model analyzed a simple system with only one prey, thus the model may not be applicable to the system described here, where the snakes prey on a variety of species that may each react differently to moonlight.

Cues for the Location of Ambush Sites

The distribution of ambush sites in the oasis does not indicate what cues the snakes use when choosing these sites. A snake may be either selecting certain habitat features or it could search for some olfactory cues, and, when these are found at a site, the snake chooses to ambush there. Our experiments in the semi-natural enclosures shed some light on the process of ambush site selection. In spite of the fact that the snakes reacted behaviorally to the scent of the gerbils offered in experiment 1, only the structure of the habitat (presence of cover) determined the final location of the ambush. Theodoratus and Chiszar (2000) also found no effect of prey odor on the location of the ambush sites (four rattlesnakes inhabited quadrants with cover and odors, and three were found in cover without odor). However, the rattlesnakes differed from *E. coloratus* in their reaction to scent, because the former spent more time in prey odor quadrants under cover (Theodoratus and Chiszar, 2000) while the latter only reacted to cover and not to gerbil odor. *Echis coloratus* did not react to odor from other prey species either. This result may indicate that the odor of prey is not used as a main cue by *E. coloratus* for the location of future prey visits.

Prairie rattlesnakes (*C. v. viridis*) in some studies did not respond to prey chemical cues to make decisions about prey presence (Duvall and Chiszar, 1990). In other cases, male snakes stayed in stations with prey chemical cues more than in control stations. Note, however, that the difference was only significant for the response of staying within 10 m, but not for shorter distances from the stimulus (Duvall et al., 1990). These results support our proposition that *E. coloratus* do not use prey odor as a major indicator for the precise location of future prey visits. Rather, *E. coloratus* selects its specific ambush site based mainly on physical characteristics of the site.

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