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BREANNA J. PUTMAN[1,3], MATTHEW A. BARBOUR[2], AND RULON W. CLARK

Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA
[1] Ecology Graduate Group, 1005 Wickson Hall, One Shields Avenue, University of California, Davis, CA 95616, USA

ABSTRACT: Foraging is a key aspect of a species' ecology and decisions made while foraging affect fitness in many ways. Although much research has focused on snake foraging, only a handful of detailed studies have been conducted on free-ranging individuals, all on *Crotalus horridus*. We used fixed videography to collect data on free-ranging Northern Pacific Rattlesnake (*Crotalus oreganus*) behavior to qualitatively test predictions regarding interspecific differences in rattlesnake foraging behavior. We analyzed foraging behaviors based on encounter rates with prey and strike rates on prey, distances moved between consecutive ambush sites, residency time at each site, and poststrike behaviors. Snakes encountered approximately 4 prey/d, with California Ground Squirrels (*Otospermophilus beecheyi*) being encountered at much higher rates than other prey types. *Crotalus oreganus* typically did not remain at hunting sites for long durations compared with other species, and generally exhibited short distance movements (<10 m) to new sites. Snakes initiated strikes during 21% of all prey encounters, and 49% of these strikes were successful. Snakes were more likely to hold on to nonsquirrel prey than squirrels after a strike. When snakes struck and released prey, the distance prey fled after a strike was positively related to the time snakes spent locating the envenomated prey. Our findings indicate that variation in rattlesnake foraging behavior both within and between species might be driven largely by differences in habitat features, including prey abundance.

Key words: Ambush; Movement; Optimal diet; Optimal foraging; Prey encounter; Strike-induced chemosensory searching; Videography

FOR DECADES, ecologists have been intrigued by how animals balance the costs and benefits of foraging (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Charnov 1976). For predators, unsuccessful hunting can lead to a large reduction in fitness. Thus, the choices made in selecting foraging sites, in spending time at each site, and in attacking and pursuing prey can inform us of the trade-offs predators face while hunting. Many foraging studies are conducted under artificial conditions, however, and foragers often do not make ecologically relevant decisions because of the way choices are presented (Sih and Christensen 2001; Stephens et al. 2004; Ydenberg 2010). Thus, we lack data on this fundamental aspect of the ecology of many organisms, making research on free-ranging predator behaviors and predator–prey interactions critical (Lima 2002).

In theory, foraging predators should attempt to maximize energy intake while minimizing energy loss (Hamilton 2010). Hence, prey biomass, vulnerability, and encounter rate are important factors for predators making diet choices. Larger bodied prey can provide predators with more energy than smaller prey, but could also present larger costs where handling time and risk to the predator are concerned (Wanzenbock 1995; Rutten et al. 2006; Mukherjee and Heithaus 2013). Thus, the largest consumable prey type in a habitat might not be the most preferred (Turesson et al. 2002; Fossette et al. 2012). Time spent hunting at a site depends on the prey encounter rate; predators should stay longer at sites with higher prey densities or biomass (Charnov 1976; Nonacs 1991). When transit time to a new site is high or when travel is costly, predators are more likely to stay longer at hunting sites (Nonacs 1991; Hamilton 2010). Prey preferences and hunting behaviors can vary across populations, likely affecting the life-history traits of predators.

Adaptations related to predation by snakes are central in the evolutionary diversification of this clade of squamates (Shine et al. 2004). All snakes are carnivores: many are ambush hunters that remain stationary at a single site to attack unsuspecting wandering prey (Cundall and Greene 2000). The sit-and-wait foraging mode of these species facilitates the use of fixed videography to record their predatory behaviors in the natural environment. Clark (2006a) introduced this idea when quantifying aspects of Timber Rattlesnake (*Crotalus horridus*) foraging, and suggested that similar methods could be applied to a variety of ambush-hunting snakes for intraspecific and interspecific comparisons. Although researchers have adopted this method to study rattlesnake behavior (Amarello 2012; M.D. Cardwell, personal communication), quantified detailed foraging behavior for free-ranging individuals and populations has only been available for one species (Clark 2006a,b; Reinert et al. 2011; but see Barbour and Clark 2012a,b; Clark et al. 2012). Reinert et al. (2011) reported that differences in local prey abundance over a small spatial scale produced varying frequencies of two alternative hunting body positions (log-oriented and non–log-oriented) in *C. horridus*. This indicates that rattlesnakes exhibit plasticity in foraging behavior based on characteristics of the local environment, particularly in prey availability. Interspecific comparisons are needed to shed light on factors influencing foraging behaviors, providing support for phylogenetic relationships.

Besides the studies on free-ranging *C. horridus,* most of our knowledge on rattlesnake foraging comes from laboratory studies, anecdotes, and morphological and dietary analyses (Cundall and Greene 2000). The diet of adult rattlesnakes mostly consists of small mammals, but rattlesnakes are opportunistic and will also eat lizards, birds, arthropods, and amphibians (Ernst and Ernst 2003). North American rattlesnakes usually hunt in the summer during both the day and night, depending on the population (Clark 2006a; Barbour and Clark 2012a). Like all predators, rattlesnakes must make

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[2] PRESENT ADDRESS: Department of Zoology, University of British Columbia, 2212 Main Mall, Vancouver, BC, Canada

[3] CORRESPONDENCE: e-mail, putman.bree@gmail.com

several decisions before successfully consuming prey. In general, they (1) find a suitable ambush site, (2) wait for prey to come within strike distance, (3) envenomate prey with a bite, (4) release the prey, (5) employ chemosensory trailing to locate the envenomated prey, and, (6) swallow the carcass (following Clark, in press). Rattlesnakes select ambush sites based on chemical cues, and often hunt while concealed within occluded microhabitats and along rodent trails (Duvall et al. 1990; Theodoratus and Chiszar 2000; Clark 2004). After a strike, rattlesnakes employ strike-induced chemosensory searching (SICS) to locate the envenomated prey by following a hierarchy of chemical cues (Duvall et al. 1980; Chiszar et al. 1992; Smith et al. 2005; Saviola et al. 2013).

We used fixed videography to study the foraging behavior of free-ranging Northern Pacific Rattlesnakes (*Crotalus oreganus*) in central coastal California. We examined whether intrinsic factors such as body size and sex influenced various measures of foraging behavior. We used the same basic methods as Clark (2006a,b) so that our results for *C. oreganus* could be compared with those for *C. horridus*. To evaluate interspecific differences in foraging behavior, we qualitatively tested three predictions of optimal foraging theory: (1) rattlesnakes should have narrower diet breadth in areas with higher prey densities (MacArthur and Pianka 1966), which we estimated from average prey encounters per day; (2) rattlesnakes should have shorter site residency times in areas with higher prey densities (Charnov 1976; Nonacs 1991); and, (3) the distances moved to new hunting sites (i.e., travel time) should be positively related to site residency times (Charnov 1976; Nonacs 1991).

Materials and Methods

Study Sites and Snake Collection

Our study took place at three sites in California: (1) the Blue Oak Ranch Reserve (BORR), Santa Clara County; and (2) Camp Ohlone and (3) Frog Pond, both within Ohlone Regional Wilderness (ORW), Alameda County. We collected data from ORW in 2009–2010 and from BORR in 2011–2012. ORW is approximately 30 km north of BORR, and within the former, Frog Pond is 3 km west of Camp Ohlone. BORR is also at a higher elevation than ORW (800 m vs. 400 m elevation above sea level, respectively), but both habitats are generally characterized by steep to moderate hills covered by mixed oak (*Quercus* spp.) woodland interspersed by grassland. We combined data from Frog Pond and Camp Ohlone into a single location termed ORW because they were studied concurrently using a slightly modified videography method, and they occur at a lower elevation than BORR.

At each site, we captured adult rattlesnakes and surgically implanted temperature-sensitive radiotransmitters (models A1-2T and SI-2T, Holohil Systems Ltd; model G3, AVM Instrument Company Ltd) using the methods of Reinert and Cundall (1982). Transmitters weighed <5% of snake body mass. After snakes recovered from surgery, we released them at their site of capture. We captured 22 adult rattlesnakes at ORW and 25 adult rattlesnakes at BORR.

Field Videography

We radiotracked snakes at least once daily, but usually every 1–2 h from May to July. *Crotalus oreganus* generally end breeding and begin their active hunting season in late April (Lind et al. 2010). Each time a snake was located, we recorded its position using a Global Positioning System (GPS) unit (Garmin Geko, ±6 m accuracy). We then positioned a battery-powered portable surveillance camera over a snake if it appeared to be actively hunting (as evident by a stereotyped ambush posture; Clark 2004; Reinert et al. 2011). At ORW, we used fixed security cameras (Swann PNP-150 and Supercircuits PC161IR-2) that recorded data onto mini digital video recorders (SVAT CVP800 and Supercircuits MDVR14-3) at 1030 frames/s (fps). At BORR, we used wireless network security cameras (Sony SNC-RZ25N) attached to network radios (Nanostation M2), which communicated with a wireless internet network erected at the field site (recording at 15–30 fps). These networked cameras allowed us to monitor and record video feeds in the field and to control the pan–tilt–zoom mechanism in real-time using laptop computers.

We continually monitored snakes with wireless video; whenever a snake moved away from a site, we relocated it using radiotelemetry and repositioned the camera over it. We measured distance moved between sites with a GPS unit when snakes moved >6 m, or measuring tape when snakes moved <6 m. Additionally, if the snake was not visible on camera for >1 h (i.e., it remained within a burrow or log), we confirmed its position using radiotelemetry. Thus, we remained confident of all snake locations even when the snake was unexposed. We consistently recorded snakes on camera between 0700 and 1900 h and less often beyond these hours. Our videography methods did not appear to alter the snakes' behavior because snakes rarely fled, rattled, or exhibited other overt behavior in response to our approaches. Furthermore, the growth rate of snakes that we monitored (for which we had repeated body measurements) was similar to that reported for other *C. oreganus* populations (*t*-test: $t_{32} = -0.49$, $P = 0.63$; Fitch 1949) indicating that our methods did not interfere with normal feeding behavior.

Behavioral Quantifications

We recorded behaviors of 11 males and 4 females from ORW, and 12 males and 7 females from BORR (these snakes exhibited hunting behavior and positioned themselves in areas amenable to videography). In total, we collected 3102 h of video. Sample video recordings from this study can be viewed at our YouTube channel (see http://www.youtube.com/user/rulonclark). Most of the data for this study were taken from our videos recorded from 2009 to 2012, but we continued to conduct fieldwork at BORR until 2014, opportunistically collecting additional foraging data, of which some are included in this study.

Ambush sites.—When we determined a snake was foraging (and not shedding, digesting, or unknown), we calculated its residency time at each hunting site. These times have a possible maximum error of 1–2 h because we did not often know the exact time of arrival to each site (Barbour and Clark 2012b). We recorded the exact time of site departure on our video cameras. At each site, we quantified hunting effort as the amount of time each snake maintained its body in one of two ambush postures: (1) when a snake positioned its body in a tight coil with its neck retracted; or, (2) when its head was visible at the entrance of a refuge such as a burrow, log, or rock. When snakes were

not visible within a refuge or were elongated, we scored their body position as nonambush. We also recorded the number of nights snakes remained in ambush until the next morning (i.e., did not retreat to refuge for the night), and the distance in meters snakes moved between consecutive sites.

Prey encounters.—Sparks et al. (2015) suggested that the majority of the adult *C. oreganus* diet consists of small rodents, and that adult snakes in California also include a higher proportion of lizards in the diet compared with populations at the northern part of the range. Thus we predicted that at our sites (based on range maps), common potential prey items would include Western Fence Lizards (*Sceloporus occidentalis*), Southern Alligator Lizards (*Elgaria multicarinata*), skinks (*Plestiodon skiltonianus* and *P. gilberti*), Pocket Gophers (*Thomomys bottae*), mice (*Peromyscus californicus* and *P. maniculatus*), woodrats (*Neotoma fuscipes* and *N. lepida*), California Voles (*Microtus californicus*), Broad-footed Moles (*Scapanus latimanus*), California Ground Squirrels (*Otospermophilus beecheyi*), and over 100 species of bird.

From our video recordings, we scored a prey encounter as occurring when a potential prey item came within 1 m of the snake or its refuge. For each prey encounter, we recorded the snake's body position as ambush or nonambush and determined the prey type (for this study: squirrel adult, squirrel pup, other rodent, lizard, or bird). Video frame rates and resolution often prevented us from identifying rodents and lizards to species. We separated squirrels into two age classes because rattlesnakes have been shown to respond differently to squirrel pups, which are more susceptible to snake predation than adult squirrels on account of their smaller body size and reduced ability to inhibit the effects of rattlesnake venom (Poran and Coss 1990; Barbour and Clark 2012b).

Strike.—For each prey encounter, we determined strike occurrence. It was sometimes not possible to determine whether strikes contacted or missed prey. In such cases, we determined strike success based on whether the snake searched for the prey after the strike. That is, we assumed that when a snake struck and did not attempt to locate prey, it either did not make contact with the prey, or it did not envenomate prey during contact. Clark (2006a) found that snakes that missed strikes always remained at the ambush site, while snakes that succeeded in striking prey exhibited SICS. For all successful strikes, we also noted whether the snake held onto or released the prey after the strike.

Strike-induced chemosensory searching.—For rattlesnakes that searched for struck prey, we determined the latency to start SICS and the length of time to successfully locate struck prey. SICS behavior was characterized as increased rates of tongue-flicking and head-scanning movements followed by abandonment of the strike site (Chiszar et al. 1977). When possible, we also recorded the distance that prey fled after a successful strike, which we were able to do for 14 strikes on prey.

Statistical Analyses

We implemented several generalized linear mixed models (GLMMs) fit by the Laplace approximation (R package lme4) to account for repeated observations of individual snakes. In all models, we included snake sex, body size (total length, cm), and study site as covariates and snake identity as a random factor. If GLMMs had overdispersed data, we
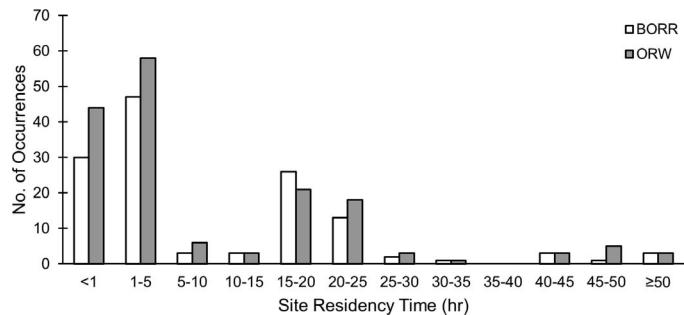

Fig. 1.—The frequency of occurrence for the duration that rattlesnakes (*Crotalus oreganus*) resided at each ambush site for two localities in California. BORR = Blue Oak Ranch Reserve, Santa Clara County; ORW = Ohlone Regional Wilderness, Alameda County.

modeled overdispersion as a random effect, with one random effect level for each observation (Elston et al. 2001; Bolker et al. 2009). We compared treatment levels using Wald's Z-tests (Bolker et al. 2009). We used separate GLMMs with a Poisson distribution (log-link function) to analyze the covariate effects on site residency times (min), time in ambush at a site (min), and distance moved between sites (m), and a GLMM with a binomial distribution (logit-link function) to examine these same effects on snakes' decision to remain in ambush posture overnight.

We used three more GLMMs with binomial distributions (logit-link function) to analyze data on striking. One model examined the probability of striking all prey types and included time of day and the above-mentioned covariates as fixed effects. The second model examined the probability of striking only squirrels and included hour of day, squirrel age class, and the above-mentioned covariates as fixed effects. We implemented a third model to determine whether the probability of strike success differed between squirrel pups and adults. In this model, we included the same fixed effects as the second model.

We used Chi-squared tests to determine whether prey types were encountered at equal frequencies and to examine whether prey types were struck at proportions equal to their overall encounter rates. We removed data associated with birds from the latter analysis because only one strike was initiated toward a bird during the entire study. Because squirrels are relatively large and can potentially inflict more damage on snakes during an attack than other prey, we performed a Fisher's Exact test to determine whether the decision to hold onto prey after a strike differed between squirrel and nonsquirrel prey.

We ran a linear regression to examine the effect of the distance envenomated prey fled following a strike on snakes' time to locate the prey (square-root transformed). Some snakes seemed unable to locate struck prey and we noted the length of time they exhibited SICS, but their behaviors were not included in our regression analysis because we did not know the distance their prey had fled.

In tests that did not account for snake identity because of low sample size (Chi-squared, Fisher's Exact, linear regression), no one snake contributed >13% of the total observations. We tested the assumptions of all statistical tests and examined all of our models for evidence of significant interactions between main effects. Analyses were performed in SYSTAT (v12.0; Systat Software Inc., Chicago, IL) and R

TABLE 1.—Results from generalized linear mixed-effects models explaining variation in measures of foraging behavior in *Crotalus oreganus* as a function of snake sex, body size, and study site, among other factors of interest. Snake identity was used to control for nonindependence. Significant effects are shown in bold.

Behavior	Factor	Estimate	SE	Z	P
Site residency time (min)	(Intercept)	5.79	0.32	18.30	<0.001
	Sex	−0.64	0.41	−1.58	0.11
	Body size	0.06	0.17	0.35	0.73
	Study site	0.16	0.28	0.56	0.58
Time in ambush at site (min)	(Intercept)	3.85	0.35	11.12	<0.001
	Sex	0.46	0.45	1.02	0.31
	Body size	−0.17	0.19	−0.89	0.37
	Study site	−0.19	0.33	−0.59	0.55
Nighttime ambush (y/n)	(Intercept)	−0.86	0.72	−1.20	0.23
	Sex	0.94	1.03	0.91	0.36
	Body size	−0.49	0.49	−1.01	0.31
	Study site	0.18	0.67	0.27	0.79
Distance moved (m)	(Intercept)	2.06	0.27	7.67	<0.001
	Sex	0.36	0.34	1.06	0.29
	Body size	−0.01	0.15	−0.07	0.94
	Study site	**−0.74**	**0.23**	**−3.27**	**<0.01**
Probability of striking all prey	(Intercept)	−2.82	0.51	−5.57	<0.001
	Sex	0.22	0.55	0.40	0.69
	Body size	−0.39	0.28	−1.38	0.17
	Study site	0.41	0.46	0.90	0.37
	Time of day	**−0.61**	**0.31**	**−2.00**	**<0.05**
	Study site × time of day	**0.77**	**0.36**	**2.11**	**<0.05**
Probability of striking squirrels	(Intercept)	−2.61	0.54	−4.83	<0.001
	Sex	−1.59	0.88	−1.81	0.07
	Body size	0.31	0.32	0.96	0.34
	Study site	−1.26	0.68	−1.85	0.07
	Time of day	−0.19	0.19	−0.99	0.32
	Squirrel age class	**1.16**	**0.40**	**2.89**	**<0.01**
	Study site × sex	**2.77**	**0.94**	**2.94**	**<0.01**
Strike success on squirrels	(Intercept)	1.12	1.63	0.69	0.49
	Sex	−3.18	2.60	−1.23	0.22
	Body size	1.41	1.21	1.17	0.24
	Study site	1.26	1.66	0.76	0.45
	Time of day	−0.45	0.58	−0.78	0.43
	Squirrel age class	1.32	1.03	1.29	0.20

(v3.1.1; R Foundation for Statistical Computing 2014), with $\alpha \le 0.05$. Unless otherwise stated, we report median values with interquartile ranges (IQR) as our measure of central tendency because most data were not normally distributed.

Results

The general foraging behavior of snakes from both populations consisted of residence within a restricted hunting area (typically within one cluster of squirrel burrow systems) at which snakes would use several different hunting sites. After several hours (or some cases, days), snakes would move a longer distance to a new hunting area (e.g., a different burrow cluster) and repeat the process. The core use area of California Ground Squirrels is <9 m (Boellstorff and Owings 1995); thus, we assumed that when snakes moved >9 m, they were attempting to prey upon a new group of squirrels.

Ambush Sites

We recorded 296 unique sites that rattlesnakes used while foraging: 131 from BORR and 165 from ORW. The majority (61%) of hunting-site residency times was <5 h, with 25% being <1 h (median = 2.87 h, IQR = 1.00–18.13 h, range = 0.07–120.50 h; Fig. 1). Snakes often moved in and out of refuges, exhibiting multiple hunting bouts at a single site. The median duration of individual hunting bouts at each site was 1.13 h (IQR = 0.50–2.99 h, range = 0.02–55.32 h). At

11% of snake locations, snakes never exhibited ambush body position (i.e., zero hunting effort). In 78% of these cases, this was because the snake sought refuge in shelter for the night, and moved to a different location the next morning. Snakes remained in ambush overnight 46% of the time. Site residency times, time spent in ambush at a site, and snakes' decision to remain out in ambush overnight were not affected by body size, sex, or study site (Table 1).

The distance moved between consecutive sites was affected by study site only (Table 1), with snakes from BORR tending to move farther distances than snakes from ORW. The median distance moved between sites at BORR was 11.26 m (IQR = 3.00–28.52 m) compared with 3.00 m (IQR = 1.00–14.25 m) at ORW. Overall, most movements from both sites were <10 m (Fig. 2).

Prey Encounters

From 3102 h of video recordings, we recorded 518 prey encounters on camera: 228 from BORR and 290 from ORW. Snakes encountered roughly 4 prey/d (0.17 prey/h). The majority (57%) of all prey encounters occurred when snakes were not visible in refuge. When snakes were visibly in ambush body position, their prey encounter rate remained relatively constant dropping only to 0.15 prey/h (37% of total encounters). Prey types were not encountered equally (χ^2 = 574.57, df = 4, $P < 0.001$; Table 2). Squirrel adults and pups were encountered at higher rates than lizards, birds, and

other rodents. Of all prey encountered, adult squirrels accounted for 53%, squirrel pups for 38%, lizards for 5%, birds for 2%, and other rodents for 2%.

Strike

When in ambush body position, rattlesnakes initiated strikes during 21% of prey encounters. On five occasions we also recorded strikes from snakes that we had classified as not hunting because they were not visible in refuge. Of the 47 strikes we recorded, 23 were successful, yielding a strike success rate of 49% (Table 2). We found that the probability of striking was influenced by time of day, which interacted with study site (Table 1). The probability of striking at BORR decreased with time of day, while ORW showed the opposite pattern with strike occurrence increasing with time of day, which likely resulted from more nighttime recordings at ORW than BORR.

Strikes were not initiated toward prey types at proportions equal to their encounter rates ($\chi^2 = 25.74$, df $= 3$, $P < 0.001$). More strikes were initiated toward squirrel pups, lizards, and other rodents and fewer strikes were initiated toward adult squirrels (Table 2). For all squirrel encounters, the probability of striking was higher for encounters with squirrel pups and showed an interaction between study site and sex (Table 1). Female subjects were more likely to initiate strikes on squirrels at BORR while males were more likely to initiate strikes on squirrels at ORW, but this interaction likely stems from uneven sampling of sexes at each site than true sex differences in foraging behavior. Although pups were attacked at higher rates than adults, the probability of strike success did not differ between squirrel age classes (Table 1).

We recorded four (out of 23) instances when snakes did not release prey after a strike. This occurred for two mice (*Peromyscus* spp.), one squirrel pup, and a California Quail chick (*Callipepla californica*). Snakes were more likely to hold onto nonsquirrel prey than squirrels after a strike (Fisher's Exact test: $P = 0.02$, $n = 23$). The snake that ate the squirrel pup did not hunt in a traditional sit-and-wait manner. Instead, it actively searched for the prey within the prey's burrow. When the snake entered the burrow, the pup was alive and started emitting a high-pitched screech. The pup was physically small (likely <100 g), and appeared to have not reached the developmental stage of full emergence from its natal burrow. The snake struck the pup and remained still within the entrance of the burrow. It started consumption after immobility and presumed death of the prey item.

Strike-induced Chemosensory Searching

After a successful strike, prey fled a median distance of 3.80 m (IQR = 0.25–13.75 m, $n = 14$). Snakes started SICS behavior <5 min after the strike in 9 out of 15 recorded instances. Although the median time to start SICS was 3 min (IQR = 2–35 min, $n = 15$), snakes waited >100 min to start searching for prey on two occasions (101 and 135 min after the strike). Because squirrel pups were attacked most frequently (other prey usually contributed to 1–2 data points/variable), we could not statistically analyze the effect of prey type on poststrike behaviors.

The median time to locate envenomated prey was 40 min (IQR = 21–115 min, $n = 13$). Snakes took longer to find prey that fled farther distances ($F_{1,9} = 72.52$, $R^2 = 0.89$, $P <$
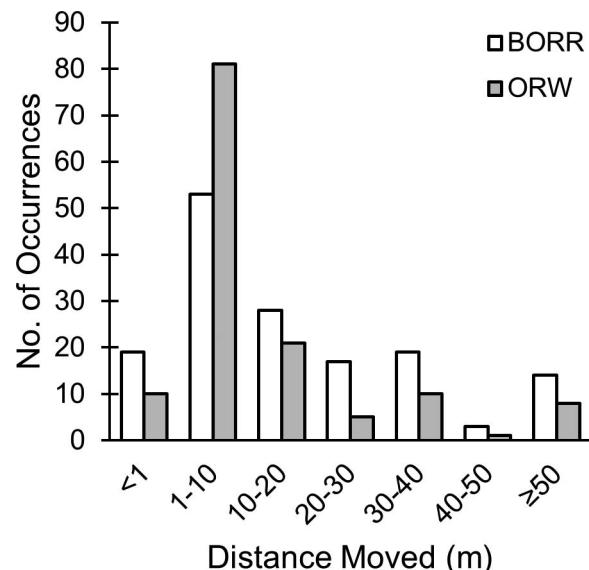
FIG. 2.—The frequency of occurrence for the distance moved by rattlesnakes (*Crotalus oreganus*) between consecutive ambush sites at two localities in California. BORR = Blue Oak Ranch Reserve, Santa Clara County; ORW = Ohlone Regional Wilderness, Alameda County.

0.001; Fig. 3). We calculated that snakes moved at a rate of 0.2 ± m/min while searching for envenomated prey. This is an underestimate because it is based on the straight-line distance from the strike site to the prey consumption site and snakes do not move in a straight line when performing SICS.

Three out of 20 strikes to squirrels appeared to involve unsuccessful SICS. As these snakes exhibited SICS, they retraced the same path for several hours going into and out of the same burrows repeatedly. One male snake from BORR struck a squirrel pup at around 0715 h and exhibited SICS behavior at 0856 h. He repeatedly searched three burrows, which were 1–2 m from each other for 305 min, and then he moved to a new burrow 16.1 m away from the strike site. We are unsure as to whether this snake found the pup because we never saw him emerge from the most-distant burrow. Another male subject from ORW struck an adult squirrel at 1317 h and began searching at 1319 h. This snake was repeatedly harassed by other ground squirrels in the area, which alarm-called and tail-flagged at him as he searched for his prey. He ceased SICS after 179 min and moved to an area 26.5 m from the strike site. We confirmed that this snake never consumed the struck squirrel, which was marked, because it was alive and active the next day. A female snake from BORR struck a squirrel pup at 1257 h and began searching for it at 1300 h. She continued to search a large portion of the hillside where she had set up ambush until around 1820 h the same day. She spent the night in a burrow, and in the morning, she resumed SICS behavior repeatedly searching the same burrows as before. After more than 1 h of searching, she set up ambush in a new area 20.3 m away. This snake spent 397 min exhibiting SICS and apparently never located the struck pup.

Unusual Foraging Behaviors

While conducting this research, we observed two unusual foraging behaviors. First, an adult male snake from ORW struck a squirrel pup, but the pup had not died when the

TABLE 2.—Number of all potential prey encountered at each of two study sites in California when rattlesnakes (*Crotalus oreganus*) were in all body positions (i.e., not visible, nonambush, and ambush), when rattlesnakes were in ambush body position only, and strike outcomes for all prey encountered (no. of successful strikes and no. of unsuccessful strikes). Prey were unknown when subjects struck at something outside of the camera field of view. BORR = Blue Oak Ranch Reserve, Santa Clara County; ORW = Ohlone Regional Wilderness, Alameda County.

Prey type	BORR				ORW			
	Total no. encountered	No. in ambush	No. successful strikes	No. unsuccessful strikes	Total no. encountered	No. in ambush	No. successful strikes	No. unsuccessful strikes
Squirrel adult	133	38	2	1	134	49	2	6
Squirrel pup	76	19	6	3	116	38	8	4
Other rodent	3	3	3	0	4	4	0	1
Lizard	0	0	—	—	22	17	1	4
Bird	1	1	1	0	11	11	0	0
Unknown	3	3	0	3	2	2	0	2

snake located it. Although the pup was immobile, the snake struck it a second time before consuming it. Second, a female snake from BORR was found scavenging a decapitated squirrel pup carcass (see at http://youtu.be/D4TVesJ9ZeM). She attempted to consume the carcass by repeatedly repositioning her mouth on the body in different ways, but seemed unable to start swallowing the prey possibly because it lacked a head (although she did locate the anterior region). She spent 7 min trying to ingest the carcass before abandoning it and retreating to a burrow.

DISCUSSION

Although they are similarly sized congeners that primarily consume small mammals via ambush hunting, *C. oreganus* exhibits differing patterns for several foraging behaviors when compared with *C. horridus* (Reinert et al. 1984, 2011; Clark 2006a,b). Our results also reveal some interpopulational differences within *C. oreganus* between our two field sites. Variation in the foraging behaviors of *C. oreganus* appears to be less affected by snake sex and body size, and are more likely driven by locally available prey and/or habitat features.

When we compare our results on *C. oreganus* to studies of *C. horridus,* we find general support for the prediction that diet breadth decreases with increasing prey encounters. We found that *C. oreganus* in California encountered approximately 4 prey/d, whereas Clark (2006a) reported that *C. horridus* in New York encountered approximately 1 prey item/d. Individuals from our populations appeared to choose sites that maximized encounters with the largest consumable prey item in the habitat (California Ground Squirrels) because this prey species made up 91% of all recorded encounters. Clark (2006a) found that a population of *C. horridus* in New York neither preferentially targeted a single prey item nor large-bodied prey items. Instead, snakes maximized encounters with nocturnal rodents such as mice (*Peromyscus* spp.) and voles (*Clethrionomys gapperi* and *Microtus pennsylvanicus*) even though the habitat contained larger sciurids (*Tamias striatus, Sciurus carolinensis,* and *Tamiasciurus hudsonicus*). Goetz (2011) found that a population of *C. horridus* in Virginia preferentially targeted gray squirrels (*S. carolinensis*), however, demonstrating that the diet of this species could also be driven by differential prey encounter rates or overall prey abundances.

The snakes in our population also showed a willingness to attack nonsquirrel prey items when given the opportunity. These results corroborate past diet studies on rattlesnakes, which suggested that these snakes are opportunistic predators (e.g., Ernst and Ernst 2003). Rattlesnakes might attack less profitable prey when preferred prey becomes hard to find (e.g., it has not been encountered for some time; Carle and Rowe 2014), although this behavioral pattern has not been quantified. Although adult squirrels were the largest consumable prey type and had the highest encounter rates at our sites, squirrel pups were struck by snakes at proportions higher than adult squirrels. Pups might be preferred because they are less effective at detecting snakes (Putman et al. 2015) and have slower reaction times to surprise attacks (Putman and Clark 2015). Pups are also less effective at physiologically inhibiting the effects of venom compared with adults (Poran et al. 1987; Poran and Coss 1990), and so they are more likely to succumb to venom quickly, potentially resulting in smaller poststrike flight distances. Our small sample size for these measures prevented us from examining relationships associated with prey ontogeny on flight distance. The above-mentioned age differences in squirrel antisnake defenses should result in pups being more vulnerable to rattlesnake attacks.

Few studies have quantified the length of time ambush-hunting snakes wait at a site, which is one of the key aspects of their foraging ecology. The rattlesnakes in our populations typically abandoned sites before 5 h had elapsed (Fig. 1), and hunting effort at each site was often lower than the total time in residence because snakes moved in and out of refuges, spending shorter periods of time engaged in individual hunting bouts. Most of these bouts lasted <3 h and could be influenced by rattlesnakes' need to thermoregulate. Our results support the predictions that site residency time is influenced by both prey encounter rate (a negative relationship) and travel time between sites (a positive relationship with distance). Clark (2006a) found that *C. horridus* typically stayed longer at hunting sites compared with the *C. oreganus* in our study (mean ± SD: 17.0 ± 13.8 h and 10.3 ± 14.3 h, respectively). These longer site residency times correspond with lower prey encounter rates (1 prey/d) and longer mean travelling distances between sites (mean ± SD, 47 ± 80.1 m) compared with *C. oreganus* (prey encountered, 4 prey/d; mean distance, 16.7 ± 27.5 m). We also found that snakes at BORR moved farther distances between sites compared with snakes at ORW, but site residency times at BORR were not longer than those at ORW (Fig. 1). This could indicate that the costs associated with travel might be higher at BORR than at ORW (Charnov 1976; Hamilton 2010), or that prey encounter rate has a stronger effect on site residency time

than the distance between sites. Further studies should test these assumptions.

Overall, we found that movements between hunting sites by rattlesnakes in both *C. oreganus* populations were short (Fig. 2). Rattlesnakes tended to move within a small area for several days, and then made occasional long-distance movements to new hunting areas (i.e., a new squirrel burrow cluster). Clark (2006a) found that *C. horridus* in New York tended to move ≤20 m to new ambush sites, but also made occasional long distance movements (up to 900 m). A similar foraging spatial use was also observed in a population of *Bothrops asper,* which hunts nocturnal small mammals (Wasko and Sasa 2009). Studies on other species are needed to verify whether short movements interspersed by long forays to new areas is a widespread spatial pattern among hunting pitvipers. Most studies that use radiotelemetry to monitor snakes do not track individuals more than once daily, so we lack data on fine-scale movements for many species; this topic merits further investigation.

The strike initiation and success rates that we measured for *C. oreganus* are nearly identical to those reported for *C. horridus* (values for the latter metric are 21% vs. 25%, respectively; Clark 2006a,b). Thus, rattlesnakes do not often strike prey during an encounter, indicating that they require specific circumstances to initiate an attack (see Clark et al. 2012 for details). Rattlesnakes frequently miss strikes when presented with captive mice in laboratory conditions (Chiszar et al. 1986; Kardong 1986; Cundall and Beaupre 2001). Both *C. oreganus* and *C. horridus* successfully envenomated prey in only approximately 50% of attacks. These results are consistent with those of Shine et al. (2002), who reported that Shedao Island Pitvipers (*Gloydius shedaoensis*) also exhibit a relatively high frequency of missed strikes. Similarities in strike responses across studies indicate that some of the mechanisms governing strike outcomes are conserved regardless of prey type or environment.

We found that snakes were more likely to release squirrel prey than nonsquirrel prey. The probability of prey injuring the snake (when held in the mouth) increases with time to death (Rowe and Owings 1990; Cundall 2009), and squirrels often take several minutes to hours to succumb to venom because of their venom resistance (Poran et al. 1987; Poran and Coss 1990). Thus, the probability of poststrike retaliation would be high if snakes did not release squirrels after a strike. We recorded several instances when snakes are forcibly pulled out of their ambush coil while envenomating squirrels, indicating that the physical struggle alone might prevent snakes from holding onto large prey. We recorded only one instance of a subject restraining a squirrel after a strike, but this squirrel was a small pre-emergent pup, and it probably lacked the motor skills necessary to escape from the snake (Coss 1991; Carrier 1996).

We found that SICS typically began within 5 min of a strike. This is consistent with what Clark (2006b) reported for *C. horridus* and with what many laboratory studies have documented (Chiszar et al. 1982; Hayes 1992, 1993). However, we also recorded two instances when snakes waited more than 1 h to start SICS. Long wait times after a strike have not been reported previously and could be caused by disturbances (e.g., predator or human presence) that prevent the snake from giving up crypsis. A laboratory study found that the appearance and movement of simulated
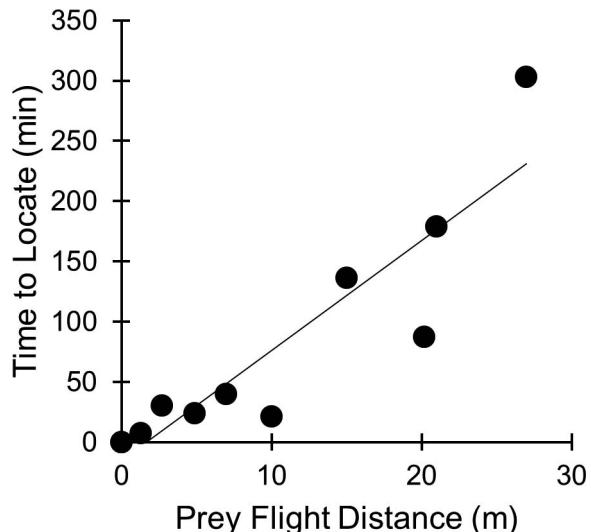

Fig. 3.—The time that rattlesnakes (*Crotalus oreganus*) spent locating envenomated prey as a function of the distance prey fled after the strike by the snake.

raptor eyes suppressed SICS behavior in rattlesnakes (O'Connell et al. 1981), but these snakes still began searching within 30 min of striking.

The distance prey fled after a strike was positively related to the time to locate the prey item (Fig. 3). Clark (2006b) estimated that the average prey-trailing rate of *C. horridus* was approximately 0.5 m/min. We found that *C. oreganus* moved at a slower pace, trailing prey at approximately 0.2 m/min. Laboratory studies have found trailing rates between 0.2 and 0.4 m/min (Golan et al. 1982; Duvall et al. 1990; Smith et al. 2000), indicating that this behavior does not vary much across environments. We also found that prey were sometimes not located following SICS. If fang placement is flawed (Kardong 1986; Cundall 2009), venom quantity is too low (Hayes 1991), or prey are resistant to venom (Perez et al. 1978), prey may survive an attack and/or create a long and complex chemosensory trail. We observed that ground squirrels occasionally do not succumb to envenomation quickly (or at all), in part because of their innate venom resistance (Poran et al. 1987), and this defense could result in a snake having difficulty locating struck squirrels. Even with the increased costs of movement (e.g., predation, energy, missed opportunities), however, free-ranging rattlesnakes appear willing to spend considerable time searching for squirrels (>5 h in SICS). Our results differ from laboratory studies, which showed that the maximum time rattlesnakes kept searching for struck prey was 4 h (Chiszar et al. 1982, 1985). For free-ranging rattlesnakes, the benefits of finding envenomated prey seem to outweigh the costs of prolonged searching.

Even though rattlesnakes are not generally considered prey specialists, the snakes in our populations positioned themselves in areas where they would maximize encounters with California Ground Squirrels. Successful attacks on squirrels directly remove individual squirrels from the population. Furthermore, the presence of snakes alone near and within squirrel colonies could also induce strong indirect effects on squirrel behavior and physiology, such as lowering foraging rates, increasing stress hormones, and lowering reproductive output (Preisser et al. 2005; Clinchy et al. 2013; Sheriff and Thaler 2014). Our study illustrates that the

foraging behaviors of *C. oreganus* reflect a preference to target squirrels, making rattlesnakes a major source of selection on this prey species.

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