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Foraging site selection in prairie kingsnakes (Lampropeltis c. calligaster): An experimental approach

Angela M. Fornell

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FORAGING SITE SELECTION IN PRAIRIE KINGSNAKES

(*LAMPROPELTIS C. CALLIGASTER*): AN EXPERIMENTAL APPROACH

by

Angela M. Fornell

THESIS

Submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE in BIOLOGICAL SCIENCES

In the Graduate School, Eastern Illinois University

Charleston, Illinois

2008

I hereby recommend that this thesis be accepted as fulfilling this part of the graduate

degree cited above

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Date	Thesis Director
_____	_____
Date	Department/School Head

Abstract

A critical component to a predator's survival is the choice of foraging sites that yield enough predatory success to meet energetic demands. To elucidate cues used to select foraging sites, I examined foraging site selection in Prairie Kingsnakes (*Lampropeltis c. calligaster*), a generalist species whose foraging mode is flexible. My objectives were to determine: the pattern of foraging site selection; the importance of certain cues that kingsnakes use when selecting foraging sites; and, whether or not kingsnakes adjust their foraging patterns in response to alterations in the microhabitat. I tested subjects in a large experimental arena under several treatment conditions that simulated various components of a natural habitat setting: presence/absence of chemical cues from prey; presence/absence of physical structure that could be used as either a shelter or ambush site; presence/absence of both chemical cues and physical structure. After subjects acclimated to treatment conditions where both chemical and physical cues were present, I also quantified changes in subject behavior in response to repositioned objects (i.e., interrupted chemical trails). Most snakes maintained an active foraging strategy under different treatment conditions, but my results indicate inter-individual variation in foraging behavior in similar microhabitats. Flexibility in foraging behavior appears to facilitate predatory success in kingsnakes, even when confronted with an altered microhabitat.

Dedication

This thesis is dedicated to my grandparents and parents. Without them who knows where

I would be…

Acknowledgements

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Introduction

A basic necessity organisms require to live is energy. This can be acquired
through photosynthesis, as in autotrophs, or by consuming another organism, as is the
case for heterotrophs such as herbivores and carnivores. An animal's task of finding food
is arguably a greater challenge than harnessing solar radiation. Herbivores may travel
great distances and graze all day in order to satisfy their daily nutritional requirements.
Carnivores may also travel great distances in search of prey, which then must also be
captured and killed before consumption. Organisms must expend energy to obtain
energy. Therefore, it is important to understand the ecological mechanisms behind the
decisions that predators make in their environment to locate prey. A greater scientific
understanding about the interactions between animals and their environment can facilitate
the conservation of biotic and abiotic processes, as well as the maintenance of general
levels of biodiversity.

Natural selection should favor those predators that effectively use cues in their
environment to find suitable prey (Downes 2002). Regardless of the foraging mode used,
snake predators assess the quality of a habitat based in part on chemical information
deposited by potential prey (Burghardt 1990, Clark 2004a,b, Tsairi and Bouskila 2004).
Energy expenditure during foraging bouts could increase in cost if a predator sought prey
in areas having low levels of either prey density or chemical information (Clark 2004a,
Slip and Shine 1988). There are still costs when foraging in a profitable area, but these
are typically negated by energetic gains due to higher encounter rates with prey (Downes
2002, Tsairi and Bouskila 2004). Burghardt (1990) reported snakes might develop

chemical search images to discriminate prey chemicals in favor of those that have been profitable in the past.

Observations of foraging behavior in a number of squamate taxa have documented the utilization of chemoreception to locate prey via scent trails (also referred to as pathways or runways) left by prey, such as small rodents (Burghardt 1990, Clark 2004a, Reinert et al. 1984, Slip and Shine 1988, Tsairi and Bouskila 2004). Few studies, however, have recorded foraging site selection as a result of using scent trails (Burghardt 1980, Clark 2004b). Research concerning kingsnake foraging ecology has been limited to laboratory-based examinations of responses to prey chemical cues by a few kingsnake species (Brock and Myers 1979, Weldon and Schell 1984), or are general descriptions of natural history (Fitch 1978, Richardson et al. 2006). This study constitutes the first experimental study of foraging site selection in Prairie Kingsnakes (*Lampropeltis c. calligaster*), and is the first study to use a simulated habitat arena to test specific foraging hypotheses in any member of this Genus. The results of this study will add to what is currently known of the natural history of this species and will enhance efforts for conservation of the Prairie Kingsnake and related species.

Natural History

Prairie Kingsnakes range from western Indiana, central Kentucky and north-western Mississippi across to most of Kansas, Oklahoma, and east Texas (Conant and Collins 1998). Adults typically range in size from 76 to 107 cm total length (Conant and Collins 1998). Fitch (1978) documented the natural history of a population in Kansas and noted that members of this species could be found in various types of grassland, open woodland and woodland edges. Most of the time, snakes were out of direct sight (e.g.,

found in small mammal burrows or in mats of dead vegetation). These observations were also supported by a study of an Illinois population where subjects were monitored using radio telemetry and often detected underground (Richardson et al. 2006). This species does not share hibernacula with other species including conspecifics presumably because Prairie Kingsnakes are known to prey on other snakes including smaller conspecifics. Kingsnakes are generalist predators, consuming a number of different prey items, such as rodents, lizards, snakes, and birds (Rodriguez-Robles and de Jesus-Escobar 1999, Weldon and Schell 1984). Prairie Kingsnakes feed mostly on mammals (48% of the ingested prey mass from the Kansas population was made up of *Microtus ochrogaster*); squamates also compose a smaller percentage of this species' diet (Fitch 1978).

As a result of the secretive nature of kingsnakes, studies of their foraging ecology are poorly represented in the literature. Yet, kingsnakes are important to the ecological health of the environments in which they live because they regulate prey populations and are a food resource for larger predators. Descriptions of their diet, defensive behavior, distribution, reproduction, and natural history are available from the literature (Fitch 1978, Richardson et al. 2006, Rodriguez-Robles and de Jesus-Escobar 1999), but little is known about their foraging site selection (but see Greene and Rodriguez-Robles 2003).

Two examples from the literature concerning *Lampropeltis* are presented here to illustrate the types of studies that have been conducted. Brock and Myers (1979) studied naïve *L. getulus* that were presented cotton swabs with different prey extracts. They found no differences between swabs, indicating that the snakes use more than chemical cues to discriminate among prey items. Greene and Rodriguez-Robles (2003) described the dietary variability of *L. zonata* in order to assess its ecological role as a predator.

They reported that this species switches from ectothermic prey as juveniles to endothermic prey as adults, similar to other species in the Family Colubridae (Burghardt 1990, Greene and Rodriguez-Robles 2003, Rodriguez-Robles and de Jesus-Escobar 1999).

Snake Foraging Ecology

A common means of describing predatory mode is the use of either active or ambush foraging tactics (Cooper 2005, Scharf et al. 2006, Tsairi and Bouskila 2004). Active foraging is characterized by a predator that moves through the habitat in search of suitable prey. On the other end of the spectrum, ambush foraging (or sit-and-wait foraging) is characterized by a predator that sits motionless at one location and waits for active prey types to come within striking distance (Cooper 2005, Scharf et al. 2006, Tsairi and Bouskila 2004).

Foraging site selection in rattlesnakes is well represented in the literature (e.g, Clark 2004a,b, Reinert et al. 1984). Timber rattlesnakes often use rodent runways to locate profitable ambush sites (Clark 2004a,b). Once a site has been located, the rattlesnake then positions its body in a particular posture and waits in ambush for the approach of a prey item (Clark 2004a, Reinert et al. 1984). Foraging mode has been shown to be similar among congeners (Perry 1999). In contrast to North American vipers, the desert snake *Echis coloratus* chooses ambush sites primarily on physical characteristics of the site, and secondarily on prey scent (Tsairi and Bouskila 2004). Rattlesnakes and *E. coloratus* are both considered ambush predators, yet each type of snake uses different cues to choose a profitable ambush site.

The use of chemosensory information by predators, ambush or active, is an important element of their foraging behavior (Burghardt 1990, Clark 2004b). The information gathered from chemical cues by ambush and active foragers differs because most ambush predators choose a site based on the presence or intensity of prey scent; hence, there is an increased likelihood of encountering a prey item (Clark 2004b). Active predators must locate a chemical trail that may lead to a prey item.

Most squamates have a highly developed tongue-vomeronasal organ system (Burghardt 1980, 1990, Halpern1992). The system is comprised of an olfactory organ projecting to the principle olfactory bulb and the vomeronasal organ projecting to the accessory olfactory bulb through the vomeronasal nerve. Odorants stimulate the olfactory organ receptors and chemicals transported by the tongue, both volatile and non-volatile, stimulate the vomeronasal organ. The vomeronasal nerve endings remain detached from the olfactory system and terminate in the accessory olfactory bulb (Burghardt 1980, Halpern 1992). This system is imperative to feeding in snakes. Snakes and many lizard species flick their tongues in the air or put their snouts directly in contact with substrate to chemically sense their environment. The recording of tongue flick rates (TFR; typically measured as the number of tongue flicks per unit time) has been a consistent way to quantify interest in prey (Ford 1995).

Rodent Prey Pathways

Many small mammals store food items (especially those whose abundance is seasonally variable), a behavior referred to as caching (Smith and Reichman 1984). A cache is defined as a place where a food source is stored for later consumption. Caching behavior tends to be more common among species inhabiting temperate regions (Smith

and Reichman 1984). Rodents that cache must be able to locate their food stores, often

using a series of non-random movements to and from their caches and other features in

the habitat (Lavenex and Schenk 1998, Smith and Reichman 1984). A pathway or

runway, typically marked by the application of urea, is established by an individual after

repeated passes (Cook et al. 2004, Lavenex and Schenk 1998). Over time, this produces

a network of scent trails used to navigate among their destinations (i.e., food and shelter).

The scents are then exploited by predators in search of rodent prey (Clark 2004b).

Rodent pathways can also function to reduce the risk of predation through a

prey's knowledge of the habitat and the escape routes within it (Gauthier and Bider

1987). Activity outside of these pathways increases during inclement weather and/or

moonless nights because these conditions may reduce a predator's ability to visually

detect rodent prey (Orrock et al. 2004). Researchers frequently use smoked tracking

paper to document the use of fallen log surfaces by small animals as a means of pathway

use within the habitat (e.g., Reinert et al. 1984).

Research Objectives

My study examines the foraging ecology of Prairie Kingsnakes. I assessed their

ability to use chemosensory cues when foraging and selecting foraging sites. I also

determined the degree to which alterations in microhabitat structure direct kingsnakes to

adjust their foraging strategy to compensate for such alterations. A change in foraging

mode might be triggered by alterations in the microhabitat, such as shifts in objects

representing habitat structure. Predators can exhibit some flexibility in foraging modes

between the extremes of active and ambush (Scharf et al. 2006). Although kingsnakes

are considered active foragers (Greene and Rodriguez-Robles 2003), they should, in

theory, change their strategy to that of an ambush predator when presented with appropriate conditions. The specific objectives of my study were to: 1) determine whether or not foraging sites are selected at random, 2) determine the importance of certain cues that *L. c. calligaster* uses when selecting foraging sites, and 3) determine if *L. c. calligaster* adjusts its foraging pattern in response to alterations in the microhabitat (i.e., repositioned logs).

Materials and Methods

Animals and husbandry

Adult Prairie Kingsnakes were caught by hand within Coles County (n=8) and two neighboring counties in the spring of 2007 and 2008 (Moultrie County, n=1; Clark County, n=1; IDNR Scientific Collecting Permit #NH06-0946). Subjects were marked using a combination of scale clips and passive integrative transponders (PIT tags) injected subcutaneously (Fitch 1987). Upon capture, I determined the sex of each subject with a set of sexing probes, and measured snout-vent length (SVL, ±1 cm), tail length (±1 cm), and mass (±0.1 g). Kingsnakes were held in captivity for at least one week prior to their use as subjects in the experiment (IACUC protocol #06-016). Subjects were housed individually in fiberglass cages (30 x 30 x 60 cm) lined with newspaper, and provided with a shelter, shedding substrate and water *ad libitum*. Heating tape ran underneath one end of the cage to provide a temperature gradient (19-30 °C). A wild-type laboratory mouse (*Mus musculus*) was offered to each subject every other week except the period within two weeks of their participation in any trials. During this two week pre-trial period, subjects were placed on a restricted diet (water alone) to motivate predatory behavior (Ford 1995). Ambient temperature (approximately 25 °C) and photoperiod (12:12 h light:dark) were established in both the housing area and the testing arena using a series of electric timers and space heaters.

Wild type laboratory mice (*Mus musculus*; n=19) were obtained from an existing colony (IACUC protocol #04-001). Mice were housed at a density of no more than six per cage (separated by sex) in standard Nalgene cages (10 x 10 x 30 cm, plastic with metal grill lid) with bedding, food (rodent grain pellets) and water *ad libitum*. Ambient

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temperature was set at 22.2 °C and photoperiod at 12:12 h light:dark. Bedding was
replaced weekly.

Experimental habitat

Foraging trials were conducted in an experimental arena (200 x 200 x 75 cm;
Figure 1). The arena was constructed from pine lumber, plywood, and tin flashing. The
tin flashing lined the arena interior along the bottom 50 cm of the walls to prevent mice
from escaping or gnawing on the frame and to deter snakes from climbing out. The
interior corners of the arena were rounded with the tin flashing to minimize edge effects
on behaviors of both mice and snakes (Krebs 1989). Because rodent and snake behaviors
can be influenced by chemical cues available on the substrate (Ford and Burghardt 1993,
Lavenex and Schenk 1998), the arena was bottomless to facilitate cleaning between
consecutive trials. The arena floor consisted of heat tape fixed to a concrete floor with a
sheet of linoleum tile (220 x 220 cm) overlaying the heat tape. The heat tape was turned
on approximately 5 min before the introduction of the snake and turned off after the
removal of the snake. Within the arena, the tile flooring was covered with hardwood
mulch (approximately 0.06 m^3) at a depth of about 2.5 cm to simulate a natural
environment. This substrate also provided the means by which mice could establish a
trail network (likely containing chemical information), which could then be utilized as a
cue directing the foraging behavior of snake predators. I suspended a string across the
top of the arena to visually divide it into two equal halves thereby making it easy to
distinguish between control and treated sides (see below).

Experimental design

Trials were conducted between 12 June 2007 and 11 July 2008. Test subjects were chosen in random order to be used in five treatments (tested in succession from 1 to 5). I allowed a minimum of 24 h to elapse between any one subject's use in trials involving treatments 1 - 3. Furthermore, a minimum of 7 d followed any subject's use in trials involving each of treatments 3 - 5 such that the subject's gut could be cleared of any ingested prey. Due to logistic constraints of the testing arena, I was unable to randomize the designation of control and treated sides. Therefore, I established the left side as the control side and the right side as the treated side of the arena. Snakes from 2007 underwent 4 replicates, while those from 2008 underwent two replicates, of all treatments. All experimental trials (90 min in duration) were recorded using a Canon GL-1 video camera suspended 2.2 m above the center of the arena floor. The camera was mounted on a remote-controlled pan-tilt tripod head (Bescor, Farmingdale, New York) such that the camera could zoom in on the subject and follow its activity throughout each trial. Because this species is diurnal (Rodriguez-Robles and De Jesus-Escobar 1999), experimental trials of snakes took place between the hours of 08:50 h and 20:08 h.

Between successive trials, all substrate was removed and walls and floor were cleaned with 70% ethanol, as were logs when used. I wore latex gloves when adding substrate to the arena and handled logs to prevent contamination with extraneous chemical odors. The substrate was distributed as evenly as possible. Each snake was placed in the center of the arena at the start of a trial with the use of a snake hook. For treatments 3, 4, and 5, a live adult wild-type mouse (separate from those participating in scenting trials) was offered at the completion of the trial to provide positive

reinforcement of predatory behavior. If the mouse was not eaten within 30 min it was euthanized and placed in the snake's cage for ≤ 24h.

The wild-type mice (n=3 to 6) used to scent pine litter were placed into a separate enclosure (121.5 x 50 x 42.25 cm, length by width by height) for approximately 20 h. I used two groups of mice that were alternated over a period of 5 days about one week prior the start of treatment 1. The features of this enclosure were similar to those of the pre-trial phase in the experimental arena (see below). This set up comprised of pine litter that was distributed as evenly as possible (at a depth of 1-2 cm) with food (rodent pellets) at one end of the enclosure and a shelter at the opposite end. This scented bedding was stored in a plastic bag at room temperature until its use. Scenting the enclosure litter in this fashion was necessary for two reasons. First, this allowed the mice to adjust to a larger space than the smaller Nalgene cages where they are housed. Secondly, mice could move naturally from food to shelter thereby depositing their chemosensory information on the substrate. This litter was then used within the testing arena during trials for the first treatment.

Treatment 1 was arranged so that there was only substrate on the control side and the soiled bedding on top of the substrate on the treated side. This tested the snakes' ability to detect the chemosensory information of the prey on the substrate. Treatment 2 lacked chemical information, but had a log placed in the center of both the control and treated sides so that they were parallel to one another (logs averaged 54.24 x 9.91 cm, length by diameter). Having logs present without chemosensory information on the logs or substrate from prey allowed me to detect associations with the physical elements in the habitat.

Prior to trials in treatments 3, 4 and 5, a wild-type mouse was placed in the treated side of the arena for a total of 20 h. After an initial 16 h the mouse was dusted with fluorescent powder (Day-Glo, Columbus, Ohio) by placing it within a quart size plastic bag with approximately 2.5 ml of powder, and then shaken gently for 5-10 sec (Lemen and Freeman 1985). The mouse was placed back into the arena for the remainder 4 h to help visualize trail patterns within the arena prior to the introduction of the snake subject. The trail patterns would otherwise not be visible to the human observer when recording snake behaviors (see below). Upon the removal of the mouse, excess powder was wiped off with a damp towel before it was returned to the colony. The same mouse was never used in consecutive trials.

Treatment 3 examined the subject responses to chemosensory cues available from the recent deposition of rodent trails. During the pre-trial phase of this treatment, a mouse was acclimated within the treated side of the arena. Food pellets and a shelter were provided at opposite ends of the arena's treated side for the mouse to establish a pathway(s). To confine the mouse to this side, a divider wall that ran the length of the arena (200 x 75 cm; constructed from plywood and tin flashing) was placed into the arena to separate the control and treated halves. It was removed after the mouse had been taken out but before the introduction of the test subject.

For treatments 4 and 5, a mouse was placed in a smaller, bottomless enclosure (148 x 58 x 31 cm; length by width by height) made of pine lumber and plywood with a fiberglass mesh screen across the top. This smaller enclosure further restricted the mouse away from the perimeter of the testing arena, so that snake behaviors would not be confounded by the mouse associating with the edge microhabitat (description below).

This enclosure was placed in the treated side of the larger experimental arena. The separation between the wall of the smaller enclosure and those of the testing arena was at least 20 cm. Similar to treatment 3, the pre-trial period of treatments 4 and 5, included the positioning of a shelter on one end of the smaller enclosure and food (rodent pellets) on the other for the mouse (similar to the process of scenting the mouse litter, described above). As with the divider in treatment 3, the smaller arena, and shelter were all removed following the pre-trial scenting period by the mouse, but before the introduction of the test subject.

In treatment 4, both a mouse and a log were placed in the treated side of the arena during the pre-trial phase. This treatment investigated the importance of chemosensory information to the predator in association to physical features within the arena landscape when foraging. In treatment 5, a mouse was present during the pre-trial period and after the removal of the mouse but before the introduction of the snake, a log was placed in the arena so that it intersected the mouse pathway. Treatment 5 tested for the similar association between chemosensory information and orientation of objects within the habitat. The control side of the arena in treatments 3 and 5 had only substrate, whereas the control side of treatment 4 had a log in it, as was the case for treatment 2.

Behavioral Descriptions

Based on recordings of the first 15 trials (involving five subjects), I categorized and described five behaviors performed by foraging Prairie Kingsnakes. Escape behavior included climbing walls, pushing against walls, and any attention directed towards the corners of the testing arena. I defined traveling as general forward movement between any two points within the arena. Resting occurred when snakes ceased to move and

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remained motionless for >1 sec. The body was oriented in either a linear or near linear posture or positioned with a single lateral flexion; in either case, the snake's head was always visible. I defined stationary searching as a snake which remains motionless in a coiled or near coiled posture and with the body positioned immediately adjacent to a rodent trail or the log when either was available in the arena. Subjects occasionally tongue-flicked in this posture and sometimes burrowed into the substrate so as to conceal a portion of their bodies. In this sense, I considered stationary searching as being equivalent to an ambush posture. Active searching occurred when subjects exhibited interest in areas where prey has previously been and when investigating the log (when present). In my observations, subjects always tongue-flicked at a rate of one flick per second or faster during active searching, and occasionally made direct contact with their labial scales against the substrate. Another behavioral component used to identify periods of active searching was alternating lateral movement of the snake's head as it progressed forward.

Data analyses

I reviewed tape recordings of the experimental trials on a Panasonic monitor (65 cm screen) and scored them using a combination of focal sampling and instantaneous sampling. When using these methods, I recorded one individual at a time (focal) at a pre-selected interval of time (instantaneous; Altmann 1984, Martin and Bateson 1993). To facilitate instantaneous sampling, behaviors should be easily distinguishable when scoring trials. In this study, a 60 sec interval was established to record the behaviors of each snake over the 90 min trial duration, thus collecting 90 samples per test subject.

Using this method I could quantify behavioral data (described above) as a frequency of occurrence for the trial duration.

I recorded the total time in contact with logs (±1 sec) along with the location of each behavior exhibited within the arena. To analyze subject location patterns, the experimental arena was visually divided into: control and treated, edge (extending out 10 cm from edge of wall) and middle (all areas except the edge). Two-sample t-tests were used to evaluate amount of time that subjects spent in contact with logs. I also used two-sample t-tests on body measurements taken on day of capture to compare the sizes of male and female subjects.

I calculated the frequency of occurrence over the trial duration that each subject spent performing the different behaviors. On many occasions, snakes spent a considerable amount of time trying to escape from the arena. Therefore, I subtracted the number of observed escape behaviors from the total number of observations (n=90) before proportions were analyzed. I then used arcsin-square root transformations to standardize these proportion values prior to statistical analyses (Sabin and Stafford 1990). I used a 3-factor analysis of variance (ANOVA) in SuperANOVA (Abacus Concepts, 1990) to assess changes in behavior as a function of treatment. The independent variables were treatment, gender and behavior type. Because the number of replicates was not equal for all subjects (n = either 2 or 4), I used the mean values for each subject across all replicates within a treatment. I adjusted significance values to more conservative levels as appropriate for any post-hoc comparisons of means.
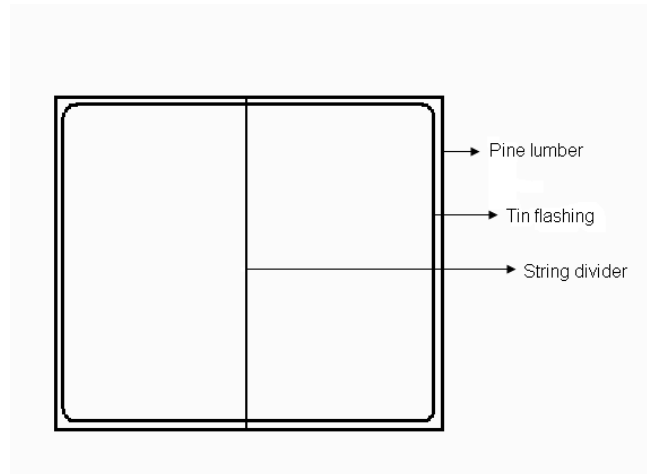
Figure 1a. The top view of the experimental arena (200 x 200 x 75 cm) where trials took place from 12 June 2007 to 11 July 2008. The arena was constructed from pine lumber with tin flashing lining the interior 50 cm from the bottom. A string was suspended to visualize the control side from the treated side.
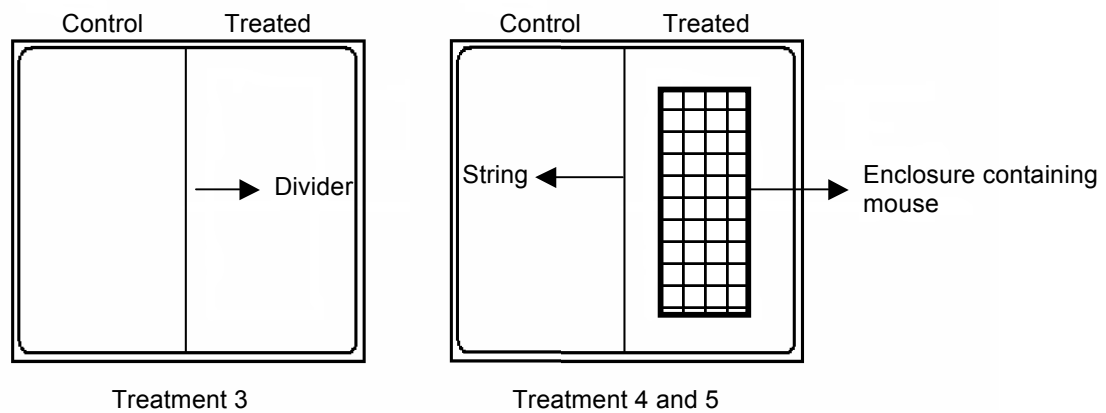
Figure 1b. Treatment 3 is illustrated with the divider (200 x 75 cm, length by height) in the center to restrict the mouse to the treated side. Treatments 4 and 5 are also illustrated with the smaller enclosure (148 x 58 x 31cm; length by width by height) to further restrict the mouse within the treated side of the test arena.

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Results

Behavioral patterns

There was no effect of treatment ($F_{4,160}$ = 0.10, p = 0.98) or gender ($F_{1,160}$ = 0.09, p = 0.76) on observed behaviors. The proportion of time subjects spent performing specific behaviors was different ($F_{3,160}$ = 130.79, p < 0.001). Snakes traveled more often than any other behavior across all treatments (Sheffe's post-hoc tests, p < 0.001; Figure 2). Resting and actively searching were performed at a similar frequency (p = 0.50), but also differed from stationary searching (p < 0.001). Stationary searching was performed least often by all subjects regardless of treatment type.

Habitat selection within testing arena

The amount of time spent in contact with logs did not differ among the different treatments (Table 1). Snakes spent more time in contact with the control log in treatment 4 than they did with the control log in treatment 2 (t = -6.37, p < 0.001). Regardless of gender or treatment condition, subjects spent more time in association with the edge areas within the testing arena ($F_{1,80}$ = 292.02, p < 0.001). Snakes spent 75±2 % of the trial duration in this microhabitat (Figure 3). Time in association with either area within the arena was not influenced by gender or treatment (F < 0.001, p ≥ 0.99).

Overall, subjects were found of on the treated side more often than on the control side of the arena, as they spent 51±1 % of the observations in the former half of the arena ($F_{1,80}$ = 3.51, p = 0.07; Figure 4). This preference was driven by female subjects exhibiting a preference for the treated side (pair-wise post-hoc comparison; F = 5.34, p = 0.02), whereas males did not (F = 0.01, p = 0.91). There was also an interaction between

treatment type and side preference ($F_{4,80} = 5.27$, p = 0.001) as snakes spent more time on the treated half of the arena in treatments 2 and 5 ($F \geq 7.04$, $p \leq 0.01$; Figure 5).

Morphometrics

Although male kingsnakes (n=7) tended to be longer and heavier than females (n=3), male and female subjects did not differ in their SVL (t = -1.7, p = 0.14) or mass (t = -1.9, p = 0.12). Tail length differed between the sexes (t = -3.05, p = 0.056) with males having longer tails (Table 2).
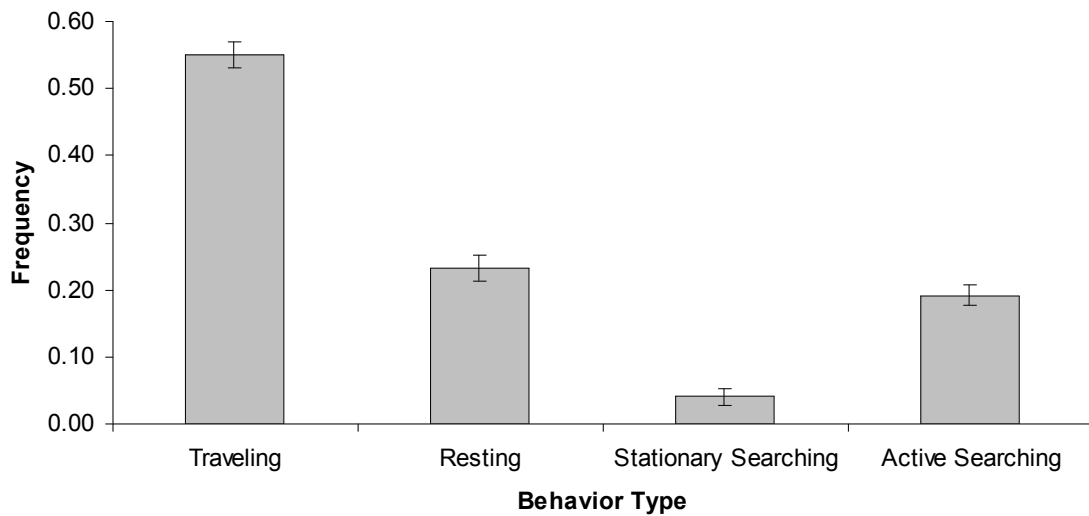

Figure 2. Proportion of total trial duration spent exhibiting each behavior type by Prairie Kingsnakes (*Lampropeltis c. calligaster*; n=10) used in foraging trials between 12 June 2007 and 11 July 2008. See Methods for detailed description of behaviors. Bars represent mean values ± 1 standard error.

Table 1. Average duration (sec) that Prairie Kingsnakes (*Lampropeltis c. calligaster;*

n=10) were observed in contact with a log in treatments 2, 4, and 5. Other treatments (1

and 3) did not involve logs as available microhabitat (see Methods for details).

Treatment #	Log Position	Mean ± SE	Min	Max
2	Control	167.20 ± 34.48	0	814
	Treated	400.53 ± 118.05	0	3365
4	Control	270.23 ± 43.17	0	831
	Treated	445.20 ± 158.48	0	4919
5	Treated	298.70±65.23	0	1782
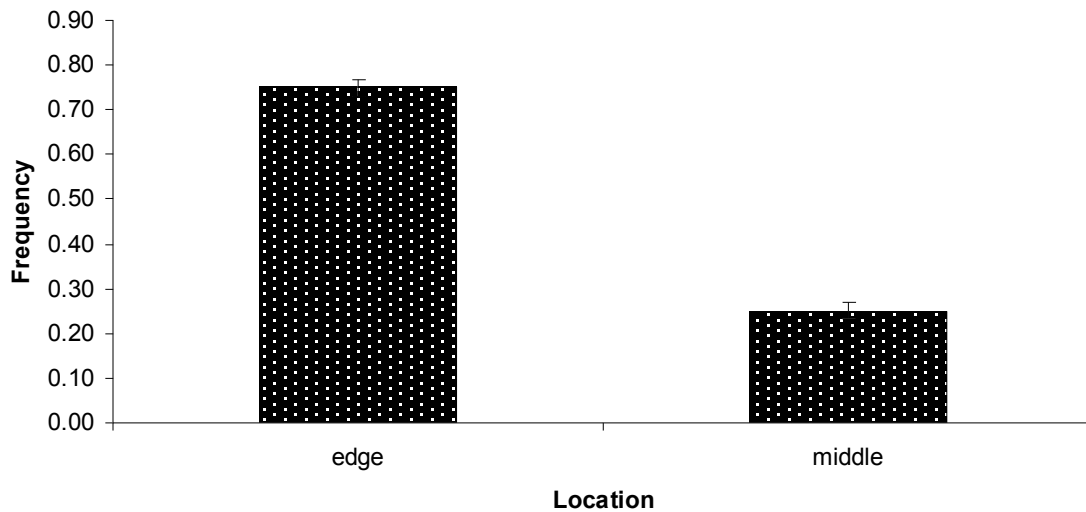
Figure 3. Proportion of trial duration that Prairie Kingsnakes (*Lampropeltis c.*

calligaster; n=10) spent in the edge and middle of the arena. Foraging trials were

conducted in a simulated habitat between 12 June 2007 and 11 July 2008. Bars indicate

mean values ± 1 standard error.

Figure 4. Proportion of trial duration subjects spent in the control and treated sides of the testing arena by Prairie Kingsnakes (*Lampropeltis c. calligaster*; n=10). Foraging trials were conducted in a simulated habitat between 12 June 2007 and 11 July 2008. Bars represent mean values ± 1 standard error.
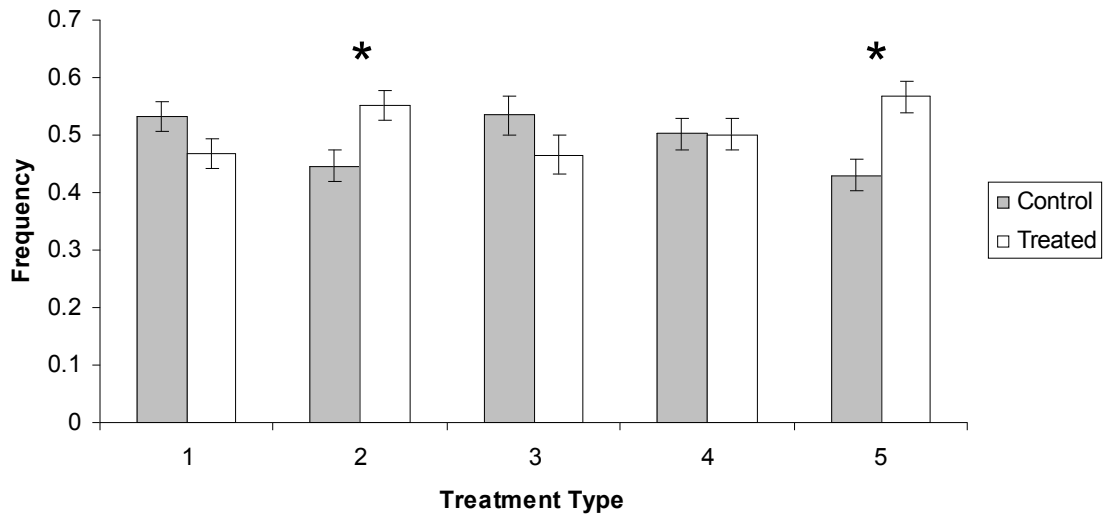
Figure 5. Proportion of trial duration that Prairie Kingsnakes (*Lampropeltis c. calligaster*; n = 10) spent in control and treated side of the testing arena as a function of treatment. Foraging trials were conducted in a simulated habitat between 12 June 2007 an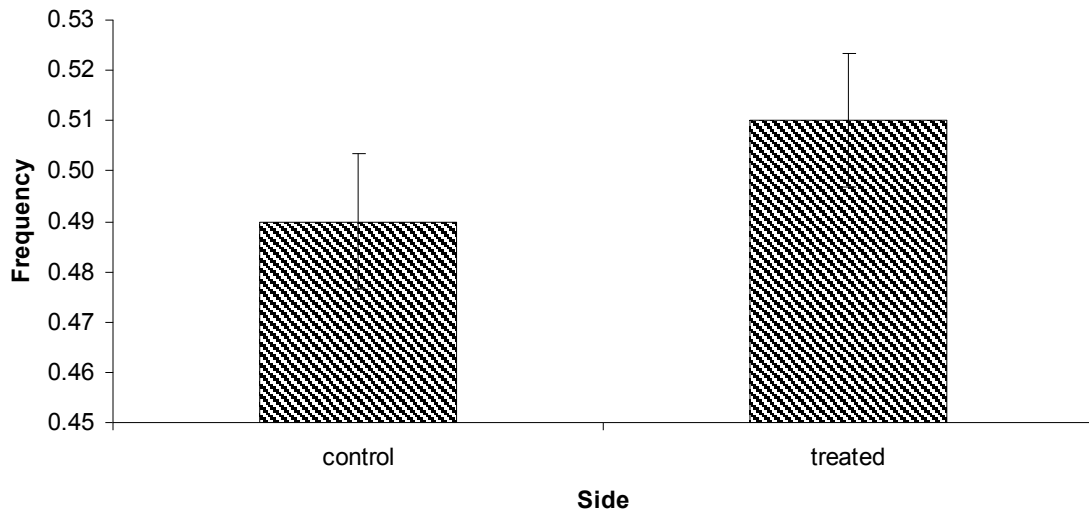d 11 July 2008. Bars represent mean values ± 1standard error; starred treatments indicate snakes spending more time on the treated side of the arena.

Table 2. Mean values and ranges for snout-vent length (SVL), tail length (TL), and mass

for female (n=3) and male (n=7) Prairie Kingsnakes (*Lampropeltis c. calligaster*) used in

foraging trials from 12 June 2007 and 11 July 2008. Means are reported ± 1 standard

error (SE).

Trait	Gender	Mean ± SE	Min	Max
SVL (cm)	F	83.50 ± 4.54	76.50	92.00
	M	94.41 ± 4.56	81.50	117.00
TL (cm)	F	10.03 ± 1.59	7.00	12.40
	M	15.26 ± 0.63	13.30	18.00
Mass (g)	F	236.83 ± 53.33	173.30	342.80
	M	367.90 ± 43.52	266.20	585.40

Discussion

Squamate reptiles exploit chemosensory information of prey in an effort to locate profitable patches of habitat (Burghardt 1980, 1990, Clark 2004a,b, Cooper 2000, Theodoratus and Chiszar 2000). Yet, there is more to a patch than just the prey item. The patch contains structural (static) elements such as vegetation, rocks, and fallen timber that are used by both predator and prey for refuge, and as landmarks for orientation (Cook et al. 2004, Orrock et al. 2004, Theodoratus and Chiszar 2000). This likely explains why Prairie Kingsnakes in my study spent more time on the treated side of the testing arena during treatments 2 and 5. Treatments 1, 3, and 4 did not show this same pattern. Treatment 2 had an unscented log in both the control and treated side while lacking prey odor on the substrate, yet more time was spent in the treated half by snakes. Treatment 5 had a similar outcome but prey odor was present only on the substrate and not on the log that intersected the pathway. This finding indicates that an important cue used by foraging kingsnakes may be first structural and then chemical. Prairie Kingsnakes are secretive and semi-fossorial like other kingsnakes (Fitch 1978, Greene and Rodriguez-Robles 2003, Richardson et al. 2006) therefore may view the log as cover, as I observed several occasions where subjects would take refuge underneath or along the underside of the log. Prey odors may not be highly detectable as they can be washed away or dissipate over time. As has been reported in other snake species (Tsairi and Bouskila 2004, Theodoratus and Chiszar 2000), kingsnakes may prioritize their choice of foraging sites based initially on structural elements in the habitat and then rely on prey odors to "fine tune" the selection of a specific foraging site.

Because most snake species rely on chemical and tactile senses when seeking prey (Burghardt and Pruitt 1975, Ford 1995), I had expected that prey chemical cues would be a primary driving force in selecting foraging sites for Prairie Kingsnakes. This expectation was not realized, however, as the proportion of time that subjects spent on the treated side in treatments 1, 3, and 4 did not differ from the control side. Unlike other species within *Lampropeltis* that feed on ectothermic prey or have a more general diet, *L. c. calligaster* feeds mostly on rodent prey (Conant and Collins 1998, Greene and Rodriguez-Robles 2003, Rodriguez-Robles and De Jesus-Escobar 1999). Given the variability in diet within the Genus, it is also plausible that the types of cues employed can be variable when choosing a foraging site. This may explain the observations from treatment 5.

Traveling by subjects was observed as often as expected, given that much of this was investigating a novel setting. It goes to reason that a predator, regardless of foraging mode, must spend some time traveling in search of profitable patches. Male subjects showed no preference for either side within the testing arena. This finding may be due to male kingsnakes having larger home ranges than females, because males are in search of potential mates (Brito 2003, Fitch 1978, Madsen 1984, Richardson et al. 2006), thus requiring a larger experimental arena than what was used in this study. Because they do not actively seek mates, female kingsnakes do not require a large home range and thus may have been able to devote more time to the treated side of the arena.

For a predator to be an optimal forager, it should not just forage in the most profitable of patches, but should also adjust its foraging tactics when suitable. According to optimal foraging theory, animals must choose the better of two patches that will yield a

greater net energy benefit and to offset costs in locating and handling the food item

(Charnov 1976, Pyke 1984). Related to this tenet is the marginal value theorem stating

that animals should respond to a patch no longer being profitable by leaving to seek prey

in a different patch (Charnov 1976). Predators must use reliable cues to find prey in

order to survive; those individuals that are unsuccessful at finding suitable prey may die.

Given that nature is stochastic, a predator cannot necessarily predict the quality of any

particular patch prior to seeking prey within it. Similarly, snake predators rarely have the

ability to detect differences in quality of neighboring patches. For these reasons, a

generalist snake, such as Prairie Kingsnakes, might benefit from being flexible in its

foraging mode while remaining within a patch (as opposed to leaving in the hopes of

finding prey elsewhere and incurring the energetic costs of doing so). Previous research

has documented behavioral shifts in foraging among different snake species in response

to changes in the biotic and abiotic variables within a patch of habitat (Mullin and

Mushinsky 1995, Mullin et al. 1998).

Prairie Kingsnakes belong to the Family Colubridae that contains many species

that are active foragers (Slip and Shine 1988). By association, I expected that this species

should actively forage for prey. A sister taxon, *Lampropeltis zonata* (California

Mountain Kingsnake), has also been described as an active forager (Greene and

Rodriguez-Robles 2003). My results validate this generalized description for the Genus

in that my subjects adopted an ambush posture least often.

The need for an ectothermic predator to thermoregulate can influence its foraging

success (Ayers and Shine 1997) as well as other behaviors. The high proportion of trial

duration that my subjects spent resting may be a result of thermoregulating, because the

floor was heated via heat tape (see Methods), even though the ambient temperature was held near a constant of 25 °C. On the other hand, resting snakes with a high body temperature might, in fact, be alert to prey items within their proximity (Ford 1995). As such, I cannot rule out the possibility that snakes that rested near logs were not adopting an ambush foraging strategy. Active foragers tend to be thermal specialists because being warm enhances their ability to catch prey and in the process of moving are not able to limit the amount of heat loss. Ambush predators, on the other hand, tend to be thermal generalists because they sit and wait for prey in what could be a poor thermal patch, hence being in a coiled position reduces the amount of heat loss (Secor and Nagy 1994, Webb et al. 2004). Because the thermal environment of the arena was relatively stable within a given trial (since the heat tape was underneath the arena floor, see Methods), the tendency for my subjects to be associated with the treated side of the arena when prey chemicals were present (as seen in treatment 5; Fig. 5) was not likely to be influenced by the thermal demands of the snakes. This conclusion is not supported by the fact that subjects in treatment 4 did not show this same trend.

Kingsnakes may have associated with the edge more frequently than the middle of the experimental arena due to their life history traits. Fitch (1978) reported finding individuals under matted vegetation or small mammal burrows. Richardson et al. (2006) tracked *L. c. calligaster* utilizing radio telemetry, observing that snakes were found underground 73% of the locations. It is possible that the snakes do not "feel safe" in an open environment (*sensu* Mullin et al. 1998), and prefer to be under cover or along an edge as a means of anti-predatory and thermoregulatory behavior. When snakes were observed along the arena edge, they were also trying to escape from the enclosure much

of the time. In hindsight, my experimental design should have adjusted the proportion of time spent along the edge in a fashion similar to the adjustment for the proportion of time snakes were recorded expressing escape behavior. Accounting for the proportion of time along the arena edge might have corrected for the edge effect that might have occurred in this study (*sensu* Krebs 1989).

Summary

My study has demonstrated that *L. c. calligaster* does not randomly select foraging sites. Kingsnakes may rely primarily on structural cues when locating profitable patches while they rely on chemosensory information secondarily to "fine tune" their selection of microhabitat in which to forage. Prairie Kingsnakes exhibited predominantly an active foraging strategy but occasionally shifted towards an ambush strategy. Although the reasons for this shift are unclear, it is evidence of this species being flexible in its foraging mode when environmental conditions are appropriate. Further studies should examine what environmental cues kingsnakes use to behaviorally shift from an active forager to an ambush forager. Such studies should also examine these foraging mode shifts differ among prey type sought by kingsnakes.

Whether lab- or field-based, experimental studies of behavioral ecology often generate more questions than answers. Such studies, especially those involving secretive species like Prairie Kingsnakes, are underrepresented in the scientific literature and often require unique technology or methodology. Richardson et al. (2006) radio tracked 10 Prairie Kingsnakes for over a year to document their habitat use, home range size, and effects of anthropogenic structures (i.e., roads). Radio telemetry has served as a good tool, but is limited by the battery life of the implanted transmitter. Repeated location of

individuals with PIT tags over longer time periods (Blomquist et al. 2008) is a promising

new direction that could be applied to kingsnake behavioral ecology. Examined over the

scope of several activity seasons that encompass more than one life history stage, a

greater understanding of kingsnake ecology might better identify their role as both a

predator and prey.

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