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Home Ranges of Gopher Snakes (*Pituophis catenifer*, Colubridae) in Central California

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Knowledge of the home range of an animal can provide insights for studies of behavioral interactions among individuals, and long-term monitoring of particular animals is necessary to determine whether they exhibit seasonal variation in space-use patterns. I radio-tracked four adult male *Pituophis catenifer* (gopher snake) in central California for 14 consecutive months to investigate spatial and seasonal movement patterns. Using the fixed kernel density estimator to produce a probability contour, the 95% home ranges of *P. catenifer* ranged from 0.89–1.78 ha, whereas their core areas (50% polygons), the most heavily used areas of their home ranges, ranged from 0.1–0.29 ha. Movements of male *P. catenifer* were similar in spring and summer and decreased in autumn and winter. The telemetered snakes were close to marshes and *Eucalyptus* woodlands but were routinely found in grassland areas, perhaps because this habitat type may provide abundant food resources and partial protection from predators. Despite their proximity, the estimated home ranges of males 2, 3, and 4 did not overlap. These findings, and those of a previous investigation of activity patterns of *P. catenifer* in eastern Nebraska, suggest that syntopic gopher snakes occupy exclusive home ranges during at least part of their active season.

WITHIN a population, individual animals typically use distinctive areas where they enact their day-to-day activities. Such areas are called home ranges. Although researchers differ in the definition of home range (Powell, 2000), the concept is used to indicate a somehow confined area that an animal uses in pursuit of its normal activities. Knowledge of the home range (= activity range) of an animal can provide insights for studies of bioenergetics (Secor, 1994), behavioral interactions among individuals (Civantos, 2000), and conservation efforts (Webb and Shine, 1997).

Pituophis catenifer (gopher snake) is a widespread snake that occurs from southwestern Canada to northern Mexico, including the Baja California peninsula, and from the Pacific Coast east to the Great Plains and Great Lakes regions of the United States (Rodríguez-Robles and de Jesús-Escobar, 2000). Gopher Snakes are primarily diurnal and are found in a variety of habitats, including woodlands, prairies, canyons, deserts, and cultivated fields (Hammerson, 1999; Werler and Dixon, 2000). As part of an ongoing investigation of the biology of *P. catenifer*, I radio-tracked four adult males for 14 consecutive months in central California to estimate their home range sizes and to determine whether they exhibit seasonal variation in space-use patterns. Because my dataset consists of frequent radio locations of individual animals over an extended period, it also provides an opportunity to assess whether snakes that are in close proximity to each other use exclusive parts of a local landscape.

MATERIALS AND METHODS

I conducted this study at Point Pinole Regional Shoreline, west Contra Costa County, California (37°59′44″N, 122°21′31″W, WGS 84 datum). The park comprises 868.9 ha of grasslands, marshes, and *Eucalyptus* forests and supports a natural population of *P. catenifer*. Four adult male (Platt, 1984; Diller and Wallace, 1996) gopher snakes (94.2–102.3 cm snout–vent length, 301.5–375.6 g) were captured at Point Pinole between 21 and 26 April 1997 and brought to the laboratory where 9.15-g radio-transmitters (Model SI-2, Holohil Systems, Ltd., Ontario, Canada) were implanted intraperitoneally following the procedure described by Reinert and Cundall (1982) and Reinert (1992). Transmitters weighed 2.4–3% of snakes' body mass and were not replaced during this study. I released the snakes at their capture sites the day after the surgeries were performed. I radio located the four males one to four times per week, between 11 May 1997 and 8 July 1998, using a TRX-2000S PLL synthesized tracking receiver (Wildlife Materials, Inc., Carbondale, IL). Male 3 was monitored only until 17 January 1998, when he was found partially eaten. Judging by the nature of the injuries in the carcass, male 3 was probably killed by a *Buteo jamaicensis* (red-tailed hawk), a year-round resident at Point Pinole (N. K. Johnson, pers. comm.) and a known, common predator of gopher snakes in central California (Fitch et al., 1946) and elsewhere (Smith and Murphy, 1973; Steenhof and Kochert, 1985). Each time I located a snake, I took five positional readings with a Garmin 12XL Global Positioning System (GPS) unit at 2-min intervals and used their average as the coordinates for that particular animal's location that day.

I calculated home ranges using the kernel density estimator (Worton, 1989; Powell, 2000). This estimator is a nonparametric statistical method that incorporates the density of known animal locations, giving more weight to frequently used areas, to produce a home range probability contour of any shape. I chose the width of the kernel (variously called the band width, window width, smoothing parameter, or *h*) using least-squares cross-validation (LSCV) and held this parameter constant for the locational dataset of a particular snake (fixed kernel). The fixed kernel estimator with LSCV produces the most accurate estimates of home-range areas and shapes of the density contour (Worton, 1995; Seaman and Powell, 1996; Seaman et al., 1999). Kernel-based methods have recently become popular and have been used to study activity ranges of a wide array of vertebrates, including turtles (Lewis and Faulhaber, 1999; Morrow et al., 2001), birds (Plissner et al., 2000; Thogmartin, 2001), rodents (Ribble and Stanley, 1998; Taulman and Seaman, 2000), and seals (Sjöberg and Ball, 2000), but to my knowledge, no previous study of snake activity patterns has employed this approach. I used the Animal Movement Analysis Extension (P. N. Hooge and B. Eichenlaub, 1997. Animal movement extension to ArcView, version 1.1. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage, AK) of the ArcView GIS 3.2 software program (Environmental Systems Research Institute, Inc., 1999) to calculate fixed kernel home-range estimates. I determined 95% probability contours (the area where the animal was found 95% of the time), and 50% polygons, which allowed me to identify core areas, the most heavily used areas of the estimated home ranges.

To facilitate comparisons with previous studies, I also estimated home ranges using the 95% minimum convex polygon (5% of the outlying points were removed using the harmonic mean method; Dixon and Chapman, 1980). The minimum convex polygon estimates the home-range area by connecting the outer locations to form a polygon. This simple and easy method has several major disadvantages (White and Garrott, 1990; Powell, 2000); therefore, it only provides a crude outline of an animal's home range.

Using my dataset to calculate mean distance traveled by gopher snakes between successive radio locations was not appropriate because the accuracy of the readings was approximately 30 m, and the telemetered animals typically moved shorter straight-line distances from one location to the next. Signals from the GPS satellites were scrambled by the U.S. military during the duration of this study and differential correction was not feasible. Nevertheless, my data were suitable for estimating total home-range and seasonal movement patterns (H. K. Reinert, pers. comm.).

Results and Discussion

The 95% fixed kernel home ranges of male *P. catenifer* at Point Pinole ranged from 0.89–1.78 ha, whereas their 50% probability contours varied between 0.1 and 0.29 ha (Table 1). The 95% polygons of each of the four telemetered individuals had disjunct areas (= ''islands'') of habitat use (Fig. 1), but there were no obvious habitat differences between those islands. Males 2 and 4 each had two home-range areas, whereas males 1 and 3 each had three. Judging by their radio locations (Fig. 1), at least males 1 and 4 used the area separating their respective home-range islands. With the exception of male 3, the radio-tracked snakes displayed single core areas (50% polygons) within their estimated home ranges (Fig. 1).

The smallest island of habitat use of Male 1, and five of the six radio locations to the north and to the west of the largest home-range island of this snake were occupied during the final 10 weeks of this study (29 April to 8 July 1998). Similarly, the smaller home-range island of male 4 and five of the nine radio locations that fell outside its 95% probability contour corresponded to dates between 29 April and 6 June 1998, but subsequent locations fell within the 95% probability polygon. These findings suggest that males 1 and 4 may have slightly shifted their

TABLE 1. FIXED KERNEL (WITH LEAST-SQUARE CROSS-VALIDATION) AND 95% MINIMUM CONVEX POLYGON HOME-RANGE ESTIMATES FOR FOUR MALE *Pituophis catenifer* AT POINT PINOLE REGIONAL SHORELINE, CONTRA COSTA COUNTY, CALIFORNIA. Number of radio locations for each snake is indicated in parentheses.

Fixed kernel			95% minimum convex polygon	
Snake	Density contour	Home-range area (ha)	Snake	Home-range area (ha)
Male 1	95%	1.57	Male 1	2.29
(n = 104)	50%	0.17	(n = 99)	
Male 2	95%	0.89	Male 2	0.97
(n = 104)	50%	0.10	(n = 99)	
Male 3	95%	1.78	Male 3	1.45
(n = 83)	50%	0.29	(n = 79)	
Male 4	95%	1.09	Male 4	2.26
(n = 103)	50%	0.17	(n = 98)	
Average	95%	1.33 (±0.41)	Average	1.74 (±0.64)
(±SD)	50%	0.18 (±0.08)	(±SD)	

home ranges when I stopped monitoring them, although male 4 returned to an area that it had previously occupied. In comparison, males 2 and 3 maintained a more constant activity range throughout this investigation. In the Sierra Nevada foothills of central California, two adult male *P. catenifer* were recaptured at distances of approximately 137–152 m from their place of release six years before, and another adult male was recaptured 61 m away after three years (Fitch, 1949), indicating significant site fidelity. Gopher snakes from eastern Nebraska also maintained similar home ranges from one year to the next (J. J. Fox, 1986, Ecology and management of the bullsnake, *Pituophis melanoleucus sayi* in the Nebraska sandhills: final report, Crescent Lake National Wildlife Refuge, Nebraska).

Pituophis catenifer at Point Pinole spend a considerable amount of time underground, since they were in burrows during 90% of radio locations (see also Sterner et al., 2002). Unlike many other large-bodied snakes, *P. catenifer* often seizes its victims in their subterranean retreat sites and nests (Klauber, 1947; Gehlbach, 1965). Further, gopher snakes beginning the shedding cycle stay underground for several days (Jennings et al., 1996; Shewchuk, 1996; pers. obs.), a behavior that may help reduce cutaneous water loss (Lillywhite and Maderson, 1982) and provide protection from predators during the vulnerable ''opaque'' period when vision is impaired.

Many North American snakes show bimodal seasonal movements, with peaks in spring and autumn (e.g., *Crotalus atrox* [western diamond-backed rattlesnake], *Micrurus fulvius* [harlequin coralsnake], *Coluber constrictor* [eastern racer], *Heterodon platirhinos* [eastern hog-nosed snake]), whereas other species have unimodal activity cycles (e.g., *Crotalus oreganus* [fide Ashton and de

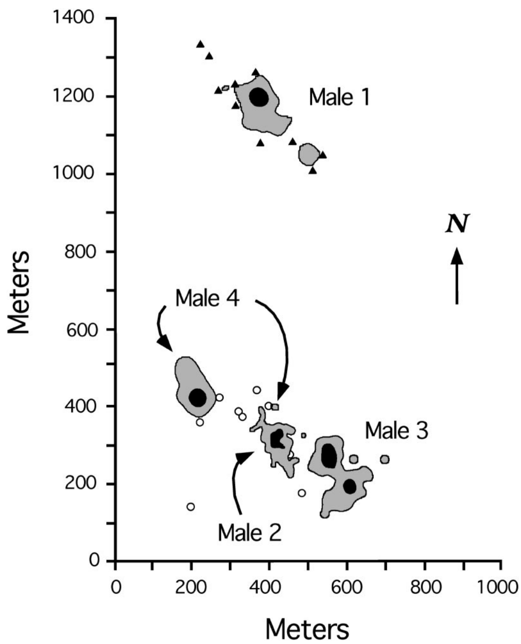

Fig. 1. Fixed kernel density home-range estimates (using least-squares cross-validation) for four male *Pituophis catenifer* at Point Pinole Regional Shoreline, Contra Costa County, California. Gray and black areas represent the 95% and 50% probability polygons, respectively. For male 1 (black triangles) and male 4 (empty circles), locations that fell outside the estimated home ranges are indicated. All radio locations of male 2 and male 3 fell within their respective 95% polygons.

Queiroz, 2001; western rattlesnake], *Tantilla coronata* [southeastern crowned snake], *Cemophora coccinea* [scarlet snake; Oliver, 1955; Gibbons and Semlitsch, 1987; Diller and Wallace, 1996]). In western Utah, *P. catenifer* was most active in May and July (Fautin, 1946), whereas the peak

TABLE 2. DIFFERENCES IN SEASONAL HOME-RANGE AREA ESTIMATES (CALCULATED USING THE FIXED KERNEL METHOD WITH LEAST-SQUARES CROSS-VALIDATION) OF MALE *Pituophis catenifer* AT POINT PINOLE REGIONAL SHORELINE, CONTRA COSTA COUNTY, CALIFORNIA. Numbers in parentheses on the Season column indicate total number of observations of males 1, 2, 3, 4, respectively, in that season.

Season	Density contour	Mean home-range area (±SD; ha) (n = 4 for all means)
Spring (32, 32, 19, 31)	95%	2.20 (±2.06)
	50%	0.40 (±0.40)
Summer (34, 34, 32, 34)	95%	1.10 (±0.27)
	50%	0.17 (±0.03)
Autumn (26, 26, 26, 26)	95%	0.43 (±0.17)
	50%	0.08 (±0.03)
Winter (12, 12, 6, 12)	95%	0.31 (±0.20)
	50%	0.05 (±0.05)

95% density contour, Kruskal-Wallis test, $H = 9.99$, df = 3, $P = 0.019$
50% density contour, $H = 10.3$, df = 3, $P = 0.016$

of activity of male gopher snakes in southwestern Idaho occurred from mid-May to early June (Diller and Wallace, 1996). At Point Pinole, there were significant differences in home-range size among seasons (Table 2). Multiple comparison tests indicated that all but the spring-summer pairwise differences of the 95% probability contours were significant, as were four of the six comparisons of the 50% polygons, the exceptions being the spring-summer and autumn-winter pairwise differences. Judging exclusively by these findings, movements of male *P. catenifer* at Point Pinole are similar in spring and summer and decrease in autumn and winter, as could be expected for ectothermic animals.

Gopher snakes are good swimmers (Howitz, 1986) and excellent climbers (Marr, 1985; Eichholz and Koenig, 1992), but despite the proximity of the telemetered animals to marshes and *Eucalyptus* woodlands, they were routinely found in grassland areas and only rarely on the edges of forested areas. Even during periods of low population densities (Krebs, 1966; Batzli and Pitelka, 1971; Pearson, 1971), *Microtus californicus* (California vole) undoubtedly is the most common small vertebrate in grasslands at Point Pinole, where it makes runways through the vegetation and burrows extensively (J. L. Patton, pers. comm.). Gopher snakes at Point Pinole and nearby localities prey on *M. californicus* (pers. obs.), and when the telemetered males were seen active aboveground, they were commonly using *Microtus* runway and burrow systems when foraging and fleeing. In addition to California voles, other prey of *P. catenifer* at Point Pinole can travel through *M. californicus* runways, including *Reithrodontomys megalotis* (western harvest mouse), *Thomomys bottae* (Botta's pocket gopher), *Elgaria multicarinata* (southern alligator lizard), and *Sceloporus occidentalis* (western fence lizard; cf. Pearson, 1959; Rodríguez-Robles, 2002). Therefore, these passages constitute excellent sites for gopher snakes to forage, and at the same time can provide at least partial concealment from potential predators that occur at Point Pinole (i.e., *Vulpes vulpes* [red fox], *Felis catus* [feral domestic cat], *Buteo jamaicensis*, *B. lineatus* [red-shouldered hawk], *Elanus leucurus* [white-tailed kite], *Circus cyaneus* [northern harrier]; pers. obs.; J. L. Patton, pers. comm.). Gopher snakes from eastern Nebraska (J. J. Fox, 1986, Ecology and management of the bullsnake, *Pituophis melanoleucus sayi* in the Nebraska sandhills: final report, Crescent Lake National Wildlife Refuge, Nebraska) and southern British Columbia, Canada (Shewchuk, 1996) also use *Microtus* runways for their foraging activities, indicating that this is a common behavioral pattern for *P. catenifer.*

Despite their proximity, the estimated home ranges of males 2, 3, and 4 did not overlap, although male 4 was occasionally found in close proximity to the 95% polygons of males 2 and 3 (Fig. 1). A previous investigation of *P. catenifer* in eastern Nebraska also suggested that individuals inhabit nonoverlapping ranges when active (J. J. Fox, pers. comm. to Gregory et al., 1987). At Point Pinole, abundant food resources could account for the sedentary behavior in gopher snakes, but other explanations are conceivable (e.g., mutual avoidance of conspecifics, territorial behavior). Additional field studies involving relatively large numbers of syntopic individuals are necessary to determine whether gopher snakes indeed occupy exclusive home ranges during at least part of their active season and, provided they do, to elucidate the factors responsible for this behavior.

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