Radiotelemetric Study of Activity and Movements of Racers (*Coluber constrictor*) Associated with a Carolina Bay in South Carolina

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Racers (*Coluber constrictor*) were monitored with radiotelemetry in an old field/forest habitat surrounding a Carolina bay in South Carolina. Racers were active on approximately 70% of days; inactive snakes usually were in ecdysis. Active racers were relocated on the ground surface (40%), above ground in shrubs and trees (35%), and underground (25%). Habitats in which racers were relocated were thickets and grassland shrubs (50%), woodland/forest (25%), and grassland (25%). Active snakes moved an average of 104 m/d within home ranges averaging 12.2 ha estimated as minimum convex polygons. The home range of each snake included at least a portion of the bay and overlapped with home ranges of other snakes. In comparison with other studies of racers in which data were collected, analyzed, and presented in the same manner as in this study, home range size and daily movement of South Carolina racers were significantly greater. Possible explanations for the greater movement include trophic level differences and a proximate response to a local drought.

COMPARATIVE studies of snake populations in wide-ranging species may provide opportunities to identify and resolve differences in life-history tactics (Dunham et al., 1988; Parker and Plummer, 1987). The racer, *Coluber constrictor*, has an extensive geographic distribution in North America (Conant and Collins, 1991), and its life history and ecology have been studied in Utah, Kansas, and Michigan (Brown and Parker, 1984; Fitch, 1963; Rosen, 1991). Interesting geographic differences in population characteristics have been reported among these northern and western racer populations (Brown and Parker, 1976, 1984; Rosen, 1991). Studies of southern and southeastern populations are needed to augment this body of information (Rosen, 1991).

Rather than being fixed characteristics of a species, activity and movement of individual snakes vary among populations, presumably reflecting differences in responses to local environments (Gibbons and Semlitsch, 1987; Gregory et al., 1987; Mace et al., 1984). In this paper, we describe the spatial use of habitat by racers in a southeastern population and compare our results with those of studies from Utah and Kansas. Because comparison of snake movements among studies is laden with difficulties (Shine, 1987; Macartney et al., 1988), we compare studies only when methodologies similar to ours were used, and we adjust results according to sample size differences.

MATERIALS AND METHODS

The study area centered on Field 3-412 and Ellenton Bay on the Department of Energy's Savannah River Site near Aiken, South Carolina. Field 3-412 is an old field (abandoned in 1952) of the lowland floodplain terrace. The primary vegetation consists of grassland (67% by area covered) interspersed with *Lespedeza* spp., various forbs, woody shrubs, and bare soil (J. R. Jensen, M. E. Hodgson, J. Pinder, B. S. Collins, and H. E. Mackey, Jr., Savannah River Operations Office Rep. DP-MS-87-111, 1987, unpubl.). Other vegetation includes thickets (22% coverage) of plum (*Prunus angustifolia*) and briars (*Rubus* spp.) and scattered clumps of trees (6%) consisting of oak (*Quercus laurifolia*) and pine (*Pinus taeda*). The old field is surrounded by either mixed hardwood forest or planted pine forests of various ages. Ellenton Bay is an approximately 10-ha Carolina bay typical of the area. A road embankment 5–6 m wide crosses the bay along its minor axis. Gibbons (1990) described the climate and aquatic habitats associated with the bay area.

Racers were collected in wire-mesh funnel traps set along a permanent aluminum drift fence surrounding Ellenton Bay. Racers were sexed and measured (SVL, mass). A temperature-sensitive radiotransmitter (Model CHP-2P, Telonics Inc., Mesa, Arizona) was implanted in each racer, following the procedures of Reinert

Snake no.	Sex	SVL (cm)	Date	No. days monitored	Days active (%)	Inactive days in ecdysis (%)	Movement on active days (m/day)	Home range (ha)
1	F	87.5	J	72	74	84	135 ± 15	13.7
2	F	76.3	J	72	75	67	116 ± 11	18.4
3	M	85.0	J	72	69	77	73 ± 11	12.7
7	F	78.5	A	51	82	67	104 ± 12	7.9
8	F	93.0	A	46	63	82	74 ± 10	6.7
9	F	75.0	A	51	75	46	134 ± 23	20.5
10	F	78.5	A	51	67	59	83 ± 10	5.3
Mean	—	82.0	—	59	72	69	104 ± 5	12.2

(1992). Transmitter mass was a maximum of 5% of snake mass. Each snake was relocated once daily, and its location was plotted on an aerial photograph of the study area. Data collected on individuals during successive daily relocations were considered to be independent (White and Garrott, 1990). At each relocation, observations on activity, behavior, habitat, and snake condition were noted at approximately the same time each day. At each relocation, snakes were considered "inactive" if their location was <5 m from the previous day's location and "active" if their location was ≥5 m from the previous day's location. Ten radiotagged racers were released at their sites of capture and monitored for various periods from mid-July to mid-Oct. 1989. Two snakes were lost to predators early in the study (Plummer and Congdon, 1992). The bulk of the data, designated as "summer," were collected on seven snakes through 30 Sept. A few data, collected 1–18 Oct., were designated as "fall." Minimum convex polygon estimates of home ranges were calculated with McPAAL Ver. 1.21 (Michael Stuwe, National Zoological Park). The alpha-level for all statistical tests was 0.05.

RESULTS

In the summer, snakes were active on 72% of days (Table 1). On about 50% of days, active snakes were relocated in shrub habitats (thickets
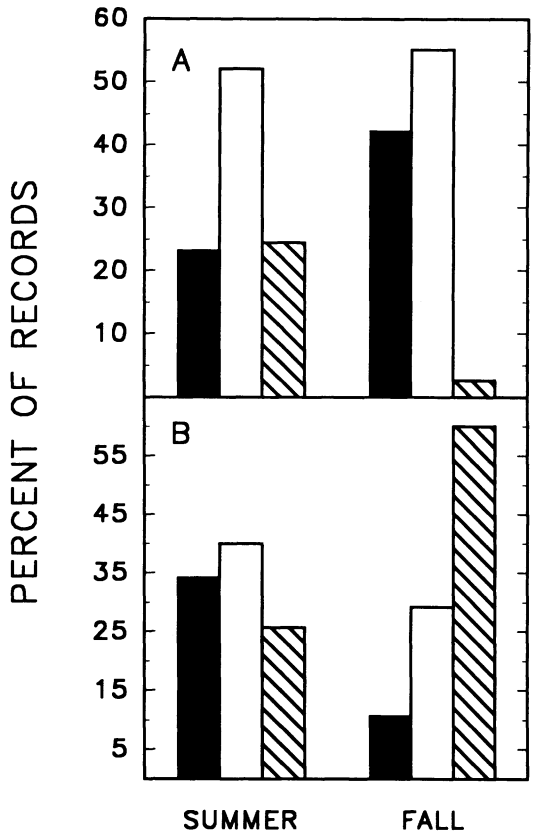

Fig. 1. (A) Percent of relocations of snakes in grassland habitat (dark bars), in thicket/grassland shrub habitat (light bars), and in tree habitat (crosshatched bars) in the summer (n = 420 relocations on seven snakes) and in the fall (n = 78 relocations on six snakes). (B) Percent of relocations of snakes above ground (dark bars), on the ground surface (light bars), and underground (crosshatched bars) in the summer (n = 300 relocations on seven snakes) and in the fall (n = 65 relocations on six snakes).

or grassland shrubs) and, on about 25% of days, in habitats dominated by either grasses/*Lespedeza* or trees (Fig. 1A). Active snakes were relocated above ground in trees or shrubs on about 35% of days, on the ground surface 40% of days, and underground in rodent burrows on about 25% of days (Fig. 1B).

On at least 70% of inactive days and on 19 occasions when snakes were inactive for >3 consecutive days, 17 (90%) were associated with snakes in ecdysis. On the remaining two occasions when snakes were inactive for >3 days, the snakes were strongly suspected to be in ecdysis based on their individual shedding histories and their behaviors. Snakes known to be in ecdysis most often took refuge underground in rodent burrows (n = 10) but also in trees (n = 2), on the ground surface (n = 1), or in com-
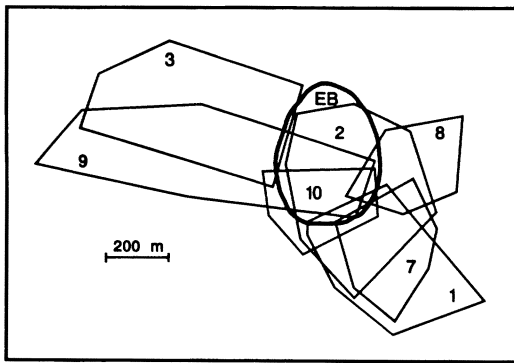
Fig. 2.   Minimum convex polygon home ranges of seven racers relative to Ellenton Bay (EB, heavy outline). Numbers identify the home ranges of individual snakes.
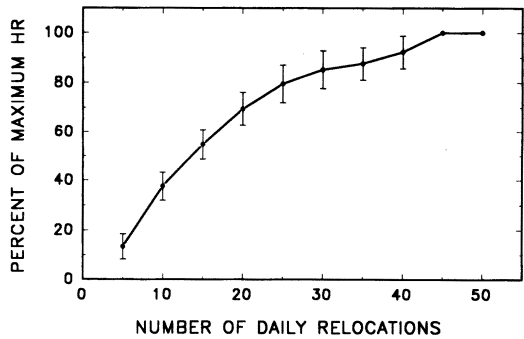

Fig. 3.   The relationship of the relative size of home range and the number of daily relocations of active (excluding days of no movement) racers. Plotted are mean ± 1 SE except for days 45 and 50 when data were available for only one snake.

binations of underground and surface or underground and above-ground locations (n = 4).

Compared to summer, snakes in the fall were less active (50%; $\chi^2 = 13.6, P < 0.01$), spending more time underground in grassland habitats (Fig. 1). Frequency of arboreality also declined in the fall (Fig. 1B). Frequency of arboreality by month was July 48%, Aug. 45%, Sept. 21%, and Oct. 10%.

Each snake was initially captured at the drift fence at Ellenton Bay. Subsequent relocations included portions of the bay in each snake's home range (Fig. 2). Water level in the bay was very low during this study, and all relocations within the bay proper were on emergent land. The home range of one racer (no. 2) included most of the bay; six relocations were within the bay proper. Two other racers (nos. 9, 10) moved over one end of the bay and averaged three relocations in the bay proper. The remaining four racers (nos. 1, 3, 7, 8) moved mostly along the bay's margin; only one relocation among the four snakes was in the bay proper. Four

telemetered snakes were recaptured five times in traps averaging 12 m (range 4–29) from the trap of initial capture for each snake. Home ranges of individual snakes overlapped extensively (Fig. 2). In summer, active snakes moved an average of 104 m/d (n = 277) within home ranges averaging 12.2 ha in area (Table 1). Neither home range size nor movement per day was related to body size of snake (Table 2). Movement decreased in fall (70 ± 9 m/d; n = 39; t = 2.42, $P < 0.01$). Size of home range increased rapidly with the number of captures of active snakes up to about 25 relocations when an average of 80% of the maximum home range was traversed (Fig. 3). At 35 relocations, home range size averaged 90% of an individual's maximum (Fig. 3).

DISCUSSION

Frequency of daily activity of racers in South Carolina (72%) was similar to that of telemetered racers in Kansas (80%; Fitch and Shirer,

TABLE 2.   COMPARISON OF BODY SIZE AND MOVEMENT CHARACTERISTICS OF RACERS IN THREE RADIOTELE-METRIC STUDIES. Movements are for summer only and do not include migratory movements. For movement rate, incl. = includes days of no movement, excl. = excludes days of no movement. Home range (HR) size in Kansas racers were calculated with McPAAL by digitizing the home ranges in figure 2 of Fitch and Shirer (1971). All home ranges were estimated by minimum convex polygon methods. Correlations of SVL and movement rate (MR) excludes days of no movement. Studies are KS = Fitch and Shirer (1971); UT = Brown and Parker (1976); SC = present study. Also included are unpublished data provided by H. S. Fitch and W. S. Brown. Means of SVL and HR include ±1 SD (range). All correlations are nonsignificant ($P > 0.30$).

Study	n	SVL (cm)	Movement rate (m)		HR size (ha)	Correlation of SVL and	
			Incl.	Excl.		HR	MR
KS	7	82 ± 4.3 (75–89)	28	37	2.5 ± 1.65	−0.08	−0.43
UT	9	71 ± 3.4 (60–77)	—	33 ± 4	0.4 ± 0.34	−0.26	−0.29
SC	7	82 ± 6.7 (75–93)	66 ± 4	104 ± 27	12.2 ± 5.86	−0.45	−0.43

1971) and to that of the closely related *Masticophis flagellum* in California (76%; Secor, 1992). In this study, frequency of daily activity in the summer appeared to be limited primarily by ecdysis and not by environmental constraints (Peterson, 1987). The restricted movement and reclusive behavior observed in shedding racers has been noted in radiotelemetric studies of several species of both viperid (Galligan and Dunson, 1979; Brown et al., 1982; Macartney, 1985) and colubrid snakes (Madsen, 1984; Weatherhead and Charland, 1985; MVP, unpubl.).

Racers in South Carolina spent similar time on the ground surface (50%) and underground (22%) compared to telemetered racers in Kansas (40%, 32%; Fitch and Shirer, 1971). Telemetered racers in Utah also spent similar time on the surface (35%) but spent more time underground (65%; Brown and Parker, 1982). Frequency of arboreality appears to be greater in racers in South Carolina (34%) than in Kansas (19%) or Utah (0%). Finding female racers to be less arboreal (7%) than males (24%), Fitch and Shirer (1971) suggested that the sexual difference was a result of the larger body size of females. South Carolina racers (one male, six females) were postreproductive and had SVLs similar to Kansas males (South Carolina 82 ± 6.7 cm, Kansas 82 ± 4.3; t = −0.06, df = 12, $P > 0.95$), yet still were more arboreal. Arboreal racers were often inconspicuous to us and were less wary than those on the ground surface. Compared to terrestrial racers, arboreal racers were more often immobile and permitted closer approach before initiating escape behavior. Such behavior contrasts with the behavior of terrestrial racers (Fitch, 1963; Fitch and Shirer, 1971; pers. obs.) and may be widespread in normally arboreal snakes (Plummer, 1981; Greene, 1988). Fitch (1963) noted that racers may climb to escape danger.

Geographic differences in life history and movement ecology among populations of racers in Utah, Kansas, and Michigan were summarized by Brown and Parker (1976, 1984) and Rosen (1991). Relatively long-range migratory movements between summer ranges and winter hibernacula occurred in each of these northern populations (39–42°N latitude). Although not studied, it is unlikely that such migratory movements occur in the more southern South Carolina racers (33°N latitude) because of the mild winters and high local availability of rodent burrows for short-term brumal refuge (Gregory, 1982; 1984). In addition, there is no evidence suggesting migratory movements in the Ellenton Bay population based on mark-recapture studies (R. A. Seigel, pers. comm.). Within the summer activity season, movements of nonreproductive racers are confined to home ranges (Brown and Parker, 1976; Fitch and Shirer, 1971; Rosen, 1991; present study), which, in some cases, are used by the same individual in successive years (Brown and Parker, 1976). Occasional excursions from the home range may occur, as when gravid females search for oviposition sites (Brown and Parker, 1976) or for unknown reasons (Plummer and Congdon, 1992).

Size of home range in snakes is considered to be an important ecological trait which may be related to resource availability (reflecting community productivity) and body size (reflecting the animal's energetic needs; Gregory et al., 1987; Mace et al., 1984; Macartney et al., 1988). Although comparisons of movements among studies should increase our understanding of why snakes move as they do, such comparative studies often are laden with difficulties (Shine, 1987; Macartney et al., 1988). We attempted to minimize bias resulting from different methodologies by comparing our data only with those from studies of racers in which home ranges were determined as minimum convex polygons using location data obtained by radiotelemetry. We found that home ranges in South Carolina racers were significantly greater than those of racers in both Kansas and Utah (Table 2; ANOVA, $F_{2,20} = 26.5$, $P < 0.001$, Scheffe). Determining home range size depends heavily on assumptions of the particular home range estimation procedure used (White and Garrott, 1990). In squamates, for example, home range size determined by the minimum convex polygon method often is a function of sample size (Rose, 1982; Madsen, 1984; Secor, 1992). Because home ranges of racers in Kansas and Utah were determined with fewer relocations than in our study, we used the relationship between number of relocations and relative home range size (Fig. 3) to adjust the mean South Carolina home range according to sample sizes given by Fitch (1963) for Kansas racers and Brown and Parker (1976) for Utah racers. The resulting mean home ranges for racers in South Carolina adjusted for sample size in Kansas (8.5 ha) and Utah (4.9 ha) still suggest that home ranges in South Carolina are larger than those in Kansas and Utah.

Because a home range estimate is a calculated value with underlying assumptions, perhaps more meaningful comparisons among studies may be made by comparing actual movement data (Gregory et al., 1987; Macartney et al., 1988; White and Garrott, 1990). Excluding days of no movement, mean daily movement within

home ranges in the summer of South Carolina racers was significantly greater than such values reported for racers in Kansas and Utah (Table 2; ANOVA, $F_{2,20} = 31.0$, $P < 0.001$, Scheffe). Movement in South Carolina racers was equivalent to that reported for Utah racers moving between hibernacula and summer ranges (100 m/d) which was more than three times their normal daily movement rates within home ranges (Brown and Parker, 1976). Our estimate of movement per day is conservative because it does not include the more extensive movements of males in the spring as they search for females, nor does it include reproductive females searching for nesting sites (Macartney et al., 1988; Plummer, 1990). Our estimate also underestimates actual distance moved because we could not account for the actual path taken by racers between relocation points (as also is true of the earlier tracking studies). Actual distances moved by a closely related species, *Masticophis flagellum*, averaged 1.4 times the measured distances between relocation points (Secor, 1992).

Differences in transmitter placement could possibly confound interstudy comparisons. Transmitters in the Kansas racers and in most of the Utah racers were positioned intragastrically which, because of possible satiation stimuli, may have increased basking and decreased foraging and, thus, decreased the frequency and length of movements (Fitch and Shirer, 1971; Fitch, 1987; Lutterschmidt and Reinert, 1990). To test this possibility, we compared Brown and Parker's (1976) data on movement per day and home range size of racers with transmitters positioned intraperitoneally (31.8 m/d, 0.18 ha, n = 4) to those with transmitters positioned intragastrically (33.7 m/d, 0.52 ha, n = 6). We found no differences in either movement per day (t = 0.22, $P > 0.80$) or in home range size (t = 1.78, $P > 0.10$), suggesting that transmitter placement did not affect movements.

Our approach to comparing home range size and movement rate among populations suggests the existence of real biological differences, i.e., South Carolina racers move more than racers in Utah and in Kansas. These differences cannot be the result of different relative "observability" among habitats or different activity levels among populations because the comparable methods of radiotelemetry eliminate these observer biases (Shine, 1987). Why then, do these racers move as they do (Gibbons and Semlitsch, 1987)? Possible influences on movement rate include differences in body size (length, SVL; and proportion, body mass/SVL). Body mass/SVL among males and nongravid females did not differ among populations (ANOVA, $F_{2,18} =$

0.22, $P > 0.80$). We found no significant relationship between SVL and either home range size or distance moved per day within populations (Table 2) or among populations (home range, r = 0.32, $P > 0.10$; movement r = 0.24, $P > 0.27$). Utah racers, with the smallest body sizes (SVL and body mass), had the smallest home range size and daily movement rate. South Carolina and Kansas racers had larger and similar body sizes (SVL and body mass) but differed significantly in home range size (t = 4.2, df = 12, $P < 0.01$) and in daily movement rate (t = 5.6, df = 12, $P < 0.001$). Relative trophic position of racers also could affect movements. Utah racers are insectivorous secondary consumers feeding primarily on locally abundant orthopterans (Brown and Parker, 1982; W. Brown, pers. comm.). Kansas racers also eat a large number of insects but also frequently eat vertebrates (Fitch, 1963). In contrast, southeastern racers (Georgia, South Carolina) appear to be exclusively tertiary consumers feeding on a variety of vertebrate prey (Hamilton and Pollack, 1956; R. Seigel, pers. comm.; pers. obs.), which typically are more widely dispersed. It appears that Utah racers have physical (body size) and physiological (trophic) attributes that are related to a more sedentary way of life. The large difference in movements between Kansas and South Carolina racers also may be partially explained by trophic differences but not by body size differences.

The greater movement of South Carolina racers could possibly have involved a proximate temporal response to a deteriorating local environment. The initial capture of each racer was at the margin of Ellenton Bay. A continuous strong attraction for the bay was apparent because all snakes included the bay in their movements as evidenced from both recapture and telemetric data. Water level in the bay typically is highly variable (Gibbons, 1990) and is known to influence the diversity and abundance of semiaquatic turtle and snake species using the bay (Gibbons et al., 1983; R. Seigel and J. W. Gibbons, unpubl. data). After a severe drought in 1985–87, the bay was essentially dry when this study was conducted in 1989 (R. Seigel and J. W. Gibbons, unpubl. data). Thick herbaceous vegetation growing on soggy soils surrounded small pools of water on each side of the embankment and extended out to the bay's normal high-water margin. The long-term drought and dry bay with a resulting probable decrease in prey availability (e.g., frogs) may have stimulated more wide-ranging foraging than when the bay was at normal levels. In lizards, size of home range may be negatively related to abun-

dance of food both naturally (Simon, 1975; Krekorian, 1976) and when manipulated experimentally (Simon, 1975). Water levels in Ellenton Bay returned to normal levels in 1990 (R. Seigel and J. W. Gibbons, unpubl. data). A study of the movements of *Coluber* at Ellenton Bay during normal hydric conditions would be an interesting test of this hypothesis.

Neither the energetic cost of locomotion in *Coluber* (Walton et al., 1990) nor the cost of activity in the energy budgets of reptiles is trivial (Congdon et al., 1982). The cost of locomotion is a major component of the activity budget in a closely related species, *Masticophis flagellum* (Secor, 1992). Relatively greater movement is energetically more expensive among squamate species (Anderson and Karasov, 1981; Huey and Pianka, 1981; Secor, 1992). The greater movement of South Carolina racers compared to that reported in racers from Kansas and Utah suggests the possibility that geographic differences in other variables relating to energetics may exist (e.g., life-history traits). Although foraging is prominent among those snake activities that can be acted on by natural selection (Gibbons and Semlitsch, 1987), whether the movement differences documented here resulted from increased foraging and are genetically based is unknown.

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