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Ecological Parameters of *Coluber constrictor etheridgei*, with Comparisons to Other *Coluber constrictor* Subspecies

Robert R. Fleet¹, D. Craig Rudolph^{2,*}, J.D. Camper³, and J. Niederhofer⁴

Abstract - In 1998, we conducted a radio-telemetry study of *Coluber constrictor etheridgei* (Tan Racer) in the Angelina National Forest in eastern Texas. Individuals were located once daily from 12 June to 14 August. We determined home-range size, movement distances, movement frequency, and habitat use for this short-term study. We also determined food habits of this population by examination of fecal samples. We compared these parameters to other Racer taxa in Utah (*C. c. mormon* [Western Yellow-bellied Racer]), Kansas (*C. c. flaviventris* [Eastern Yellow-bellied Racer]), and South Carolina (*C. c. priapus* [Southern Black Racer]). Compared to these populations, Texas Racers exhibited larger home ranges and greater movement frequency and distances during the summer than Utah or Kansas populations, but approximately equal to those of the South Carolina population. Available data on food habits suggests that all populations are consumers of invertebrate and vertebrate prey. We hypothesize that the basic diet of *C. constrictor* is composed of invertebrates captured by active foraging in areas of abundant herbaceous vegetation, that differences in home-range size and movement distances result from variations in patchiness of suitable foraging habitat across populations, and that the proportion of vertebrate prey in the diet of *Coluber* populations increases as home-range size and movement distances increase due to increasing patchiness of foraging habitat, resulting in increasing encounters with vertebrate prey.

Introduction

Coluber constrictor L. (Racer) (Serpentes, Colubridae) ranges from southern Canada and the northern US to northern Central America and from the east to west coast, but is largely absent from the arid southwestern US and northern Mexico. The species has eleven described subspecies (Wilson 1978). Ten of the eleven subspecies range east of the Rocky Mountains. *Coluber c. mormon* Baird and Girard (Western Yellow-bellied Racer) occurs to the west from Utah to the west coast (Wilson 1970).

Life history and ecology of *Coluber c. mormon* was studied in Utah (Brown and Parker 1976, 1982); *C. c. flaviventris* Say (Eastern Yellow-bellied Racer) in Kansas (Fitch 1963, Fitch and Shirer 1971), and *C. c. priapus*

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Dunn and Wood (Southern Black Racer) in South Carolina (Plummer and Congdon 1994). These studies describe considerable variation in ecological characteristics between populations; among these are home-range size (minimum convex polygon), movement frequency and distance, and prey selection. This paper is the result of our study of a southern population of *Coluber c. etheridgei* Wilson (Tan Racer) which we conducted to gain insight into the ecological and environmental forces driving differences in these ecological parameters between populations.

Methods

Study areas

Two study areas in the Angelina National Forest (ANF) were utilized. One, approximately 2 km SE of Zavalla, TX in Angelina County, had overstory vegetation consisting of *Pinus palustris* Mill. (Longleaf Pine) and *Pinus echinata* Mill. (Shortleaf Pine) and understory vegetation dominated by *Ilex vomitoria* Ait. (Yaupon), *Liquidambar styraciflua* L. (Sweetgum), *Callicarpa americana* L. (American Beautyberry), *Myrica cerifera* L. (Wax-myrtle), *Vitis rotundifolia* Michx. (Muscadine), and *Rubus* spp. Composition and structure of the vegetation had been altered as a result of a wildfire 4–5 years prior to our study, resulting in a thick understory and many dead snags in the overstory.

A second study area of rolling Longleaf Pine savanna, approximately 12 km southeast of Zavalla, TX, had an overstory dominated by Longleaf Pine with the upland and sideslope understory consisting mainly of sparsely distributed *Quercus incana* Bartr. (Bluejack Oak), *Q. stellata* Wang. (Post Oak), *Sassafras albidum* (Nutt.) Nees (Sassafras), Yaupon, Sweetgum, *Pteridium aquilinum* (L.) Kuhn (Bracken Fern), *Toxicodendron radicans* (L.) (Poison Ivy), and *Schizachyrium scoparium* Michx. (Little Bluestem). Numerous first order stream drainages run through these areas. Dominant midstory and understory vegetation of these drainages are *Ilex coriacea* (Pursh.) Chapm. (Bay-gall), *Magnolia virginiana* L. (Sweet Bay), *Persea borbonia* (L.) Spreng. (Red Bay), American Beautyberry and Muscadine. Understory structure and composition of this study area resulted from a controlled-burn management scheme that was intended to maintain the Longleaf Pine savanna ecosystem.

Snake capture

Snakes ($n = 5$) were captured on the study areas from mid-March to 4 June 1998 in drift fence/funnel trap arrays (Burgdorf, et al. 2005). Transmitters measuring 40 x 8 x 5 mm with a mass of 3.2 g (P. Blackburn, science equipment specialist, Stephen F. Austin State University [SFASU]) were implanted subcutaneously using procedures adapted from Reinert and Cundall (1982) and Weatherhead and Anderka (1984).

Data collection

Beginning on 12 June 1998, five snakes were located once daily using a ATS (Advanced Telemetry Systems) receiver and hand-held directional an-

tenna. At each relocation, the snake's position and activity (if visible) was recorded. A flag, marked with the snake's identification and date, was placed in the ground to indicate daily location. Relocation points were revisited and locations recorded using a handheld Trimble Pathfinder II GPS (global positioning system) unit. Daily relocations continued until 14 August 1998.

Data analysis

GPS points were differentially corrected with Pathfinder Office software using US Forest Service base station files downloaded from the Pineville, LA base station. Home ranges were determined using CALHOME software program. ArcView GIS was used to determine daily movements. Statistical analysis was carried out using STATISTICA software package.

Home ranges were calculated using four different methods—minimum convex polygon, harmonic mean, adaptive kernel, and bivariate normal—using two different percentages, 95% and 100% of the locations.

Using the 100% minimum convex polygon (MCP) of the snakes in this study and the MCP home ranges of the snakes in South Carolina and Utah, a general ANOVA was used to test for significant difference among the three. Three planned comparisons were used to discover which populations' home ranges differed.

Mean daily movement rates of the Texas, South Carolina, and Utah Racers were tested for significant difference using a general ANOVA. Planned comparisons between populations were used to determine which populations differed.

Results and Discussion

Home range

Home range in the context of this study is the area covered by the radio-telemetered Racers in the course of their daily activities during the short-term time period from 12 June to 14 August 1998. Using all of the GPS-acquired snake locations, the mean home ranges for the five snakes by the minimum convex polygon (MCP), harmonic mean (HM), adaptive kernel (AK), and bivariate normal (BN) methods were 15.4 ha, 19.2 ha, 32.2 ha, and 61.5 ha, respectively. The 95% home ranges for these methods were also calculated (Table 1). The MCP and HM home-range estimates are similar at both the 100% and 95% level. The BN method oversimplifies an animal's spatial use patterns and provides home-range estimates that are far greater than the other three methods (Kie et al. 1996).

Plummer and Congdon (1994) considered home-range size in snakes 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). Snout-vent length (SVL), a measure of body size, of our snakes was compared against home-range size and was not found to be related to home-range size (Table 2). Plummer and Congdon (1994) also found no correlation between SVL and home-range size for the South Carolina, Kansas, and Utah Racers (Table 2).

Home-range size in Texas, South Carolina, Utah, and Kansas were found to be significantly different (ANOVA: $F_{2,20} = 19.48$, $P < 0.001$). Three planned comparisons of this ANOVA were carried out revealing the following: there was no significant difference in home-range size between Texas and South Carolina Racers (ANOVA: $F_{1,18} = 1.13$, $P = 0.2671$); there was a significant difference between home ranges of Texas and Utah Racers (ANOVA: $F_{1,18} = 30.82$, $P < 0.001$); and there was a significant difference between the home ranges of the South Carolina and Utah Racers (ANOVA: $F_{1,18} = 23.18$, $P < 0.001$). Both the Texas and South Carolina Racers' home ranges were greater than the Utah Racers' (Table 2). No ANOVA was carried out with the Kansas Racers because individual home ranges were not provided in Brown and Parker (1976). Plummer and Congdon (1994) determined that the South Carolina home ranges were significantly greater than the Kansas home ranges, and because Texas Racers' home ranges are larger than those of the South Carolina snakes, it is reasonable to assume that the home ranges of Texas Racers are also larger than those of the Kansas snakes.

Daily movement

Problems arise in using home-range size for comparisons because "determining home range depends heavily on assumptions of the particular home-range estimation procedure used" (Plummer and Congdon 1994:23). Considering this, Plummer and Congdon suggest that actual movement data may make for more meaningful comparisons among studies.

Table 1. Mean home ranges (ha) of *Coluber constrictor etheridgei* in eastern Texas. Home ranges calculated by minimum convex polygon, harmonic mean, adaptive kernel, and bivariate normal methods using 100% and 95% of locations.

Snake	SVL (cm)	Minimum convex polygon		Harmonic mean		Adaptive kernel		Bivariate normal	
		100%	95%	100%	95%	100%	95%	100%	95%
Female	84.1	8.6	7.4	10.3	6.0	20.0	19.9	45.0	19.5
Male	71.5	18.2	14.5	17.0	16.5	29.3	22.8	66.9	29.0
Male	76.5	9.3	4.0	32.6	5.1	19.7	6.0	29.8	12.9
Male	73.4	26.5	18.4	24.5	17.4	57.1	28.1	102.3	44.4
Male	76.5	14.5	12.3	11.5	9.9	25.9	16.0	63.4	27.5
Mean	76.4	15.4	11.3	19.2	11.0	32.2	18.6	61.5	26.7

Table 2. Comparison of mean SVL, mean daily movement (m/day), and home range (minimum convex polygon) of *Coluber constrictor* from radiotelemetry studies in Utah, Kansas, Texas, and South Carolina. Mean movements were calculated using active season data only. Movement distances and home ranges are reported as means \pm 1 SD.

Study	n	SVL (cm)	Mean		Correlation of SVL and	
			movement	Home range	Home range	Movement/day
Utah	9	71	33 \pm 4	0.4 \pm 0.34	-0.26	-0.29
Kansas	7	82	37	2.5 \pm 1.65	-0.08	-0.43
Texas	5	76	99 \pm 27	15.4 \pm 7.34	-0.71	-0.18
South Carolina	7	82	104 \pm 27	12.2 \pm 5.86	-0.45	-0.43

Five *Coluber c. etheridgei* were monitored for a total of 280 tracking days (mean = 56 days per snake) and were active 83% of those days (Table 3). Mean movement per day on active days was 99 m, with a mean minimum movement of 12 m and a mean maximum movement of 415 (Table 3). Fourteen days (30%) were portions of periods when snakes were inactive for more than three consecutive days, possibly suggesting ecdysis or digestion of a large meal. These numbers are very similar to what Fitch and Shirer (1971) reported in their study of Kansas Racers, where 80% of the tracking days involved movement, with a maximum movement of 454 m in one day. The Kansas mean movement per day of 37 m is definitely lower than that found in our study. The lower movement per day for the Kansas Racers may be explained by the force-feeding of the transmitters to the snakes in that study. This placement could possibly have caused the smaller mean movement per day due to the snakes acting as if having full stomachs and not searching as actively for food.

Frequency of daily activity of Racers in eastern Texas (83%) was similar to that of *Coluber c. flaviventris* in Kansas (80%; Fitch and Shirer 1971). Plummer and Congdon (1994) suggested that frequency of daily activity in the summer is apparently primarily related to ecdysis and not to environmental constraints. Environmental constraints, such as extremely high temperatures, are also probably not limiting for daily activity in Texas Racers since our observations indicate that the Racers made daily movements in summer during the cooler periods of the day and on cloudy days.

Average daily summer movement of Texas, South Carolina, and Utah Racers were significantly different (ANOVA: $F_{2,18} = 25.93$, $P < 0.001$; Table 2). A planned comparison of the daily movements of the Texas and South Carolina Racers revealed no significant difference (ANOVA: $F_{1,18} = 0.11$, $P = 0.743$; Table 2). A planned comparison between Texas and Utah daily movements revealed that Texas movements were significantly greater (ANOVA: $F_{1,18} = 30.07$, $P < 0.001$ Table 2). Through another planned comparison South Carolina daily movements were determined to be significantly greater than in Utah (ANOVA: $F_{1,18} = 41.69$, $P < 0.001$; Table 2). No individual movement data were given in Fitch and Shirer (1971), but Plummer and Congdon (1994) determined that South Carolina daily movements were significantly greater than in Kansas. This suggests that Texas daily movements would also be greater than in Kansas.

Table 3. Mean, minimum, and maximum daily movement (m) of *Coluber constrictor etheridgei* in eastern Texas.

Snake	SVL (cm)	Days tracked	Days active (%)	Mean	Minimum	Maximum
Female	84.1	53	87	104 ± 14.9	6	485
Male	71.5	40	75	67 ± 13.8	6	333
Male	76.5	63	89	95 ± 15.5	8	632
Male	73.4	63	81	135 ± 16.4	18	388
Male	76.5	61	82	92 ± 8.3	22	239
Mean	76.4	56	83	99 ± 10.1	12	415

Plummer and Congdon (1994) suggested that their approach to comparing daily movement rate may indicate biological differences between populations of Racers. One suggestion they made for these biological differences is the influence of body size. However, they found no significant relationship between snout–vent length (SVL) and daily movement distance within or among populations. We also found no significant relationship between SVL and daily movement distance in our Texas population (Table 3).

Another explanation Plummer and Congdon (1994) suggest for these differences is the relative trophic position of the Racers. Utah Racers have smaller body sizes and are mostly secondary consumers, feeding mainly on insects. These two factors make them more suitable for a sedentary life style, thus possibly explaining their small daily movements and home ranges. Kansas and South Carolina Racers have larger, similar body sizes, but South Carolina Racers have significantly greater movement rates and home-range sizes. Kansas Racers feed mostly on insects, but also feed on vertebrate prey, which made up the greatest biomass of their diet (Fitch 1963). South Carolina Racers are apparently tertiary consumers feeding exclusively on vertebrates (Plumer and Congdon 1994). They conclude that these differences in home-range sizes and daily movement rate can be explained by trophic differences because the vertebrate prey of the South Carolina Racers are more widely dispersed. *Coluber c. etheridgei* prey records (Table 4) show that Texas Racers feed (numerically) mostly on insects (63%), while having home ranges and daily movement rates similar to the South Carolina Racers. Further, examination of food records for South Carolina Racers gathered from the Savannah River Ecology Lab (SREL) since Plummer and Congdon's (1994) study, indicate that these Racers are not feeding exclusively on vertebrates. Thus, differences in home range and daily movement rates does not appear to be explained by trophic differences. An alternative explanation of these differences between populations can be suggested after an examination of foraging behavior of the Texas population.

Table 4. Prey records of *Coluber constrictor etheridgei* and *Coluber constrictor anthicus* in eastern Texas.

Prey taxon	<i>C. c. etheridgei</i>		<i>C. c. anthicus</i>	
	Number	Percent	Number	Percent
Orthopterans	26	27.4	32	65.3
Other insects	30	31.6	6	12.2
Other invertebrates	4	4.2	1	2.0
Total invertebrates	60	63.2	39	79.6
Lizards	24	25.3	7	14.3
Snakes	3	3.2	1	2.0
Birds	2	2.1		
Mammals	6	6.3		
Total vertebrates	35	36.8		

Foraging behavior

On 11 separate occasions, our Texas Racers were observed exhibiting what was described by Fitch (1963) as foraging behavior. This behavior consisted of a fully or nearly fully extended body with the head and front of the body elevated about 10 cm from the ground. Their behavior was either slow movements of the head from side to side with the head occasionally lowering to the ground, or jerky, seemingly erratic movements of the head from side to side with the head frequently being lowered to the ground. The snakes were seen frequently extending their tongues and touching them to the ground. All observations of this apparent foraging behavior were in areas that had more open understory and more abundant ground cover than surrounding areas, with large, nearly continuous patches of *Vitus rotundifolia* that ranged in height from around 6 cm up to about 0.5 m. These areas had an abundance of invertebrates, especially orthopteran insects, which have been noted in other studies as being a large portion of the Racers' diet (Brown and Parker 1982, Fitch 1963).

Prey items

Examination of scats taken from Tan Racers captured on the Angelina National Forest and the Big Thicket National Preserve yielded 95 prey records (Table 4). Numerically the majority were invertebrates, dominated by orthopterans, but the 35% that were vertebrates probably made up the majority by biomass. We also examined scats from *Coluber c. anthicus* (Cope) (Buttermilk Racer), a taxon geographically contiguous with *C. c. etheridgei*. Similarly, the majority of the food records were invertebrates, dominated by orthopterans, but 20% were vertebrates (Table 4). By contrast, Brown and Parker (1982) reported the diet of the Utah population to be 96% insects (mostly orthopterans), with the remainder being mammals (3%) and snakes (1%).

Fitch (1982), working with 986 food records from the Kansas population obtained from animals captured on the principal study area, the Fitch Natural History Reservation (FNHR), ascertained that insects, especially orthopterans, made up 76% of the food items. Vertebrates accounted for nearly 24% of the food records. Estimates of biomass from these records and others from nearby areas indicated that vertebrate prey accounted for 86% of the prey biomass.

Prey of the South Carolina population, studied on SREL, was reported by Plummer and Congdon (1994) from literature records (Hamilton and Pollack 1956) to be exclusively vertebrates. However Hamilton and Pollack (1956) actually reported 1.7%, by volume, of food records of *Coluber c. priapus* to be lepidopteran larvae. Furthermore, examination of more recent food records from the SREL Racer population indicates that these Racers do consume invertebrate prey items, although the amount is unclear (*C. Winne*, Savannah River Ecology Lab, Aiken, SC, pers comm). In addition, we have examined seven scats from Racers captured 175 km NE of the SREL, near the intergrade zone between *C. c. priapus* and *C. c. constrictor*. These scats contained remains of two rodents, one lizard, and 12 arthropods.

Relationship between habitat use, food habits, movement distance and frequency, and home-range size

The fundamental food niche of the Racer is that of an insect (primarily orthopteran) feeder that acquires prey by active foraging in areas of abundant grassy/herbaceous ground cover. Vertebrate prey, more thinly distributed on the landscape, are taken opportunistically as the Racers move in and between suitable foraging habitat. Fitch (1999, 2006) monitored the composition and change of the snake community on the FNHR in eastern Kansas for over 50 years. The FNHR, a 590-acre farm, was set aside in 1947, and its wildlife population was studied as succession was allowed to proceed. The area initially was evenly divided between deciduous forest, pastures, and formerly cultivated fields. The open areas rapidly became prime Racer habitat with abundant ground cover, and Racer populations increased. As succession proceeded, these areas of rich ground cover were invaded by trees and the Racer habitat became increasingly fragmented into small, widely separated patches, and the Racer population declined. By the 1990s, only small patches of tall grass persisted between the trees. There seemed to be, at that time, no resident adult Racers, and Racer captures (34 in the decade) were mostly hatchlings that were transients from other habitats.

Amount and distribution of key foraging habitat is the significant factor in explaining the variation between populations of Racers, in distance and frequency of movement, home-range size, and composition of the diet (Fig. 1). The Utah Racer population (Brown and Parker 1982) existed in a

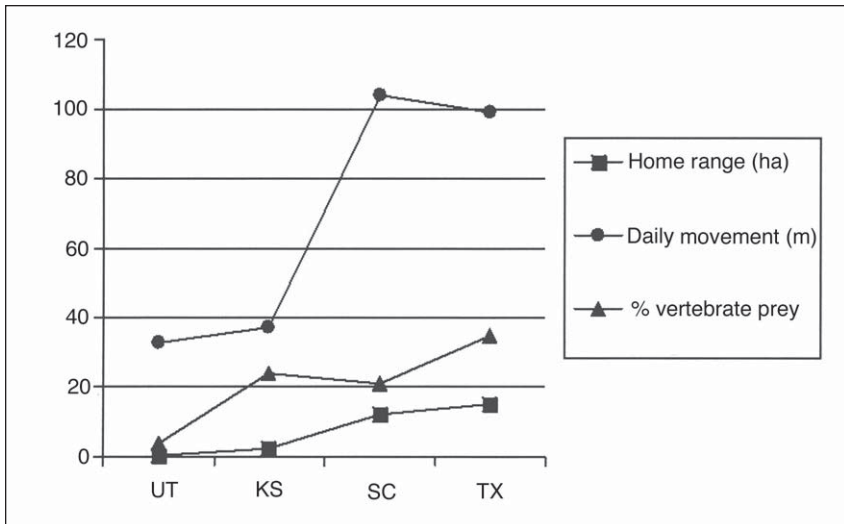


Figure 1. Comparisons of ecological parameters for *Coluber constrictor mormon* in Utah (Brown and Parker 1976), *C. c. flaviventris* in Kansas (Fitch, 1963), *C. c. priapus* in South Carolina (Plummer and Congdon, 1994), and *C. c. etheridgei* in Texas (this study).

uniformly suitable habitat of abundant ground cover. These snakes did not need to make frequent or long-distance movements to reach rich foraging territory, thus resulting in low movement frequency and distance and small home ranges. Since these snakes were traveling little, there was scant opportunity to encounter vertebrate prey which resulted in the numerical and biomass dominance of insects (orthopterans) in their diet.

The Kansas Racer population (Fitch 1963, Fitch and Shirer 1971) on the FNHR preferred habitats of tall grass prairie, weedy pasture and fields, and woodland edges. These preferred foraging habitats were less uniformly distributed on the landscape and the Racers exhibited greater movement frequency and movement distance in utilizing these habitats, resulting in larger home ranges. Larger home ranges resulted in increased encounters with vertebrate prey and thus their increased representation in the diet of the Kansas Racers.

Our Texas population as well as the South Carolina Racers (Plummer and Congdon 1994) exist in a considerably more forested environment than the Kansas Racers. The southern pine forests of east Texas and South Carolina have few and widely scattered forest openings with suitable ground cover for Racer foraging. On our study area within the Angelina National Forest, rich grass/herbaceous ground-cover areas occur along forest roads, small streamside zones, and occasional openings in the forest canopy caused by wind thrown or beetle-killed trees.

Foraging Racers from these populations would be forced into longer and possibly more frequent movements between the widely separated foraging sites resulting in the largest home ranges reported for the species, and the large proportion of vertebrate prey items in the diet due to the greater opportunity for vertebrate encounters in their large home ranges.

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