Short-term movements of the South American rattlesnake (*Crotalus durissus*) in southeastern Brazil

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Ecological studies of movements in animals require extensive knowledge of direction, distance and frequency of movements. The purpose of this study was to describe the daily and seasonal movements in a population of the South American rattlesnake, *Crotalus durissus*. The study population inhabits a *cerrado* area in southeastern Brazil. Snakes were tracked with externally attached radio-transmitters and thread bobbins. Larger animals tended to make more extensive daily movements, moving further from the initial site of capture. There were no differences in average daily movements between sexes. Site fidelity was higher in the dry season for both sexes. Both sexes moved distances twice as long as those calculated by drawing a straight line between consecutive points. The movement pattern of *C. durissus* seemed to be similar to that observed in other tropical pit vipers, such as species of the genus *Bothrops*.

Key words: daily movement, radio telemetry, seasonal movement, spool-and-line tracking device

INTRODUCTION

Studies concerning spatial ecology and habitat use require detailed information on components of movement, such as direction, distance and frequency (Gregory et al., 1987). In general, animals exhibit a preference for locations in their environment with distinct characteristics, which may be defined as microhabitats (Gibbons & Semlitsch, 1987; Huey et al., 1989; Huey, 1991; Reinert, 1993). Many studies have characterized snakes as immobile animals; however, sedentary levels vary according to the species, their foraging habits (Fitch & Glading, 1947; Duvall et al., 1985; Sazima, 1988) and environmental conditions (Madsen, 1984; Gibbons & Semlitsch, 1987; Shine, 1987; Reinert, 1993).

Most studies on snake movements have been conducted in temperate regions (Gibbons & Semlitsch, 1987; Gregory et al., 1987; Brown et al., 2005). Despite considerable information about the biology of the South American rattlesnake (*Crotalus durissus*; Salomão et al., 1995; Almeida-Santos & Salomão, 1997; Vanzolini & Calleffo, 2002a), few studies have been conducted in the wild (Bastos et al., 2005; Tozetti & Martins, 2008). The neotropical rattlesnake (*C. durissus*) is widespread throughout many parts of South America (Campbell & Lamar, 2004). Several subspecies have been described (Hoge, 1966) but taxonomic distinctions among them remain problematic (see detailed revision in Vanzolini & Calleffo, 2002b). In a mtDNA-based study, Wüster et al. (2005) showed that all South American populations of *C. durissus* are phylogenetically closely related, and considered the previously recognized Brazilian subspecies *C. d. collilineatus* and *C. d. cascavella* as synonyms of *C. d. terrificus*, which therefore includes our study population. Given the unstable subspecies nomenclature, we will limit discussion to the species level.

In the tropics, the activity peak of *C. durissus* occurs between April and May (dry cold season; Salomão et al., 1995). The reproductive cycle is biennial (Almeida-Santos & Salomão, 1997; Almeida-Santos et al., 2004), ovulation occurs between September and October (wet warm season) and pregnancy between September and April (from wet warm to early cold season; Almeida-Santos & Salomão, 1997; Almeida-Santos et al., 2004).

The species is highly common in dry and open vegetation types in Brazil, especially in the *cerrado*, a savanna-like biome (Colli et al., 2002). The *cerrado* vegetation covers two million square kilometres, representing more than 20% of the area of Brazil (Ratter et al., 1997) and constituting an important proportion of the distribution of *C. durissus*. This biome is a highly heterogeneous landscape, including many physiognomies that range from fields of grass to relatively dense gallery forests (Coutinho, 1978). The *cerrado* climate is typical of the rather moister savanna regions of the world, with an average precipitation of 800–2000 mm for over 90% of the area and a very pronounced dry season during the southern winter, while average annual temperatures are 18–28 °C (Dias, 1992). The spatial heterogeneity associated with marked seasonality has profound effects on the ecology of ectotherms (Colli et al., 2002). The *cerrado* is the main habitat of *C. durissus* and one of the 25 most important terrestrial biodiversity hotspots (Myers et al., 2000), and is possibly the most threatened tropical savanna in the world (Silva & Bates, 2002). At present, very few remnants of these open formations are protected in southeastern Brazil (Kronka et al., 1998), highlighting the importance of studies concerning the native fauna and flora (see Silva & Bates, 2001). Despite the close association between *C. durissus* and *cerrado*, this species has also been recorded in fragmented forest habitat, representing a recent invasion into disturbed areas of Atlantic forest (Bastos et al.,

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2005) revealing an ability to colonize new habitats. The general purpose of this study was to describe the daily and seasonal movements in a population of *C. durissus* in one of the last *cerrado* remnants in southeastern Brazil. The present study provides new information about movements of a rattlesnake species that, unlike the majority of species from North America, is not well studied.

MATERIALS AND METHODS

Field work was conducted at the Itirapina Ecological Station (IES: 2300 ha; 22°13'24"S; 47°54'03"W; approximately 700 m elevation), municipality of Itirapina, state of São Paulo, southeastern Brazil. Regular sampling was carried out between October 2003 and October 2004. The study site represents one of the last remnants of protected open *cerrado* in the state of São Paulo. It consists of gallery forests, swamps, flooded areas, grasslands, shrubby grasslands and shrubby grasslands with trees. The climate is mesothermal, with two well defined seasons, a dry cold (April–August) and a wet warm season (September–March).

Snakes were captured by systematically surveying unpaved roads (maximum vehicle speed 35 km/h) and during occasional encounters. Each captured individual was weighed, measured and marked using passive integrated responder (PIT) tags. To obtain data on short-term movements, 15 snakes (11 males and four females) were equipped with radio-transmitters (model SI-2; 9 g, 33 mm × 11 mm; Holohil Systems Ltd, Ontario, Canada) and five snakes (two males and three females) were equipped with spool-and-line tracking devices (thread bobbins; Wilson, 1994; Tozetti & Toledo, 2005; Tozetti & Martins, 2008). This device was constructed using quilting cocoons (produced by Hiltex Ltda) containing 300 m of cotton thread (4.7 g, 4 cm long, 1.2 cm wide). A case for each cocoon was made by wrapping it in plastic food wrap fastened with a piece of adhesive tape 2 cm wide. A hole was made in the plastic case from which the line ran free as the snake moved. Both spools and radio-transmitters were externally attached at the dorsal posterior portion of the snake's body using adhesive tape (Tozetti & Martins, 2007), which naturally detached upon shedding. For all snakes the final weight of the device was less than 5% of the individual's body mass (Hardy & Greene, 1999). Although intraperitoneal implantation is the most widely used radio attachment technique, we adopted external attachment to avoid surgical procedures. This was necessary because the legislation concerning wild animal care at the study site limits surgery licenses due to the risk of mortality following injection of anaesthetic (Reinert & Cundall, 1982; pers. obs.). A series of alternative attachment methods has been developed to avoid this risk (see Ciofi & Chelazzi, 1991), including the one adopted by us and described by Tozetti & Martins (2007, 2008), with positive aspects that include: 1) the simplification of the process of transmitter battery recovery; and 2) unlike in surgical implants (see Hardy & Greene, 1999), animals with external radio-transmitter attachment resume their normal behaviour immediately after manipulation.

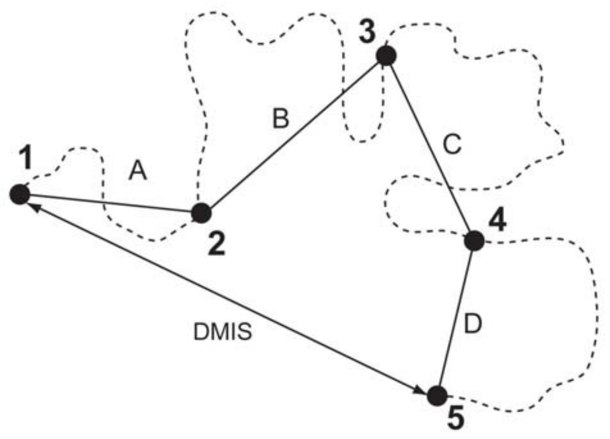

Fig. 1. Diagram of measurements taken from hypothetical relocations of a snake tracked with radio-transmitter (solid line) or thread bobbin (dashed line). The numbers indicate relocations in chronological order from 1 to 5. Legend: A, B, C and D = straight-line distances between consecutive relocations = SLD; A+B+C+D = total distance moved (TDM); arrowed line indicates the measurement of distance moved from initial site (DMIS); dashed line represents the thread trail from which the effective distance moved (EDM) is obtained.

After attachment, snakes were released at the capture site. We followed the trail of thread (abandoned line) or signal from radio-transmitters daily. Radio signals were received with a portable telemetry receiver using a four-element hand-held Yagi antenna. Radio locations included a visual observation of the tracked individual, except when it was underground, eliminating triangulation errors. For every encounter with *C. durissus*, we recorded environmental conditions (air temperature and relative air humidity) and the snake's surface body temperature using a non-contact infrared thermometer (Raytek model RAYMT4U), eliminating the need to handle the animal. Straight line distances between the radio locations were determined using a measuring tape (for a maximum distance travelled of 100 m) or GPS equipment (Garmin, model 12 XL, for longer distances). All measurements were converted into Universal Transverse Mercator (UTM) coordinates. For each individual, we estimated the total distance moved (TDM, in metres) by calculating the sum of straight-line distances between sequential relocations (considering total sample duration or TSD). We also estimated the mean daily straight-line distance moved or DDM (= TDM/TSD; in m/day) and the distance moved from initial site or DMIS (= distance from last to first location/TSD; in m/day; see Fig. 1 for details). To evaluate the snake's tendency to remain near the initial site we calculated site fidelity SF (= TDM/DMIS). Higher SF values reflect a tendency to move around the initial site (e.g. zigzag or circular movements). For animals equipped with threads, the line abandoned between loca-

Table 1. List of South American rattlesnake (*Crotalus durissus*) individuals monitored by radio-transmitters and thread bobbins at the Itirapina Ecological Station, State of São Paulo, southeastern Brazil.

Snake	Sex	Total size (mm)	Duration of track (days)	Number of relocations	Method	Season
61BED1A	F	771	36	9	radio	wet
61C0023	F	735	183	33	radio	dry
61BE8EA	F	970	195	23	radio	dry
61C0BEO	F	1085	59	14	radio	dry
61C0686	M	637	21	4	radio	wet
61C360B	M	708	57	12	radio	wet
61C007D	M	775	37	14	radio	wet
61BCD61	M	785	45	10	radio	wet
610D9DC	M	1010	14	7	radio	wet
618A8A9	M	1035	5	3	radio	wet
61C4308	M	1168	2	1	radio	wet
61C0025	M	1055	39	5	radio	dry
610B167	M	1190	191	21	radio	dry
1C94997	M	1196	44	9	radio	dry
61COB5F	M	1256	111	16	radio	dry
000124BCE4	M	1240	9	4	thread	dry
000610D05F	F	1335	4	4	thread	wet
000618D311	F	537	1	1	thread	wet
00061BF70C	F	840	1	1	thread	wet
00061C013B	M	655	2	3	thread	dry

tions was cut and reattached to a stake close to a snake's present location. The length of abandoned line gave us the effective distance moved by the snake (EDM; Fig. 1). We also measured the straight-line distance (SLD) between sequential locations. Both EDM and SLD are presented as m/day (sum of point-to-point distances/ number of monitored days). During relocations only visual contact was established with snakes.

We used the Mann–Whitney *U*-test to compare differences among DDM, DMIS, EDM, SF and SLD between sexes and seasons. To compare SLD and EDM we used the Wilcoxon matched pairs test. The relationships between body size and movements were compared using Spearman rank order correlation tests (r). The relationships between movements and environmental variables (substrate and air temperature and air relative humidity) were examined using a multiple regression analysis. For all cases differences were considered significant when $P<0.05$ (Zar, 1999).

RESULTS

Radio-tracking

Between October 2003 and October 2004 we radio-tracked 15 adult rattlesnakes (11 males and four females; Table 1). The mean duration of tracking was 59.45 (range 2–191) days. Animals equipped with external transmitters were observed moving through dense vegetation or sheltered in deep and narrow burrows. Animals were also observed basking, foraging and even capturing and ingesting a prey item offered by us. This indicates that the presence of adhesive tape does not apparently interfere with the distention of the body during the passage of food, as previously noted by Tozetti & Martins (2008). There was no significant difference between sexes when comparing daily distances moved (DDM for males = 19.4 m/day; females = 12.5 m/day; U=20; P=0.39; n=15; Table 2). A significant positive correlation was found between body size and DDM (r_s=0.63; P=0.008; n=15), although the correlation between body size and distance moved from initial site (DMIS) was not significant (r_s=0.59; P=0.59; n=15). Differences in DDM between dry and wet season were not significant (U=19; P=0.18; n=15; Table 2), nor were differences in DDM between dry and wet seasons for males (U=11; P=0.57; n=11; Table 2) or females (U=0; P=0.08; n=4; Table 2). Also, no significant differences were found in DMIS between sexes (U=24; P=0.43; n=15; Table 2) or seasons (U=24; P=0.43; n=15; Table 2). There were no significant differences in DMIS between seasons for males (U=9; P=0.34; n=11) or females (U=2; P=0.56; n=4; Table 2).

No significant differences in site fidelity (SF) were found between sexes (U=19; P=0.33; n=15; Table 2). However, considering both sexes together, SF was higher in the dry season (U=11; P=0.03; n=15; Table 2). Significant negative correlations were obtained for daily distance moved (DDM) and environmental variables (multiple r^2=0.84, df=4.5, F=12.5, P=0.008). We detected a negative relationship between DDM and air relative humidity (beta = –0.80) and between DDM and air temperature (beta = –2.41). We also detected a positive relationship between DDM and substrate temperature (beta = 1.98)

Spool-and-line device

Five snakes (two males and three females) were tracked using the spool-and-line (Table 1) method between January and July 2004. The average duration of tracking with the spool-and-line method was 3.4 days (Table 3). All

Table 2. Average daily distance moved (DDM), distance moved from initial site (DMIS) and site fidelity (SF; see details in Methods) obtained from adult males and females of the South American rattlesnake (*Crotalus durissus*) radio-tracked at the Itirapina Ecological Station, State of São Paulo, southeastern Brazil. Values presented as mean ± standard deviation (range); *n* = number of individuals.

	DDM (m/day)	DMIS (m/day)	SF
Male (*n*=11)	19.4±14.3 (3.4–48.2)	13.2±14.7 (1.7–43.7)	2.9±3.0 (1.0–11.0)
Female (*n*=4)	12.5 ±9.6 (2.4–28.2)	3.8±3.7 (0.6–10.0)	6.1±5.7 (1.0–13.8)
All snakes – dry season (*n*=15)	17.5±9.4 (8.1–32.2)	5.9±6.0 (0.6–16.3)	6.3±5.3 (1.1–13.8)
All snakes – wet season (*n*=15)	17.0±16.0 (2.4–48.2)	13.6±16.1 (1.2–43.7)	2.0±1.5 (1.0–4.7)
Male – dry season (*n*=11)	18.2±10.3 (8.1–32.2)	8.5±7.0 (1.7–16.3)	4.1±4.6 (1.1–11.0)
Female – dry season (*n*=4)	16.6±10.3 (8.6–28.2)	2.5±1.8 (0.6–4.3)	9.1±5.5 (3.0–13.8)
Male – wet season (*n*=11)	20.1±16.9 (3.4–48.2)	15.9±17.7 (2.2–43.7)	2.2±1.7 (1.3–4.7)
Female – wet season (*n*=4)	6.3±5.5 (2.4–10.2)	5.6±6.2 (1.2–10.0)	1.5±0.6 (1.0–1.9)

males were captured and monitored by spool-and-line device during the dry season and females during the wet season. Males and females did not differ significantly regarding straight-line distances moved (SLD; U=17; *P*=0.57; *n*=13; Table 3) or effective distances moved (EDM; U=18; *P*=0.67; *n*=13). Also, no significant correlation was found between body size and SLD (r_s= –0.1; *P*=0.87; *n*=5 or EDM (r_s= –0.1; *P*=0.87; *n*=5). The mean EDM was 1.76 times longer than SLD (Table 3), although this difference was not statistically significant (*t*=18; *P*=0.099; *n*=12). Nonetheless, this result suggests that sinuous movements were more frequent than straight ones.

DISCUSSION

Our findings revealed that even when distances travelled are long, sinuous movements (common in snakes; Laundré et al., 1987) may result in short distances from the initial point. Monitored individuals exhibited an erratic combination of short (e.g. 0.5 m/day) and long movements (e.g 100 m/day). During data collection, we ensured that the snake was not disturbed (see Nilson, 1999). This suggests that changes in movement pattern occur based on the suitability of the microhabitat selected (Pianka, 1966; Brown et al., 2005).

Daily distances travelled by individuals of *C. durissus* ranged from 2.4 to 48.2 m/day, suggesting a higher similarity with *C. horridus* (9.6–36.9 m/day; Reinert & Rupert, 1999) than with *C. viridis abyssus* (25.8–42.1 m/day; Reed & Douglas, 2002) or *C. cerastes* (0.0–373.6 m; Secor, 1994). However, differences in methods, number of individuals and study duration make comparisons difficult.

Monitored animals were less active or motionless (generally inside termite mounds or rodent burrows) just before shedding. Thus, ecdysis seems to be an important factor to be considered in short-term studies of movements. Despite the limited number of samples obtained with the spool-and-line method, the primary contribution of our findings is that cocoons are effective in enabling researchers to follow free-ranging *Crotalus*. Furthermore, it provides the real distance travelled, instead of point-to-point movement estimates, as reported in most studies. Our results show that movement analysis from straight-line distances underestimates real movement by a factor of about two. The negative relationship between mean daily distance moved, air temperature and relative air humidity could be associated with males searching for females for mating, which occurs in the dry/cold season (Salomão & Almeida-Santos, 2002). However, these movements seem to be more intense during the warmer hours of the day, as shown by the positive relationship detected between daily distance moved and substrate temperature. This result suggests that snakes are able to move considerable distances even in the colder months throughout the year. This ability is of importance for future studies on the home ranges and migratory potential of *C. durissus* and for management plans in fragmented *cerrado* landscapes.

Table 3. Average values of straight-line distances between consecutive relocations (SLD, m/day), effective distance moved (EDM, m/day) and the ratio EDM/SLDobtained for adult male and female South American rattlesnakes (*Crotalus durissus*) tracked with the spool-and-line method at the Itirapina Ecological Station, State of São Paulo, southeastern Brazil. Values presented as mean ± standard deviation (range; number of samples).

	Mean duration of monitoring (days)	No. of locations	SLD (m/day)	EDM (m/day)	EDM/ SLD
All snakes	3.4	2.6	12.4±6.8 (2.23–37.1; 12)	20.0±9.7 (3.95–50.32; 12)	1.76
Males	5.5	3.5	10.2±6.6 (2.23–29.1; 6)	14.9±11.0 (3.95–43.78; 6)	1.5
Females	2.0	2.0	13.8±7.9 (5–37.1; 6)	23.4±9.7 (5.3–50.32; 6)	1.93

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