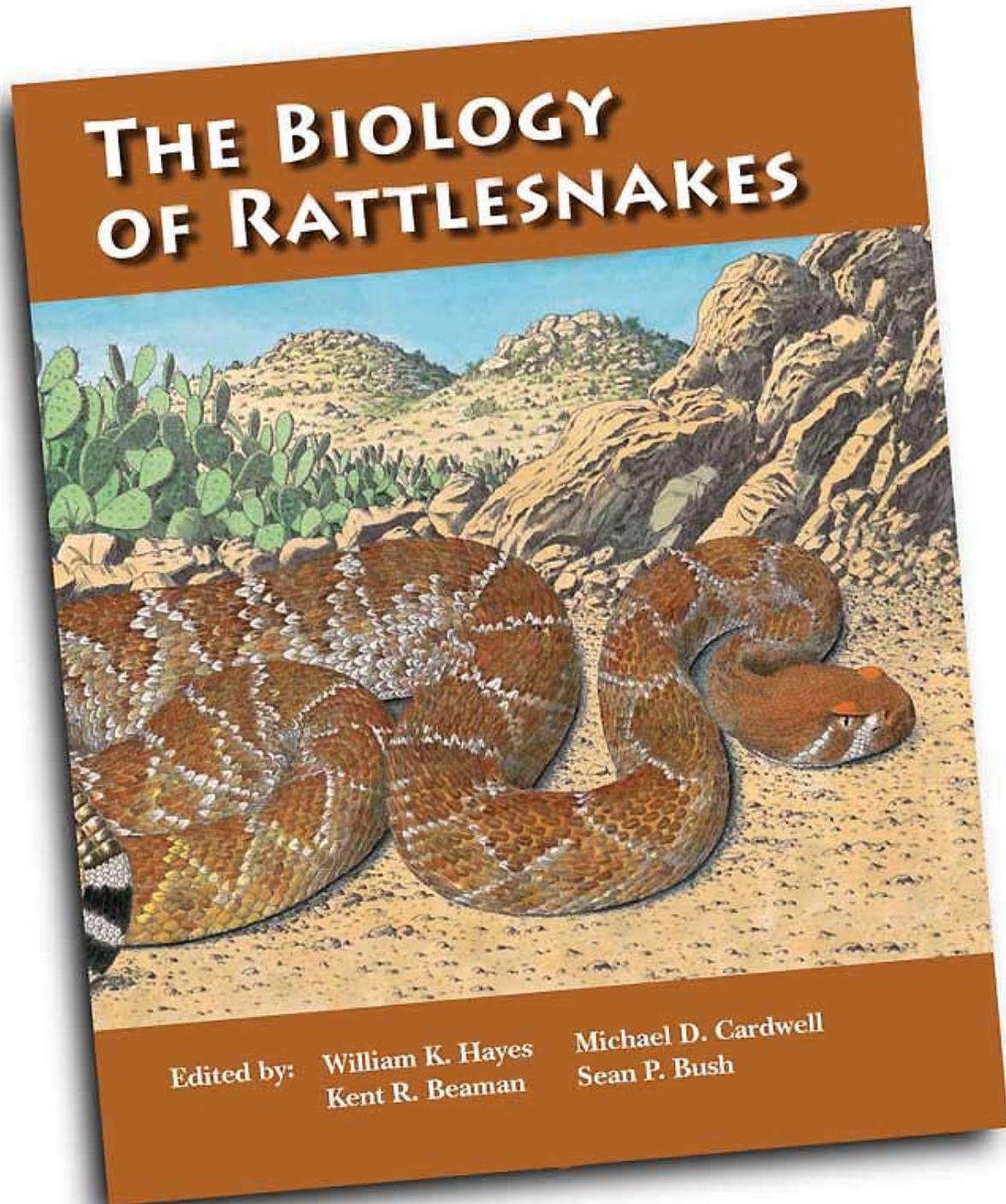


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Seasonal and Annual Variation in Home Range and Movements of Tiger Rattlesnakes (*Crotalus tigris*) in the Sonoran Desert of Arizona

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ABSTRACT.—The Tiger Rattlesnake (*Crotalus tigris*) was one of the least-studied rattlesnake species in the United States before we began a long-term research program in 1997. In this paper, we present data from the first 5 yr of research on selected aspects of *C. tigris* spatial ecology in the Sonoran Desert of Arizona. We implanted radio transmitters into 31 (15 female and 16 male) adult *C. tigris*, which we located 2,453 times over a 5-yr period (1997-2001). Males had larger home ranges than females. Annual variation in home range size and location was also greater in males than in females. Although movement frequency was similar, males exhibited a conspicuous spike in activity during the summer rainy season, whereas females did not. Males moved greater distances than females in summer, but not in spring or fall. Although male *C. tigris* are larger than females, difference in body size did not explain variation in home range size and movement patterns. Both males and females moved on relatively straight vectors during spring and fall as they traveled to and from den sites. However, during the summer mating season, males moved back and forth across their home ranges, while females tended to maintain relatively stable distances from their dens until returning in fall. The maximum distance moved from winter dens was similar for males and females. Males moved more during an unusually wet year compared to a drier-than-average year, indicating that precipitation may play a role in movement patterns. We suggest that differences in male and female spatial ecology can best be explained in the context of mating system dynamics. Tiger Rattlesnakes appear to engage in prolonged mate searching polygyny, characterized by males that move long distances in search of receptive females, which are a scarce resource due to greater-than-annual periodicity in reproductive cycles.

INTRODUCTION

Prior to this study, the Tiger Rattlesnake (*Crotalus tigris*) was one of the least studied rattlesnake species in the United States (Ernst, 1992). Much of what was known about *C. tigris* came from a small number of field observations and museum specimens, consisting mainly of physical descriptions, scale counts, and information on distribution (Baird, 1859; Amaral, 1929; Klauber, 1931; Gloyd, 1940; Campbell and LaMar, 1989). Knowledge of the natural history of this secretive species was largely anecdotal (Gloyd, 1937; Klauber, 1956; Wright and Wright, 1957; Fowle, 1965; Armstrong and Murphy, 1979; Lowe et al., 1986) until Beck (1995) obtained data on home ranges, movements, and body temperatures of three males over a 2-yr period. Herpetologists have recognized for decades the need for a detailed study of *C. tigris* (Klauber, 1931; Gloyd, 1940).

Our goal was to greatly expand our knowledge of the natural history and ecology of *C. tigris* by intensively studying a large sample of animals using radiotelemetry and mark-recapture. For this paper, we examined seasonal and annual variation in home ranges and movement patterns in a population of *C. tigris* from the Sonoran Desert of southeastern Arizona. We present data from the first 5 yr (1997-2001) of what has become a 12-yr study of multiple

populations. In the future, we will present data from continuing research on spatial ecology from additional populations, and from ongoing research on various aspects of *C. tigris* ecology (e.g., habitat use, growth, reproduction, diet, and conservation genetics).

MATERIALS AND METHODS

Study area.—We studied *C. tigris* in and adjacent to Saguaro National Park in the Rincon Mountains near Tucson, Arizona. The study area, roughly 12 km² in size, was characterized by steep rocky slopes, ridges with exposed bedrock, and bajadas dissected by numerous washes, some of which were characterized by relatively well developed soil terraces and xeroriparian vegetation. Vegetation was typical of Sonoran Desertscrub, Arizona Upland Subdivision (Turner and Brown, 1982). Common plants included Saguaro (*Carnegie gigantea*), Foothill Paloverde (*Cercidium microphyllum*), Brittlebush (*Encelia farinosa*), Prickly Pear and Cholla (*Opuntia* spp.), and Velvet Mesquite (*Prosopis velutina*). Tiger Rattlesnakes are only found in southern Arizona and the state of Sonora, Mexico, at elevations ranging from sea level to ca. 1,650 m; our study area was located towards the northern limit of the species range, where elevation varied from ca. 900–1,100 m.

Telemetry.—We began searching for *C. tigris* on foot in 1997 and continued to add new snakes to our study into 2001. We tracked individuals for varying periods of time, primarily due to premature failure of transmitters, although

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Table 1. Sex, size, tracking dates, and home range estimates (ha) of Tiger Rattlesnakes (*Crotalus tigris*) from Saguaro National Park in southeastern Arizona, 1997-2001. We did not calculate home ranges for snakes with <30 locations during the active season. ID = snake identification number, *N* = number of tracking occasions, *N_a* = number of locations used to calculate home range, SVL = snout-vent length (mm), mass (g), K = kernel, MCP = minimum convex polygon.

ID	Sex	N	Na	Tracking Dates	SVL	Mass	95% K	50% K	MCP
3	F	175	130	08/1997 – 11/2000	592	259	3.7	0.4	2.6
9	F	236	189	08/1997 – 12/2001	637	261	5.2	0.8	7.6
17	F	99	86	09/1997 – 03/1999	600	291	10.9	2.0	7.3
21	F	45	39	03/1998 – 03/1999	627	251	4.9	0.6	3.1
25	F	35	32	07/1998 – 07/1999	647	275	1.2	0.1	0.8
40	F	44	30	08/1998 – 03/1999	650	264	3.9	1.1	1.7
44	F	39	-	09/1998 – 10/1999	635	243	-	-	-
45	F	10	-	08/1999 – 04/2000	692	256	-	-	-
62	F	11	-	08/2001 – 11/2001	640	217	-	-	-
71	F	9	-	08/2001 – 10/2001	511	113	-	-	-
115	F	26	-	06/2001 – 12/2001	682	230	-	-	-
133	F	22	-	06/2001 – 11/2001	550	140	-	-	-
136	F	22	-	06/2001 – 11/2001	511	95	-	-	-
152	F	7	-	08/2001 – 09/2001	554	167	-	-	-
170	F	7	-	10/2001 – 12/2001	546	190	-	-	-
Mean					604.9	216.8	5.0	0.8	3.9
SE					15.1	15.9	1.3	0.3	1.2

ID	Sex	N	Na	Tracking Dates	SVL	Mass	95% K	50% K	MCP
5	M	94	80	08/1997 – 12/1998	680	283	10.2	0.8	9.3
6	M	98	79	08/1997 – 03/1999	667	292	72.1	10.6	125.3
16	M	120	102	09/1997 – 11/2000	650	261	10.9	1.3	21.1
18	M	106	94	09/1997 – 12/1998	694	317	22.4	2.1	23.3
20	M	149	125	09/1997 – 09/2000	680	325	6.9	0.5	15.4
22	M	208	169	10/1997 – 12/2001	687	355	16.5	2.2	29.3
24	M	167	135	05/1998 – 01/2001	694	348	9.8	1.2	11.9
27	M	66	49	07/2000 – 12/2001	755	308	11.2	2.7	6.0
39	M	12	-	08/2001 – 12/2001	734	312	-	-	-
61	M	113	75	04/2000 – 03/2001	682	305	9.3	1.2	8.4
70	M	107	84	04/2000 – 12/2001	684	288	22.4	3.9	8.9
72	M	76	54	05/2000 – 04/2001	712	345	4.4	0.7	10.7
74	M	126	95	03/2000 – 12/2001	736	378	19.4	3.0	13.1
85	M	35	-	07/2000 – 10/2000	689	265	-	-	-
90	M	94	63	07/2000 – 06/2001	689	308	9.4	1.4	4.5
91	M	95	70	07/2000 – 12/2001	712	298	8.7	1.4	8.0
Mean					696.6	311.8	12.4	1.7	13.1
SE					6.8	8.1	1.6	0.3	2.0

several snakes were predated and a few were lost and later found. We surgically implanted (procedure modified from Reinert and Cundall, 1982) temperature-sensitive transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) weighing <5% of snake mass. We released rattlesnakes at their capture location within 24 h of surgery.

Field procedures.—We varied our sampling effort seasonally and annually, due to changes in snake activity patterns. We generally located snakes monthly during winter,

bi-weekly during spring and fall, and 2-4 times per week during summer when snakes were most active. We used a global positioning system (GPS) receiver to record snake locations (<7 m accuracy). We recorded whether or not a snake was visible (either on the surface or easily observable under cover) and if it had moved since last located.

Data analyses.—We did not include locations <24 h after capture or <7 d after transmitter implantation surgery in any analyses. We defined seasons as winter (21 December–19

March), spring (20 March–20 June), summer (21 June–19 September), and fall (20 September–20 December). We calculated home ranges using locations from spring, summer, and fall only, because snakes did not move during winter.

We estimated home range size (ha) for snakes with ≥ 30 locations (Millspaugh and Marzluff, 2001). We calculated minimum convex polygons (MCP) for comparison with other studies, but used the fixed kernel method for analyses. We calculated 50% and 95% activity kernels using the optimal smoothing factor with least squares cross-validation (LSCV) in Animal Movement Analysis (Hooge and Eichenlaub, 1997), an ArcView (ESRI, Inc., Redlands, California, USA) extension.

To examine annual variation in movements and home range characteristics, we used a multi-response permutation procedure (MRPP) embedded in Blossom Statistical Software (Cade and Richards, 2005). We chose MRPP rather than traditional analyses such as ANOVA, because it is a nonparametric test, thereby avoiding the difficult problem of choosing, *a priori*, a multivariate distribution with reasonable goodness of fit (Mielke, 1981). Using MRPP allows for comparison of the average distances between the geometric centers of home ranges with all other possible combinations to determine if the location of the home range is different among years (Cade and Richards, 2005). In our case, we compared movements of males and females across years (e.g., each group consisted of all the snakes of a given gender that we radiotracked in multiple years). For MRPP, we used locations from each snake during summer and fall only, when rattlesnakes were most active, and we did not include tracking occasions when snakes did not move.

We took subsets of consecutive movements (“paths,” as defined below) to examine seasonal and sexual differences in movement speed (m/d). Each path had to meet specific criteria to be included in the analysis: the snake had to be monitored for at least 30 d; maximum time between tracking locations could not exceed 20 d; mean tracking interval could not exceed 7 d. Paths started and ended at snake overwintering sites in spring and fall, respectively. We divided total distance moved by path duration for each snake in each season to calculate travel speed. If a snake had more than one path for a given season (i.e., in different years), we randomly selected one path to eliminate pseudoreplication.

To examine seasonal changes in movement frequency, we calculated mean movement frequency (% move) for each snake in each season. We only used location records if time since last location (tracking interval) was 1–7 d. We excluded snakes with < 5 locations per season. We log-transformed ($\log_{10} [\% \text{ move} / (1 - \% \text{ move})]$) movement frequency data to conform to distribution assumptions of analyses of variance (ANOVA). To eliminate pseudoreplication, we only included one seasonal movement frequency per snake by randomly excluding its other seasonal movement frequencies, because snakes had data points for multiple seasons.

We used ArcView extension Path, with Distances and Bearings (Jenness, 2005), to calculate distance, bearing, and

angular concentration (r) on paths. We assessed seasonal differences in path straightness by comparing mean values of r for snakes in different seasons. To eliminate pseudoreplication, we only included one seasonal r per snake by randomly excluding its value in other seasons, because snakes had data points for multiple seasons. We square-root transformed r to conform to distribution assumptions of ANOVA.

RESULTS

We implanted transmitters into 31 adult *C. tigris* (15 females, 16 males), which we located 2,453 times during the study period. In fall 1998, one male (CRTI 6) made an atypical movement to what turned out to be a new den 2.7 km from his 1997–1998 den. The following spring, his transmitter failed before he emerged from hibernation. Therefore, we were uncertain if he moved to a new area during the following active season or if he returned to his previous home range. However, since his movements were dramatically different than those of any other snake in this study, or any snake we have monitored during subsequent research on *C. tigris* (58 snakes from 2002–2005), we excluded him from home range analyses.

Males had larger home ranges than females (Table 1). Controlling for sex, body size (snout-vent length) did not explain variation in home range size (all $P > 0.21$). Kernel home range estimates of males were larger than females (ANOVA: $N = 19$, 95% kernel: $F_{1,17} = 8.50$, $P = 0.01$; 50% kernel: $F_{1,17} = 3.96$, $P = 0.06$).

Males appeared to exhibit greater annual variation in home range location than females, as revealed by MRPP analyses, but due to the small number of females with at least 30 locations per year in multiple years ($N = 3$), we did not make statistical comparisons. However, only one female varied her home range annually, and several other females with slightly < 30 locations showed little variation in annual home range location. In contrast, 82% ($N = 9$) of males varied in annual home range location.

Males moved more (m/d) than females in summer ($N = 24$, $t = 4.7$, $P = 0.0006$), but not in spring or fall (P s > 0.1 ; Fig 1). In addition, males moved significantly more in summer than in spring or fall (ANOVA: $F_{2,12} = 4.7$, $P = 0.032$), but females did not (ANOVA: $F_{2,8} = 2.8$, $P = 0.12$); however, we had low power to detect seasonal differences in movement rates of females due to small sample sizes.

We calculated the Euclidean distance that snakes moved from their dens as the active season progressed (Fig. 2). The maximum distance from the den was similar for males (490 m) and females (447 m), but males continued to traverse their home ranges throughout the active season, sometimes passing within < 50 m of their dens. In contrast, once females moved away from their dens, they tended to maintain their distance until they returned in fall.

We assessed seasonal differences in path straightness (Batschelet, 1981) by comparing r values among snakes. Summer paths had lower r values than fall or spring (ANO-

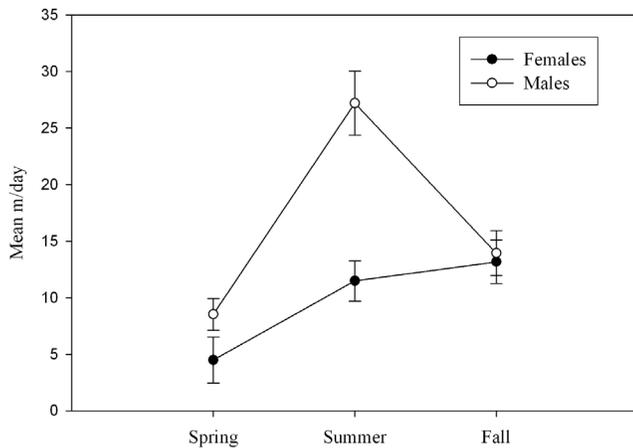


Figure 1. Seasonal movements (m/d) for male and female Tiger Rattlesnakes (*Crotalus tigris*) from Saguaro National Park in southeastern Arizona, 1997-2001. Males moved significantly more in summer than in spring and fall, but females did not. Males moved significantly more than females in summer, but not in spring and fall.

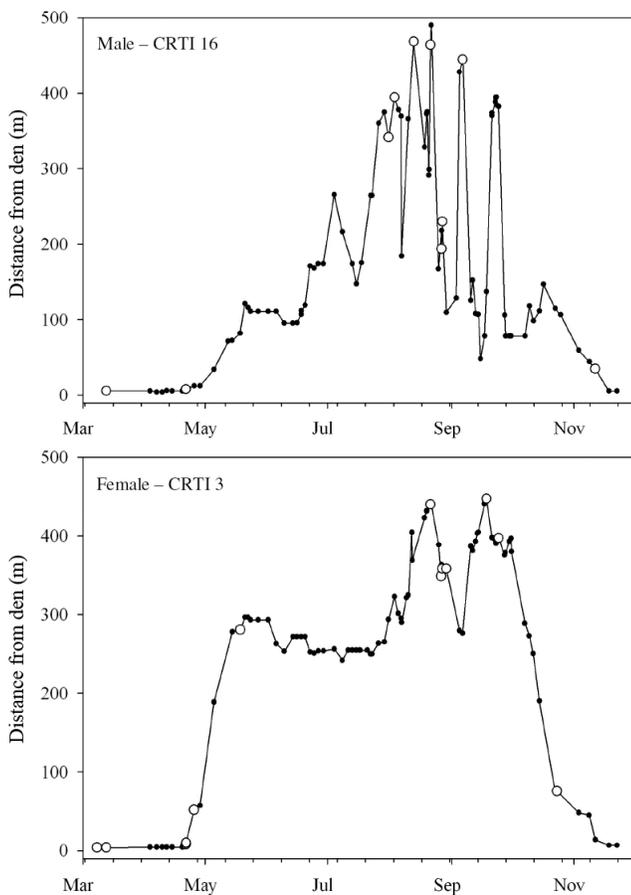


Figure 2. Distance from den over the course of one year (1998) for representative Tiger Rattlesnakes (*C. tigris*: male CRTI 16 and female CRTI 3) from Saguaro National Park in southeastern Arizona, 1997-2001. Maximum distance from dens was similar for males and females, but males tended to move back and forth across their home ranges during the summer mating season, whereas females tended to maintain small, stable activity centers.

VA: $F_{2,23} = 6.6$, $P = 0.0054$), meaning fall and spring movement paths were straighter than in summer (Fig. 3).

To examine annual variation in movements related to precipitation (Fig. 4), we compared total meters moved during an unusually wet year (1998) by male *C. tigris* during the monsoon season (July-September) to a drier-than-average year (2000). We only included males that we tracked more than five times in each month, and we only included 1 yr for each individual to avoid pseudoreplication. As expected, males moved more during 1998 ($N = 7$, mean = 3,538 m) than 2000 ($N = 5$, mean = 2,116 m; ANOVA: $N = 12$, $F_{1,19} = 8.10$, $P = 0.02$).

DISCUSSION

Home ranges.—Home range size (MCP) of male *C. tigris* from a previous study (Beck, 1995) averaged 3.4 ha, which was less than one-third that of our average of 13.1 ha, and even smaller than our 3.9 ha average for females. Although Beck studied *C. tigris* in the foothills of the Tucson Mountains, approximately 40 km from our study site in the foothills of the Rincon Mountains, both sites are nearly identical in elevation and characterized by highly similar habitats. Differences in home range size between the two studies could be due to any number of potential interacting factors. For example, the study sites may have differed in prey abundance and/or habitat quality. It is also possible that home range size differed in response to the configuration of prominent landscape features, such as the distance from rocky slopes where snakes overwinter to surrounding washes where snakes spend most of their time during the active season. The contrast in home range size reported by Beck may provide us with important data on inter-population variation in *C. tigris* spatial ecology, although it is also possible that the differences can be attributed to small sample size, as Beck only had data from three snakes.

Male *C. tigris* had larger home ranges than females, which is typical of most rattlesnake species studied to date (e.g., Reinert and Zappalorti, 1988; Duvall et al., 1990; Weatherhead and Pryor, 1992; Brown 1993; Secor, 1994; Prival et al., 2002; Reed and Douglas, 2002; Marshall et al., 2006; Waldron et al., 2006; Parker and Anderson, 2007; see also other chapters in this volume). Although males are larger than females on average, we did not detect a significant difference in home range size when taking body size into account. Theoretically, larger individuals should require larger home ranges to obtain resources needed to fulfill increased energy requirements (Mace and Harvey, 1983). Therefore, it is important to account for potential variation in home range size related to body size, especially in sexually dimorphic species like *C. tigris*.

We believe that the most likely explanation for the difference in home range size between males and females is related to mating system dynamics in the context of a highly variable environment like the Sonoran Desert. In any given year, due to extreme variation in resource availability, fe-

males may forego reproduction. Males are forced to search for receptive females, which are essentially a scarce resource. In this mating system, referred to as prolonged mate-searching polygyny (PMSP), selection may favor males based on their ability to find a female (Duvall et al., 1992). For rattlesnake species living in northern climates with relatively short active seasons, PMSP makes intuitive sense. Indeed, the overwhelming majority of detailed research on rattlesnake spatial ecology has been conducted on species with more northerly distributions, living in colder climates (e.g., *C. viridis*, *C. horridus*, *Sistrurus catenatus*). However, we also see PMSP in *C. tigris* in the Sonoran Desert of Arizona, where winters are relatively mild and the active season is longer. We have also observed male-male combat on three occasions, indicating that the mating system has components of female defense polygyny as well (Duvall et al., 1992). Nevertheless, rainfall variation is high in the Sonoran Desert, and prolonged drought is common, leading to highly variable resources and subsequent increased periodicity in reproduction, which in turn leads to dramatic gender-based differences in home range characteristics.

To meet energy requirements, rattlesnakes may be expected to expand their home ranges in low-resource years and contract their home ranges in high-resource years, regardless of sex. However, male *C. tigris* exhibited greater annual variation in home range placement than females. Again, this likely reflects strong differences in male and female mating strategies, combined with environmental conditions. Males tended to expand their home ranges in wet years, presumably because they spent less time meeting energy demands and more time attempting to reproduce. Home range expansion was likely facilitated by weather conditions conducive to increased movement (e.g., increased relative humidity and warmer night time temperatures). In contrast, females maintained stable home ranges regardless of resource availability. Perhaps stable home ranges provide benefits, such as experience with productive ambush sites, familiarity with basking and shedding sites, enhanced communication via chemosensory stimuli, and reduced exposure to predators. However, none of these reasons can explain why females did not contract their home ranges during high-resource years, when they are more likely to be gravid and sedentary (e.g., King and Duvall, 1990; Graves and Duvall, 1993; Beaupre and Duvall, 1998). Although pure speculation, perhaps females increase their chance of being encountered by males by being more predictable in their location. Obviously, a full understanding of underlying causation in gender-based differences in spatial ecology will require more directed research, including an increase in studies that focus on rattlesnake species with more tropical distributions characterized by less variable climates. Surprisingly, *C. tigris* is one of the most southerly distributed rattlesnake species to be intensively studied, even though it is still a decidedly temperate species, subjected to a prolonged winter inactivity period lasting approximately five months (November-March).

Movement patterns.—Male *C. tigris* showed a conspicuous spike in activity (as measured by movement frequency and distance moved per day) during the summer rainy season compared to spring and fall, but females did not. Once again, this spike in activity is likely due to increased mate searching on the part of males, facilitated by environmental conditions conducive to above-ground activity. Interestingly, unpublished data (Goode et al.) on the ratios of *C. tigris* with obvious food boli and/or feces in the hindgut indicate that males feed less during the summer mating period than in spring and fall. The fact that males feed less during the

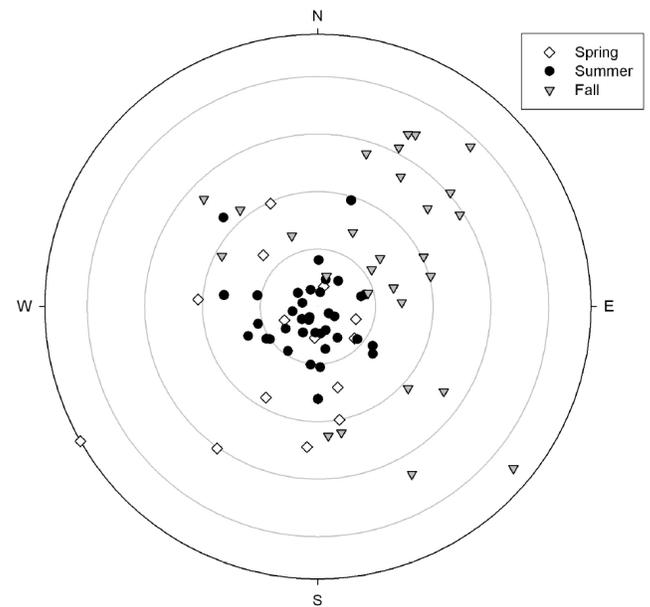


Figure 3. Polar graph depicting directionality of movements of Tiger Rattlesnakes (*C. tigris*) from Saguaro National Park in southeastern Arizona, 1997-2001, as a function of season. Both males and females tended to maintain directional movement vectors to and from dens during spring and fall, but did not show directionality in movements during summer.

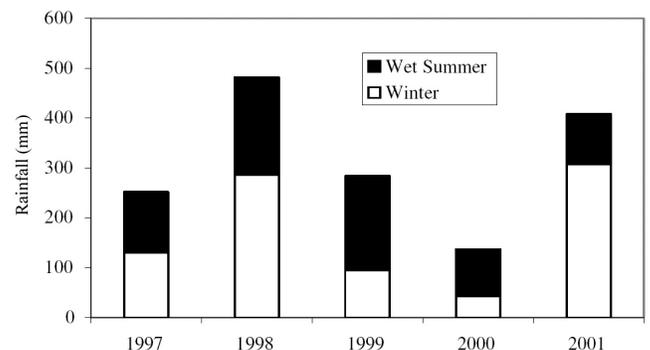


Figure 4. Annual rainfall from our Tiger Rattlesnake (*C. tigris*) study site in Saguaro National Park, southeastern Arizona, 1997-2001. Rainfall in the Sonoran Desert was bimodal, with peaks in summer (monsoon season) and winter. Data are presented in “water years” to give a more accurate picture of variation in rainfall.

mating season stresses the importance of finding mates, and implicates mating rather than foraging as the primary reason for dramatic increases in movement (c.f. Cardwell, 2008).

Rattlesnakes living in more northern climates are known to travel long distances to and from hibernacula (*C. viridis*, 5.7 km, Duvall et al., 1985; *C. horridus*, 7.2 km, Brown 1992). Straight-line movements to and from summer activity centers have been well documented for *C. viridis* in Wyoming (Duvall et al., 1990; King and Duvall, 1990; Duvall and Schuett, 1997) and in Alberta, Canada (Jørgensen and Gates, this volume). When traveling to and from overwintering sites, *C. tigris* tend to make relatively straight movements, but they do not range long distances from dens compared to their northern congeners. During the summer activity season, males especially tend to move back and forth across their home ranges, often encountering several females during the mating period.

Research on the effects of precipitation on snake activity is surprisingly scant, especially on temperate species. Limited research from tropical regions indicates that effects of precipitation are highly variable among species, with little or no discernable patterns (Henderson and Hovers, 1977; Brown et al., 2002). There is wide agreement among herpetologists and hobbyists that snake activity in the Sonoran Desert increases dramatically with the advent of the summer monsoon season, in spite of the lack of references documenting this "fact." The literature on annual differences in movement patterns associated with variation in precipitation is even scantier, although Prival et al. (2002) documented an increase in movements in response to summer monsoon precipitation by *C. pricei* in Arizona. We were only able to compare differences in movements between one unusually wet year and one drier-than-average year. As predicted, males moved more during the wet year, but several years of data will be required to make robust conclusions about the association between movement patterns and precipitation.

Research on rattlesnakes has contributed a great deal to our understanding of snake ecology in general (Beaupre and Duvall, 1998). However, it is important to recognize that the bulk of our knowledge of snake ecology is based on studies of single populations over relatively narrow time frames. Although this study covered a 5-yr period, it was still difficult to obtain a comprehensive picture of *C. tigris* spatial ecology. Variation in natural systems is partly to blame for the difficulty in obtaining robust data sets, but research techniques are also implicated. For example, radiotelemetry has undoubtedly revolutionized the study of secretive species like snakes (Reinert, 1992), but due to the intensive amount of work required to track a large number of individuals, obtaining statistically meaningful results can be extremely challenging. It should come as no surprise that the core of our knowledge is mostly confined to male snakes of relatively large species, because subdividing sample size into sex and age-class categories, let alone multiple populations, makes rigorous analyses all but impossible. In-

creasing the difficulty of our task is the fact that researchers commonly experience significant problems with transmitters, such as premature failure.

It seems as if there is no shortcut to understanding the mysteries of rattlesnakes, and that only long-term, detailed research will provide us with the hard-won data on natural history that is so essential to our task. Therefore, we stress the importance of truly long-term research on multiple populations that incorporates spatial replication. In this vein, we have continued to study additional *C. tigris* populations. It will be interesting to examine population variation in a variety of ecological parameters as we continue with our long-term research program. We hope to use our increasing understanding of inter-population variation to examine how changes in land use and interactions with environmental factors may affect different populations at different times.

ACKNOWLEDGMENTS

This study would not have been possible without the contributions of numerous people and organizations to whom we extend our sincere appreciation. For able assistance in the lab and field, we thank S. Breeden, T. Edwards, E. Kuklinski, R. Gann, C. Fatzinger, J. Borgmeyer, I. Cornelius, C. Boal, C. Davis, B. Bibles, C. Billington, F. Kranenburg, J. Treiber, M. Wall, A. Kellar, A. Diaz, and K. Beaupre. We are grateful to P. Anning, J. Jarchow, C. Scott, S. Cameron, J. McNally, D. Duvall, B. Brandner, S. Basford, and C. Schwalbe for technical advice, expertise, and financial and equipment support. J. Peterson, S. Riplog-Peterson, and the Eisentraut family were very gracious in allowing us to conduct research on their land. For their patience and support, A. Tuijl and R. Tuijl-Goode deserve special thanks. We extend our gratitude to the entire staff of Saguaro National Park, especially N. Kline, D. Swann, and M. Weesner. And finally, we would like to single out L. Norris and the National Park Service Desert Southwest Cooperative Ecosystem Studies Unit for their generous support of MG's research program. We thank the following organizations for funding: Arizona Game and Fish Department Heritage Fund, Southwestern Parks and Monuments Association, Tucson Zoological Society, Reid Park Zoo Teen Volunteers, Denver Zoological Society, National Park Service, Desert Southwest Cooperative Ecosystem Studies Unit, University of Arizona, and Saguaro National Park. This research was authorized by scientific collecting permits issued to M. Goode by the Arizona Game and Fish Department, and handling of research subjects was approved by the University of Arizona's Institutional Animal Use and Care Committee (Protocol #03-023).

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