Microgeographic Variation in Tiger Rattlesnake Ecology and Life History: The Importance of Long-Term, Natural History-Based, Multiple-Population Research

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We studied multiple populations of Tiger Rattlesnakes (*Crotalus tigris*) in the Sonoran Desert from 1997–2010, using mark-recapture and radiotelemetry to obtain a robust data set on various aspects of Tiger Rattlesnake biology. We report on variation in body size, diet, growth, and reproduction at three intensively studied sites near Tucson, Arizona, USA. We discuss possible reasons for observed differences within and among populations, and emphasize the importance of long-term studies that encompass multiple populations to better understand effects of environmental variation and local adaptation. We also stress the need to incorporate an intensive natural history-based approach to elucidate patterns that can subsequently be examined using a more focused, question-driven approach.

A review of the literature reveals that, with few exceptions (e.g., Fitch 1999), most of what we know about snakes comes from relatively short-term, single-population studies (see discussion in Parker and Plummer 1987). Studies on multiple populations of snakes have tended to focus on geographic variation in populations separated by relatively long distances, often from disparate habitat types (e.g., Plummer 1987, Gregory

The view overlooking the ninth green at Stone Canyon. Note the artificially mesic habitat associated with the golf course.

and Larsen 1993, Ashton 2001, Luiselli et al. 2001, Zuffi et al. 2009). Comparatively few studies have examined microgeographic variation (see King 1993, Beaupre 1995, Jenkins et al. 2009) in snake populations, especially from similar habitats (see Kephart 1982, Meshaka and Delis 2010). In spite of these shortcomings, ecologists recognize the need to examine long-term variation within and among populations of a species if we are to understand the critical roles played by environmental variation and local adaptation (Stearns 1992).

In 1997, when we began to study Tiger Rattlesnakes (*Crotalus tigris*) in the Sonoran Desert of Arizona, our goal was to conduct a long-term study that would enable us to learn as much as possible about the secret lives of these seemingly elusive snakes (cf., Goode et al. 2008). Fourteen years later, with countless hours spent in the field, at times practically living with our research subjects, we have amassed a rich dataset on multiple populations. Using a classic natural history approach, we have relied on intensive field observations to uncover patterns in nature, often followed by question-driven research designed to gain a more thorough understanding of Tiger Rattlesnake ecology (e.g., Greene 2005). In spite of criticisms from those wedded to experimental hypothesis testing, we unapologetically favor a rigorous natural history approach, because it often leads to a better understanding of the life histories of free-ranging animals. Also, although increasingly overlooked, hard-won natural history data often are critical for conservation and key for identifying patterns that can lead to the development of hypotheses that can be tested in a more focused scientific framework, even in some cases disentangling cause and effect through field experimental manipulation (e.g., Bartholomew 1986).

In this paper, we provide selected data on important aspects of Tiger Rattlesnake ecology and life history from three intensively studied populations subjected to different local environmental conditions. In one population, a subset of individuals has been exposed to anthropogenic influences (i.e., a low-density residential development and associated golf course) that appear to have led to dramatic changes in fundamental life history traits. These changes are likely due to greatly increased productivity brought on by year-round irrigation of the golf course and landscaping associated with roads, public facilities, and private residences.

Methods

Study Sites.—We collected data on Tiger Rattlesnakes from several sites throughout the Tucson Basin and southern Arizona. However, in this paper, we only included data from three populations located in the Rincon and Tortolita Mountains (Fig. 1), because these were the only sites where we conducted intensive mark-recapture and radiotelemetry research. The two sites within the Rincon Mountains, Tanque Verde Ridge (TVR) and Rocking K Ranch (RK), were originally chosen as part of a project investigating effects of urban development on Tiger Rattlesnakes along the boundary of Saguaro National Park along the southeastern edge of Tucson. The two sites are situated approximately 4 km apart. The Tortolita Mountain site, Stone Canyon (SC), is located on the northwestern side of Tucson, approximately 50 km from the other two sites. Stone Canyon is a large, affluent development, which when completed will consist of a resort, golf course, and over 450 residential estates situated on one- to five-acre lots. The golf course was built in 2000, and as of 2010, approximately 150 homes were constructed. All three sites consist of massive rocky ridges with steep rocky slopes dissected by relatively small ephemeral washes, some of which are characterized by well-developed xeroriparian vegetation. Vegetation is typical of Sonoran Desertscrub, Arizona Upland Subdivision (Turner and Brown 1982). Common plants include Saguaro (*Carnegia gigantea*), Foothill Paloverde (*Cercidium microphyllum*), Brittlebush (*Encelia*

DON SIAS

A Tiger Rattlesnake (*Crotalus tigris*) in an ambush posture waits for a potential meal. We have documented interpopulation variation in Tiger Rattlesnake diet at three sites.

JOHN F. BINNS

Fig. 1. Map of Tucson, Arizona and surrounding mountain ranges, showing the locations of our three study sites (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon).

farinosa), Prickly Pear and Cholla (*Opuntia* spp.), and Velvet Mesquite (*Prosopis velutina*). The elevational range is approximately 850–1,100 m.

Capture, Handling, and Marking.—We encountered Tiger Rattlesnakes while road cruising, during foot surveys, and while radiotracking a large number of snakes implanted with radiotransmitters. We captured rattlesnakes with tongs and transported them to the lab in cloth snake bags placed inside coolers. We permanently marked snakes by injecting a PIT tag under the skin, sealing the injection site with superglue. We assigned each snake an identification number corresponding to the sequence in which it was captured, and a unique paint mark applied to the dorsal half of the first 3–4 rattle segments conveyed this number. This allowed us to identify snakes in the field without capturing them, and it enabled us to determine shedding frequency.

Data Collection.—In the laboratory, we placed rattlesnakes in a clear plastic restraining tube and anesthetized them using 1–2 ml isoflurane (Abbott Laboratories, Abbott Park, Illinois). We contend that anesthetizing rattlesnakes is critical, because it facilitates accurate data collection, eliminates or reduces stress and pain associated with handling, and minimizes the likelihood of harm to both rattlesnakes and researchers. Accurate SVLs are essential for reliable quantification of growth, especially in adult Tiger Rattlesnakes, which typically grow in fractions of a millimeter per month. Anesthesia also facilitates collection of feces, which are easily removed from the hindgut via gentle and repeated pressure applied toward the cloaca. We washed and sorted fecal samples into identifiable prey remains, consisting of hair, scales, claws, bones, teeth, and the occasional feather. For the purposes of this paper, we have only provided data on fecal samples containing hairs and scales, because they are easily identifiable, and can be unambiguously assigned to either mammal or lizard, by far the two most important prey groups of Tiger Rattlesnakes.

Assessment of reproductive condition in females, via palpation of follicles, ova, or embryos, also is far more reliable in anesthetized individuals. We have compared data from palpation to ultrasound readings, and we have found this manual method to be highly accurate (M. Goode, unpubl. data), although fully formed embryos can be difficult to palpate even in a fully anesthetized snake. We assessed reproductive condition either in the fall, when gravid females contain small, hard follicles before entering hibernation, or in the spring, when gravid females contain larger, vitellogenic follicles upon emergence from hibernacula. Tiger Rattlesnakes tend to give birth in rock outcrops, making it difficult to obtain data on litters. However, diligent radiotracking of gravid females enabled us to obtain such information for numerous snakes. In a few cases, we assumed that a gravid female gave birth, even though we did not see the litter, because the recaptured female had lost a significant amount of mass. Similar decreases in mass were consistent with those in snakes known to have given birth and for which we were able to obtain post-parturient masses.

Results

Body Size (SVL).—We drew upon our rich mark-recapture data set (Table 1) to examine within- and among-population variation in SVL, which varied among the three populations, and within the SC population, where Tiger Rattlesnakes associated with the golf course environment were much larger than their off-course counterparts (Fig. 2).

Growth.—We used ANCOVA with initial snout-vent length as a covariate to detect differences in growth rates. Analyses revealed no difference in growth rates among the three populations (Fig. 3a). However, when comparing SC snakes, individuals associated with the golf course and

Table 1. Numbers of captures and recaptures of Tiger Rattlesnakes (*Crotalus* tigris) at our three study sites and other locations in Arizona from 1997–2010 (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon, Catalinas = Santa Catalina Mountains, Tucsons = Tucson Mountains). Only data from RK, TVR, and SC were used in analyses.

Site	Captures	Recaptures
RK	59	24
TVR	145	77
Catalinas	126	1
SC	646	532
Tucsons	61	0
Other	72	0
Total	**1,109**	**634**

JOSH CAPPS

Overspray and runoff from the constant irrigation required to maintain turf have created permanent riparian areas along Stone Canyon's fairways and greens.

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Body sizes of Tiger Rattlesnakes (*Crotalus tigris*) varied among populations and within the Stone Canyon population.

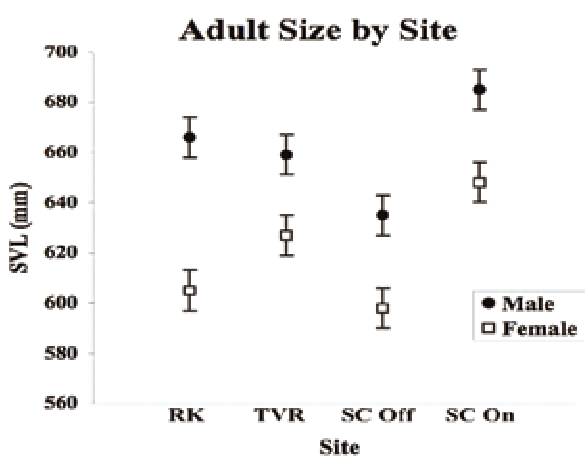


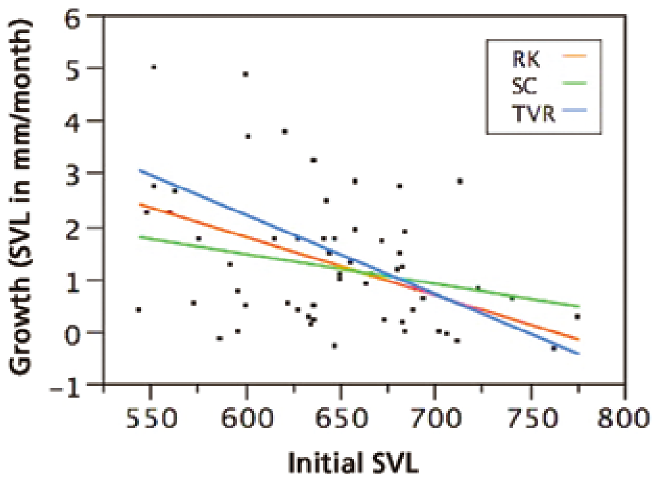
Fig. 2. Average adult male and female Tiger Rattlesnake (*Crotalus tigris*) body sizes (SVL = snout-vent length) at RK, TVR, and SC from 1997–2010 (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon). The SC population is divided into those snakes with home ranges that include part of the golf course (SC-on) and those with home ranges that do not include part of the golf course (SC-off).

development grew significantly more rapidly than their off-course counterparts (Fig. 3b). We only used radiotransmittered snakes for on- and off-course comparisons, because we could be certain that off-course snakes never included the golf course in their home ranges.

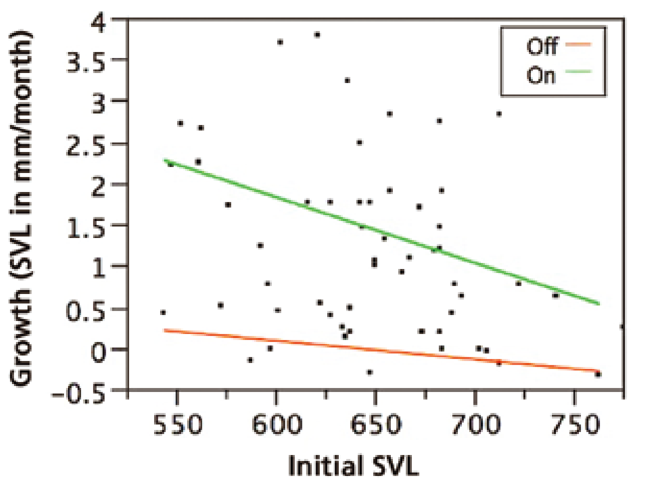
Diet.—Fecal analysis revealed important among-population differences in diet (Fig. 4). Tiger Rattlesnakes at TVR were primarily small-mammal eaters, whereas rattlesnakes at RK consumed primarily lizards, even though the two populations are only 4 km apart. At SC, rattlesnakes ate a far greater proportion of mammals, but the difference between on- and off-course snakes was negligible.

Reproduction.—Palpation of female Tiger Rattlesnakes revealed slight among-population variation in reproductive status. However, we observed a dramatic increase in within-population variation at SC (Fig. 5), where a roughly two-fold increase in the proportion of gravid females was associated

A Tiger Rattlesnake (*Crotalus tigris*) consuming a Western Whiptail (*Aspidoscelis tigris*). Tiger Rattlesnakes consumed lizards in greater proportions at Rocking K than at Tanque Verde Ridge or Stone Canyon.



Source	DF	Sum of Squares	F Ratio	Prob > F
Site	2	1.151030	0.4065	0.6681
InitialSVL	1	14.797037	10.4516	0.0022
Site*InitialSVL	2	2.691094	0.9504	0.3933



Source	DF	Sum of Squares	F Ratio	Prob > F
Off/On	1	9.5082340	13.1397	0.0013
InitialSVL	1	1.9868555	2.7457	0.1100
InitialSVL*Off/On	1	0.6457620	0.8924	0.3539

Fig. 3. A. ANCOVA of growth rates of Tiger Rattlesnakes (*Crotalus tigris*) at three sites from 1997–2010, using initial SVL as a covariate to detect differences in growth rates (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon). **B.** Within-population comparison of growth rates for on- and off-course snakes at SC from 2002–2010. We considered on-course snakes to be those with home ranges that included part of the golf course and off-course snakes to be those with home ranges that did not include part of the golf course.

Table 2. Mean litter sizes (± 1 SE) of Tiger Rattlesnakes (*Crotalus tigris*) at RK, TVR, and SC (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon). The SC population is divided into those snakes with home ranges that include part of the golf course (SC-on) and those with home ranges do not include part of the golf course (SC-off).

Site	Mean Litter Size
RK	2.2 ± 0.3
TVR	2.4 ± 0.4
SC-on	3.4 ± 0.5
SC-off	2.4 ± 0.3

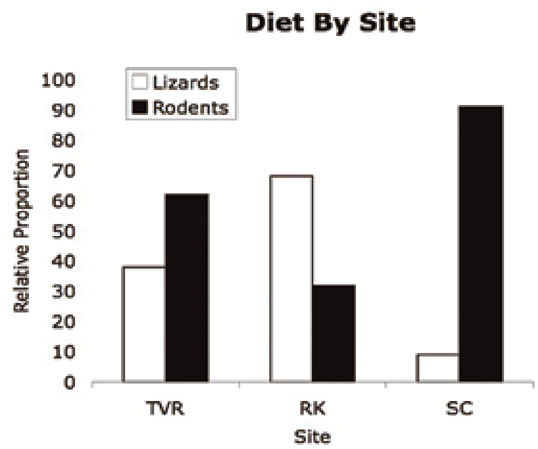


Fig. 4. Proportions of mammals and lizards in the diets of Tiger Rattlesnakes (*Crotalus tigris*) at RK, TVR, and SC based on examination of fecal samples (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon).


MATT GOODE

An adult Tiger Rattlesnake (*Crotalus tigris*) eating a White-throated Woodrat (*Neotoma albigula*). Snakes at Stone Canyon ate a far greater proportion of small mammals than at the other two sites.

with the golf course and development. Mean litter size (a critical life history trait with obvious fitness consequences) of snakes occupying the golf course and development portion of SC was 3.4, which represents an approximately 30% increase over off-course, TVR, and RK snakes (Table 2).

Discussion

Using a long-term, natural history-based, intensive field approach, we were able to uncover important within- and among-population differences in Tiger Rattlesnake ecology and life history. Our findings suggest that life history traits are relatively plastic, apparently responding to changes in local environmental and ecological conditions, even over relatively short distances. Although our data will eventually be rigorously analyzed in the context of life history theory, our goal here was to simply describe micro-geographic differences observed in Tiger Rattlesnakes populations.

The most striking results from our research were the consistent differences found in snakes living within the golf course and development area at SC. This area is dramatically different than TVR, RK, and nearby off-course sites, because it is characterized by a growing residential development and associated golf course. Data on water availability at SC indicate that seasonal drought is essentially eliminated at the golf course site (Fig. 6). In addition, intensive irrigation of mostly native vegetation along the golf course and roads, and in landscaped areas around public facilities and homes, results

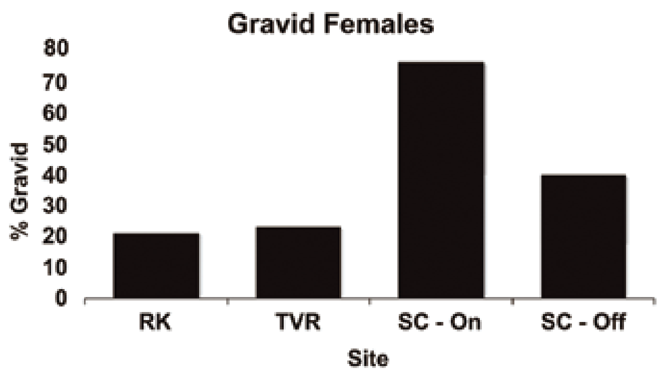


Fig. 5. Among-population comparison of the reproductive status of female Tiger Rattlesnakes (*Crotalus tigris*) at three sites and within-population comparison at SC from 1997–2010 (RK = Rocking K, TVR = Tanque Verde Ridge, SC = Stone Canyon). The SC population is divided into those snakes with home ranges that included part of the golf course and off-course snakes to be those with home ranges that did not include part of the golf course.

in thick, mesic tracts of vegetation that essentially act as permanent riparian areas in an otherwise dry environment. The dramatic difference between natural and irrigated areas is most pronounced in spring and early summer, when the Tucson region receives only trace precipitation. In essence, the existence of year-round water at SC greatly extends the active season of many species. In addition, unusually high productivity leads to increased plant reproduction, providing forage and cover for a wide variety of animals. Apparently, Tiger Rattlesnakes are taking advantage of this enhanced resource environment, allocating extra energy to growth and reproduction. Indeed, 8 of 16 female Tiger Rattlesnakes from on-course areas at SC have given birth in two successive years, and one individual produced a litter in each of three successive years. In comparison, only 5 of 31 females from all other sites combined have been gravid in successive years.

In the case of diet and prey availability, systematic surveys indicate that the relative abundance of lizards is greater at RK than at TVR, which corresponds to the relative proportion of lizards consumed by Tiger Rattlesnakes at both sites (Goode and Wall 2002). Small-mammal trapping at all three sites indicates that relative abundance of small mammals at SC

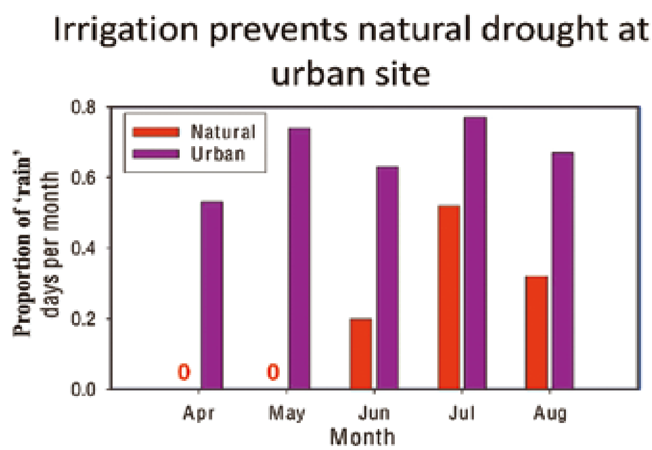


Fig. 6. "Rainfall" (i.e., irrigation) patterns at Stone Canyon verses natural rainfall patterns in Tucson, Arizona in 2007. Courtesy of Jon Davis and Dale DeNardo, ASU.

Two neonate Tiger Rattlesnakes (*Crotalus tigris*). Litter sizes from females occupying the golf course were approximately 30% higher than those from other populations.


DON SIAS

Although Tiger Rattlesnakes (*Crotalus tigris*) appear to be benefiting from the energy-rich environment of the Stone Canyon golf course, they also face risks posed by increased human activity.

is dramatically higher than at TVR and RK, with trap success rates ranging from as low as 5% at RK to as high as 75% at SC (M. Goode, unpubl. data). Again, these differences are likely attributable to stark differences in water availability, leading to increased seed and leaf production and higher rodent populations at SC.

Our study underscores the importance of long-term studies on multiple populations. A study of shorter duration might have led us to a erroneously conclude that Tiger Rattlesnakes at TVR feed primarily on small mammals and gravid females have small litters every 2–5 years. By adding the RK population, we discovered that Tiger Rattlesnakes found only 4 km away actually consumed more lizards than small mammals, even though they occurred at the same elevation and were using an essentially identical vegetative community. Furthermore, dietary analysis at SC revealed yet another difference, with snakes consuming small mammals in much higher proportions than in the other two populations. Documenting interpopulation variation in diet is important, because it provides insight into the fundamental ecology of an organism, and allows for predictions to be made about behavior, physiology, and reproduction (Taylor et al. 2005).

Tiger Rattlesnakes clearly are responsive to changes in their environment, and snakes living in an energy-rich environment (e.g., SC on-course) are taking advantage of additional resources to increase their reproductive output. However, concluding that golf courses and developments are beneficial for Tiger Rattlesnakes would oversimplify the complexity of this relationship, and we caution against such an interpretation. Data from SC indicate that humans regularly kill snakes, including Tiger Rattlesnakes. Indeed, mortality rates in general appear to be much higher at SC than TVR and RK, including what appears to be natural predation. Road mortality at SC also has been relatively high, and it continues to increase as more homes are built. The critical question from a conservation standpoint is whether or not increased female reproductive output at SC can offset increased mortality. Will SC become an ecological trap, providing Tiger Rattlesnakes with all their needs only to bring them into contact with humans? Only a long-term study such as ours will be able to answer that question.

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Young Aruba Whiptail (*Cnemidophorus arubensis*) from Aruba sitting on a tonalite block (a type of andesite rock). Distinguishing the sexes is difficult in young and subadult animals. When males become larger, they change color from yellow-brown or light brown to gray and blue. In an animal of this size that would be noticeable, thus the lizard in the picture is very likely a female.