DAILY AND SEASONAL ACTIVITY PATTERNS OF THE MASSASAUGA (Sistrurus catenatus): An Automated Radio-telemetry Study

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Abstract.—Many snake species substantially shift their daily activity patterns throughout the year. Understanding if, when, and why these changes occur can improve our understanding of snake ecology and conservation. However, quantifying these fine-scale activity shifts is logistically difficult as manual radio-telemetry provides little information on what animals are doing between intermittent tracking events. Furthermore, newer tracking technology (i.e., satellite or global positioning trackers) often cannot be used for snakes due to size or shape constraints. We used automated radio-telemetry to assess fine-scale daily and seasonal activity patterns of the Massasauga (Sistrurus catenatus) at a site in northern Michigan, USA. During the active seasons (April to October) of 2015 to 2017, we recorded 16,816 detections of nine adult Massasaugas and found that, on average, an individual was actively moving during 15% (range: 3-27%) of detections. Massasaugas were principally diurnal at this site with 73% of the 960 recorded movements occurring during daylight hours. However, Massasaugas were more frequently active around sunset during the warmest months of the summer. These results suggest that Massasaugas at northern latitudes need only make minor shifts in activity from day to evening to avoid hot summer temperatures rather than shifting to nocturnal activity as has been reported for other snake species. Snakes showed a clear seasonal pattern in activity with a peak in summer, presumably corresponding with reproductive behavior. Our study highlights the value of using automated radio-telemetry to monitor fine-scale activity patterns of free-ranging inconspicuous wildlife.

Key Words.-conservation; crepuscular; diurnal; movement patterns; nocturnal activity; snake behavior; spatial ecology

INTRODUCTION

Organisms may alter their daily activity patterns throughout the year in response to changing temperatures (Weatherhead et al. 2012), prey availability (Margues and Puorto 1998), or to reduce their risk of predation (Dorcas and Peterson 1998). Snakes in particular appear capable of switching between diurnal and nocturnal activity seasonally (Gibbons and Semlitsch 1987; Abom et al. 2012). Studies determining if species alter their activity patterns, when such shifts occur, and the proximate causes of these changes have provided valuable information about the thermoregulatory behavior (Weatherhead et al. 2012; Sperry et al. 2013), foraging ecology (DeGregorio et al. 2015), and natural history (Moore 1978; Slip and Shine 1988) of several snake species. However, documenting the timing of snake activity and occurrence of seasonal shifts can be logistically challenging.

Traditional methods for quantifying snake daily activity patterns are based on capture/encounter rates (e.g., Shine 1979; Lillywhite and Brischoux 2012), observations of captive snakes (Moore 1978), or manually tracking snakes using radio-telemetry (Durner and Gates 1993). However, each of these methods has limitations (e.g., intermittent and unreliable encounter rates, captivity effects, or infrequent tracking events), and automated data collection has become the preferred method for quantifying activity patterns of freeranging animals (Rodgers 2001; Cagnacci et al. 2010). Incorporation of global positioning systems (GPS) into radio-transmitters or deployment of satellite transmitters are the most common methods to automate collection of activity data, but both methods are difficult or impossible for snakes, which typically have transmitters surgically implanted as opposed to externally attached (but see Riley et al. 2017) and because many species are relatively small-bodied (Dorcas and Willson 2009).

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Recently, several researchers have demonstrated and validated the ability of automated radio-telemetry systems (ARTS) to semi-continuously monitor the location and activity of snakes (Ward et al. 2013; Sperry et al. 2013).

Automated radio-telemetry systems receive signals from conventional radio-transmitters via multiple directional antennas attached to multiple receivers and use differences in signal strength to detect movements of focal animals (Cochran et al. 1965; Kays et al. 2011). These systems can continuously monitor the activity of numerous individuals and can generate extensive data sets without repeatedly disturbing the animal. This system has recently been used to successfully quantify the seasonal and diel activity patterns of several colubrid snakes, such as Gray Ratsnakes (Pantherophis spiloides; Ward et al. 2013) and Black Racers (Coluber constrictor; DeGregorio et al. 2016). The system can provide researchers near continuous monitoring of animal activity; however, it cannot provide fine-scale behavior or habitat use data, so the method is most valuable when paired with manual radio-telemetry studies. Here, we use ARTS to study the seasonal and daily activity patterns of the federally listed Massasauga (Sistrurus catenatus) at a site in Michigan, USA, near the northern extent of the geographic range of the species.

The Massasauga is a small-bodied (< 100 cm total length) rattlesnake found in the central portion of North America including throughout the Great Lakes region of the continent. Massasaugas typically hunt by ambushing small mammals from stationary positions. As an ambush hunter, the daily activity patterns of the Massasauga may be different from the actively foraging colubrid species previously studied with ARTS (e.g., Ward et al. 2013). Several studies have found seasonal variation in Massasauga movement with peaks in activity corresponding to movement to and from hibernacula (Reinert and Kodrich 1982; Seigel 1986; Marshall et al. 2006) or mate-searching (Jellen et al. 2007). Less attention has been paid to the daily, short-term activity patterns of this species, although there is some evidence that it may shift seasonally from diurnal to crepuscular or nocturnal activity (Seigel 1986; Dreslik 2005). A more complete understanding of Massasauga activity can inform conservation by identifying periods of time when snakes might be most vulnerable to human activity (Shepard et al. 2008) and provide a basis for exploring the species natural history and behavioral ecology. Our goals here were to use ARTS to (1) quantify how frequently Massasaugas are active, (2) assess the times of the day (or night) they are most active, and (3) explore how their daily activity patterns change throughout the active season.

MATERIALS AND METHODS

Study site.—We studied snakes at the Camp Grayling Joint Maneuver Training Center in Grayling, Michigan, USA (44.6615°N, 84.7148°W). Camp Grayling is a military facility that encompasses nearly 60,000 ha across three counties in the northern Lower Peninsula of Michigan. The installation is primarily focused on military training, but portions of the base are also open to the public for recreation. Our specific study site was an approximately 800 ha area located on the periphery of the installation where training activity is minimal. The site consists of patchy and fragmented forests composed of oak (Quercus spp.), maple (Acer spp.), Quaking Aspen (Populus tremuloides), Red Pine (Pinus resinosa), Jack Pine (Pinus banksiana), Black Spruce (Picea mariana) and Arborvitae (Thuja occidentalis). A large utility right-of-way runs through the site and separates higher, drier pine-dominated forests from lower, wetter scrub-shrub wetlands and mixed forests. The Manistee River and a smaller creek traverse the site and are bordered by Speckled Alder (Alnus incana).

Radio-telemetry.—From May 2015 to June 2017, we captured adult Massasaugas for transmitter implantation by visually searching around known or likely overwintering sites in the spring. We captured additional snakes opportunistically throughout the active season. In snakes selected for radio-telemetry, we surgically implanted a 5.0 g or 9.0 g temperaturesensitive radio-transmitter (model SB-2T or SI-2T, respectively; Holohil Systems, Ltd., Carp, Ontario, Canada) into the body cavity following methods adapted from Reinert and Cundall (1982). Implanted transmitters were, on average, 4.4% of the body mass of an individual (range: 3.1-5.4%). While each snake was anaesthetized, we recorded the weight (g) and snout-to-vent (SVL) length (cm), confirmed its sex by probing its cloaca, and determined the reproductive status of females by palpating their abdomens for developing follicles. We held implanted snakes for two to five days after surgery and released them at their respective capture locations. We manually located each individual approximately every 48-72 h during daylight hours (0800-2000) using a handheld receiver (R-1000, Communications Specialists, Inc., Orange, California, USA) and antenna (three element mini Yagi, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA).

During May 2015, we constructed three ARTS (JDJC Corp., Fisher, Illinois, USA) to semi-continuously track the activity of radio-implanted snakes. Each ARTS consisted of an automated receiving unit (about \$4,500 USD) connected to an array of six, three-element Yagi antennas (about \$200 each) attached to the top of a tower (about \$300 USD) and powered by a 12-volt deep cycle marine battery (about \$80 USD). We used guyed, 50G Rohn television antenna towers, each consisting of three, 3-m tall sections for a total height of approximately 9 m. The azimuths of the six antennas were spaced at 60° to give 360° coverage. Each receiving unit was programmed to search at intervals of 3-10 min for the radio frequency of each transmitter implanted in a snake. The search interval was determined by the number of transmitters that each receiving unit was programmed to search. Thus, when relatively few snakes were being tracked, the search interval was faster (3 min) and when more snakes were being tracked, the search interval was slower (10 min). All data were recorded on memory cards and we downloaded data every two weeks. We placed the three towers approximately 500 m apart in locations that would maximize the number of snakes within range of a tower at any given time.

Detecting the activity of a snake relies upon detecting changes in the bearing from ARTS to the radio-tagged snake and the amount of energy received by the receiving unit from the transmitter (signal strength: recorded in dBm). Thus, snake movements should result in simultaneous changes in both signal strength and bearing. However, it is important to note that postural changes by the snakes (e.g., coiling, uncoiling) may also alter the orientation of the transmitter antenna to the ARTS antenna and may change the signal strength. Postural change may be interpreted as a movement, thus careful thresholds must be decided upon to differentiate between movements and postural changes. To determine these thresholds, we used tests previously conducted by DeGregorio et al. (2016) using the same ARTS systems and radio-transmitters. In this study, the authors placed radio-transmitters throughout the landscape around the ARTS and, at set times, altered their orientation by either coiling or uncoiling them or changing their orientation and distance relative to the ARTS. After each transmitter was manipulated 10-15 times, it was determined that a snake could be considered to have moved if the bearing of the snake changed by $> 1.5^{\circ}$ and its signal strength changed by > 350 dBm between successive readings. These results should not vary between individuals or snake species as long as the equipment components are the same. These conservative thresholds allowed us to reliably differentiate true transmitter movements from background noise, signal variation, and postural changes while also allowing us to detect relatively small snake movements (2–3 m). Before analysis, we filtered the data to eliminate spurious or weak records using the recommendations of Ward et al. (2013).

To assess daily trends in Massasauga movement, we quantified the total number of detections for each individual and the proportion of those detections in which the snake had moved since the previous detection (hereafter movement frequency). For example, if we recorded 1,000 detections for a snake and it had moved during 180 of those detections, this individual had a movement frequency of 0.18. Because we detected snakes semi-continuously, movement frequency can be considered the proportion of time a snake was actively moving. We calculated the movement frequency for each snake for every hour of the day for each month of the active season (April to October).

We assessed daily and seasonal trends in Massasauga activity patterns using a generalized linear mixed model (PROC GLIMMIX in SAS, SAS Institute, Cary, North Carolina, USA). Our response variable was movement frequency, and we assessed the effects of the fixed factors: year, month, hour of day, time period, sex, as well as the interaction term of month x time period. We defined time period as either day, night, sunrise, or sunset. The latter were delineated using average sunrise and sunset times for the 15th day of each month. The sunrise period included all activity occurring one hour before or one hour after sunrise, and the sunset period included all activity occurring one hour before or one hour after sunset. We used snake ID as a random effect to account for repeated ARTS readings recorded per individual and individual variation in activity. To specifically explore the factors influencing nocturnal activity by Massasaugas, we used a generalized linear model to assess the influence of the fixed factors: snake ID, sex, month, and year on the response variable of individual movement frequency. We restricted the analysis to the night hours (1 h after sunset to 1 h before sunrise).

RESULTS

Over the course of three active seasons (May to October 2015 and April to October 2016 and 2017), we used automated radio-telemetry to investigate the activity patterns of nine individual Massasaugas including three non-gravid females and six males. Three of the male snakes were tracked during both 2015 and 2016. We recorded 16,816 detections in which signal strength and noise values exceeded the conservative thresholds we set to filter spurious or unreliable records. The number of detections per individual snake averaged 1,401 (range: 21–8,608). Of those detections, snakes were actively moving during 964 of the events. Individual movement frequencies ranged from 3% to 27% with an average movement frequency of $15 \pm 0.09\%$ (± 1 SD).

Massasauga movement frequency varied seasonally (by month: $F_{6,16780} = 24.32$, P < 0.001: Fig. 1) with snakes being most active in June, July, and August (least squares means = 0.11, 0.18, 0.26, respectively). Although we lacked the statistical power to analyze the interactive effect of sex and season, patterns were

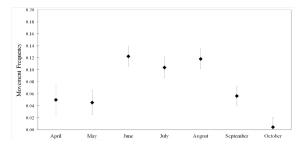


FIGURE 1. Mean monthly movement frequency (±1 standard error) of nine Massasaugas (*Sistrurus catenatus*) tracked via automated radio-telemetry in northern Michigan, USA, during the active season in 2015–2017.

qualitatively similar with both sexes most active in July and August and least active at the beginning and end of the season (April to May and September to October).

Massasauga movement frequency also varied daily (by time period: $F_{3,16779} = 50.45$, P < 0.001), but daily activity patterns shifted throughout the active season (month x time period interaction: $F_{18,16779} = 13.38$, P < 0.001; Fig. 2). In general, snakes were most active during the day and least active during the early morning hours (Fig. 3). However, activity during the sunset period was low during the beginning and end of the active season and relatively high during the hotter months of the summer with a peak in August (Fig. 2). Activity during the night was consistent but infrequent during all months of the active season (Fig. 3).

Overall, Massasaugas were principally diurnal with approximately 73% of all recorded movements (703 of 964) occurring during daylight hours. Of the 6,131 snake detections occurring at night, snakes were actively moving 167 times (2.7%), and all but one individual was recorded moving at least once. Nocturnal movement frequency averaged 0.4% and ranged from 0 to 1.1% per individual. Individual variation was the strongest factor influencing the amount of nocturnal activity ($F_{\rm 8,28}$ = 17.180, P = 0.021). We found no evidence that movement frequency at night varied monthly ($F_{\rm 6,22}$ = 0.082, P = 0.521), by sex ($F_{\rm 1,22}$ = 0.028, P = 0.290).

DISCUSSION

Overall, individual Massasaugas were active approximately 15% of the time (individual range: 3–27%). Contrary to our prediction that as an ambush

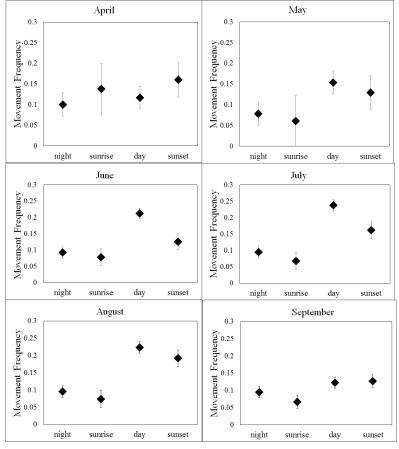


FIGURE 2. Mean frequencies of time period movements (\pm 1 standard error) by month of nine Massasaugas (*Sistrurus catenatus*) tracked via automated radio-telemetry in northern Michigan, USA, during the active season in 2015–2017. October is not displayed due to the low number of movements.

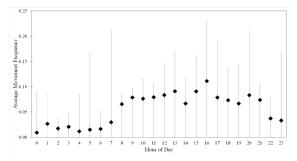


FIGURE 3. Mean frequency of hourly movement (± 1 standard error) of nine Massasaugas (*Sistrurus catenatus*) tracked via automated radio-telemetry in northern Michigan, USA, during the active season in 2015–2017.

hunter this species would be less frequently active than the colubrid species previously studied with ARTS, Massasaugas had similar movement frequency to the active, diurnal hunting *C. constrictor*, and were more active than the central-place foraging *P. spiloides* (Ward et al. 2013; DeGregorio et al. 2016). Data from manual radio-telemetry showed that Massasaugas move shorter distances per day than either of the colubrids (DeGregorio et al. 2011, 2016), suggesting that the Massasaugas movement pattern may consist of traveling to a spot, shuttling around the area for a bit while foraging, and then moving to a new spot several days later as would be expected for an ambush forager.

Using ARTS, we found a peak in Massasauga movement frequency in late summer, which has also been found in manual radio-telemetry studies at this site (DeGregorio et al. 2011) and others (Shepard et al. 2008). This increase is most likely associated with mating behavior (Jellen et al. 2007). We expected ARTS to be largely confirmatory with respect to seasonal patterns in activity, but that it would have a distinct advantage over manual radio-telemetry when it came to providing insight into diel activity patterns. Indeed, we found this to be the case and we were able to examine at an unprecedented scale how Massasauga diel activity varied throughout the active season with a focus on nocturnal activity.

Many snakes switch to nocturnal activity during summer to avoid hot daytime temperatures (Gibbons and Semlitsch 1987). Given the high latitude of our study site, daytime temperatures do not consistently exceed the preferred temperature range of the Massasauga (30–33.6° C; Harvey and Weatherhead 2010). Indeed, Massasaugas at our site were primarily diurnal with 73% of all movements occurring during daylight hours. Approximately 9% of movements occurred during the hours spanning sunset and activity during this time period peaked during the hottest months of the year. This increase in evening activity is consistent with reports of a summer shift to crepuscular activity by Massasaugas in Missouri (Seigel 1986) and Illinois (Dreslik 2005) in the USA. Given that we recorded little nocturnal activity at our site, it appears that Massasaugas need only make minor shifts in activity from day to evening to avoid hot summer temperatures.

Fewer than 1% of Massasauga movements occurred around sunrise. This is most likely a response to environmental temperature as these hours are consistently the coldest during a 24 h cycle. At northern latitudes, these temperatures are typically far from the preferred temperature range of Massasaugas (Harvey and Weatherhead 2010). Snakes should benefit from remaining inactive until their body temperature warms up enough for efficient locomotion. Indeed, most of the daytime activity we recorded for Massasaugas was during the warmest parts of the day during the warmest parts of the summer, indicating that Massasaugas are primarily diurnal at our site.

The automated radio-telemetry system is a versatile tool for exploring the ecology of snakes or other small-bodied wildlife species, and may help to provide useful information for species conservation that would not otherwise be possible. However, the system costs much more than manual radio telemetry and may not be necessary in all studies. In our case, the use of ARTS provided an extensive data set on the activity of the imperiled Massasauga. During our study, we also recorded approximately 500 relocations using manual radio-telemetry, but ARTS allowed us to expand our investigation of seasonal activity patterns to explore daily activity patterns on a temporal scale not yet accomplished for this species and proved to be a great compliment to manual radio-telemetry. A firm understanding of Massasauga activity patterns can provide land managers the information needed to plan activities such as vegetation mowing or road closures to avoid times of day and season when the snakes are most active and likely to be encountered. Modifications to the ARTS system can allow monitoring of body temperature for snakes equipped with temperaturesensitive radio-transmitters or generate location data if ARTS towers are placed on the periphery of telemetered animals, allowing for even greater insight into species biology.

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