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Vulnerability of Northern Pine Snakes (*Pituophis melanoleucus* Daudin, 1803) during fall den ingress in New Jersey, USA

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***Abstract.*—The management of threatened and endangered species often falls to various state agencies which may have different and conflicting goals. The Pine Barrens of New Jersey are managed for different objectives, including fire management, tree cutting, recreational activities (hiking, hunting, off-road-vehicle use), wildlife protection, and conservation. Managing competing claims requires ecological information on critical issues and vulnerabilities for determining the impacts of each claim. The Northern Pine Snake (*Pituophis melanoleucus*), an iconic Pine Barrens species that is threatened in New Jersey, is normally dispersed during spring and summer, but the snakes converge in the fall to communal hibernacula, where they spend the winter and leave in the spring. Here, the activity of Northern Pine Snakes near hibernacula in the fall is described to examine their vulnerability to various competing claims, such as fire or off-road vehicle use. Two hypotheses are tested: (i) that snakes enter the hibernaculum once (and stay), and (ii) that the total period of ingress for all Northern Pine Snakes is limited to just a few weeks in the fall. Activity of PIT-tagged snakes at hibernacula entrances was monitored with a passive, continuously-recording AVID TracKer and temperatures were monitored with a continuously recording thermometer placed at the soil surface. The behavior of marked snakes (18 in 2017, 25 in 2018), indicated that the period of activity around the hibernaculum entrance was: 1) longer than expected (i.e., over two months), 2) involved multiple ingress and egress of individual snakes, and 3) sometimes involved movement between two or among multiple nearby hibernacula. Northern Pine Snakes generally did not move in or out of hibernacula when temperatures were below 9° C. Daytime high and nighttime low temperatures greatly influenced movement. Although the daily high and low temperatures when snakes moved were correlated ($r = 0.54$ in 2017; 0.51 in 2018, $P < 0.0001$), the daily high and low temperatures were more highly correlated ($r = 0.71$ in 2017; 0.79 in 2018), indicating factors other than temperature influence snake activities. Most snakes entered and exited between 1000 and 1800 h, although some moved as late as 0030 h. These data can inform science-based decisions about when to allow tree cutting, fire management, and off-road vehicle races (e.g., increased human activity). Most snakes are concentrated around hibernacula (but not necessarily near the entrances) from early October until early December (or the end of December for two hatchlings). Therefore, a significant proportion of snakes are vulnerable to disturbances that could impact their population viability. Vulnerabilities are discussed in terms of competing claims and conservation.**

Keywords. Behavior, competing claims, hibernation, reptiles, Serpentes, Squamata, wildlife management

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Introduction

Managers are often required to make environmental resource decisions with incomplete knowledge, with little time, and often under conditions of competing claims for resources and associated habitat. Human alteration of natural lands is a key driver of global biodiversity loss (Pimm and Raven 2000; Wilcove et al. 2000). Claims for land can come from those who want to either use the resource itself (e.g., hunting, fishing, wildlife collecting), use important components of the habitat (e.g., logging), or improve the habitat for people (e.g., trail or road building, fire suppression). Indeed, managers of different resources (e.g., timber, wildlife) are often in conflict, asserting competing claims for the same resource or habitat. These need to be carefully considered and resolved in a manner that reduces the risks to the habitat and wildlife, while enhancing human benefits. For example,

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managers of forests must balance cutting (or harvesting) trees against re-forestation, the adverse effects of cutting trees against the benefits of cutting them, and the relative importance of the different benefits and costs (McLeod and Gates 1998; Todd and Andrews 2008). Similarly, fire suppression has some benefits (e.g., reduced potential for fire damage to nearby communities and industries), as well as costs if it does not occur (e.g., allowing dry debris to build-up, creating the potential for a very hot canopy fire when it does occur). Each option (e.g., logging, fire suppression) has both benefits and costs to the plants and animals living in the forests (Roth and Franklin 2018; Steen et al. 2010). In addition, most animals face one or more challenges to their survival, including predators, competitors, poachers, and resource users, as well as threats to their habitat from development, wildfire, or resource use. What may be good for one animal group may not be good for another. For example, creating gaps in forests may be good for deer management and for snakes requiring open nesting areas, but is not good for interior-nesting forest birds (Blouin-Demers and Weatherhead 2001; Gerald et al. 2006; MWPARC 2009). The complex situations forest managers face can only be resolved by examining the ecological and societal benefits and costs of different options.

Setting priorities for conservation is a challenging and necessary effort (Pimm et al. 2001). The biodiversity crisis facing the Earth suggests that the conservation needs of threatened and endangered species should be considered first when managing habitats and ecosystems (Wilson et al. 2009; Gaiarsa et al. 2015). Economic, societal, and political issues also play important roles in conservation decisions (Polasky 2008; Wilson et al. 2011). However, it is equally important to understand the roles of species vulnerability (IUCN 2009), habitat loss (Wilson 1992; Pimm et al. 1995; Gibbons et al. 2000), habitat fragmentation and patch size (Forman and Godron 1986; Hilton-Taylor 2000; Kjoss and Litvaitis 2001; Sanderson et al. 2002), restricted range or habitats (Segura et al. 2007; Cardillo et al. 2008), human disturbances (Parent and Weatherhead 2000), human infrastructures (e.g., roads, Andrews et al. 2008), and environmental stochasticity (Tanentzap et al. 2012), among others (Gaiarsa et al. 2015). Non-random distributions in time and space are important aspects of vulnerability for animals, particularly those that are slow moving or temperature-dependent (Croak et al. 2013), including ectothermic vertebrates (Kapfer et al. 2010). Understanding temporal and spatial use of core areas is critical for conservation and management (Semlitsch and Bodie 2003). All of these factors become more important for understanding life histories and conservation when they are considered within a framework of human-related activities and impacts (e.g., fire management, logging, development; Kapfer et al. 2010).

One of the iconic species of the New Jersey Pine Barrens is the Northern Pine Snake (*Pituophis melanoleucus* Daudin, 1803), a top-level predator that can reach 2 m in length. The Northern Pine Snake is listed as a threatened species in New Jersey and as threatened or endangered in other parts of its range in the southern United States (Burger et al. 2017, 2018). New Jersey appears to have the most stable population of this species (thus, a more global responsibility for its conservation, Golden et al. 2009; Burger and Zappalorti 2016; Burger et al. 2017). This paper examines the behavior of individually PIT-tagged Northern Pine Snakes during their fall ingress into hibernation sites (hibernacula or winter dens) in relation to conservation of the species with respect to forest management (e.g., logging, fire suppression) and other human activities (e.g., poaching, off-road vehicle [ORV] races, and traffic). There are competing claims for the habitat (e.g., snake use and ORV use), for habitat management (e.g., fire management and deer management), and for the snakes themselves (e.g., population stability and poaching, Burger and Zappalorti 2016). The activities of snakes in the fall were monitored around several hibernacula using new passive PIT-tag recording devices located at the hibernaculum entrances. This technical application is described with the intent of illustrating its use for other such studies. The overall goal was to test the null hypothesis (H_o) that Northern Pine Snakes return to their hibernacula and enter only once, remaining there for the duration of the winter hibernation period. If H_o is rejected, this could indicate increased vulnerability in time and space for a snake that is already threatened in New Jersey.

Hibernation behavior in this species has been studied previously in terms of hibernaculum site selection, use and fidelity, structure of hibernacula, and the defensive behavior of snakes disturbed during hibernation (Burger et al. 1988, 2000; Burger and Zappalorti 2016, 2017). Hibernaculum sites of other species of pine snakes (*P. ruthveni* and *P. melanoleucus lodingi*) were studied in Mississippi where the former used burrows of small mammals, and the latter used decayed pine stumps and roots for hibernation (Rudolph et al. 2007). Dispersal rates around hibernation sites were also examined in Gopher Snakes (*Pituophis catenifer deserticola*) in British Columbia (Williams et al. 2012). Some studies on hibernation in other snake species include hibernation site selection (Harvey and Weatherhead 2006), body temperatures while hibernating (Costanzo 1986; Hein and Guyer 2009), cold tolerance (Joy and Crews 1987), factors affecting spring emergence (Todd et al. 2009), spring emergence patterns (Hirth et al. 1969; Gregory 1974; Shine et al. 2006), and gene flow among snakes in different hibernacula (Clark et al. 2008; Anderson 2010). However, without individually marked snakes, and the availability of the recent remote recording ability of the Avid Power TracKer VIII, it was previously impossible to determine the activity of individual snakes near hibernation sites, the final entry temperatures for fall ingress, or the final dates of entry into hibernacula, each of which were incorporated into the present study.

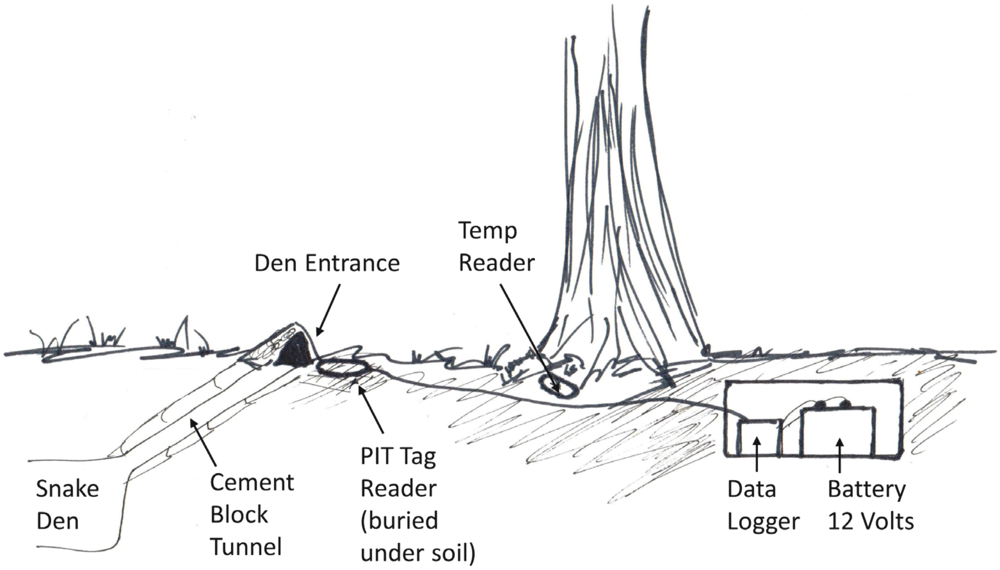

Fig. 1. Schematic of deployment of the Tracker device at the entrance of a hibernaculum.

Methods

Northern Pine Snakes have been studied in the Pine Barrens of New Jersey for over 35 years, including marking each snake with an individual PIT tag (Burger and Zappalorti 2011). They are large constrictors that reach the northern limit of their range in southern New Jersey. The New Jersey population is separated from other populations by several hundred km (Golden et al. 2009; Burger and Zappalorti 2011, 2016). They dig their own nest burrows, and dig or modify hibernacula (Burger and Zappalorti 2011). They hibernate communally, along with other snake species.

Northern Pine Snake studies have examined breeding and hibernation biology, risks and threats Northern Pine Snakes face, habitat selection, movement and home ranges, and contaminant exposure. While movement has been studied throughout the year with the use of radio-tracking, these previous studies did not provide detailed movement of the community of snakes using hibernacula (Burger and Zappalorti 2011). During this period Northern Pine Snakes were studied in Burlington, Cumberland, and Ocean counties, however, the exact locations of the studies were not disclosed because of the very high risk of poaching of Northern Pine Snakes (Burger et al. 2017, 2018).

The present study used passive continuous recording devices on snakes as they left and entered the hibernacula. In 2017 one hibernaculum was monitored to test the feasibility of using this tracking method, and in 2018, five hibernacula were monitored (four units monitored snakes for the entire year in Bass River State Forest, and one additional site was only monitored in the fall in Berkeley Township, Ocean County, known as “Davenport Den”). Any tagged snake passing by, entering, or leaving one of these monitored hibernacula was recorded. Data were generally down-loaded every 2–3 weeks throughout the year. A recording device was placed at the entrance of each hibernaculum, and buried so it was not visible (Fig. 1). The device used was the AVID Power TracKer VIII, a multi-mode reader with memory for PIT tags, made by AVID Identification Systems, Inc., in Norco, California. A TracKer unit was placed at each hibernaculum entrance and covered with a 1 cm layer of sand to prevent vandalism. The unit has a 6-inch coil reader with leads that can be up to 4 m long and lead to a device that can record and store up to 2,500 events, recording the PIT Tag, the time of day, and the date for each event. The power source was a 12-volt marine battery. The recorder and battery were placed in a plastic box, covered with a board for stability (and to prevent collapse if someone stepped on it by accident), buried beneath 10 cm of soil, and covered with leaves and twigs for camouflage (Fig. 1). None of the equipment was visible on the surface to prevent injury of the snakes, theft, or vandalism. The technology requires that snakes are fitted with PIT tags. Although the recorders were operating all year, this report only examines snake activity from 15 October to 31 December 2017 (at one hibernaculum) and from 1 October to 31 December 2018 (at five hibernacula).

The soil surface temperatures were recorded continuously, all year, near one of the hibernaculum entrances at Bass River State Forest using an Elitech RC-5USB Temperature Data Logger. The device was placed in a plastic bag and covered with a 1 cm layer of sand and moss to disguise its location. In previous studies, this small recorder has worked for well over a year on its original battery.

This study was only possible because: 1) Many Northern Pine Snakes use the same traditional hibernation and nesting sites (Burger and Zappalorti 2011; Burger et al. 2012; Zappalorti et al. 2014), 2) Gravid female Northern Pine Snake use the same hibernating and nesting sites (Burger and Zappalorti 1992, 2015), 3) Hatchlings can

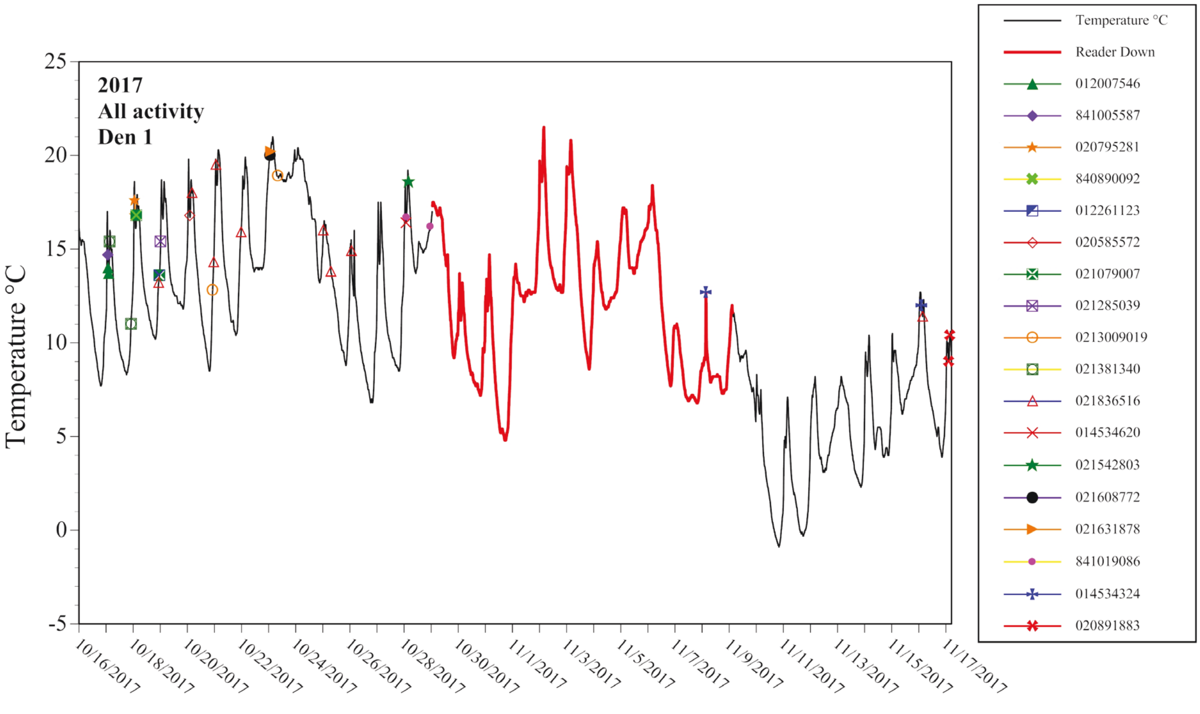

Fig. 2. All activity of snakes at den 1 (Bass River State Forest) in 2017 as a function of date and soil surface temperature. The colored markers indicated by 9-digit numbers in the legend represent individually tagged snakes. Data for snakes during the period from 29 October to 11 November (red line) were not recorded because the maximum number of data points the receiver could store was reached.

be easily found at nesting areas, fitted with PIT tags, and then followed at the hibernacula, and 4) Therefore, most of the individual snakes using a given hibernation site are PIT-tagged. Further, the sexes and ages of all snakes were known because they had been followed since they were hatchlings or two-to-three years old. The hibernacula in this study had been studied for over 30 years, and were well-known to the snakes and the researchers (Burger and Zappalorti 2011; Burger et al. 2012). For each snake, the first reading hit of the season was assumed to be its initial entry.

Analyses included calculating frequencies, percentages, means, and standard deviations for various behavior parameters of the Northern Pine Snake around hibernation sites in the fall. Data were analyzed using standard SAS software (Statistical Analysis Systems, Cary, North Carolina, USA), including Kruskal-Wallis One-Way Analysis of Variance (ANOVA), with 95% confidence intervals. Kendall tau was used to determine correlations among ambient soil surface temperatures and the temperatures at which snakes exhibited activity. The best models for explaining variations in snake activity as a function of temperature and date were developed using SAS (ProcGLM) procedures. Variables included were den, year, age, sex, date (only for the temperature model), and maximum and minimum daily sand surface temperatures.

Results

Date and temperature: The two primary factors that might account for entry of Northern Pine Snakes into hibernacula in the fall are date and ambient temperature. The factors entering the best model ($F = 34$, $P < 0.0001$, $r^2 = 76$) for Julian date of activity (e.g., entering/leaving) were maximum daytime sand temperature ($P < 0.001$), den number ($P < 0.04$), and perhaps age ($P < 0.08$). The factors entering the best model ($F = 122$, $P < 0.0001$, $r^2 = 90$) explaining variation in the temperature of snake activity (i.e., soil surface temperature when a snake entered, left, or passed by the hibernaculum) were maximum daytime sand temperature ($P < 0.001$), minimum nighttime temperature ($P < 0.0001$), and sex ($P < 0.04$). These factors are explored in greater detail below.

Seasonal activity patterns: While there was virtually no activity around the hibernacula in August or September, by early October snakes returned to the vicinity of the dens and began passing by, entering, and leaving hibernacula. In 2017, the equipment was only deployed in mid-October (when activity was expected to begin) at Bass River State Forest, but many snakes were already active around den 1 (Fig. 2). In the first year the reader was initially placed 0.3 m down the tunnel to the hibernaculum, and this resulted in one snake sitting in the entrance, and running the recorder until it reached the max-

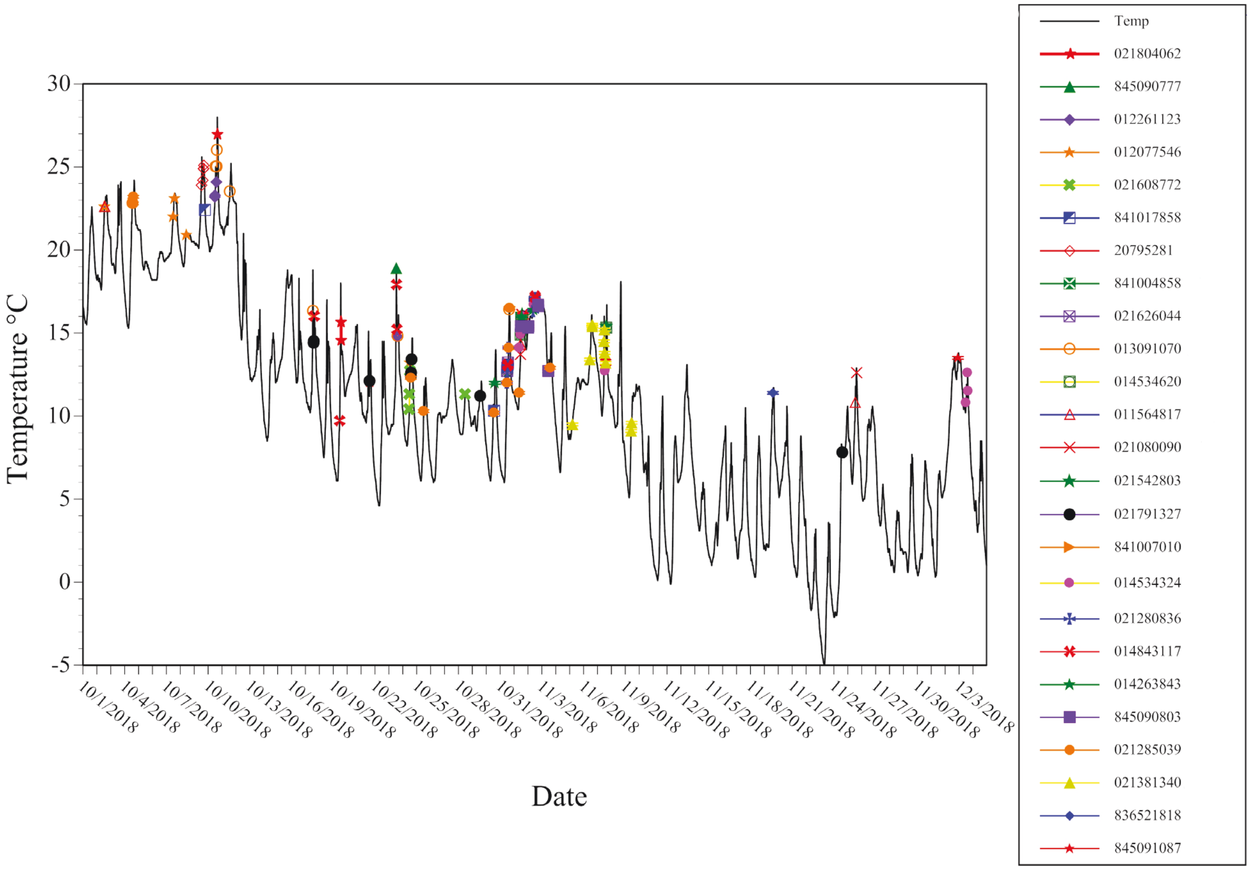

Fig. 3. All activity of snakes at four dens in Bass River State Forest in 2018 as a function of date and soil surface temperature.

imum number of data points it could store (n = 2,500). Figure 2 also indicates the period when the recorder was not recording. Because of this, the recorder was moved up to the entrance on 9 November 2017 (so that even if a snake was in the tunnel, watching the outside world with its head at the entrance, it would not record the activity more than a few times). During this down period from 29 October to 9 November some snakes entered (and may have left) without being recorded. Even so, the pattern clearly shows 18 different snakes (ages 0 [hatchling] to 16 years) entering, leaving, and re-entering from 16 October to 17 November 2017. The recorder continued monitoring through December but due to freezing surface temperatures, there was no more activity.

In 2018, the activity of 25 Northern Pine Snakes began on 2 October and continued to 7 December at Bass River State Forest (Fig. 3). The pattern was similar to that in 2017 in that there was daily temperature variation, and the snakes entered and left numerous times. It is, however, important to acknowledge these patterns because they show that activity is rather constant. Thus, the first hypothesis of a restricted time period of activity around the hibernacula was rejected.

Additionally, the Davenport Den (Ocean County) was monitored in the Fall of 2018. In winter of 2017–2018 only one two-year old Northern Pine Snake and two Corn Snakes *Elaphe guttata* (now *Pantherophis guttatus*) used this hibernaculum. In the fall of 2018, it was used by two hatchlings and the same two-year old. There were thus no large snakes that might influence the activity of the small Northern Pine Snakes; and the hatchlings were extremely active. The activity at this hibernaculum started on 1 November and ended on 28 December 2018. Since there were so few snakes at this hibernaculum, the individual activity patterns of the hatchlings are given in greater detail below.

Time of Day: As might be expected for ectothermic species, snakes were most active during the day and more so on warm sunny days. Most activity occurred between 1000 and 1700 h in both years (Fig. 4). In 2017, 77% of the activity occurred between 1000 and 1600 h; in 2018, 84% of the activity occurred in this same time period. However, in 2017 one snake left at 2000 h, and in 2018, one entered at 2045 h, and another entered at 0100 h at night. These rarely observed nocturnal activities occurred during relatively high temperatures (> 14° C).

Temperature effects: The activity of the snakes was plotted against the soil surface temperatures for 2017 and 2018 as a function of date (Figs. 2 and 3). In both years, the October surface temperatures were high, and they generally decreased throughout the fall. Snakes did not enter or leave at the lowest daily temperature (at night), but sometimes entered or left at the highest temperatures for the day. Most of the activity occurred at temperatures of 10° C or above. In both years there was little activity when the surface temperature fell below 8° C at night.

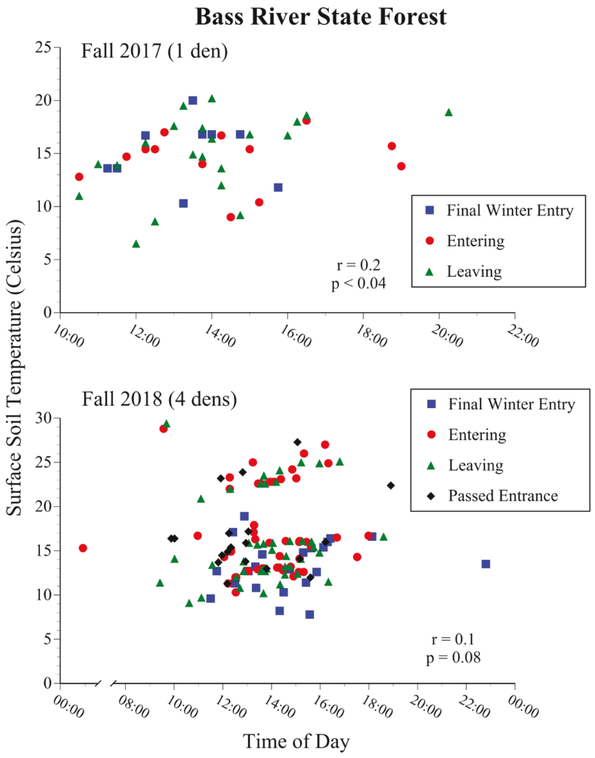

Fig. 4. Fall activity of snakes in Fall 2017 and Fall 2018 as a function of time of day and surface soil temperature. Activity type is noted by each symbol.

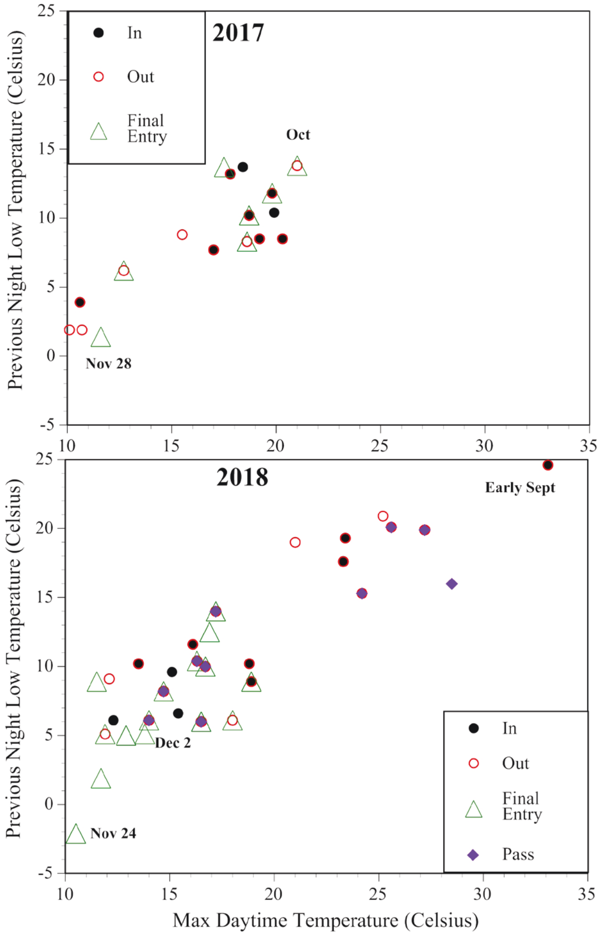

Fig. 5. Activity of snakes in Fall 2017 and Fall 2018 as a function of the maximum daytime temperature and the previous night's low temperature.

However, it is noteworthy that for both years, snakes entered or left the hibernacula, even after prolonged periods of daily low temperatures that reached 0° C in 2017, and even -5° C in 2018 (Figs. 2 and 3).

Although the daily high and low temperatures and snake movements were correlated ($r = 0.54$ in 2017; 0.51 in 2018; both $P < 0.0001$), the daily high and low temperatures for each day were more highly correlated ($r = 0.71$ in 2017; 0.79 in 2018, Fig. 5). Figure 5 indicates when snakes either entered or left a hibernaculum, or made their final entry for the winter. Note that some snakes entered at the same temperature point, and so there are fewer points than snakes. There are fewer points in 2017 because only one hibernaculum was monitored; while the 2018 data refer to all four hibernacula at Bass River State Forest. Final entries were usually at lower temperatures than other activities (Fig. 5).

Individual behavior: Figures 2–3 indicate frequent activity at hibernacula; individual snakes typically entered and left more than once (rejecting the initial hypothesis). The activity of individual snakes was examined only for 2018; individual activity in 2017 was not examined because equipment failure for a short period made it impossible to know whether any snakes left or entered during that period. Some snakes entered a den and remained for the winter (32%), but most did not (68%). At the Bass River study site, some snakes visited all four of the monitored hibernacula on the same day, often returning to the first one they entered. Snakes entered or left hibernacula an average of 5.6 ± 0.7 times, switched dens an average of 1.4 ± 0.3 times, and visited 1.8 ± 0.2 dens at Bass River State Forest in 2018. Movement was a function of age: older snakes moved more often than younger ones (Table 1). At Bass River State Forest, hatchlings moved an average of only 2.3 ± 1.3 times (Table 1).

However, at the Davenport den, where there were only two hatchlings and one 2-year old, the movement pattern was very different. Hatchlings used the hibernaculum as a home base, and went in and out many times before final entry. Sometimes they remained near the entrance, but they mainly moved a few meters away (e.g., the hatchlings were not immediately located). The seasonal patterns of the two hatchlings are shown in Fig. 6. The two hatchlings moved 48 and 66 times, while the 2-year old moved only 16 times. The lack of older, larger Northern Pine Snakes at the den may have allowed the hatchlings to move more freely.

Activity around each den (entering, leaving) varied significantly ($X^2 = 98$, $P < 0.0001$), and the percentage of hits at each den varied: den 1 = 25%, den 2 = 59%, den 4 = 12% and den 5 = 4% of total activity at Bass River. The total activity around the four dens at Bass River State Forest was 139 hits for 25 snakes. At the Davenport den

Table 1. Movement of Northern Pine Snakes among four monitored hibernacula at Bass River State Forest, New Jersey, USA, in 2018.

		Age of Snake (yr)				
		0–1	**2–3**	**5–7**	**Over 7**	**X^2**
Any Reading						
	mean	2.3 ± 1.3	2.8 ± 0.9	6.8 ± 2.5	7.1 ± 0.8	8.7 (0.03)
	min/max	1/6	1/5	1/11	3/12	
Den Switches						
	mean	0.3 ± 0.3	0.5 ± 0.5	1.5 ± 0.7	2.0 ± 0.4	8.0 (0.05)
	min/max	0/1	0/2	0/3	0/5	
Dens Visited						
	mean	1.3 ± 0.3	1.3 ± 0.3	1.8 ± 0.3	2.2 ± 0.2	7.9 (0.05)
	min/max	1/2	1/2	1/2	1/4	

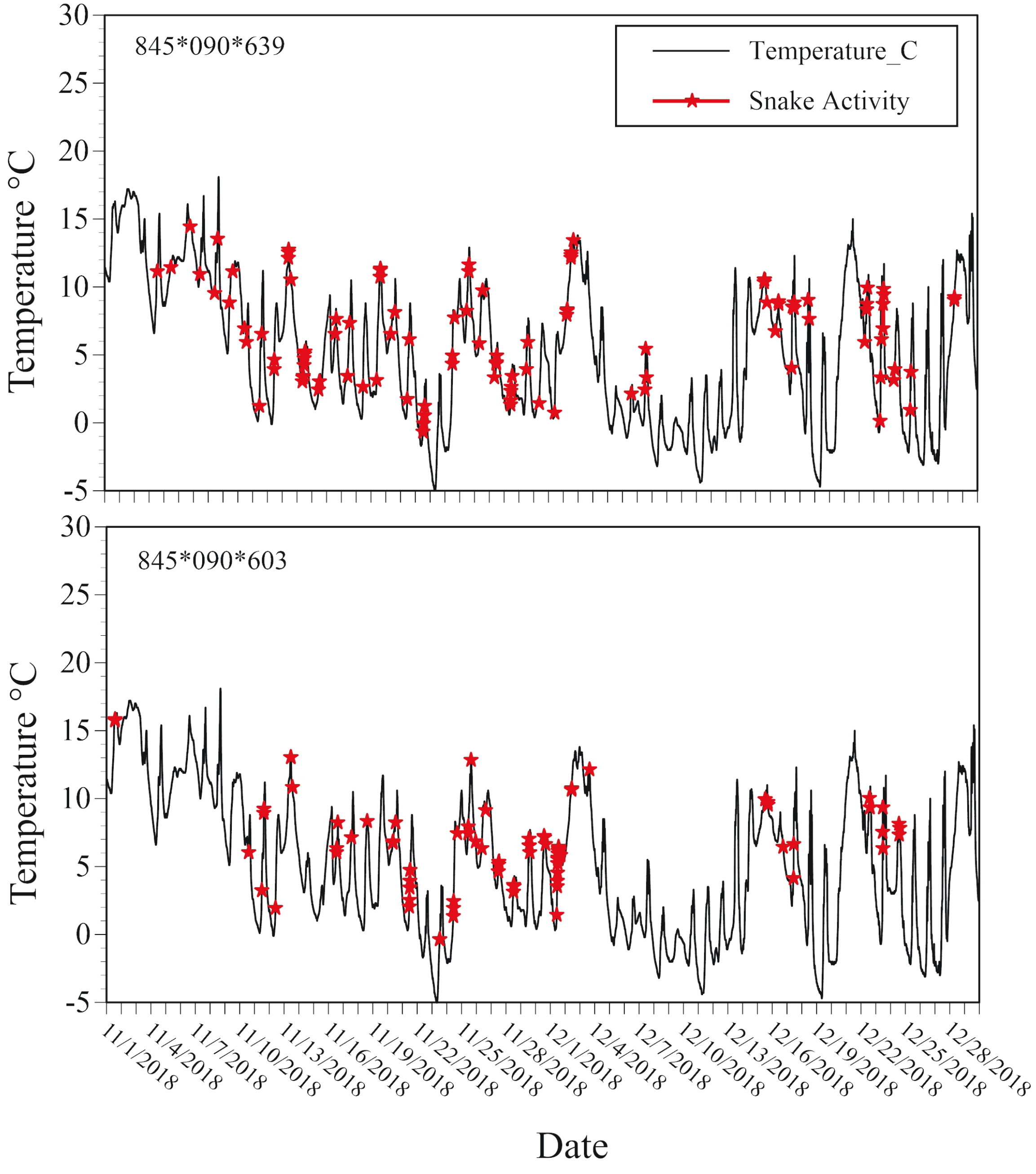

Fig. 6. Activity of two hatchlings (tag numbers 845090639 and 845090603) in the fall of 2018 at den (Davenport) as a function of date and soil surface temperature.

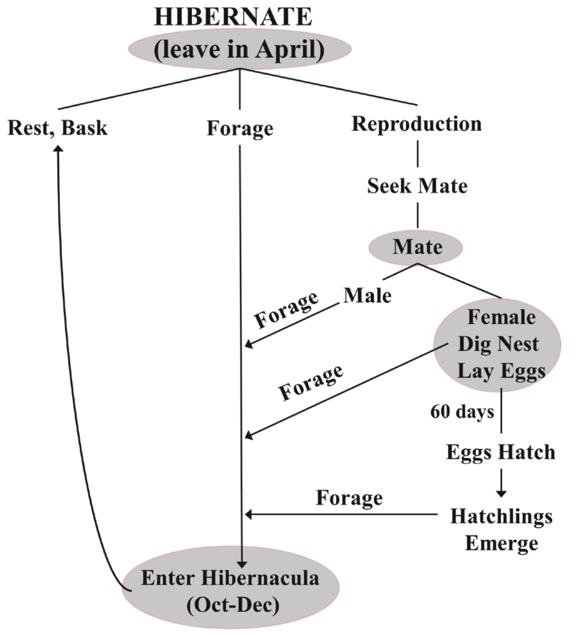

Fig. 7. Schematic of life cycle of Northern Pine Snakes, indicating periods of high vulnerability to human disturbances, such as fire, off-road vehicles, hunting, and poaching.

it was 120 hits for only three snakes, and the two hatchlings accounted for most of this activity.

Discussion

Methodological issues and using the Power TracKer VIII: Any study of animals in the wild is fraught with variability and uncertainties in the methods used, in environmental variation, and in the behavior and ecology of the species. Data from 2017 indicated that the PIT-tag recording devices could be used in the field with 12-volt marine batteries, since they operated properly, and the data could be retrieved. However, the main problem encountered initially related to placement of the receiver – when it was partway down the hibernaculum entrance, it recorded continuously as some snakes simply rested in the tunnel, peering out of the entrance and filling all the available data points. When the coil was moved to the front of the entrance, this problem did not exist, but then it was difficult to determine if a snake merely passed by the entrance, or entered. This issue could be partly managed by seeing where the individually marked Northern Pine Snake turned up next. The main difficulty with the Power TracKer was that the batteries need to be changed to allow charging every 2–3 weeks depending upon temperature (battery life was shorter at cold temperatures). Batteries need to be charged on the "slow setting" rather than the "rapid method;" as the former provided a longer-lasting charge in the field. Bad weather, heavy rains and snow, and downed trees from severe storms made getting to the study site to change the (20 kg!) batteries every couple of weeks very challenging.

Poaching of Northern Pine Snakes is known to be a major threat (Burger and Zappalorti 2016), so I opted not to use solar power or place cameras that might call attention to the den entrance. Visible solar panels would alert poachers or vandals to the exact location of hibernacula entrances, and would also encourage theft. Protecting the equipment is important since each set-up costs about $3,000 for the TracKer, leads, batteries, plastic case for the recorder and batteries, and a wood cover to prevent excessive rain from entering the plastic case. The continuously recording thermometers were only $25, and the manufacturer's battery lasted at least a year. Lastly, the tracker should be put in place when the snakes are underground to ensure that they leave a scent trail when they leave so that other snakes (particularly hatchlings) can find the entrance.

With any field study there are weather-related and other environmental variables that can influence the behavior of the snakes. Exceptionally warm weather in 2018 resulted in an extended period of ingress into the hibernacula. No snake entered or left den 1 in 2017 (the only den monitored that year) after 17 November, but in 2018 snakes continued to move in and out of the five dens monitored into late December.

Finally, there are uncertainties that relate to the behavior and ecology of the snakes. These uncertainties were related to age, sex, and individual responses. Age clearly entered as a factor in explaining the observed Northern Pine Snake behavior, but this would not have been clear if the snakes were not of known ages. The behavior of hatchlings varied depending upon the composition of the hibernaculum community (see below). Hatchlings moved very little when they were part of a community that included snakes of different ages (and sizes), but hatchlings moved often when there were no larger (older) snakes present.

Activity patterns around hibernacula in the fall: Northern Pine Snakes in the present study were very active around the hibernacula for over two months. At Bass River State Forest, snakes moved in and out an average of six times, often switching dens. The hypotheses that activity around a hibernaculum was restricted in time, and that snakes entered a hibernaculum and stayed were both rejected. Individuals moved from den to den over a few days or a few weeks, partly dependent upon weather. That Northern Pine Snakes left a given den and did not enter another den for several days, but then returned, indicates that there are some other suitable places to shelter when the temperatures drop at night. Nonetheless, the snakes came back to one of their original dens when the weather warmed up enough to move.

The factors that played a role in activity were season (date), temperature (daytime high and nighttime low), age, and hibernaculum number. The Northern Pine Snakes appeared to prefer two of the dens over the others. However, even snakes that first entered one of the "preferred dens" moved to other dens before returning. One might predict that older snakes, aware of the advantages and disadvantages of one den over another, might move less than young snakes that are less familiar with their environment and den options. This, however, was not the case. The reason for increased switching with increasing age is unclear. However, in the absence of larger (older) snakes, the two hatchlings at the Davenport den (an isolated hibernaculum) used it as a home base, and moved in and out frequently, depending upon temperature. These two hatchlings did not finally enter for the winter until 28 December.

Factors affecting entry into hibernacula: Clearly there are seasonal and temperature effects; Northern Pine Snakes enter hibernacula to avoid freezing winter temperatures, as do other snakes in northern climates. Although other studies have examined the temperatures of snakes during hibernation (Costanzo 1986; Hein and Guyer 2009), or emergence in the spring (Todd et al. 2009), little is known about the temperatures at which snakes enter hibernacula in the fall. To study fall behavior requires: 1) individually marked snakes, 2) a method of recording each snake's entrance in the fall (date, time of day), and 3) devices to continuously record the soil surface temperature to capture the temperature when snakes enter. A long-term study was required for the first criterion, and recent technological developments were required for the latter two. The development of this new technology makes it possible to more accurately examine both the seasonal and temperature influences on snakes entering and emerging from hibernacula, as well as indicating the degree to which snakes move in and out during both entry and emergence, before finally dispersing in the spring to forage, mate, and nest.

In this study, date and sand surface temperature determined when snakes entered and left hibernacula, and snakes moved an average of about six times before settling in for the winter. Three other factors seemed to also affect movement: den number, age of the snakes, and for hatchlings, the presence of older (larger) snakes. Snakes clearly preferred two of the monitored dens over the other two, and both of the preferred dens were deeper than the other two, and they were older in terms of usage history (Burger and Zappalorti 2011).

The age of the snakes influenced their movement; older snakes moved more often, switched dens more often, and visited more dens than did younger snakes. This was unexpected since younger snakes might be expected to explore a range of different sites before settling down. Hatchlings using the four hibernacula at the Bass River State Forest showed significantly less activity than older snakes (an average of only two movements/snake). However, the two hatchlings that used the Davenport hibernaculum showed activity 48 and 66 times. They not only entered and left (and were not visible around the hibernaculum or in the surrounding area), but sometimes basked very near the entrance, moving swiftly down the entrance when approached by the researchers. They appeared to be using the hibernaculum as a refuge and an overnight site for nearly two months before remaining for the winter (refer to Fig. 6). This difference in hatchling behavior at the two sites may relate to the relative risk posed by much larger snakes using the same hibernaculum. If large, heavy (up to 1,350 g) adult snakes are entering and leaving, they pose a risk to hatchlings (30–50 g), and adults could injure them while both are moving through the tunnels. The only dead snakes found in hibernacula over the years (with one exception of small mammal predation) were those squashed flat by older, larger snakes lying on top of them for long periods of time.

Vulnerability, risk, and competing claims: Northern Pine Snakes are most vulnerable when they are roaming above ground (even though they are partially fossorial), and when they are concentrated in one small area. They are above ground at intermediate temperatures; in the hot summer they spend a great deal of time in hollow fallen logs, under leaves and needles, or underground; in the winter they hibernate 1–2 m below ground. Behaviorally they are vulnerable when they are mating (spatially scattered), nesting (females, spatially clumped), and entering or leaving hibernacula (clumped around hibernacula). The vulnerability of Northern Pine Snakes is greatest when these two features (above ground and clumped) overlap, which occurs when entering hibernacula for the winter. This situation occurs when entering hibernacula for all Northern Pine Snakes, and for females when they are nesting (Burger and Zappalorti 1992, 2011, 2016; Burger et al. 2017, 2018, Fig. 7). The data presented in this paper clearly show that the period of ingress into hibernacula is at least two months in duration, spanning both October and November, and can extend through December if the weather is not too cold. The data also show that there is frequent activity, not just one entry into the hibernaculum by each snake. The dens at Bass River State Forest that were studied are about 30–120 m from each other. That snakes come and go indicates that the spatial area of activity is greater than just around the immediate entrance to a hibernaculum.

Only once was a Northern Pine Snake seen above ground in the fall, although later analysis of the recorded data indicated that just minutes before or after our presence, snakes entered or left the hibernaculum. In one case, a snake came up five minutes after we finished downloading the data, and I only saw it because I went back to pick up a piece of equipment. It was lying in the tunnel, with its head about 2 cm from the entrance. This observation emphasizes the importance of having continuously recording equipment; observation alone would not yield this key information.

The major risks that Northern Pine Snakes face are natural predators (hawks, mammals, and other ophiophagus snake species), commensal predators (dogs, raccoons), poachers, loss of habitat, and human disturbance (direct and indirect). Human disturbance can take the form of people disrupting snake behavior (e.g., during snake copulation, nesting, or entering/leaving hibernacula), disrupting snake habitat (e.g., off-road vehicles, ORV races through the Pine Barrens, prescribed burns, tree-cutting), or a combination of these activities. Many of these activities represent competing claims for the same Pine Barrens habitat (either quantity or quality of the habitat).

The resolution of competing claims for Pine Barrens habitat, or management of that habitat, is partly a societal decision. However, the specific needs of wildlife, and of specific species such as the Northern Pine Snake, cannot be considered unless there are data to show what those needs are, when (and what) their vulnerabilities are, and when interference will jeopardize their populations. In many cases, a situation can be resolved by bringing together the relevant people and agencies, and determining the best course of action. Clearly, debris and dry leaves that will result in a hot fire that could destroy local human communities or businesses (as well as wildlife) need to be reduced, and fire management is a reasonable option. Likewise, hunting, ORV races, and other human activities are reasonable uses of public forests such as the Pine Barrens. Protection of endangered and threatened species is another public goal (as well as being a legal one) that must be considered. Even accepting the latter as an important public goal does not completely solve the problem, however, because different species may have different requirements and vulnerable periods. For each species, relative abundance and total distribution need to be considered, with species which have very restricted ranges getting priority treatment. A consensus needs to be reached both about the specific habitat and ecological requirements of different endangered, threatened, or otherwise vulnerable species, and about the specific requirements of other groups with competing claims (e.g., foresters, recreationists, fire managers). Armed with this knowledge, managers can make science-based, societally-based, and cost-effective decisions about managing the habitat and the associated wildlife species that occur there.

Conclusions

Plants and animals in the Pine Barrens, and everywhere else, face competing claims to their habitat along with of the risks of disruption or disturbances from other animals, poachers, recreationists, foresters, resource managers, firemen, developers, and the general public. Resolving competing claims requires having knowledge of the specific needs of vulnerable species and habitats, as well as the needs of the people and managers. One high risk vulnerable period for Northern Pine Snakes is when they enter or leave their winter hibernation sites. This paper provides data showing that the fall ingress period to hibernacula is prolonged (over two months), and involves frequent snake activity above ground. During October and November in the Pine Barrens, Northern Pine Snakes are moving toward hibernacula, concentrating there, and entering and leaving frequently until they eventually stay underground for the winter. Thus, this is a highly vulnerable period when snakes are concentrated, and any disruptions (such as fires or off-road vehicle races) have the potential to injure or kill Northern Pine Snakes that are threatened in New Jersey, and threatened or endangered throughout most of their range. New Jersey has perhaps the largest, and most stable population of Northern Pine Snakes throughout the range of the species (Golden et al. 2009; Burger et al. 2016, 2017), therefore state wildlife agencies have a special responsibility to ensure its continued survival.

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