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Habitat Features of Black Rat Snake Hibernacula in Ontario

KENT A. PRIOR AND PATRICK J. WEATHERHEAD

Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada

ABSTRACT.—**Suitable over-wintering habitat is critical to the survival of snake populations at higher latitudes. The identification and protection of traditional, communal hibernation sites (hibernacula) is important for the conservation of threatened species, while the assessment of hibernacula availability may help determine the extent to which population distributions are limited by habitat suitability. In this paper, we quantified surface habitat characteristics of 10 hibernacula and the composition of basking trees used by a threatened population of black rat snakes (*Elaphe o. obsoleta*) at the northern limit of the species' range. Hibernacula were typically situated on relatively rocky, south-facing slopes. The co-occurrence of these features was sufficiently unique as to distinguish hibernacula from (1) a series of random sites, but not from (2) a set of intuitively identified "potential hibernacula" in the surrounding landscape. This implies that additional requisite elements (e.g., underground structure and micro-climatic conditions), which we were unable to quantify, set actual hibernacula apart from sites that appear to be otherwise suitable (i.e., "potential hibernacula"). Basking trees found at hibernacula tended to be relatively large and decayed or dying with numerous cavities. Unused trees exhibiting these characteristics were also available at both random sites and potential hibernacula indicating the suitability of those sites for basking. Our results suggest that rat snake hibernacula cannot be predictably located by simply searching for key surface habitat features in the landscape. The current data are equivocal as to whether or not this most northern population is limited by the availability of suitable over-winter habitat since the possibility that essential subterranean features of hibernacula are limiting remains to be tested. We recommend the continued use of radio-telemetry to identify and protect additional hibernacula, the preservation of basking trees at known hibernacula, and further research to determine the internal structure and micro-environments of hibernacula.**

Different life history features of wildlife are often closely tied to precise habitat needs. Even relatively sedentary taxa like snakes may have specific and contrasting habitat requirements for over-wintering, breeding, nesting, and foraging (e.g., Burger and Zappalorti, 1986; Burger et al., 1988; Scott et al., 1989; Barry et al., 1992). As such, the use of traditional sites for communal hibernation (hibernacula) by snakes (Gregory, 1984; Sexton et al., 1992) is of particular interest to both conservation biologists and behavioral/evolutionary ecologists.

From a conservation perspective, communal hibernation necessarily places local snake populations (or snake communities in the case of multi-species hibernacula) in potential jeopardy. This is because traditional hibernacula may be used by many individuals representing a significant proportion of a local population (e.g., 60–80%, Prior and Weatherhead, unpubl. data) which is collectively and annually susceptible to both natural and human-induced catastrophe. In fact, humans have exploited knowledge of the hibernation behavior and habitat requirements of rattlesnakes (Crotalidae) to such an extent (i.e., "rattlesnake round-ups") that populations have seriously declined or been extirpated altogether from parts of the U.S. (Galligan and Dunson, 1979; Warwick, 1990; Brown, 1993). Thus, protection of hibernacula may be critical to the conservation of threatened species. If hibernacula are found to occur in very specific habitats, then one could protect hibernacula by protecting essential habitat.

Behavioral and evolutionary ecologists recognize that the quantification of the over-winter habitat needs of species may also be useful in understanding whether populations are limited by appropriate habitat for hibernation (Gregory, 1984). The selection of suitable hibernacula by snakes is fundamental to the persistence of populations in cold climates and thus, may dictate the relative position of the northern (or southern) range limits for a number of species (see Rosen, 1991). That communal hibernation may be a response to limited availability of suitable habitat does not preclude the possibility that the behavior serves some social/physiological function(s) as well (e.g., enhances mating success, minimizes probability of fatal over-winter dehydration).

While snake hibernation per se has received some attention (e.g., Gregory, 1982, 1984; Costanzo, 1989; Ultsch, 1989; Weatherhead, 1989), there have been very few quantitative descriptions of communal hibernacula (Drda, 1968; Burger et al., 1988). As suggested above, contributions to this field may be particularly valuable when they focus on threatened species and/or peripheral populations. Black rat snakes (*Elaphe o. obsoleta*) occurring in Ontario meet both criteria. The most northerly population of this species (the "Frontenac Axis population") occurs in eastern Ontario and northern New York and has been provisionally designated as "threatened" in Canada (Prior and Weatherhead, unpubl. data). Active season habitat does not appear to be particularly limiting within the range of this population (Weatherhead and Charland, 1985). Their preferred habitat, a mixture of deciduous forest, old field, and forest/field edge, is more abundant now than it was 100 years ago at the height of land-clearing for timber and agriculture (Kelly, 1990; McInnis, 1990). However, nothing is known about the availability of suitable communal hibernacula across this region.

Therefore, the objectives of this paper were to (1) quantify variability in the above-ground habitat characteristics of communal hibernacula occupied by black rat snakes at the northern edge of the species' distribution, and (2) contrast hibernacula habitat with that available in the surrounding landscape in order to determine whether appropriate habitat might be limiting.

Materials and Methods

Study Area.—At the extreme northeastern part of the species' range, the Frontenac Axis population of black rat snakes is confined to an area of approximately 5000 km^2 in eastern Ontario and northern New York ($\approx$44°15′-44°55′ N, 75°20′-76°45′ E, see maps in Conant, 1975; Cook, 1984). Detailed surveys have shown this population to be geographically disjunct from all others, the nearest population being $\approx$120 km to the south, near Syracuse, New York (A. R. Briesch, unpubl. data; W. F. Weller and M. J. Oldham, unpubl. data). The Frontenac Axis itself is an exposed, south-easterly extension of the Precambrian (Canadian) Shield and represents the dominant geological feature of the study area. Topography throughout the region is irregular with a strongly rolling upland terrain (Rowe, 1972), numerous granite outcrops, and many lake and river systems. The soils are composed of thin, very stony glacial till (Hoffman et al., 1967; Gillespie et al., 1966). Extensive second growth, mixed coniferous-deciduous forests (Great Lakes-St. Lawrence Forest Region; after Rowe, 1972) cover much of the area while the abandonment of marginal agricultural land has also resulted in considerable shrubland.

Sampling.—We studied 10 communal hibernacula distributed across the Ontario portion of the Frontenac Axis population range. All hibernacula were originally identified during radio-telemetry studies (e.g., Weatherhead and Hoysak, 1989) and are located at Murphy's Point Provincial Park (three sites), Queen's University Biological Station (two sites), Charleston Lake Provincial Park (two sites), La Rue Mills (one site), and on Hill Island within St. Lawrence Islands National Park (two sites). For conservation reasons exact locations of hibernacula remain confidential.

At each hibernacula we quantified five structural habitat variables that we believed adequately characterized the sites and might also reflect the relative suitability of the sites for snakes. The habitat features we measured included, (1) slope in degrees (mean of three measurements with an inclinometer taken 5 m from the main opening of the hibernaculum), (2) aspect in degrees (orientation of slope at the main opening measured with a hand-held compass), (3) percent canopy closure (25 point samples [×4] within a 45° cone while standing at the main opening [modified after Reagan, 1974]), (4) percent shrub cover (mean percent cover within four, randomly positioned 1-m^2 quadrats located within 10 m of the main opening), and (5) percent rock cover (mean percent surface rock and bedrock cover within four, randomly positioned 1-m^2 quadrats located within 10 m of the main opening). We were unable to quantify the underground structure of the hibernacula because the openings were too small to allow access and the threatened status of the population precluded excavation of the sites.

We also measured the same five variables at one "potential hibernacula," and two randomly positioned sites per hibernaculum, for a total of 40 sites collectively. Potential hibernacula were located during time-constrained searches (1 h), fell within 50–500 m of the hibernaculum, and represent sites that we felt appeared as if they might serve as suitable hibernation sites for rat snakes on the basis of visual inspection of habitat (i.e., prior to any empirical quantification). In essence, potential sites were found using our familiarity with the 10 actual hibernacula across the region as a guide. As a necessary criterion, all potential hibernacula had to include existing holes or cavities leading underground, though we had no way of determining the extent of these spaces. Comparisons among actual and potential hibernacula were used to assess whether any other hibernacula-type habitat was available in the surrounding landscape. Random sites were located through selection, by means of a random number generator, of a compass bearing and distance (between 50–500 m) from the hibernaculum. At these sites, we also searched the immediate area until we found an underground opening and began sampling from there. Comparisons among hibernacula and random sites provided an assessment of whether hibernacula habitat differed from the surrounding habitat generally. All potential hibernacula and random sites were checked a minimum of five times during spring emergence (1994) in order to document possible use of these sites by snakes.

Following emergence from hibernation and prior to dispersal to summer home ranges, black rat snakes in the Frontenac Axis population typically bask arboreally for several days within the immediate vicinity of the hibernaculum (Prior and Weatherhead, unpubl. data). During spring emergence (mid-April–late May) in both 1993 and 1994, we quantified the arboreal basking habitat used by rat snakes at eight of the hibernacula. (Emergence at the two Charleston Lake hibernacula was not monitored, so we have no detailed information on the basking habits of snakes at these sites). During daily visits to hibernation sites throughout the emergence period one of us (KAP) and an assistant carefully scanned the trees for snakes for an average of 30 min per site. Because snakes in coniferous trees were relatively more inconspicuous than those found in (bare) deciduous trees we were particularly thorough about searching coniferous trees for snakes in order to minimize any potential bias in our data. For the purpose of analysis we defined snakes as "basking arboreally" when we saw them in a stationary position, either draped or coiled on the branch or trunk of a tree, at a height of 1 m or more off the ground. When possible, basking snakes were captured by hand, measured, weighed, sexed, marked (with both a PIT-tag and non-toxic acrylic paint) for future identification, and then released back at the place of capture.

We recorded four features of the trees used by the snakes, including; tree species, diameter (cm) at breast height (DBH), presence or absence of cavities and hollows in the branches and trunk, and a "relative condition rank." The condition rank of basking trees was assessed by visual inspection according to the following criteria; 1 = healthy tree with no visible sign of decay, 2 = live tree with as much as 50% of the crown dead, 3 = live tree with greater than 50% of the crown dead and numerous dead branches intact, and 4 = dead snag with few or no branches intact. We then matched each basking tree with a randomly selected, "unused tree" for which we quantified the same four features. Unused trees were chosen by selecting the first tree encountered along a transect (orientation randomly selected) radiating from individual basking trees. By definition, unused trees were never seen to be occupied by rat snakes during three years of study (1992–1994). By comparing the attributes of basking and the randomly selected unused trees at hibernacula we were able to determine whether the snakes might be actively selecting a subset of the trees available to them.

We also quantified five randomly selected trees at each potential hibernaculum and random point (see above). As such, randomly selected trees were representative of those available to rat snakes had there actually been hibernacula at those locations. Comparisons among randomly selected trees at both potential hibernacula and random locations and the pooled sample of basking and unused trees at hibernacula allowed us to assess whether the type of trees available to snakes for basking at hibernacula were unique and thus, potentially limiting.

Statistical Analyses.—We used correlation-based principal components analysis (PCA) to objectively reduce the dimensionality of the original habitat variable set to a smaller number, of mutually uncorrelated composite variables or components. Slope aspect (°) was recoded to binary form (i.e., 90–269° = south, 270–89° = north) prior to inclusion in the PCA (see Green, 1979, pp. 73–95 for a discussion of the use of binary data in PCA). Analysis of variance (ANOVA) was then used to test for differences among samples sites (i.e., hibernacula, potential hibernacula, random points) with respect to habitat-based PC scores. Scheffé F-tests were used for post-hoc comparisons of means when required. As above, we also used PCA and ANOVA to test for differences among (1) basking and unused trees at hibernacula, and (2) sample sites (i.e., hibernacula, potential hibernacula, random) with respect to the trees available for basking. Where necessary, data were either arcsine- or log-transformed to achieve normality. All analyses were performed using Statview II (Feldman et al., 1987) software.

Results

Typical habitat descriptions for each of the three sample sites (actual hibernacula, potential hibernacula, random points) can be derived using information obtained from the mean habitat variables for each type (Table 1). In general, hibernacula tended to be situated on moderately sloping and relatively rocky hillsides that faced south-south-east. However, this data summary does not convey a sense of the great variability in hibernacula habitats used by rat snakes across the region. The following examples illustrate this point. Hibernacula occurred (1) on a talus slope in a steep-sided valley of broken rock and boulders, (2) on an open grassy

TABLE 1. Surface habitat characteristics (mean ± standard error) of black rat snake hibernacula (N = 10), potential hibernacula (N = 10) and random sites (N = 20).

Variable	Hibernacula	Potential hibernacula	Random sites
Slope (°)	17.56 ± 3.12	20.85 ± 1.84	7.53 ± 1.11
Aspect (°)	158.0 ± 17.0	191.0 ± 25.0	28.00 ± 80.0
% Canopy closure	74.0 ± 3.92	84.4 ± 2.10	84.90 ± 3.57
% Shrub cover	10.28 ± 2.71	3.88 ± 1.65	10.89 ± 2.34
% Rock cover	27.20 ± 10.61	31.50 ± 6.18	11.13 ± 2.42

slope, 30 m from a beaver (*Castor canadensis*) pond, (3) on relatively level ground amid a mature, closed-canopy forest, (4) on the steep, rocky shore of an island in a large lake, and (5) in a shallow depression, atop a forested ridge.

A PCA of habitat features reduced the original five structural variables to two orthogonal components that collectively explained 70% of the total variation among all sites (Table 2). Additional components had eigenvalues of less than 1.0 and were therefore considered uninformative (Dunteman, 1989). The first component primarily reflected variation in slope and percent rock cover, and to a lesser degree the aspect of the slope. PC2 was interpreted as a contrast between percent shrub cover and percent canopy closure.

A plot of the two sets of PC scores for all sample types illustrates an apparent distinction among random sites and both actual hibernacula and potential hibernacula along the PC1 axis (Fig. 1). Unlike random sites, actual hibernacula and potential hibernacula tended to have relatively high PC1 scores (i.e., steeper and more rocky with southern aspect). This impression was supported statistically by an ANOVA of the PC1 scores ($F = 21.24$, df = 39, $P = 0.0001$) and post-hoc means tests (Scheffé F-test; actual hibernacula vs. random sites, $F = 12.82$, $P \leq 0.05$ and potential hibernacula vs random sites, $F = 15.44$, $P \leq 0.05$). No differences were found among the sites with respect to PC2 scores ($F = 1.89$, df = 39, $P = 0.164$) suggesting that hibernacula were not unique with respect to degree of shrub cover and canopy closure.

TABLE 2. Factor loading matrix for principal-components analysis of 5 habitat variables.

Variable	PC1	PC2
Slope	+0.844	+0.068
Aspect	+0.694	−0.108
% Canopy closure	−0.431	−0.789
% Shrub cover	−0.339	+0.837
% Rock cover	+0.814	−0.048
% Variance explained	43.1	26.8

The most common tree species found at the hibernacula covered a broad range including; oaks (*Quercus* spp., 31%), white pine (*Pinus strobus*, 23%), white cedar (*Thuja occidentalis*, 15%), maples (*Acer* spp., 11%), and ironwood (*Ostrya virginiana*, 8%). With the exception of white cedar, both potential hibernacula and random sites exhibited similar species composition, respectively; oaks (23%, 20%), white pine (13%, 24%), cedar (2.5%, 2.5%), maples (28%, 16%), and ironwood (10%, 10%). The predominance of cedar in the actual hibernacula samples was largely due to its' abundance at a single site at Murphy's Point.

Throughout the two spring emergence periods we observed a total of 163 individual black rat snakes basking in trees near (≤30 m from the main opening) all but one of the eight hibernacula investigated in this regard. Many trees were occupied by more than one snake at a time and some individuals were observed repeatedly in the same tree(s). However, in order to avoid

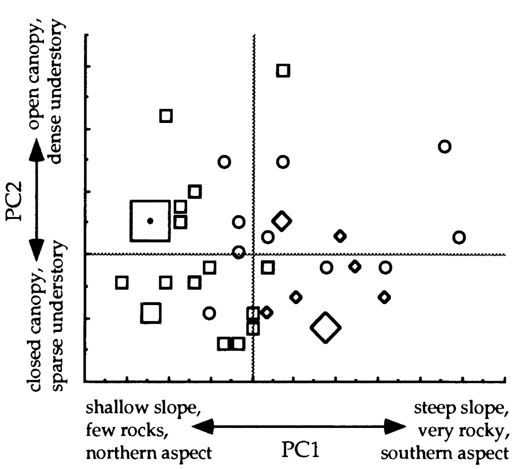

FIG. 1. Plot of principal component scores derived from 5 habitat variables. Sample sites include; actual hibernacula (circles), potential hibernacula (diamonds), and random sites (squares). Enlarged symbols represent overlapping datapoints in which the relative size of the symbol is indicative of the density of like points.

TABLE 3. Characteristics (means ± standard error) of basking trees and randomly selected unused trees found at hibernacula, potential hibernacula, and random sites.

Sample site	Tree class	N	DBH (cm)	Percent deciduous	Condition	Percent with cavities
Hibernacula	Basking	39	31.15 ± 2.4	69.2	1.82 ± 0.18	87.2
	Unused	39	17.37 ± 1.3	50.0	1.25 ± 0.08	3.3
	Pooled	78	24.26 ± 1.6	57.7	1.54 ± 0.10	50.0
Potential Hibernacula	Unused	40	25.08 ± 1.9	85.0	1.72 ± 0.15	32.5
Random Sites	Unused	80	24.82 ± 1.3	66.3	1.63 ± 0.11	27.5

pseudo replication, any tree that was occupied is represented only once in the dataset and following analyses.

The number of basking trees used by snakes at each hibernaculum ranged from 0 to 11. In total, 39 basking trees were quantified, the majority of which (51%) were oaks. In general, basking trees tended to be older, partly dead or decaying deciduous trees with numerous cavities in the trunk and larger limbs (Table 3).

A PCA of the characteristics of trees found at actual hibernacula reduced the original four variables to two orthogonal components that collectively explained 74% (PC1 = 51.5%, PC2 = 22.9%) of the total variation among basking and unused, randomly selected trees (Table 4). The first component reflected variation in the presence of cavities, DBH or girth, and general health status or condition, while PC2 explained variation due to tree type (i.e., coniferous vs. deciduous). Basking trees tended to have relatively high PC1 scores (Fig. 2) indicating that they were usually the largest and most unhealthy trees available in the vicinity of hibernacula. In contrast, there was no apparent difference between basking and unused trees with respect to PC2 scores suggesting that trees used for basking were no more likely to be deciduous than they were coniferous. An ANOVA of PC scores supported this interpretation. We found a significant difference between the attributes of basking and unused trees at hibernacula as described by PC1 ($F = 52.38$, $df = 77$, $P = 0.0001$), but not PC2 ($F = 0.76$, $df = 77$, $P = 0.385$). Thus, rat snakes appear to be selecting the older, decaying trees for basking among the wide assortment of those available to them around hibernacula. Whether such trees are deciduous or coniferous does not seem to be particularly important to the snakes.

Finally, a PCA of the characteristics of trees found at actual hibernacula, potential hibernacula, and random locations derived two orthogonal factors that collectively explained 69% (PC1 = 44.9%, PC2 = 24.5%) of the total variation among sites (Table 4). As in the previous analysis, PC1 reflected variation in the presence of cavities, DBH, and condition, while PC2 explained variation due to tree type (i.e., coniferous vs. deciduous). Ordination of the PC scores

TABLE 4. Factor loading matrices for principal-components analyses of 4 tree characteristics within hibernacula (basking, unused trees) and among sites (hibernacula, potential hibernacula, random).

Treatment	Characteristic	PC1	PC2
Hibernacula	Tree DBH	+0.798	+0.314
	% Deciduous	−0.467	+0.839
	Tree condition	+0.731	−0.142
	% with cavities	−0.817	−0.300
Among sites	Tree DBH	+0.752	+0.253
	% Deciduous	−0.306	+0.917
	Tree condition	+0.688	−0.141
	% with cavities	−0.812	−0.231

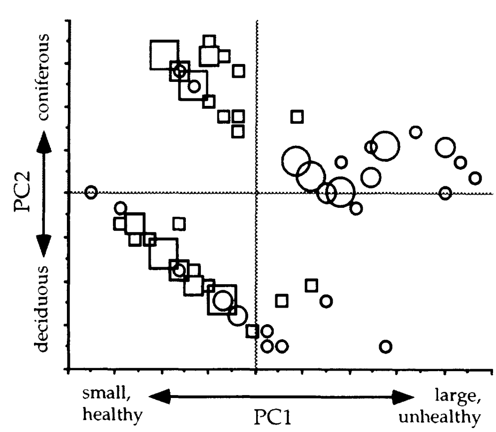

FIG. 2. Plot of principal component scores derived from 4 characteristics of trees measured at hibernacula. Trees sampled include; actual basking trees (circles) and unused trees (squares). Enlarged symbols represent overlapping datapoints in which the relative size of the symbol is indicative of the density of like points.

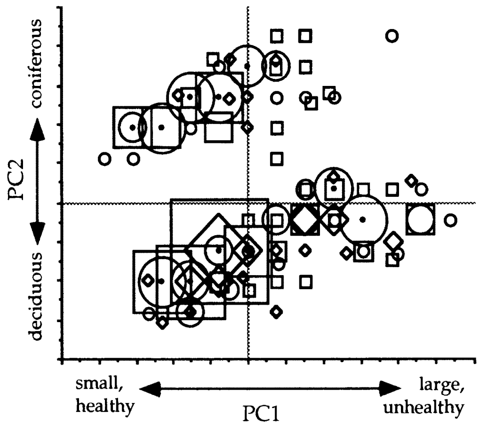

FIG. 3. Plot of principal component scores derived from 4 characteristics of trees measured at different sites including; hibernacula (circles), potential hibernacula (diamonds), and random sites (squares). Enlarged symbols represent overlapping datapoints in which the relative size of the symbol is indicative of the density of like points.

provides no clear distinction between site types along the PC1 axis (Fig. 3). ANOVA supported this view ($F = 0.51$, df = 197, $P = 0.598$), implying that the general structure of the trees around the three types of sites was similar and therefore that "potential basking trees" (large and decaying with cavities) were not absent from either potential hibernacula or random sites. However, potential hibernacula exhibited relatively low PC2 scores (i.e., predominantly deciduous, see Fig. 3). Indeed, ANOVA revealed a significant difference in the attributes of trees found across sites with respect to PC2 values ($F = 5.1$, df = 197, $P = 0.0065$). A post-hoc means test confirmed that potential hibernacula had disproportionately more deciduous trees than were found around actual hibernacula (Scheffé F-test, $F = 5.1$, $P \leq 0.05$). However, because our previous analyses suggested that rat snakes do not necessarily prefer to bask in coniferous over deciduous trees, or vice versa, we conclude that trees which are apparently suitable for basking are readily available at potential hibernacula.

DISCUSSION

Communal hibernacula occupied by black rat snakes of the Frontenac Axis population are typically situated on relatively rocky, south-facing slopes. These habitat features were sufficiently unique as to allow us to distinguish hibernacula from a series of randomly selected locations in the surrounding landscape. However, for several reasons we regard these findings to be of limited value in the establishment of guidelines to identify and protect hibernacula throughout this region of eastern Ontario.

First, the broad variability in habitat features exhibited by the hibernacula we surveyed implies that many hibernacula would not be detected if one searched for them only on southern oriented rocky slopes. For example, at least four of the communal hibernacula we quantified during this study do not fit the image of an "average hibernacula" as conveyed by our data. As such, these four major sites clearly would not have been found had natural resource managers or biologists simply used "rocky, south-facing slopes" as a search image in their quest for hibernacula.

Second, we were able to locate many "potential hibernacula" which were, by our criteria, indistinguishable from real ones. Needless to say, none of the potential hibernacula proved to be (previously undiscovered) actual hibernacula. This strongly suggests that looking for hibernacula on the basis of surface habitat features alone would only rarely result in the discovery of actual hibernacula.

While surface habitat features may not be a good predictor of hibernacula locations, the trees used for arboreal basking at extant hibernacula seem to be distinct from those generally available. The snakes tended to prefer relatively large, partially dead and/or hollow trees as opposed to the younger, more healthy trees available to them. This suggests that rat snakes select specific attributes or a class of trees for basking around hibernacula. The presence of high quality, "potential" basking trees at both potential hibernacula and random sites suggests that basking-type trees are not limiting in the landscape generally.

From the perspective of species conservation, these findings indicate that both the identification and protection of black rat snake communal hibernacula in Ontario will have to proceed on a site by site basis. One cannot predictably find new hibernacula by simply looking for specific or critical habitat features within a landscape. Therefore, radio-telemetry remains the most effective and practical means of locating hibernacula in large, semi-remote areas like parks and ecological reserves. The preferential use of specific trees by rat snakes suggests that opportunities for arboreal basking should be considered in management plans designed to preserve the suitability of communal hibernacula. Specifically, mature and decaying trees and snags should not be cleared from the vicinity of actively used hibernacula. Similarly, where possible such features might be re-created at degraded sites prior to attempts at repatriating extirpated populations.

From a biological or evolutionary perspective our findings are equivocal as to whether or not appropriate hibernacula habitat is limiting in the Frontenac Axis region of eastern Ontario.

At this point we are unable to determine if rat snakes at this (extreme) latitude are (1) geographically constrained by the limitations of over-winter habitat, and/or (2) hibernating communally simply in response to low habitat availability. However, it is unlikely that communal hibernation in black rat snakes is a consequence of some social function or advantage as has been proposed for other species (Gregory, 1984; Duvall et al., 1993). For example, there is no evidence that black rat snakes realize enhanced mating success from hibernating communally since they mate during early summer after dispersal from hibernacula (KAP, pers. obs.).

Surface characteristics alone appear to be insufficient to ascertain the suitability of a site to serve as a communal hibernaculum for rat snakes. That is, surface features may not necessarily reflect essential subterranean structure and conditions, though features like percent rock, degree of slope, and aspect (as they relate to thermal and hydric conditions) are probably not irrelevant. That all hibernacula we studied faced "south" (i.e., mean aspect = 158.0 ± 17.0°) probably holds some biological significance. Southerly exposed hibernacula are likely to experience minimal frost penetration and early spring snow melt, both of which may ameliorate over-winter conditions (see Sexton et al., 1992).

Critical internal attributes of hibernacula may be both distinctive and not particularly common in the environment. Unfortunately, little is known about the internal composition and environment of natural hibernacula. The information available to date has come from either destructive excavations (Burger et al., 1988), investigations of hibernacula occurring in caves large enough to allow human access (Drda, 1968; Sexton and Hunt, 1980), and telemetry studies (e.g., Jacob and Painter, 1980; Weatherhead, 1989). A steady decline in the internal temperature through the over-winter period may be typical of communal hibernacula (Drda, 1968; Sexton and Hunt, 1980), including those used by black rat snakes at this latitude (Weatherhead, 1989). Beyond this, traditional communal hibernacula used by rat snakes must generally be (1) structurally stable, (2) deep enough that the snakes do not reach fatal, low temperatures (0–2 C), and (3) sufficiently humid to preclude over-winter dehydration. The use of remote sensing technology (e.g., ground-penetrating radar) in the future may allow detailed mapping of the internal characteristics of otherwise inaccessible hibernacula. Ultimately, we require additional information about the characteristics of good hibernating sites (e.g., subterranean structure, internal micro-climatic conditions) and need to assess these variables at potential sites more thoroughly before we can draw conclusions regarding the availability of hibernacula (Gregory, 1984).

Acknowledgments.—Several background telemetry studies were responsible for originally locating the hibernacula described in this paper. Thus, the efforts of research teams associated with Murphy's Point Provincial Park, Charleston Lake Provincial Park, St. Lawrence Islands National Park, and the Weatherhead Lab (Carleton University) provided us with the opportunity to conduct the study. We thank L. Harbidge (SLINP), J. Ives (MPPP), and A. Thompson (CLPP) for permission to work inside the respective parks, and R. Andress, A. Caissie, P. Chamberland, D. Jivcoff, M. Ogilvie, and T. Taylor for assistance in the field. We are indebted to S. Thompson for sharing with us his knowledge of and enthusiasm for rat snakes, and thank A. Briesch, W. Weller and M. Oldham for providing unpublished data. K. Dufour provided valuable input regarding data analyses and comments by J. R. Lee and R. Seigel helped improve this paper. Financial support was provided by a research grant from the Canadian Parks Service, an Ontario Graduate Scholarship to KAP, and an NSERC operating grant to PJW.

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