A PRACTICAL MODEL OF BICKNELL'S THRUSH HABITAT IN THE NORTHEASTERN UNITED STATES

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DRAFT – PLEASE DO NOT CITE

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ABSTRACT

Bicknell's Thrush (*Catharus bicknelli*) is a rare habitat specialist that breeds in dense balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) forests at high elevations in the northeastern United States. Ongoing and projected loss of this forest type has led to increased demand for information on the availability of suitable habitat. We used elevation, latitude, and forest type to construct a model of Bicknell's Thrush habitat. The model predicted the species to be present in conifer-dominated forests above an elevation threshold that descends with an increase in latitude. The slope of the threshold (-84.5 m/1° latitude) reflects climatic effects on forest composition and structure. To test model performance, we conducted point count and playback surveys along 1-km routes established in conifer forests above and below the threshold. The model performed at a significant level ($P < 0.01$), accurately predicting the status of the species on 64 of 76 (84.2%) routes. When sites within 50 vertical meters of the threshold were excluded, accuracy improved to 94.2%. This habitat model is a practical tool for conservation planning at local and regional levels.

Bicknell's Thrush (*Catharus bicknelli*), once considered a subspecies of Gray-cheeked Thrush (*C. minimus*), gained full species status in 1995 (American Ornithologists' Union 1995). It has since been considered one of the most "at-risk" passerines in eastern North America. Partners in Flight ranks Bicknell's Thrush as the top conservation priority among neotropical migrants in the Northeast (Pashley et al. 2000), while the International Union for the Conservation of Nature classifies the songbird as "vulnerable" on its list of threatened species (BirdLife International 2000).

Although there is no conclusive evidence of widespread population declines, reports of regional declines (Rompré et al. 1999, Rimmer et al. 2001a) and local extinctions (Christie 1993, Atwood et al. 1996, Nixon 1999, Lambert et al. 2001) have elevated concern for this rare species.

Bicknell's Thrush is a habitat specialist that occupies a naturally fragmented breeding range from the Catskill Mountains of New York to the Gulf of St. Lawrence and Cape Breton Island (Atwood et al. 1996, Rimmer et al. 2001b). It is the region's only endemic bird species. In New York, northern New England, and the nearby Estrie region of Québec, Bicknell's Thrush inhabits montane forests dominated by balsam fir (*Abies balsamea*), with lesser amounts of spruce *(Picea rubra* and *P. mariana)*, white birch *(Betula papyrifera* var. *cordifolia)*, and mountain ash *(Sorbus americana*, *S. decora)* (Atwood et al. 1996, Connolly et al. 2002, Rimmer et al. 2001b). Structural attributes of Bicknell's Thrush habitat include a dense softwood understory (Sabo 1980, Hale 2001, Pierce-Berrin 2001), low canopy height (Sabo 1980, Noon 1981, Hale 2001), and high incidence of snags, stumps, and dead fallen trees (Connolly 2000). These features typify chronically disturbed sites and regenerating fir waves (Sprugel 1976). Favorable conditions may also arise following disturbance by hurricane, ice storm, debris avalanche (Reiners and Lang 1979), or logging (Connolly 2000). Habitat suitability decreases with greater prominence of hardwoods (Sabo 1980, Noon 1981, Atwood et al. 1996, Hale 2001, Connolly et al. 2002) except in New Brunswick, where Bicknell's Thrush occurs in regenerating, highland clear cuts dominated by young birch trees (Nixon et al. 2001).

Climate change could greatly reduce or eliminate balsam fir habitat in the Northeast, as growing conditions become more favorable for southern hardwoods (Iverson and

Prasad 2002). Over the long term, a shift in forest composition may impair the viability of Bicknell's Thrush populations in the region. Meanwhile, ski area expansion, communications tower construction and wind power development incrementally reduce and fragment montane fir forests with unknown consequences for Bicknell's Thrush (Rimmer et al. 2001b). In order to conserve and properly manage remaining Bicknell's Thrush habitat, natural resource managers require reliable, site-specific occurrence information. Since it is not feasible to survey all potential habitat, a predictive habitat map is required for effective conservation planning.

Wildlife habitat maps enable natural resource managers to identify suitable habitat and predict effects of management alternatives. When constructed in a geographic information systems (GIS) environment, such maps can be efficiently produced and consistently applied over large areas. However, the value of a GIS habitat model depends on its predictive capability. Therefore, model validation is a critical step in the habitat mapping process, one that has been frequently overlooked (Verner et al. 1986, but see Edwards et al. 1996, Dettmers and Bart 1999). Validation procedures yield measures of model performance that provide a basis for determining appropriate applications to research and management. An accurate GIS model is a flexible tool that focuses limited resources where they will have the greatest effect.

In a previous study, Atwood et al. (1996) identified forest type, latitude, and elevation as important factors underlying the distribution of Bicknell's Thrush in New England and New York. The goal of our study was to construct and test a predictive habitat model that incorporates forest type and accounts for the effect of latitude on Bicknell's Thrush's elevational occurrence.

METHODS

To investigate the effect of latitude on the elevational occurrence of Bicknell's Thrush, we examined records from the original Bicknell's Thrush distribution survey. Between 1992 and 1995, Atwood et al. (1996) surveyed 430 sites across a wide range of elevations (0 to 1600 m) in Maine, Massachusetts, New Hampshire, New York, and Vermont. We plotted the elevations at which they did and did not detect Bicknell's Thrush in four zones of latitude: 42-43° N (n = 24 sites), 43-44° N (n = 89), 44-45° N (n = 228), and 45-46° N (n = 83; Fig. 1). Six of the original 430 sites occurred north of 46° and were excluded from the analysis. For mountain sites, we plotted summit elevations because summits were typically included and actual elevations were not consistently recorded. The use of broad zones was necessary to obtain an adequate spread of elevations within each category and to dampen the effect of sampling error, evident in the high number of suitable sites that produced no observations of Bicknell's Thrush (see discussion).

To build the habitat model, we first entered the elevation of each zone's lowest, occupied mountain into a linear regression. This produced a minimum-elevation threshold for suitable habitat at any given latitude. Next, we converted the linear threshold into an elevation mask, formed as a grid of 30-m cells in ArcInfo GIS 8.2 (Environmental Systems Research Institute 2001). Cell values throughout the grid were set to correspond with the lowest-elevation occurrence of Bicknell's Thrush, as predicted by the regression. Next, in ArcView GIS 3.2 (Environmental Systems Research Institute 1999) we laid the elevation mask over a digital elevation model of the Northeastern United States (U.S. Geological Survey 1999). Summits, ridgelines, and slopes that emerged above the mask were designated “high-elevation habitat units”. To identify potential Bicknell’s Thrush habitat within these units, we mapped conifer-dominated stands. For this, we used forest composition data from the National Land Cover Dataset, which classifies 30-m cells based on canopy dominance (USGS 1992).

To test model performance, we conducted surveys between 2000 and 2002 on 57 mountains (> 800 m) not surveyed by Atwood et al. (1996). These mountains were scattered throughout the region and were selected based on availability of trails and volunteer observers. On each mountain, we established 5 survey stations, separated by 200 to 250 m, in areas dominated by conifer. Where conifer cover was limited, we located survey stations in mixed forests.

Trained technicians and volunteers performed point count surveys under acceptable weather conditions between 04:00 and 08:00 EDT (usually between 04:30 and 06:30 EDT) from 1 to 21 June. Observers listened quietly for five minutes, recording the number of Bicknell’s Thrushes seen or heard at each station. They also recorded Bicknell’s Thrushes seen or heard along the route, between counts. Observers who completed the route without detecting Bicknell’s Thrush broadcasted playbacks at each station on their way back to the starting point. Playbacks consisted of a three-minute, standardized recording of Bicknell’s Thrush songs and call notes, followed by two minutes of silent listening. Playbacks were stopped upon first detection of the target species. Observers who completed the playback survey without encountering Bicknell’s Thrush conducted follow-up, playback surveys at dusk or dawn before 15 July. This time, playback stations were located at 100-m intervals along the route. If no observations of Bicknell’s Thrush were made during the second visit to a given site, the species was presumed to be absent. Observers conducted the full sampling sequence (point counts and up to two playback surveys, as needed) in at least one of the three years. Follow-up playbacks were not conducted on mountains lying more than 70 m below the elevation mask.

Observers reported incidental encounters with Bicknell's Thrush on 19 additional mountains not surveyed by Atwood et al. (1996). These observations, made during one or more breeding seasons between 2000 and 2002, were added to the 57 original test routes in a chi-square analysis of the model's predictive capability. The null hypothesis for this test was that the habitat model performs no better than chance in predicting the presence or absence of Bicknell's Thrush at a given site. An accuracy level of 50% would be expected in that case, yielding an equal measure of correct and incorrect classifications. Thus, expected values in a two-by-two contingency table involving our 76 sites would be 38 correct classifications and 38 incorrect classifications. A significant result, with correct classifications exceeding incorrect classifications, would indicate a robust model.

We repeated the chi-square test for the 24 sites occurring within 50 vertical meters of the model's elevation mask. We used Systat 10.2 for these analyses (Systat Software Inc. 2002) and determined results to be significant at $P < 0.05$.

With the same combination of systematic surveys and incidental sightings, we recorded the presence or presumed absence of Bicknell's Thrush on 131 mountains first sampled by Atwood et al. (1996). Due to lack of independence, these sites were excluded from the chi-square analysis. However, we present these data to demonstrate improvements in sampling methodology and to provide further context for model evaluation.

RESULTS

Survey results from Atwood et al. (1996) showed a strong, linear relationship between zone of latitude and elevation of the lowest mountain on which Bicknell's Thrush was detected. The lower limit of Bicknell's Thrush habitat, as indicated by the regression line in Figure 1, descends 84.5 m for every one-degree increase in latitude ($n = 4$, $y = -84.5 + 1084.5$, $R^2 = 0.979$, $p < 0.01$). The sloping grid, developed in GIS to express this relationship, masks elevations as high as 1,093 m in the Catskills and includes areas as low as 759 m in north-central Maine. Throughout the region, 662 distinct, high-elevation habitat units contain 111,346 ha of conifer-dominated forest. These areas represent potential Bicknell's Thrush habitat (Fig. 2). The amount of modeled habitat within a given high-elevation unit ranged from 0 to 10,825 ha (mean = 166.2 ha, SE = 28.3 ha), with the largest measures occurring in New Hampshire's White Mountains and in the High Peaks region of New York's Adirondack Mountains. The model shows that New Hampshire has the greatest area of potential Bicknell's Thrush habitat in the U.S. (49,586 ha; 44.5 % of U.S. breeding habitat), followed by New York (26,850 ha; 24.1%), Maine (26,130 ha; 23.5%), and Vermont (8,780 ha; 7.9%).

The Bicknell's Thrush habitat model correctly classified 64 out of 76 sites (84.2%) that had never been surveyed for this species (Fig. 3). Fifty-seven of 68 (83.8%) were correctly classified as occupied by Bicknell's Thrush, while 7 out of 8 sites (87.5%) were correctly classified as unoccupied. The test of the model for overall goodness of fit produced a significant result ($X^2 = 20.15$, $df = 1$, $P < 0.01$).

	Correct	Incorrect
Expected	38	38
Observed	64	12

Model performance within 50 m of the elevation mask was poor (62.5% accuracy; X^2 = 0.76, df = 1, P = 0.38).

	Correct	Incorrect
Expected	12	12
Observed	15	9

Mountains occurring within 50 m of the mask accounted for 8 out of 11 errors of commission (misclassification of unoccupied sites as occupied) and the lone error of omission (misclassification of an occupied site as unoccupied). The average, vertical deviation of misclassified mountains from the elevation mask was 51.1 m (SE = 10.8 m). When the 24 peaks within 50 m of the elevation mask were excluded from the analysis, 49 of 52 mountains (94.2%) were correctly classified.

When all new and resampled sites were combined, the model correctly classified 187 of 207 (90.3%) sites. Classification accuracy at sites beyond 50 m of the buffer was 97% (160 of 165 sites correctly classified).

DISCUSSION

The slope of the latitude-elevation relationship for Bicknell's Thrush occurrence (-84.5 m/1° latitude) is nearly identical to the latitude-elevation relationship for treeline in the northern Appalachian mountains (-83 m/1° latitude); it also resembles that of the spruce-fir / deciduous forest ecotone (-100 m/1° latitude) (Cogbill and White 1991). The similarity in these slopes and the known association of Bicknell's Thrush with naturally disturbed forest stands suggest that the same factors governing stratification of mountain forest types regulate the availability of suitable habitat for Bicknell's Thrush. On a local scale, these include topography (slope shape, slope position, steepness, and aspect), substrate, and disturbance (Cogbill and White 1991). At regional and continental scales, temperature appears to be the primary, controlling factor (Wolfe 1979).

Cogbill and White (1991) found that the lower and upper spruce-fir ecotones were correlated with mean July temperatures of approximately 17° C and 13° C, respectively. If a warming climate were to elevate these isotherms, an upslope advance of hardwoods, and a corresponding loss of Bicknell's Thrush habitat, might be expected. Tree species distribution models project a major loss or extirpation of balsam fir habitat from the Northeast in four out of five climate change scenarios (Iverson and Prasad 2002). However, damage to hardwoods from ice- and snow-loading could moderate effects of climate change on forest composition at high elevations. The balsam fir's conical form allows it to shed snow more effectively than broad-branching hardwoods (Nykänen et al. 1997). Steep slopes might also provide refugia for balsam fir, which readily establishes in shallow, mineral soils (Frank 1990). Nevertheless, the persistence of Bicknell's Thrush in the Northeast may depend upon its ability to adapt to changing forest conditions.

A warming climate could enable mountaintop encroachment from species believed to be restricted to lower elevations by colder temperatures, including both a potential competitor of Bicknell's Thrush and a known pest of balsam fir. Swainson's Thrush (*Catharus ustulatus*) is a potential competitor (Noon 1981) whose distribution overlaps the lower reaches of Bicknell's Thrush habitat (Able and Noon 1976). A rise in summer temperatures could reduce separation between the two species by nullifying Bicknell's Thrush's greater tolerance for cold, considered by Holmes and Sawyer (1975) to confer a thermoregulatory advantage. Balsam woolly adelgid (*Adelges piceae*) is an exotic pest introduced from central Europe. It is currently controlled in the Northeast by cold winter temperatures, but has decimated balsam fir stands in the southern Appalachians (Iverson et al. 1999).

The mechanisms by which a warming climate may affect neotropical migrants are numerous and largely unpredictable, although even small changes could have far-reaching effects on productivity and survivorship (Rodenhouse 1992). Susceptibility to extinction is high for species like Bicknell's Thrush that occupy restricted and patchy habitat within small ranges (Huntley et al. 1997). In recent decades, extirpations of Bicknell's Thrush have occurred at coastal locations in Canada (Tufts 1986, Christie 1993, Nixon 1999) and along the southern periphery of the species' breeding range (Atwood et al. 1996, Lambert et al. 2001). Although there is no evidence for a link to climate change, the observed pattern is consistent with range shifts attributed to global warming in other animal species (Parmesan and Yohe 2003, Root et al. 2003). Our model of Bicknell's Thrush habitat provides the opportunity to predict changes in the species' distribution under different climatic conditions. Information gained through this exercise might be used to develop strategies to mitigate anticipated habitat loss.

Overall, the habitat model's ability to predict the occurrence of Bicknell's Thrush was high (84.2%), showing excellent performance (94.2%) beyond 50 vertical meters of the elevation mask. The model's poor performance (62.5%) within 50 m of the mask and the spread of classification errors on either side of the mask indicate a smooth gradient between suitable and unsuitable habitat. The 100-m transition zone roughly corresponds with the ecotone in which hardwoods disappear and balsam fir achieves dominance.

Able and Noon (1976) described this band as a principal distributional limit for songbirds on northeastern mountains and measured its breadth as approximately 100 m in the Adirondack and Green Mountains. Cogbill and White (1991) provided a similar measure (87 m) for the average breadth of the deciduous forest/spruce-fir ecotone in the Adirondack and northern Appalachian Mountains. Our findings are consistent with these measures and verify this boundary as an important organizer of avian community structure across four degrees of latitude.

Low densities of Bicknell's Thrush may have impaired observer ability to detect the species at some locations, particularly during silent counts (Penteriani et al. 2002). Even playbacks can fail to elicit detectable responses from Bicknell's Thrush (Nixon et al. 2001), which may exhibit agonistic postures in dense vegetation rather than vocalize (Noon 1981). Indeed, the failure to detect Bicknell's Thrush at many apparently suitable sites during the 1990's strongly suggests sampling error. The source of this error may lie in limited sampling (a single visit to 80 locations) and a relatively loose timeframe for broadcasts ("usually within three hours of sunrise or sunset"; Atwood et al. 1996). The likelihood of error during model testing (2000-2002) was reduced by multiple visits and strict broadcast guidelines. The effect of this methodological improvement is evident when detection frequencies from the two surveys are compared (Figs. 1 and 3).

Accuracy rates vary widely among habitat-relationship models that have been tested for songbirds (e.g., 20-33%, Bart et al. 1984; 60-90%, Rice et al. 1986; 53-93%, Kilgo et al. 2002). Models constructed for habitat specialists are more likely to generate accurate predictions than those developed for generalists (Kilgo et al. 2002). This presents conservation planning opportunities for rare species with narrow habitat requirements, like Bicknell's Thrush. Our model of Bicknell's Thrush habitat can be used as a practical tool to guide research, stewardship, and land protection initiatives in the mountains of New York and northern New England. Specific applications include: identification of monitoring and research sites, reserve design, recreational planning, regulatory review and impact assessment (as for tower construction or ski area expansion), and assignment of management responsibility to specific landowners.

To evaluate tradeoffs in each of these applications, it is important to consider the significance of model error. In general, excessive commission error may result in undue expenditure of limited resources at marginal sites, while excessive omission error may result in failure to identify important, occupied sites. Fortunately, GIS provides the flexibility to adjust the Bicknell's Thrush elevation mask to achieve an acceptable ratio between these two types of error. Such adjustments can be made according to project resources and objectives. For example, a risk-averse strategy to protect Bicknell's Thrush habitat might lower the elevation mask to identify all potential breeding areas, including those along the lower spruce-fir ecotone. Though sparsely populated by Bicknell's Thrush, this zone is extensive in mountainous landscapes and could contribute substantially to overall numbers (Hale 2001). A research initiative seeking to maximize encounters with the species might take a more selective approach and raise the mask.

In its current position, the elevation mask is appropriate for general applications, since it achieves similar levels of omission and commission error. For projects that require certain information on the status of Bicknell's Thrush at sites within 50 m of the elevation mask, we recommend the use of playback surveys in June and early July. If initial attempts to verify presence fail, additional effort is advised in at least two successive years or until presence is confirmed. Repeat surveys will reduce errors associated with low density (i.e., low detectability) and irregular occupancy of marginal sites.

The model's estimate of Bicknell's Thrush habitat in the Northeast (111,346 ha) falls within the previously published range of values derived from land cover and land area above the 915-m contour line (100,000 to 150,000 ha; Atwood et al. 1996). However, the addition of latitude as a variable eliminates areas in southern portions of the range once thought suitable for Bicknell's Thrush and adds sites at northern latitudes once considered too low. Despite this important advance, the model does not distinguish early- to mid-successional forests from older age classes of lesser importance to the species. Extensive surveys (Noon 1981, Hale 2001, VINS unpubl. data) and intensive, radio-telemetry studies (VINS unpubl. data) indicate that Bicknell's Thrush makes little use of large patches of mature, montane conifer that lack well-developed shrub and subcanopy layers. Nonetheless, such stands may be an ice storm, fir wave, or hurricane away from developing the structural characteristics of suitable habitat. Likewise, the habitat value of a young forest sheltered from disturbance may diminish over time.

Conservation and mitigation strategies should recognize that the location of suitable habitat patches shift due to the dynamic nature of forests at high elevations. Rather than focusing at the stand level, a prudent long-range approach would treat the entire unmasked area as the management unit. Such an approach would benefit other species that inhabit high-elevation northeastern mountains, including Black-backed Woodpecker (*Picoides arcticus*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Blackpoll Warbler (*Dendroica striata*), and White-winged Crossbill (*Loxia leucoptera*).

We advise caution in the application of this model north of 45° N latitude. Unmasked areas in this region include approximately 40,000 ha of managed timberland in Maine, some of which occurs as mixed, regenerating forest (VINS unpubl. data). The Canadian Wildlife Service has documented use of this forest type by breeding Bicknell's Thrushes in an adjacent, highland region of Quebec (Aubry pers. comm.). Furthermore, model testing in northern Maine was limited, allowing for the possibility that Bicknell's Thrush occurs lower than predicted by the model. Such a possibility is supported by Wolfe's (1979) treeline model, which slopes gradually from 20° N to about 45° N and then begins to steepen. Cogbill and White's (1991) models of Appalachian mountain ecotones maintain their linear shape until about 47° N, where the relationship between elevation and the spruce-fir / deciduous ecotone changes to a steeper slope. Records of Bicknell's Thrush at low elevations in Québec (175-1160 m; Ouellet 1993) and New Brunswick (450-700 m; Nixon et al. 2001) underscore the need for further model testing in northern Maine.

The absence of evaluation sites below the mask in the Catskills (42° N to 42.5° N) is of less concern. We are confident that the model is sufficiently inclusive in this area, since it captures virtually all of the region's upland spruce-fir and encompasses four summits that lack conifer forest altogether.

Recently developed and evolving modeling techniques will enable construction of regional models of habitat importance for Bicknell's Thrush, based on topographic and lithographic features (Banner 2002), remotely sensed forest physiognomy (Hale 2001), and/or landscape structure (Hale 2001, Lambert et al. 2002). Incorporation of abundance data into more sophisticated models will permit reasonable estimates of population size and provide a benchmark for establishing range-wide population objectives. However, construction and validation of such models will require considerable time and resources. Though basic in its parameters and predictions, the current model is accurate and effective for most applications. It is built from elevation and land cover data that are widely available, inexpensive, consistent across state boundaries, and easily updated. Furthermore, it depicts habitat over a major portion of the species' range. Together, these qualities make it a practical tool for conservation planning.

ACKNOWLEDGMENTS

We thank the scores of dedicated volunteers who helped with the fieldwork. They were recruited with assistance from: the Adirondack Mountain Club, Appalachian Mountain Club, Audubon New York, Green Mountain Club, Maine Department of Inland Fisheries and Wildlife, Wildlife Conservation Society, and Wonalancet Outdoor Club. We also thank our research assistants: N. Banfield, C. Dugan, M. Gaige, C. Rabatin, and S. Schulte. We are grateful for site access provided by: the Carthusian Monastery, Essex Timber Company, Green Mountain Club, Maine Department of Environmental Conservation, Maine Department of Inland Fisheries and Wildlife, National Park Service, New York State Department of Environmental Conservation, The Nature Conservancy, Stowe Mountain Resort, Stratton Mountain Resort, U.S. Forest Service, University of Vermont, and Vermont Agency of Natural Resources. We thank the New York State Breeding Bird Atlas for sharing Bicknell's Thrush site records. J. Schlagel and A. Toepfer provided technical assistance with the habitat model. J. Goetz, S. Hale, and R. Renfrew made helpful comments on an earlier draft of the manuscript. We are grateful for funding from the U.S. Fish and Wildlife Service.

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Figures

Figure 1. Elevational occurrence of Bicknell's Thrush (BITH) in four zones of latitude, based on 1992-1995 surveys. Linear regression incorporates lowest-elevation record from each zone (n = 4), designated by triangles. Regression line represents threshold used to create an elevation mask in the GIS habitat model.

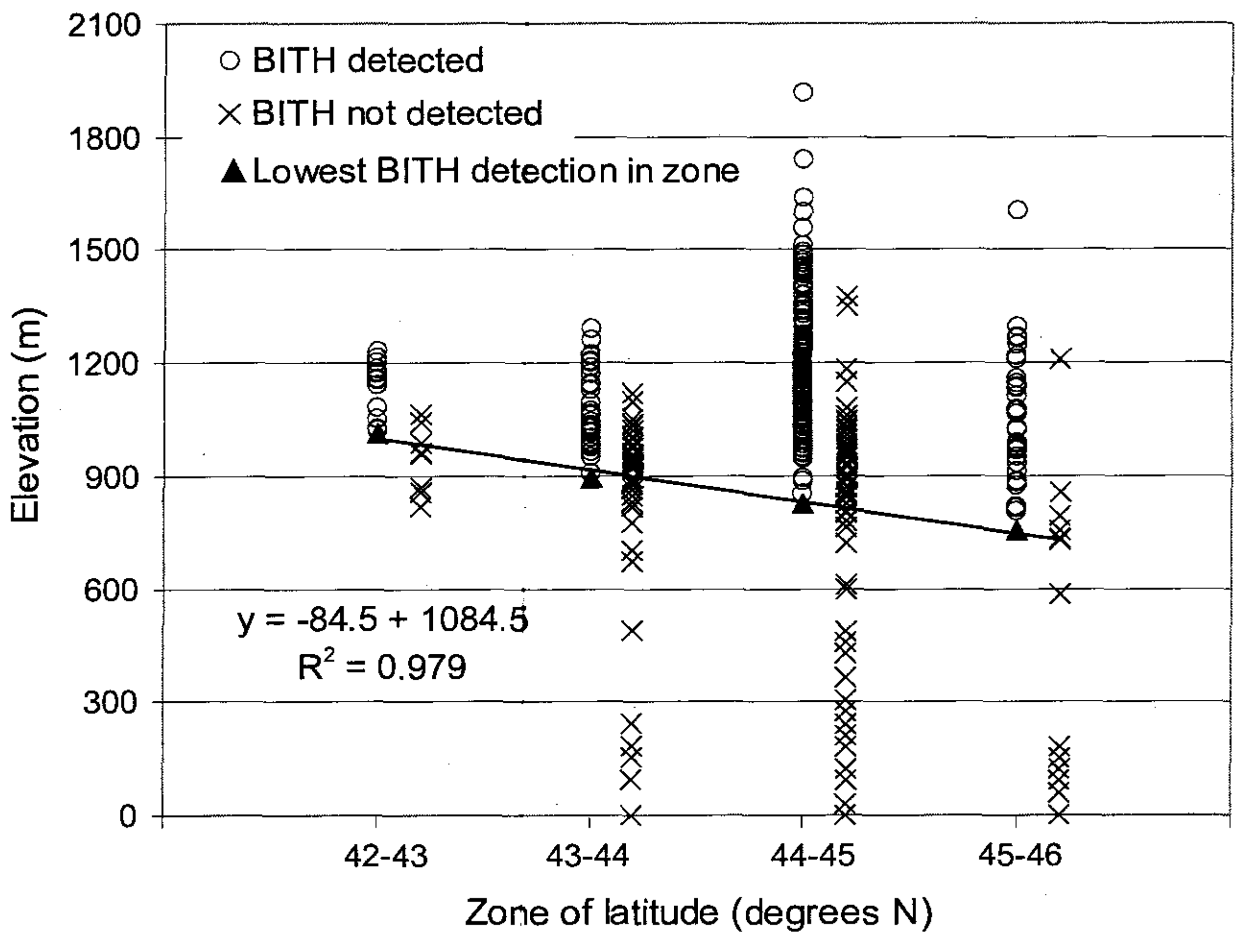

Figure 2. A model of Bicknell's Thrush (BITH) habitat in the northeastern United States.

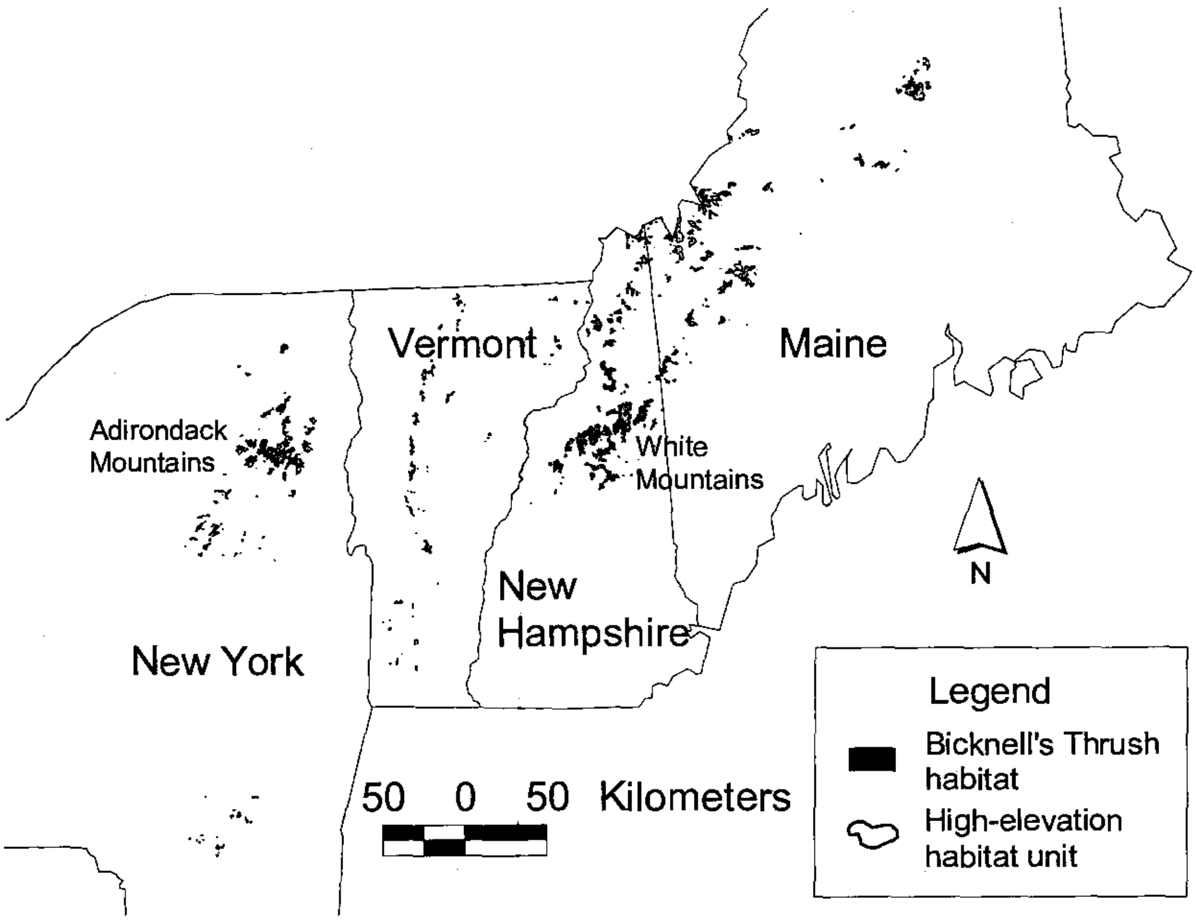

Figure 3. Elevational occurrence of Bicknell's Thrush (BITH) in relation to elevation mask and 50-m buffer, based on 2000-2002 surveys. Large symbols represent new survey locations; small symbols represent sites first surveyed by Atwood et al. (1996).