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FRONTISPIECE. Bicknell's Thrush (*Catharus bicknelli*) in its favored high-elevation, coniferous-forest habitat in the northeastern United States. Lambert et al. mapped the distribution of Bicknell's Thrush based on their model that predicts presence above an elevation threshold that decreases with increasing latitude. Original painting (acrylic and gouache) by Barry Kent MacKay.

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

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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 species' status throughout the region. We used elevation, latitude, and forest type to construct a model of Bicknell's Thrush distribution in New York, Vermont, New Hampshire, and Maine. The model predicts the species to be present in conifer-dominated forests above an elevation threshold that descends with increasing latitude. The slope of the threshold (−81.63 m/1° latitude) reflects climatic effects on forest composition and structure. The distribution model encompasses 136,250 ha of montane forest, including extensive areas of the White Mountains in New Hampshire and Adirondack Mountains in New York. 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 accurately predicted the presence or presumed absence of Bicknell's Thrush on 61 of 72 routes (84.7%). When areas within 50 vertical m of the threshold were excluded, accuracy improved to 98.1%. The distribution model is a practical tool for conservation planning at local and regional levels. Potential applications include projecting effects of climate change on Bicknell's Thrush distribution, assessing risks of habitat alteration, and setting priorities for conservation and management. *Received 9 February 2004, accepted 20 December 2004.*

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 (Pashley et al. 2000) ranks Bicknell's Thrush as the top conservation priority among Neotropical migrants in the Northeast, while the International Union for the Conservation of Nature (BirdLife International 2000) classifies the species as ''vulnerable'' on its list of threatened species. Although there is no conclusive evidence of widespread population declines, reports of regional declines (Rompré et al. 1999, Rimmer et al. 2001b) 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, Nova Scotia (Atwood et al. 1996, Rimmer et al. 2001a). 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 rubens* and *P. mariana*), white birch (*Betula papyrifera* var. *cordifolia*), and

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mountain ash (*Sorbus americana* and *S. decora*) (Atwood et al. 1996, Rimmer et al. 2001a, Connolly et al. 2002). Structural attributes of Bicknell's Thrush habitat include a dense understory of softwoods (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 habitat conditions for Bicknell's Thrush also may arise following disturbance by hurricane, ice storm, debris avalanche (Reiners and Lang 1979), or logging (Connolly 2000). Habitat suitability generally decreases with greater prominence of hardwoods (Sabo 1980, Noon 1981, Atwood et al. 1996, Hale 2001, Connolly et al. 2002); however, in the spruce-fir highlands of New Brunswick, Bicknell's Thrush inhabits both young conifer stands and regenerating hardwoods (Nixon 1996, Nixon et al. 2001).

Bicknell's Thrush also occurs in maritime spruce-fir forests at sites scattered along both shores of the St. Lawrence Seaway (Gauthier and Aubry 1996) and throughout the Gulf of St. Lawrence (Nixon 1999). Locations in the Gulf include the western tip of Anticosti Island, the Magdalen Islands (Gauthier and Aubry 1996), Cape Breton Island and small islands offshore of Cape Breton (Erskine 1992; D. Busby pers. comm.). Historic or sporadic records exist for several additional locations around the Bay of Fundy (Erskine 1992, Christie 1993).

In the northeastern United States, climate change could greatly reduce or eliminate balsam fir habitat as growing conditions become more favorable for hardwood species (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. 2001a). In order to conserve and properly manage remaining Bicknell's Thrush habitat, natural resource managers require reliable, site-specific occurrence information. Because it is not feasible to survey all potential habitats, 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 produced efficiently and applied consistently 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. 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 distribution model that incorporates forest type and accounts for the effect of latitude on the elevational occurrence of Bicknell's Thrush.

METHODS

To investigate the effect of latitude on the elevational occurrence of Bicknell's Thrush, we examined records from distribution surveys of Bicknell's Thrush conducted between 1992 and 1995. In these surveys, Atwood et al. (1996) surveyed 443 locations across a wide range of elevations (0 to 1,451 m) in New York, Vermont, New Hampshire, and Maine. We plotted the elevation and latitude of each survey location, including those where Bicknell's Thrush was detected ($n = 234$) and was not detected ($n = 209$). If multiple individuals were observed during a survey, we plotted the lowest-elevation encounter. If no individuals were observed during a survey that spanned a range of elevations, we plotted the highest point surveyed.

Next, we used the Quantreg library in R (http://lib.stat.cmu.edu/R/CRAN) to estimate the 0.05 quantile regression (Cade and Noon 2003) of elevation as a linear function of latitude for locations where Bicknell's Thrush was observed. This produced an elevation threshold above which 95% of the detections occurred. We then converted the linear threshold into an elevation mask, formed as a raster data set of 30 × 30 m cells in ArcMap 8.2 (Environmental Systems Research Institute 2002). Cell values were calculated with the 0.05 quantile regression equation: elevation $= -81.63(\text{latitude}) + 4{,}474.9$ m. Next, we laid the elevation mask over a digital elevation model of the northeastern United States (U.S. Geological Survey 1999). Summits, ridgelines, and slopes emerged above the mask as a vast complex of 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 Data set, which classifies 30 × 30 m cells based on canopy dominance (Vogelmann et al. 2001).

To test model performance, we conducted surveys between 2000 and 2002 on 53 mountains ($>$800 m in elevation) 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 five survey stations, separated by 200 to 250 horizontal m, in areas dominated by conifers. Routes were designed to include the highest forested areas accessible by trail, often the summit, as well as adjacent ridges and slopes. Where conifer cover was limited, we located survey stations in mixed forests.

Trained technicians and volunteers performed point-count surveys under acceptable weather conditions (no precipitation, temperature $>$2° C, wind speed $<$32 km/hr) from 1 to 21 June. Surveys were conducted between 04:00 and 08:00 EDT, usually between 04:30 and 06:30. Observers listened quietly for 5 min, 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 survey stations. Observers who completed the route without detecting Bicknell's Thrush broadcast playbacks at each station on their way back to the starting point. Playbacks consisted of a 3-min, standardized recording of Bicknell's Thrush songs and call notes, followed by 2 min of silent listening. Playbacks were stopped upon first detection of the 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 1 of the 3 years. Follow-up playbacks were not conducted at six locations that were $>$80 m below the elevation mask. Atwood et al. (1996) surveyed 95 locations below this level without a confirmed encounter of Bicknell's Thrush.

Observers reported incidental encounters with Bicknell's Thrushes on 19 additional mountains not previously surveyed. These observations, made during one or more breeding seasons between 2000 and 2002, were added to the 53 original test routes for a total of 72 independent sample locations (New York: $n = 34$, Vermont: $n = 19$, New Hampshire: $n = 16$, Maine: $n = 3$). Twenty-one of the 72 locations were within 50 vertical m of the elevation mask. Also during 2000–2002, with the same combination of systematic surveys and incidental sightings, we recorded the presence or presumed absence of Bicknell's Thrush on 130 mountains first sampled by Atwood et al. (1996) (New York: $n = 30$, Vermont: $n = 56$, New Hampshire: $n = 26$, Maine: $n = 18$). Nineteen of 130 resampled locations occurred within 50 vertical m of the elevation mask. For model assessment, we used one elevation and one latitude value for each sample unit (1-km survey route or site of incidental encounter). At locations where Bicknell's Thrush was present, we calculated average elevation and latitude values based on all points of encounter. Where the species was not encountered, we calculated averages from the five survey stations.

We entered presence-absence data from new and resampled locations into separate error matrices (Table 1) and calculated a variety of accuracy measures (after Fielding and Bell 1997), including correct classification rate, sensitivity (proportion of true positives correctly predicted), specificity (proportion of true negatives correctly predicted), false pos-

TABLE 1. Error matrices for new Bicknell's Thrush survey locations and for resampled locations (first surveyed by Atwood et al. 1996), from 2000–2002 surveys.

Matrix		Observed present	Observed absent
New locations	Predicted present	56	10
	Predicted absent	1	5
Resampled locations	Predicted present	114	5
	Predicted absent	1	10

itive rate, false negative rate, positive predictive power, and negative predictive power. We also calculated prevalence, the proportion of locations at which Bicknell's Thrush was present. This variable affects the predictive power of species distribution models (Fielding and Bell 1997, Manel et al. 2001). Finally, we calculated Cohen's kappa, a statistic that measures the proportion of specific agreement after accounting for prevalence.

RESULTS

Survey results from Atwood et al. (1996) show a strong, linear relationship between latitude and the lowest elevations occupied by Bicknell's Thrush (Fig. 1). The lower limit of the species' distribution, as estimated by the 0.05 quantile regression, descends 81.63 m for every one-degree increase in latitude ($\beta_1 = -81.63$, 95% CI = −112.08 to −38.13; $\beta_0 = 4{,}474.86$, 95% CI = 729.50 to 5,753.27). The regression slope differed significantly from zero (H_0: $\beta_1 = 0$) for this quantile (quantile rankscore test, $P < 0.001$).

The elevation mask, developed in GIS from the 0.05 quantile regression, covers areas as high as 1,045 m in the Catskills (42° N). In northern Maine (46.3° N), areas as low as 695 m emerge above the mask. Throughout the region, 720 distinct land units occur above the

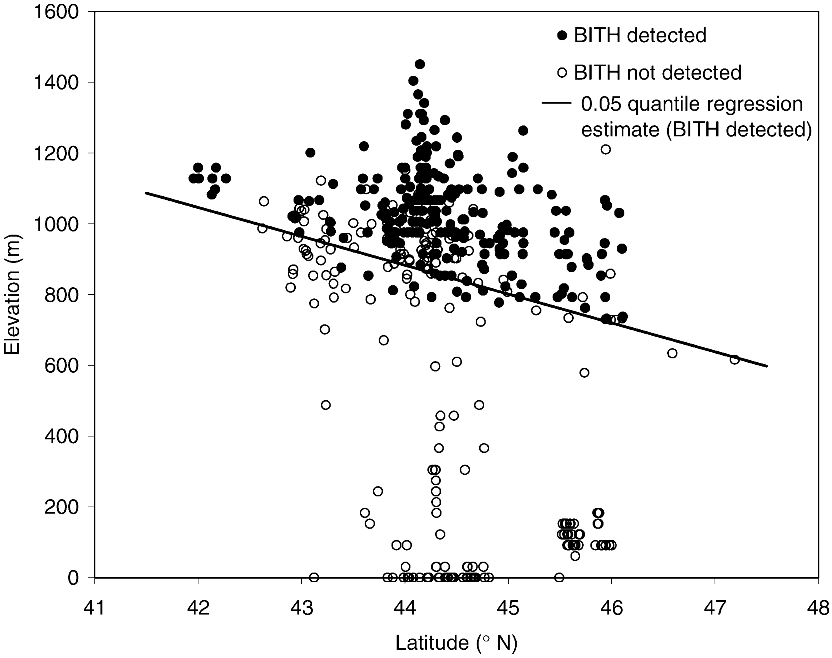

FIG. 1. Elevation and latitude of locations where Bicknell's Thrush (BITH) was detected ($n = 234$) and not detected ($n = 209$) during 1992–1995 surveys in the northeastern United States. Line is 0.05 quantile regression estimate of elevation as a linear function of latitude, incorporating only locations where Bicknell's Thrush was detected: elevation = −81.63 (latitude) + 4,474.9 m.

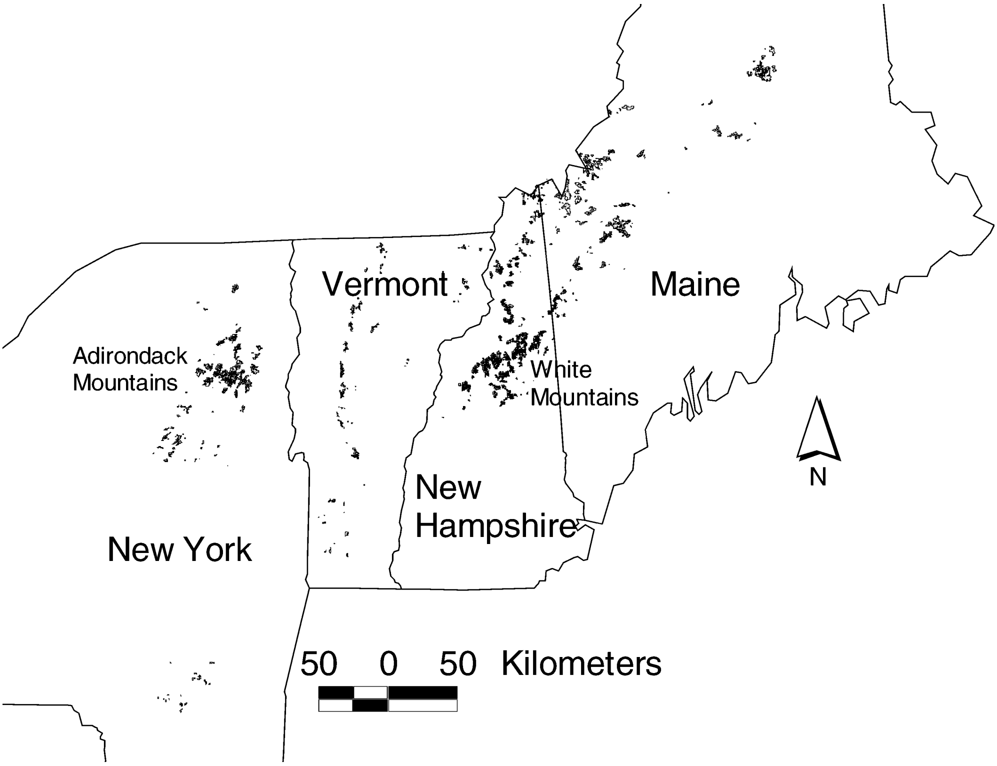

FIG. 2. Predicted distribution of Bicknell's Thrush in the northeastern United States. Shaded areas represent conifer forests (Vogelmann et al. 2001) above the model's elevation mask.

mask and contain 136,250 ha of conifer-dominated forest (Fig. 2), nearly all of which (99.7%) occurs in 387 units containing at least 5 ha of conifer—an amount sufficient to contain the average home range of a male Bicknell's Thrush (4.5 ha; Rimmer et al. 2001a). The average extent of conifer forest within the 387 units is 351.0 ha ± 56.8 SE, with highest values occurring in the White Mountains of New Hampshire and in the High Peaks region of New York's Adirondack Mountains. Of all states, New Hampshire has the most potential Bicknell's Thrush breeding habitat (59,024 ha; 43.4%), followed by Maine (33,662 ha; 24.7%), New York (31,985 ha; 23.5%), and Vermont (11,580 ha; 8.5%).

The Bicknell's Thrush distribution model correctly classified 61 of 72 locations (84.7%) that had never been surveyed for this species (Fig. 3, Table 2). Fifty-six of 57 occupied locations (98.2%) were correctly classified, compared with just 5 out of 15 (33.3%) unoccupied locations. Locations within 50 vertical m of the elevation mask accounted for both errors of omission (false negatives) and 9 out of 10 errors of commission (false positives). The average, vertical deviation of misclassified locations from the elevation mask was 28.2 m ± 5.2 SE. When the 21 locations within 50 m of the elevation mask were excluded from the analysis, 51 of 52 locations (98.1%) were correctly classified.

The model correctly classified 124 of 130 locations (95.4%) first surveyed by Atwood et al. (1996). Four of the six errors occurred within 50 m of the elevation mask. When all new (n = 72) and resampled (n = 130) sites were combined, the model correctly classified 185 of 202 (91.6%) locations. Classification accuracy >50 m above and below the elevation mask was 98.8%, with 160 of 162 locations correctly classified.

Prevalence of Bicknell's Thrush was high among new locations (0.792) and resampled locations (0.877; Table 2). Cohen's kappa, which accounts for prevalence, measured

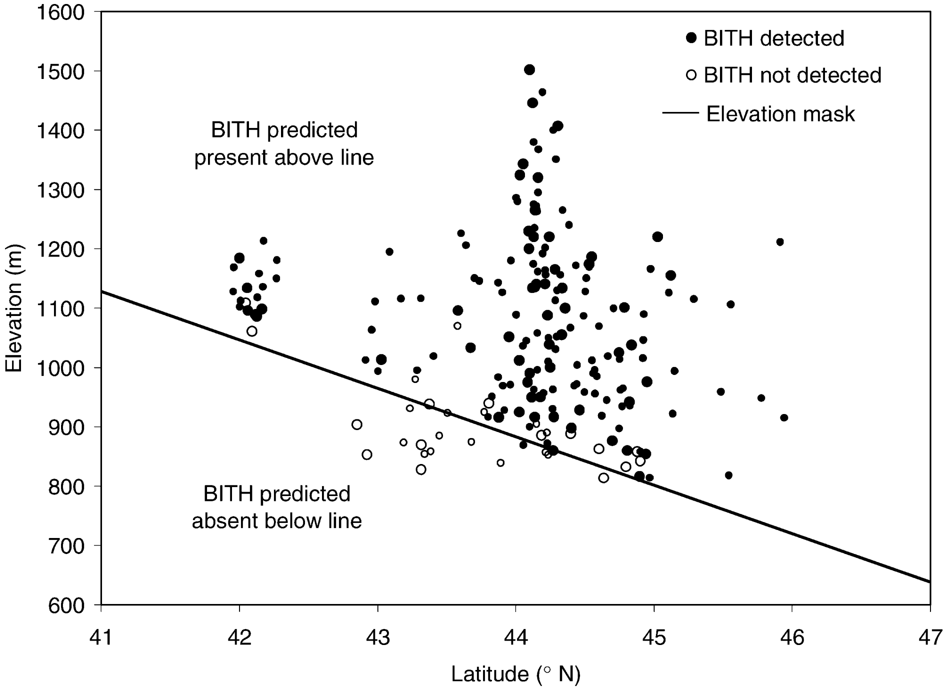

FIG. 3. Elevation and latitude of locations where Bicknell's Thrush (BITH) was detected ($n = 172$) and not detected ($n = 30$) during 2000–20002 surveys in the northeastern United States, shown in relation to elevation mask. Large circles represent new survey locations ($n = 72$); small circles represent locations first surveyed by Atwood et al. (1996) and resampled for this study ($n = 130$).

0.405 among new routes and 0.745 among resampled routes. Values of 0.4–0.6 indicate moderate model performance. Higher values (up to 1.0) are achieved when model performance ranges from substantial to perfect (after Landis and Koch 1977).

TABLE 2. Accuracy measures for Bicknell's Thrush distribution model. Values are calculated after Fielding and Bell (1997) with data from 72 new locations and from 130 (resampled) locations (2000–2002) first surveyed by Atwood et al. (1996).

	New locations	Resampled locations
Correct classification rate	0.847	0.954
Sensitivity	0.982	0.991
Specificity	0.333	0.667
False positive rate[a]	0.667	0.333
False negative rate[b]	0.018	0.009
Positive predictive power	0.848	0.958
Negative predictive power	0.833	0.909
Prevalence	0.792	0.877
Kappa	0.405	0.745

[a] Rate of commission error.
[b] Rate of omission error.

DISCUSSION

The slope of the latitude-elevation relationship for Bicknell's Thrush occurrence (−81.63 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 stands of balsam fir in the southern Appalachians (Iverson et al. 1999).

The mechanisms by which a warming climate might 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 distribution model achieved high measures of classification accuracy, positive predictive power, and negative predictive power (Table 2). However, such levels can be achieved by chance alone where the prevalence of a species is high (Olden et al. 2002), as it was in this study. Cohen's kappa provides a measure of improvement over chance that places prediction success in perspective (Fielding and Bell 1997, Manel et al. 2001). The kappa values we calculated for new routes (0.406) and resampled routes (0.745) correspond with moderate and substantial model performance, respectively. An improved test of the model, including low and middle elevations, would almost certainly yield higher kappa values because more locations would be correctly classified as unoccupied. By concentrating sampling effort at high elevations, we limited the interpretive value of this statistic.

The model's predictive success was nearly perfect at locations >50 m above or below the elevation mask (Fig. 3). By comparison, error rates were high within 50 m of the mask, where hardwoods become scarce and conifers achieve 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 factor in organizing avian community structure across four degrees of latitude.

Low densities of Bicknell's Thrush may have resulted in reduced detectability 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 1990s may indicate sampling error. Such error could have resulted from 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 possibility of error during model testing (2000–2002) was reduced by multiple visits and strict broadcast guidelines. The higher frequency of detection above the elevation mask, compared with the results of Atwood et al. (1996), provides evidence of improved methodology.

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 distribution 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.

For projects that seek 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. Six or more visits may be required to detect all individuals in a given year (Nixon et al. 2001). If initial attempts to verify presence fail, additional effort is advised in at least 2 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. Our own repeat surveys confirm their value. Since 2003, we have observed Bicknell's Thrush at 6 of 15 locations where it was predicted to occur, but was not detected during model assessment (Vermont Institute of Natural Science [VINS] unpubl. data).

The model's estimate of Bicknell's Thrush habitat in the Northeast (136,250 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 or stunted forests from tall stands, which are 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 Thrushes make little use of large patches of mature, montane conifer that lack well-developed shrub and subcanopy layers. Nonetheless, such stands may be just 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 shifts due to the dynamic nature of forests at high elevations. Rather than focus 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 nest in montane forests of the Northeast, such as 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 >40,000 ha of managed timberland in Maine (VINS unpubl. data), some of which occurs as mixed, regenerating forest. The Canadian Wildlife Service has documented use of this forest type by breeding Bicknell's Thrushes in highland regions of Québec (Y. Aubry pers. comm.), New Brunswick (Nixon 1996), and Nova Scotia (D. Busby pers. comm.). Furthermore, model testing in northern Maine was limited, allowing for the possibility that Bicknell's Thrush occurs at lower elevations 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 (175–1,160 m; Ouellet 1993), New Brunswick (450–700 m; Nixon et al. 2001), and Nova Scotia (<175 m; D. Busby pers. comm.) underscore the need for further model testing in northern Maine.

The absence of evaluation sites below the mask in the Catskills (42.0–42.5° 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.

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.

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