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Allan M. Strong*
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INTRODUCTION

The response of natural communities to disturbance has received considerable attention among ecologists. Part of the fascination with disturbances and post-disturbance ecology has been the rich descriptive literature that has come from the studies of cataclysmic events, such as the formation of new volcanic oceanic islands, the eruption of Mount Saint Helens, fires in Yellowstone National Park, or recent hurricanes. These natural disturbances have led to important insights regarding our understanding of interspecific competition, life history strategies, spatial stochasticity, and successional processes. Perhaps equally important has been our ability to put these cataclysmic disturbances into a more robust theoretical framework that has allowed us to better understand organism

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^{1.} See, e.g., I.W.B. Thornton et al., Colonization of the Krakatau Islands by Vertebrates: Equilibrium, Succession, and Possible Delayed Extinction, 85 PROC. NAT'L. ACAD. SCI. 515 (1988).

^{2.} See, e.g., Douglas Larson, The Recovery of Spirit Lake, in EXPLORING ECOLOGY AND ITS APPLICATIONS 178 (Peter Karieva ed., 1998).

^{3.} See, e.g., Monica G. Turner et al., Effects of Fire Size and Pattern on Early Succession in Yellowstone National Park, 67 ECOLOGICAL MONOGRAPHS 411 (1997).

^{4.} See generally Joseph M. Wunderle, Jr., Responses of Bird Populations in a Puerto Rican Forest to Hurricane Hugo: The First 18 Months, 97 CONDOR 879 (1995).

habitats.¹⁷ A unique aspect of mountain resorts is that the traditional pattern of development maximizes the degree of habitat fragmentation over (for the most part) a relatively small proportion of a mountain slope. Within a ski area, trails are designed to enhance visual isolation among trails and to provide skiers with a diverse set of trails with varying degrees of difficulty. To achieve the most diversified recreational experience, ski trails need to be spread out across the face of the mountain. Further, to "sell" the diversity of runs available, mountain resorts typically advertise the total number of trails, creating competition to increase the amount of habitat fragmentation. The result is a landscape that is not fragmented randomly, but one in which habitat fragmentation is indeed maximized. Thus, a more detailed evaluation of the effects of mountain resorts on animal populations and their habitats is warranted.

This Paper begins with a review of selected species' responses to natural disturbances and a discussion of whether or not these responses allow us to predict responses to anthropogenic disturbances. examines these anthropogenic disturbances in the context of the three most important effects of mountain resorts on wildlife habitat: habitat loss. habitat fragmentation, and habitat modification. These three aspects of human-induced habitat change are by no means mutually exclusive, but provide a convenient means for subdividing our review. Part II discusses our spatial analysis, quantifying the hypothetical population declines associated with habitat loss, fragmentation, and modification. In Part III, the Paper assesses certain species for risk of population decline based on three life history characteristics: home range size, gap-crossing ability, and edge sensitivity. Next, we evaluate some of the effects of mountain resorts on wildlife populations at a landscape level, followed by an analysis of the cumulative effects of mountain resort development on certain wildlife populations. Finally, we recommend some local management practices that may mitigate the negative effects of ski trails on high elevation wildlife We conclude that better long-term and landscape scale planning may aid in minimizing conflicts over expansion and development in and around mountain resorts, and our societal biases about species' identities may influence our management actions.

^{17.} Antonio Rolando & Ian James Patterson, Range and Movements of the Alpine Chough Pyrrhocorax graculus in Relation to Human Developments in the Italian Alps in Summer, 134 J. FUER ORNITHOLOGIE 338 (1993); S. Tsuyuzaki, Environmental Deterioration Resulting from Ski-Resort Construction in Japan, 21 ENVTL. CONSERVATION 121, 121–25 (1994); Johanne B. Ries, Landscape Damage by Skiing at the Schauinsland in the Black Forest, Germany, 16 MOUNTAIN RES. & DEV. 24, 24–40 (1996); see also Urbanska, supra note 15, at 1655 (discussing effects of mountain resorts on plant species).

SPECIES RESPONSES TO DISTURBANCES

The classic approach to understanding a species' response to disturbances is through an assessment of life history strategies along the rand K-selection 18 spectrum. 19 r-selected species are those that are highly adapted to disturbances. These species typically show extreme variation in population size as new colonizers disperse to recently disturbed sites and show immediate, but temporary, exponential population growth. These high population growth rates are short-lived because r-selected species allocate more energy to reproduction than to competition. Biotic and abiotic changes in the environment decrease the quality of the site for rselected species as more species begin to colonize the disturbed site and per capita resources decrease. Because newly disturbed sites are temporally ephemeral, these species put most of their energy into reproduction, with large cohorts, mobile offspring, and minimal parental care.

In contrast, K-selected species are those that are better adapted to more constant environments. They are long-lived, better competitors, and put less energy into reproductive output and more into parental care. Reproductive events are small, and substantial energy is devoted to each individual offspring. These species are poor dispersers, and individuals may move only a few home ranges from their parents before settling into a new site. Therefore, their populations tend to be relatively constant in size.

Few species show the extreme variation in the life history traits described here. In fact, species that occupy the extremes of the continuum are often species that are habitat specialists, and therefore endangered due to human modification of the environment.²⁰ Most species fall somewhere between these two extremes and show a mixture of life history traits. However, we are still able to make some predictions about how a species will respond to disturbance by studying a species' energetic investment in reproduction and its competitive ability. Our understanding of species' response to disturbance is often limited to natural disturbances or relatively common land use practices, such as succession following clearcuts or

^{18.} The symbols "r" and "K" refer to variables in widely used mathematical expressions describing population dynamics. The symbol "r" refers to the growth capacity or exponential growth rate of a population while "K" refers to the carrying capacity or specific resource limit of the environment for a population. ROBERT E. RICKLEFS, ECOLOGY 565 (1990). K-selected species express traits that enable adaptation to low-resource or overcrowded environments, while r-selected species express traits such as early maturity and increased reproductive capacity that enable rapid population

^{19.} See generally Eric R. Pianka, On r and K selection, 104 Am. NATURALIST 592 (1970). 20. See, e.g., Deborah Rabinowitz et al., Seven Forms of Rarity and their Frequency in the Flora of the British Isles, in Conservation Biology and the Science of Scarcity and Diversity 182 (Michael E. Soulé ed., 1986).

abandonment of agricultural fields. Therefore, making the leap from natural disturbances to human-caused disturbances is complicated in that anthropogenic disturbances have only recently begun to be studied in earnest. Our predictive ability is hampered by a lack of empirical data, particularly over longer time scales. Further, there are frequently secondary, or even tertiary, effects that go beyond the immediate human-induced disturbance.

Secondary effects of human disturbance are particularly poorly understood in mountain resorts. For example, land clearing for a ski trail will necessarily eliminate some amount of forested habitat. Most of the use of those ski trails will occur in the winter when most animals are either in hibernation or have migrated away from the area, minimizing the effects of disturbance. Increasingly, however, economic pressure to make mountain resorts attractive to visitors during all four seasons opens up ski trails to hiking and mountain biking during the summer breeding season, when adults are under the energetic constraints of raising young.²¹ Thus, these complex secondary effects limit our ability to predict accurately how species will respond to human-induced habitat modifications. Only now are we beginning to realize the pervasiveness of some of these land use changes.

A. Habitat Loss

Species vary in their degree of specialization. Habitat specialization is one life history trait of extreme r- or K-selected species that makes them susceptible to habitat loss. However, specialization can also occur through other aspects of a species' life history, such as food habits, den sites, temperature limits, or mating strategies. For those species that are specialized in at least one component of their annual cycle, habitat loss can critically limit their population.

The Bicknell's thrush is a migratory songbird that is extremely specialized in its habitat requirements during the nesting season, breeding in montane fir habitat above approximately 900 meters, varying to some degree with latitude. This specialized habitat requirement limits the species to about 110,000 hectares in New York, Vermont, New Hampshire,

^{21.} See Hans Gander & Paul Ingold, Reactions on Male Alpine Chamois Rupicapra r. rupicapra to Hikers. Joggers and Mountainbikers, 79 BIOLOGICAL CONSERVATION 107 (1997) (observing that alpine chamois abandon pastures near hiking and biking trails); Don White, Jr., et al., Potential Energetic Effects of Mountain Climbers on Foraging Grizzly Bears, 27 WILDLIFE SOC'Y BULL. 146, 150 (1999).

^{22.} Christopher C. Rimmer et al., *Bicknell's Thrush* (Catharus bicknelli), *in* THE BIRDS OF NORTH AMERICA, NO. 592, at 7 (Alan Poole & Frank Gill eds., 2001).

and Maine, which constitutes 0.4% of the total area of these states.²³ Suitable habitat for the Bicknell's thrush is distributed across about 858 mountaintops because of the naturally fragmented spatial distribution of these high peaks. Consequently, their distribution, even in an undisturbed landscape, is small and patchy. Within these high elevation forests, Bicknell's thrush are further limited in their distribution by the specificity of their breeding habitat. They select forested sites with high stem densities of balsam fir that have been recently disturbed.24 Under natural conditions, these sites regenerate every 80 to 100 years in a process known as fir wave migration, 25 where the mortality of exposed portions of the overstory due to high winds releases successive areas of understory fir regeneration. In certain situations, clearing of mountain fir forests for ski trails and associated infrastructure can mimic this regeneration process as the windward side of ski trails are similarly characterized by high mortality of the overstory trees and dense regeneration below. However, suitable habitat created by ski trails rarely extends more than 10 meters into the forest, and the cleared portion of the ski trail is habitat that the Bicknell's thrush will rarely, if ever, use. In fact, observations of radio-tagged individuals on Mount Mansfield have shown that during daily crossings of their home ranges, individuals will take circuitous paths to avoid extremely wide ski trail openings.²⁶ Thus, for a habitat specialist such as the Bicknell's thrush, forest clearing above 900 meters will regulate the long-term carrying capacity of the mountain.

Another group of habitat specialists are the aquatic salamanders. Unlike the Bicknell's thrush, these species appear to be affected more by modification of the habitat within the ski area, rather than by direct habitat loss. Three species of aquatic salamander exist in the mountain forests of Vermont: the two-lined salamander (Eurycea bislineata), the northern dusky salamander (Desmognathus fuscus), and the spring salamander (Gyrinophilus porphyriticus). Rather than having both terrestrial and aquatic stages as do several other salamanders, these species inhabit streams or stream banks during all phases of their life cycle. Because these species "breathe" through their skin, they require highly oxygenated streams.

Amount of land area in 4 states > 900 meters

Total land area in 4 states

^{23.} Christopher C. Rimmer et al., Vt. Inst. of Natural Science, Bicknell's Thrush (Catharus bicknelli) Conservation Assessment (2001). This unpublished report to the Green Mountain National Forest used a simple GIS analysis:

^{24.} Id.

^{25.} Douglas G. Sprugel, Dynamic Structure of Wave-regenerated Abies balsama Forests in the North-Eastern United States, 64 J. ECOLOGY 889, 906 (1976).

^{26.} Kent P. McFarland & Christopher C. Rimmer, Monitoring Bicknell's Thrush Home Range and Movements Via Radio Telemetry During Breeding (1997-1999) (unpublished database) (on file with the Vermont Institute of Natural Science).

In a 1999 study, Hagen quantified abundances and body sizes of the above three salamanders in streams within the boundaries of seven Vermont ski areas, and streams in adjacent undisturbed areas.²⁷ She used timed counts in each stream to sample salamanders, turning over all rocks greater than 10 centimeters in diameter. All salamanders encountered were then tallied and measured. Her results revealed a significantly lower population of spring salamanders and northern dusky salamanders within ski area streams (Figure 1), and also that the northern dusky salamanders within ski areas were shorter in snout-to-vent length. In contrast, ski area development did not appear to affect two-lined salamanders. hypothesized that the changes in species' distributions were a result of clearing streamside vegetation and increased siltation rates in streams within ski areas. These disruptions of the ecological integrity of streams may have a negative effect on salamanders because of higher temperatures, siltation of refugia under rocks, and a decreased prey base.²⁸ Because these species are highly specialized in their habitat requirements, they may serve as useful bioindicators of the quality of high elevation streams.

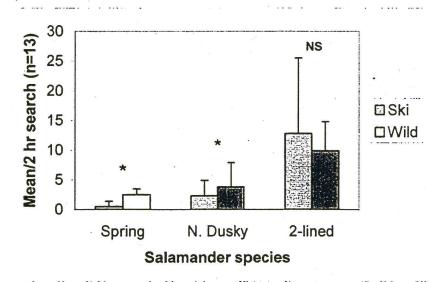


Figure 1. Relative abundances of three species of aquatic salamanders in streams on seven Vermont ski areas and adjacent watersheds in relatively undisturbed forest, May-July, 1999.

Kimberly Hagen, The Effects of Ski Area Development on Populations of Stream Salamanders in Central Vermont 7 (1999) (unpublished M.S. thesis, Antioch University) (on file with author).

^{28.} Id.; Manuel C. Molles, Jr., & James R. Gosz, Effects of a Ski Area on the Water and Invertebrates of a Mountain Stream. 14 WATER, AIR & SOIL POLLUTION 187, 203-04 (1980).

The American black bear (Ursus americanus) is a species that has more general habitat requirements than either the Bicknell's thrush or aquatic salamanders, inhabiting most forested landscapes in the northeast. However, this species is fairly intolerant of disturbance and can create management conflicts when bears are found in areas with high human population densities.²⁹ Additionally, the species goes through an energetic bottleneck in the fall and must consume substantial quantities of high energy food (mast crops such as beech (Fagus grandifolia), hickory (Carya), and acorns (Quercus)) to deposit sufficient fat prior to hibernation.30 Further, females give birth during winter and must have adequate energy stores for fetus development.31 During this critical autumn period, black bears' preferred food source is beech nuts, and each fall they may travel forty to eighty kilometers from their normal home range to forage in traditional mature beech stands.32 Because of the energetic constraints of bears during this time period, human disturbance or development of these key mast areas can have a significant negative effect on bear populations. Therefore, although bears are not specialized in their general habitat requirements, they are specialized in their food habits during crucial parts of their annual cycle, making habitat loss a critical factor in their population dynamics.

The Vermont Environmental Board has denied building permits under Act 250, the state development permit mechanism, in order to protect habitat for both Bicknell's thrush and black bears. 33 Criterion 8A of the Act evaluates a proposed development on the basis of whether or not it "will destroy or significantly imperil necessary wildlife habitat."34 defines "necessary wildlife habitat" as "concentrated habitat which is identifiable and is demonstrated as being decisive to the survival of a species of wildlife at any period in its life including breeding and migratory Bicknell's thrush habitat is readily identifiable based on elevation, latitude, vegetation type, and structure, 36 and due to its limited

^{29.} Serge Larivière, Ursus americanus, 647 MAMMALIAN SPECIES 1 (2001).

^{30.} Kenneth D. Elowe & Wendell E. Dodge, Factors Affecting Black Bear Reproductive Success and Cub Survival, 53 J. WILDLIFE MGMT. 962, 963-966 (1989).

^{31.} Id.

^{32.} George B. Kolenosky & Stewart M. Stratheam, Black Bear, in WILD FURBEARER MANAGEMENT AND CONSERVATION IN NORTH AMERICA 442, 446 (Milan Novack et al. eds., 1987).

^{33.} Act 250, VT. STAT. ANN. tit. 10, §§ 6001-6108 (1997); see also Robert F. Gruenig, Killington Mountain & Act 250: An Eco-Legal Perspective, 26 VT. L. REV. 544, 554-56 (2002).

^{34.} Act 250. VT. STAT. ANN. tit. 10. § 6086(a)(8)(A) (1997).

^{35.} Id. § 6001(12) (1997).

^{36.} Identifying Bicknell's thrush habitat is somewhat more complicated than depicted here. The species selects early successional montane fir forest, which is ephemeral by nature. Therefore,

areal extent, fulfills the concentrated habitat requirement of the definition. Long-lasting claw marks on trees permit ready identification of key mast areas for black bears. Additionally, because these areas are typically localized, they are also considered concentrated habitat. Application of this definition to the habitats of Bicknell's thrush and black bears therefore leads to the conclusion that Act 250 could be invoked to protect these species.

Could Act 250 be used to protect habitat for other species? Most species with specialized habitat requirements by definition require concentrated habitat. Thus, perhaps Act 250 could be invoked to protect habitat for species that require distinct hibernation sites (such as rocky outcroppings for bobcats), species with specific breeding areas (such as amphibians and vernal pools), or species such as aquatic salamanders that utilize highly oxygenated streams. Modifying the interpretation and application of this law to cover additional species with specialized habitat requirements may, however, depend on the political and economic climate in the state.

B. Habitat Fragmentation and Modification

Habitat fragmentation is the division of large patches of forest or other habitat into small, or more isolated, patches. In the strictest sense, this issue is distinct from the issue of habitat loss, and addresses the spatial distribution, configuration, and size of remnant patches.³⁷ The break up of continuous forest into small patches has the greatest effects on areasensitive species (species that require large areas of continuous habitat), species that have such strict habitat requirements that they are unable to cross gaps between fragments, and species that are intolerant of edge effects. Mountain resorts exert a unique form of fragmentation because habitat loss is not particularly severe, but fragmentation is extreme. For example, the developers of the Stowe Mountain Resort (west of Route 108) fragmented the 557 hectare forest into 123 discrete forest patches, but conducted relatively minimal forest clearing, with 77% of the original forest acreage remaining.³⁸

When we consider the effects of habitat fragmentation on wildlife populations, two components are important. First, individuals within

although it is relatively straightforward to identify current Bicknell's thrush habitat, over longer time scales, all montane fir habitat will eventually provide high quality habitat for this species.

^{37.} See RICHARD T.T. FORMAN & MICHEL GODRON, LANDSCAPE ECOLOGY 83–120 (1986).

^{38.} Allan M. Strong, Manually Digitized Interpretation of Digital Orthophotomaps (unpublished database) (on file with University of Vermont School of Natural Resources). See infra Part II.

isolated remnant habitat patches are separated from populations in adjacent patches over time. This leads to spatially-structured metapopulations: populations that are spatially separated, but linked demographically and genetically by occasional dispersal of individuals between patches.³⁹ This spatial separation of populations is of management concern because over time reduced gene flow may lead to increased inbreeding, decreased genetic heterozygosity, and decreased fitness of isolated populations.⁴⁰

The second component is the modification of the habitat along the edges of the remaining patches such that patch edges no longer provide suitable habitat for forest interior species. Scientists have long considered edge effects a significant negative consequence of habitat fragmentation because abiotic effects, such as wind and solar radiation, create light, dry microclimates along the edges of isolated patches. Research has shown that edge effects may penetrate as far as 500 meters into forest fragments, depending on the species or parameter in question. Edge effects may also affect biotic interactions, as species that are more tolerant of disturbances may find that edges provide high quality habitat. This, in turn, can change the species composition of forest fragments, often increasing species richness, but also changing the realm of biotic interactions for forest interior species.

II. SPATIAL ANALYSIS

To quantify the relative effects of habitat loss, fragmentation, and modification on wildlife populations, we measured the size and extent of the forest patches on Stowe Mountain Resort and Stratton Mountain. We used digital orthophotography available through the Vermont Mapping Program. Orthophotographs consist of a "pair of [overlapping] aerial photographs mathematically and optically corrected . . . to meet national

^{39.} Jekka Hanski & Michael Gilpin, Metapopulation Dynamics: Brief History and Conceptual Domain, 42 BIOLOGICAL J. LINNEAN SOC'Y. 3, 7 (1991).

^{40.} F. Thomas Ledig, Heterozygosity, Heterosis, and Fitness in Outbreeding Plants, in Conservation Biology: The Science of Scarcity and Diversity 77, 104 (Michael E. Soulé ed., 1986).

^{41.} Dennis A. Saunders et al., Biological Consequences of Ecosystem Fragmentation: A Review, 5 Conservation Biology 18, 20 (1991).

^{42.} Jiquan Chen et al., Vegetation Responses to Edge Environments in Old-Growth Douglas-Fir Forests, 2 ECOLOGICAL APPLICATIONS 387, 395 (1992).

^{43.} See generally Kevin R. Crooks & Michael E. Soulé, Mesopredator Release and Avifaunal Extinctions in a Fragmented System, 400 NATURE 563 (1999) (describing the decline of a predator, the coyote, its decline in a fragmented landscape, and the subsequent increase of smaller carnivores and decrease in nesting birds).

^{44.} VERMONT MAPPING PROGRAM, VERMONT DEP'T OF TAXES, at http://www.state.vt.us/tax/ Vermont%20ortho%20Program.htm (providing both online digital images and information for ordering printed images and CD-ROM's) (last visited Mar. 20, 2002).

map accuracy standards, but still have the readability of an aerial photograph." Vermont imagery is available at 1:5,000 scale with 0.5 meter pixels. Interpretation of photos is fairly straightforward, particularly when identifying ski trails and developed areas versus forested habitat. However, to keep our results conservative, we assigned areas that could not be classified unambiguously as forest.

We modeled two hypothetical species to assess the effects of forest loss and fragmentation on wildlife populations. Both species were forest generalists (present throughout all forest habitat types) with limited gap crossing abilities such that their home ranges could not extend outside a single forest fragment. We selected one species with an assigned territory of 1.0 hectare (e.g., a typical forest-dependant songbird) and a second species with an assigned 10.0 hectare territory (e.g., a small predator such as the ermine (*Mustela erminea*)). We consider these occupied areas to be territories rather than home ranges because we are assuming that once an area is occupied by an individual (or a breeding pair), the area will be unavailable to conspecifics.

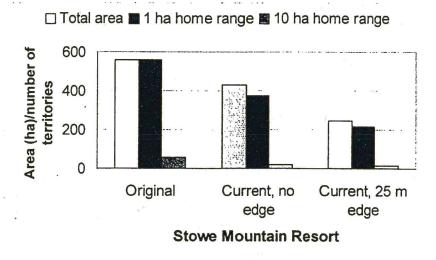


Figure 2. Effects of fragmentation and edge effects on forest area and populations of two hypothetical species with limited gap-crossing abilities on Stowe Mountain Resort. One species occupies a territory of 1.0 hectare, and the second, a territory of 10.0 hectares.

^{45.} Id.

^{46.} RICHARD M. DEGRAAF & MARIKO YAMASAKI, NEW ENGLAND WILDLIFE: HABITAT, NATURAL HISTORY, AND DISTRIBUTION 349 (2001).

We also investigated how our estimates of population size might be affected if each species were sensitive to edge effects that extend twenty-five meters into the interior of each fragment. Twenty-five meters is an underestimate of the extension of edge effects for some species (for example, the ovenbird (Seiurus aurocapillus)), but may be an overestimate for some edge-tolerant species. Consequently, the value is simply illustrative of how edge effects can further modify the impacts of forest fragmentation resulting from ski trail construction.

The results of this analysis show that the slope of Mount Mansfield (west of Route 108) occupied by Stowe Mountain Resort originally supported 557 individuals with a 1.0 hectare territory and 55 individuals with a 10.0 hectare territory (Fig. 2). These values decrease to 376 and 20 individuals, respectively, with the current levels of fragmentation. If we incorporate edge effects of 25 meters, then these values further decline to 217 and 14 individuals. This is a population decrease of 61% and 75%, respectively, compared to the mountainside in an undisturbed condition.

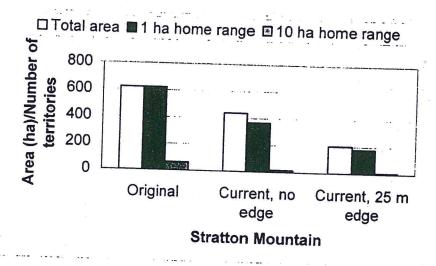


Figure 3. Effects of fragmentation and edge effects on forest area and populations of two hypothetical species with limited gap-crossing abilities on Stratton Mountain Resort. One species occupies a territory of 1.0 hectare, and the second, a territory of 10.0 hectares.

^{47.} Yvette K. Ortega & David E. Capen. Effects of Forest Roads on Habitat Quality for Ovenbirds in a Forested Landscape, 116 AUK 937, 937-38 (1999); David Flaspohler et al., Effects of Forest Edges on Ovenbird Demography in a Managed Forest Landscape, 15 Conservation Biology 173, 173 (2001).

Perhaps the most important finding is that these decreases in population size occur with only a 23% decrease in the total forest area.

The results are more extreme for Stratton Mountain. Originally, we predicted a population of 621 individuals with a 1.0 hectare territory and 62 individuals with a 10.0 hectares territory (Fig. 3). These values decrease to 367 and 17 individuals respectively, with the current levels of fragmentation. If we incorporate edge effects into the analysis, then we find a further decline to 180 and 7 individuals; respective populations decrease 70% and 89%. Compared to Stowe, Stratton Mountain has an overall greater loss of total forest area of 30%, which is a proportionally small change compared to the decline in population size.

III. SPECIES RISK ANALYSIS

The results of this spatial analysis strongly show that the percent of total forest area lost can be a misleading indicator of total habitat availability, particularly when highly fragmented. Recall, however, that this analysis is for hypothetical species that are intolerant of edge effects and have no gap crossing ability. Thus, the actual loss of habitat and subsequent decline in population size will vary depending upon a species' tolerance of these factors. Certainly, many species will be affected less severely, but ecologically sensitive species will likely be affected more drastically. Most importantly, this analysis gives us a framework by which we can better evaluate the effects of ski area development on animal populations. Modifying the parameters used in this modeling exercise is relatively simple and could allow us to address species that vary in their life history traits and their sensitivity to habitat fragmentation. For example, would our results change if a species is able to cross gaps, but only those that are less than or equal to ten meters wide? What if a species is sensitive to edges within one hundred meters of a ski trail edge? What if a species has a thirty-five hectare territory, but is able to cross gaps greater than or equal to fifty meters?

Our modeling results explicitly take into account home range size and edge sensitivity, and make an implicit assumption about a species' gap crossing ability. Although our model does include the latter parameter, if a species can cross gaps then its territory placement will be less constrained, thereby mitigating the effects of fragmentation. Of these three variables, most studies have focused on home range size because radio telemetry or mark-recapture studies can document it with ease. As our results show, species with larger home ranges, generally larger-bodied animals, will be

more sensitive to fragmentation.⁴⁸ A plethora of studies documenting the loss of large carnivores from most of North America's fragmented landscapes support this finding.⁴⁹

Certainly social behavior will mitigate the effects of home range size. Species that are strictly territorial will be more susceptible to fragmentation as conspecifics will not be tolerated within the same area. However, lack of territoriality does not necessarily make a species less susceptible to fragmentation. For example, ski area development in the western United States has negatively affected the elk (*Cervus elaphus*). Similarly, forest loss and fragmentation may negatively affect wide-ranging irruptive seed-eating birds that follow coniferous cone crops.

Edge sensitivity is more difficult to assess and has only been studied thoroughly for migratory songbirds. For most species of songbirds, edge effects can be severe because edges attract generalist predators such as raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), jays (*Cyanocitta cristata*), crows (*Corvus brachyrhynchos*), and nest parasites (for example brown-headed cowbirds (*Molothrus ater*)) that significantly reduce nesting success along forest edges.⁵² On Mount Mansfield, preliminary analyses show that open-cup nesting songbirds have significantly decreased nest success rates along ski trail edges as compared to nests farther from human-caused forest openings.⁵³ However, other factors also play a role in determining productivity.

Although studies for other taxa have been more haphazard, research on root voles (*Microtus oeconomus*) demonstrates that connectivity is critical to maintaining population processes and genetic structure in an experimentally fragmented ecosystem.⁵⁴ Dispersing juvenile amphibians

^{48.} Douglas A. Kelt & Dirk H. Van Vuren, The Ecology and Macroecology of Mammalian Home Range Area, 157 Am. NATURALIST 637, 639 (2001).

^{49.} See, e.g., Paul Beier, Determining Minimum Habitat Areas and Habitat Corridors for Cougars, 7 Conservation Biology 94 (1993); Reed F. Noss et al., Conservation Biology and Carnivore Conservation in the Rocky Mountains, 10 Conservation Biology 949, 957 (1996).

^{50.} James R. Morrison et al., *The Effects of Ski Area Expansion on Elk*, 23 WILDLIFE SOC'Y BULL. 481, 485–87 (1995) (finding a decline in elk inhabitation of ski areas).

^{51.} ROBERT ASKINS, RESTORING NORTH AMERICA'S BIRDS: LESSONS FROM LANDSCAPE ECOLOGY 103-05 (2000).

^{52.} J. Edward Gates & Leslie W. Gysel, Avian Nest Dispersion and Fledgling Success in Field-Forest Ecotones, 59 ECOLOGY 871, 875-76 (1978); David S. Wilcove, Nest Predation in Forest Tracts and the Decline of Migratory Songbirds, 66 ECOLOGY 1211, 1213 (1985).

^{53.} Kent P. McFarland & Christopher C. Rimmer, Montane Bird Nesting Database (1992–2001) (unpublished database) (on file with the Vermont Institute of Natural Science).

^{54.} Harry P. Andreassen & Rolf A. Ims, The Effects of Experimental Habitat Destruction and Patch Isolation on Space Use and Fitness Parameters in Female Root Vole Microtus oeconomus, 67 J. ANIMAL ECOLOGY 941, 950 (1998); see generally Jon Aars & Rolf A. Ims, The Effect of Habitat Corridors on Rates of Transfer and Interbreeding Between Vole Demes, 80 ECOLOGY 1648 (1999)

avoid open areas.⁵⁵ Generally, species that require humid microclimates, species that feed on leaf litter fauna or use the leaf litter for cover, and species that are sensitive to human disturbance or predation show a greater degree of edge sensitivity. For example, forest fragmentation negatively affects the ovenbird, a ground-foraging and ground-nesting migratory songbird, because of increased nest predation and parasitism rates.⁵⁶ However, ovenbirds also show avoidance of forest edges; this appears to be influenced by the abundance of insects, their primary food source, which are present in lower numbers near the dry edges of forest fragments.⁵⁷

Gap crossing ability is probably the least well-known trait affecting sensitivity to fragmentation, and most species probably show extreme variation based upon life cycle stage. Traits that make species susceptible to gaps in forest cover are strict habitat requirements, complex life cycles that entail seasonal movements between different habitat types. susceptibility to predation, limited mobility, and sensitivity to disturbance.⁵⁸ Because birds are highly mobile, they are rarely limited by gap crossing ability. However, this trait may vary throughout the annual cycle. For example, an individual Bicknell's thrush, which will cross thousands of forest gaps while migrating from Vermont to the Dominican Republic, will arrange its home range in such a way that it minimizes the number of wide ski trails it must cross during its daily foraging activities.⁵⁹ Many species of amphibians make seasonal movements from breeding ponds to terrestrial foraging sites.⁶⁰ Because these species have relatively limited rates of movement, they are susceptible to predation during these seasonal movements. The attributes of ski trail gaps probably make them less formidable obstacles than roads, suburban subdivisions, or agricultural fields. For most species, however, mortality rates will likely increase in ski trail openings when compared to travel within forested habitats.

Given these life history characteristics, we can make some preliminary predictions about which species may be susceptible to population declines

⁽describing an experimental study of the effects of corridors in 12 experimentally fragmented root vole populations).

^{55.} See, e.g., Philip G. deMaynadier & Malcolm L. Hunter, Jr., Forest Canopy Closure and Juvenile Emigration in Poolbreeding Amphibians in Maine, 63 J. WILDLIFE MGMT. 441, 446 (1999).

^{56.} Scott K. Robinson et al., Regional Forest Fragmentation and the Nesting Success of Migratory Birds, 267 SCIENCE 1987, 1989 (1995).

^{57.} Dawn M. Burke & Erica Nol, Influence of Food Abundance, Nest-Site Habitat, and Forest Fragmentation on Breeding Ovenbirds, 115 AUK 96, 101 (1998).

^{58.} GARY K. MEFFE & C. RONALD CARROLL ET AL., PRINCIPLES OF CONSERVATION BIOLOGY 291–294 (2d ed. 1997).

^{59.} McFarland & Rimmer, supra note 26.

^{60.} Kenneth C. Dodd & Brian S. Cade, Movement Patterns and the Conservation of Amphibians Breeding in Small, Temporary Wetlands, 12 CONSERVATION BIOLOGY 331, 332 (1998).

near mountain resorts based on home range size, gap-crossing ability, and edge sensitivity (Table 1). Numerous species will experience susceptibility to population declines from the development of mountain resorts due to only one aspect of their life history strategy. We have, however, limited the results in Table 1 to species that are sensitive to fragmentation through at least two of the attributes listed above.

Table 1. Species that may suffer population declines as a result of habitat fragmentation associated with mountain resorts.⁶¹

Species	Edge Sensitive	Large Homerange	Poor Gap- Crossing
Jefferson Salamander		_	Ability
(Ambystoma jeffersonianum)	X		, · X
Red-spotted Newt			
(Notophthalmus viridescens)	X		X
Northern Spring Peeper	2		
(Pseudacris crucifer)	X		X
Wood Frog (Rana sylvatica)	X		х
Northern Goshawk (Accipiter			^
gentilis)	X	X	X
Northern Saw-Whet Owl			
(Aegolius acadicus)	X	\mathbf{X}	
Barred Owl (Strix varia)	X	X	Х
Migratory Songbirds		Λ.	^
(Passeriformes)	X		X
Shrews (Sorex spp.)	X		X
Southern Red-Backed Vole	37		^
(Clethrionomys gapperi)	X		X
Woodland Jumping Mouse	34		
(Napaeozapus insignis)	X		X
Black Bear (Ursus			
americanus)		X	X
Bobcat (Lynx rufus)		. X	Х
Fisher (Martes pennanti)		X	X,
-		7.	^

Two species that appear to be at risk as a result of all three factors are the Barred Owl (Strix varia) and the Northern Goshawk (Accipiter gentilis). These two species have home ranges that are greater than 150 hectares, and they are sensitive to forest fragmentation and human disturbance. ⁶² These

^{61.} See generally DEGRAAF & YAMASAKI, supra note 46.

^{62.} John R. Squires & Richard T. Reynolds, Northern Goshawk (Accipter gentilis), in BIRDS OF NORTH AMERICA, NO. 298, at 21, 23 (Alan Poole & Frank Gill eds., 1997); Kurt M. Mazur & Paul C.

are preliminary assessments, and further research is necessary to test these species' responses to high elevation developments. More refined spatial databases with special habitat features, such as rock ledges, vernal pools, snags, or mast trees, would further enhance our risk assessments for species of concern. But, our analysis indicates that general effects of further ski trail construction can be assessed remotely, and that the effects on particular species can be modeled and predicted given some knowledge of their life history traits.

Applying the results of these modeling analyses to an actual landscape presents several difficulties. The most significant obstacle is that, in frequently-studied fragmented landscapes, the fragment of interest is nested in a matrix of dissimilar habitat (for example, forest fragments surrounded by agricultural habitat). Only a few studies have observed forest fragments within a predominantly forested landscape, 63 exactly the situation found surrounding most mountain resorts. The degree to which fragmentation alters connectivity will depend on the spatial scale of the investigation: a fragmented forest patch, a series of fragments along a ski slope, an entire mountain, or a mountain ridgeline. A forest-dwelling flightless carabid beetle may be unable to move from one forest patch to another, and consequently their populations may be rapidly extirpated from isolated forest patches within a ski area.⁶⁴ A red-backed salamander (Plethodon cinereus) might easily be able to move from one forest patch to another, but will be forced into suboptimal habitat (ski trails) to move across the landscape. In contrast, a black bear that chooses to avoid ski trails can more easily cross from one part of a ridgeline to another by simply moving around the perimeter of the resort, perhaps in a matter of hours. Because gap-crossing ability remains a poorly understood component of most species' life history, we will continue to have difficulty in assessing how these species respond to fragmentation without additional detailed studies.

IV. DISRUPTION OF ECOLOGICAL PROCESSES

It is naïve to believe that we can manage for all species simultaneously, and certainly unreasonable to try, even over relatively large landscapes.

James, Barred Owl (Strix varia). in BIRDS OF NORTH AMERICA, No. 508. at 7, 12-13 (Alan Poole & Frank Gill eds., 2000).

^{63.} See, e.g., David I. King et al., Effects of Clearcutting on Habitat Use and Reproductive Success of the Ovenbird in Forested Landscapes, 10 CONSERVATION BIOLOGY 1380, 1383-1384 (1996).

^{64.} Hank H. De Vries & Pieter L. Den Boer. Survival of Populations of Agonum ericeti Panz. (Col., Carabidae) in Relation to Fragmentation of Habitats, 40 NETHERLANDS J. ZOOLOGY 484, 486 (1990).

However, mountain ecosystems support a unique suite of species, therefore management simply for biodiversity or species richness is inappropriate in high elevation forests. In fact, biodiversity in these harsh climates may be naturally low because of the extreme environmental conditions.65 Consequently, artificial increases in biodiversity through inadvertent species introductions or anthropogenic habitat modifications may lead to population declines of habitat specialists through competition and habitat degradation. 66 Many species whose life history traits lie to the r-side of the continuum have populations that are stable or expanding as a result of human habitat modification at all elevations. Thus, increases in American robins (Turdus migratorius) or indigo buntings (Passerina cyanea) on a ski area may increase the total number of species present, but should not be interpreted as an overall increase in habitat quality. In fact, the increase in these generalist species could be construed as an indication of declining habitat quality for many species through the modification of ecological Furthermore, increases in species with general habitat processes. requirements will probably bring an increase in generalist predators and parasites. Research has shown that the increase in these species has negative effects on high elevation species nesting in European ski areas.67 This results primarily from direct habitat modification, and indirect effects, such as increased food waste, that attracts nest predators such as gulls (Larus) and corvids to areas in which they had not previously been present.

White-tailed deer (Oidocileus virginianus) are "keystone herbivores" in forested ecosystems, in that their consumption of plant material affects the structure of the forest to such a degree that the abundances of other species are affected.⁶⁸ The composition of the landscape around mountain resorts is such that we have created excellent habitat for white-tailed deer, with forested habitat punctuated by ski trail openings. Increased white-tailed

^{65.} John G. Blake & Bette A. Loiselle, Diversity of Birds Along an Elevational Gradient in the Cordillera Central, Costa Rica, 117 AUK 663, 663 (2000) (noting that "[d]eclines in bird-species richness with elevation are common); Erica Fleishman, et al., An Empirical Test of Rapoport's Rule: Elevational Gradients in Montane Butterfly Communities, 79 ECOLOGY 2482 (1998). "Monotonic declines in species richness with increasing elevation have been documented in both temperate and tropical regions for [a variety of species]." Id. at 2489.

^{66.} Robert A. Garrott et al.. Overabundance: An Issue for Conservation Biologists, 7 CONSERVATION BIOLOGY 946, 946 (1993).

^{67.} See Adam Watson, Bird and Mammal Numbers in Relation to Human Impacts at Ski Lifts on Scottish Hills, 16 J. APPLIED ECOLOGY 753, 759, 763 (1979); Roy Dennis, Birds and Conservation Problems of the High Tops, 4 ROYAL SOC'Y PROT. BIRDS CONSERVATION REV. 48, 50-51 (1990) (asserting that development of ski areas has brought increased visitor use to the Scottish Highlands negatively impacting bird habitat).

^{68.} Donald M. Waller & William S. Alverson, The White-Tailed Deer: A Keystone Herbivore. 25 WILDLIFE SOC'Y BULL. 217 (1997).

deer populations negatively affect forest songbird populations through their effect on vegetation structure.⁶⁹ The impact of white-tailed deer on forest songbird populations could conceivably have additional ecosystem effects. Recent research has shown that songbirds can indirectly affect forest growth rates through their consumption of herbivorous insects.⁷⁰ Thus, as songbird populations decline, herbivorous insect populations increase, and biomass production by understory trees and shrubs further decreases. Therefore, additional fragmentation could negatively affect forest productivity.

At the landscape level, an important consideration regarding the degree to which a mountain resort contributes to ecosystem function is the resulting infrastructure in the surrounding community at the base of the mountain. To what degree is the construction of new hotels, bed and breakfasts, restaurants, condominiums, gas stations, convenience stores, golf courses, and gift shops generated as a result of the resort clientele? Further, what effect does this secondary development have on landscapelevel processes? One effect of these associated businesses is the creation of habitat that is suitable for synanthropic species, which can have negative consequences for native wildlife. Eurasian starlings (Sturnus vulgaris) and house sparrows (Passer domesticus) are generally not found far from human habitation and outcompete native species for nest cavities. 71 Brownheaded cowbirds are nest parasites and have been implicated in the declines of forest nesting songbirds, particularly in the midwestern United States.⁷² Their populations have been increasing in the eastern United States⁷³ and although they do not settle at high elevations, grassy slopes at low elevations provide suitable habitat that, if not currently occupied, may be in the future. Other species attracted to refuse associated with human habitat, such as American crows, raccoons, skunks, and gulls, are all avian nest predators and may reach artificially high densities in human-modified habitats.74 A related concern is the habituation of bears to human refuse, which continues to hinder grizzly bear (Ursus arctos horribilis) recovery in

^{69.} David S. deCalesta, Effect of White-Tailed Deer on Songbirds Within Managed Forests in Pennsylvania, 58 J. WILDLIFE MGMT. 711, 715 (1999) (finding negative effect on intermediate canopynesting songbirds, but no effect on upper canopynesting or ground-nesting songbirds).

^{70.} Robert J. Marquis & Christopher Whelan, Insectivorous Birds Increase Growth of White Oak through Consumption of Leaf-Chewing Insects, 75 ECOLOGY 2007, 2012 (1994).

^{71.} Patricia A. Gowaty & Jonathan H. Pilsner, Eastern Bluebird (Sialia sialis), in THE BIRDS OF NORTH AMERICA No. 381, at 24 (Alan Poole & Frank Gill eds., 1998).

^{72.} Robinson, supra note 56, at 1987.

^{73.} Margaret Clark Brittingham & Stanley A. Temple, Have Cowbirds Caused Forest Songbirds to Decline?, 33 BIOSCIENCE 31, 31 (1983).

^{74.} JOHN W. TERBORGH, WHERE HAVE ALL THE BIRDS GONE? 49-51, 67 (1989).

the Rocky Mountain range, 75 because bears that threaten human safety are quickly removed from the population.76 Thus, secondary effects of mountain resorts will likely continue to have substantial impacts on wildlife

One of the challenges of a legal approach to maintaining the ecological integrity of a mountain resort area is that we have a limited understanding of how individual species contribute to ecosystem processes such as predation, herbivory, or competition. As Aldo Leopold noted with his usual foresight, "to keep every cog and wheel is the first precaution of intelligent tinkering."77 As of yet though, we have no legal mechanism to maintain constant levels of herbivory or to keep nest predation at historic levels.

VI. CUMULATIVE EFFECTS OF DEVELOPMENT

Perhaps one of the most important issues regarding development in and around mountain resorts is that of the cumulative effects of development. Habitat fragmentation occurs in a landscape context, such that ski trail construction is not simply a loss of 1.0 or 2.0 hectares, but adds to the current amount of habitat that has already been altered, a factor not currently considered in development permits.78 The behavioral properties of ecosystems have been studied by modeling random landscapes, which have led to some useful theoretical results, some of which have been supported through empirical studies.⁷⁹ Modeling results indicate that when a landscape is fragmented to the point at which less than 58% remains forested, then the landscape no longer percolates or retains connectivity.80

This result implies that there is a threshold at which the landscape will no longer be perceived as connected for at least certain species. This "percolation threshold" will vary depending upon the species' home range size, its ability to cross habitat gaps, and its tolerance of habitat edges.⁸¹

^{75.} Matthew M. Reid & Richard Meis, Ski Yellowstone and Grizzlies: A Case Study of Conflict, WESTERN WILDLANDS, Winter 1985, 5, at 6.

^{76.} Id. at 6.

^{77.} ALDO LEOPOLD, ROUND RIVER: FROM THE JOURNALS OF ALDO LEOPOLD 147 (Luna Leopold ed., 1953).

^{78.} Act 250, VT. STAT. ANN. tit. 10, § 6086 (2001).

^{79.} See generally Therese M. Donovan & Allan M. Strong, Linkages Between Theory and Population Dynamics: A Review of Empirical Evidence, in LANDSCAPE THEORY AND RESOURCE MANAGEMENT: MAKING THE MATCH (John A. Bissonnette ed., 2002).

^{80.} Robert H. Gardner et al., Neutral Models for the Analysis of Broad-Scale Landscape Pattern, I LANDSCAPE ECOLOGY 19, 25-27 (1987).

^{81.} See generally Kimberly A. With, Is Landscape Connectivity Necessary and Sufficient for Wildlife Management?, in FOREST FRAGMENTATION: WILDLIFE AND MANAGEMENT IMPLICATIONS 97 (Rochell et al. eds., 1999) (discussing a study of species' perceptions of landscape connectivity in forests with different levels of fragmentation).

Evidence of threshold effects on distribution come primarily from largescale studies or meta-analyses where regional differences in habitat cover vary widely. For instance, Rosenberg studied the occurrence of scarlet tanagers (Piranga olivacea) across North America, and found that "sensitivity to fragmentation varies geographically and may be lower in regions with greater overall forest cover."82 Similarly, Andrén reviewed studies on birds and mammals in habitat patches in landscapes with different proportions of suitable habitat.83 He concluded that patch size and isolation are not important when landscapes consist of greater than 30% habitat, but that in landscapes with less than 30% habitat, patch size and isolation complement the effect of habitat loss so that the effect is greater than habitat loss alone.84 The existence of these thresholds suggests that the loss of an additional few hectares may have dramatic effects on ecosystem function. These thresholds will be greater for species that have large home ranges, poor gap-crossing abilities and are intolerant of habitat edges, such that fragmented landscapes will deteriorate faster for species with those life history traits.

Our own modeling results indicate that at least for Stowe Mountain Resort and Stratton Mountain, the landscapes are well above current predicted thresholds at which percolation no longer exists. However, as discussed above, landscapes surrounding ski areas are not fragmented randomly but are designed to maximize habitat fragmentation. Consequently, in these unique landscapes, additional studies will be required to evaluate what the effects of relatively small incremental habitat losses will be on populations of species of management concern.

Is it possible for us to assess how much development can be permitted before having adverse effects on wildlife populations? One means of evaluating these effects is by using population viability analysis (PVA). This method seeks to determine what the effects of a management practice might be on population persistence through some predetermined length of time. Using PVA allows managers to determine the particular stages in a species' life cycle that make it vulnerable to extinction and how this might be exacerbated by a particular management action. For example, a proposed ski trail cuts through an area that supports two nesting female

^{82.} Kenneth V. Rosenberg et al., Effects of Forest Fragmentation on Breeding Tanagers: A Continental Perspective, 13 CONSERVATION BIOLOGY 568, 568 (1999).

^{83.} Henrik Andren, Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review, 71 OIKOS 355 (1994).

^{84.} Id. at 362

^{85.} See generally Mark S. Boyce, Population Viability Analysis, 23 ANN. REV. ECOLOGY & SYSTEMATICS 481 (1992).

^{86.} Id.

Bicknell's thrush. Will the decrease in nesting habitat affect the viability of the population on the mountain, or in the region, or across its range? A PVA would examine the current temporal variation in population size and extrapolate that variance, incorporating the loss of two females. Thus, at least in theory, the analysis could help determine whether the risk of population persistence would be exacerbated by declines in carrying capacity on the breeding grounds.

Although this appears to be a useful means of determining the effects of habitat loss or modification on the population of a species of concern, a substantial amount of information is necessary to produce PVA's that have reasonably narrow confidence intervals. Consequently, one of the questions that will arise is who should pay for data collection and the PVA? Should the burden of proof be on persons with economic interests, ecological concerns, or impartial third parties? More contentious discussions will probably result from the interpretation of such analyses. Even if sufficient data were available to conduct a rigorous PVA, how would we address the results? Is a ten percent increase in the probability that a species will be extirpated from a mountain in the next one hundred years an acceptable risk; one that we can live with given the economic and recreational benefits of mountain resorts to society? These are difficult issues and resolution can come only through dialogue among stakeholders.

V. MANAGEMENT RECOMMENDATIONS

Fragmentation on ski areas may be addressed through the design and management of ski trails and the management of skier traffic across the mountain. Below, we suggest several management recommendations that we believe would minimize the impacts of ski area expansion on wildlife habitat. Most importantly, ski trails should be located to minimize the creation of new forest islands and to avoid cutting through large patches of intact habitat. In situations where one or more islands can be combined into a single, larger island, habitat will be improved for forest interior species.

Buffering of edge effects is possible by managing vegetation to create a "feathered" edge along ski trails, gradually decreasing vegetation height from the forest interior to the trail edge. For Bicknell's thrush (and other passerines found at high elevations), vegetation management is warranted mainly in areas where the adjacent forest is conifer dominated and characterized by a high stem density in the understory, often forming a dense thicket. Taller trees (greater than 5 meters in height) may be present, but these are often damaged by wind, ice, and/or insects and do not form a complete canopy, thus promoting understory growth. In these areas, which

may include only one (usually the wind-exposed) side of a ski trail, low firspruce can be allowed to extend along the edge outward for 6-7 meters (or wider) at heights of 0.3-1.0 meters (or higher). An attempt should be made to gradually decrease tree height from the forest to the grassy trail edge. When these areas are cut back, woody vegetation should be maintained at heights of 0.3 meters or more. This management practice maintains a wider ecotone of dense vegetation, creating more habitat for nesting birds while decreasing the ease of search for predators that use edge habitats.

Buffer zones should also be created around streams to maintain the integrity of habitat and water quality. Although this may be difficult within ski trails, recent advances in stream restoration⁸⁷ may suggest suitable plant species that provide adequate cover and erosion protection without the subsequent structure that interferes with ski trail maintenance. Care must be taken, however, not to introduce aggressive exotics that may preserve stream quality at the expense of native species.

To minimize adverse impacts to Bicknell's thrush and other forestnesting birds, existing gladed trails in suitable habitat should be kept as narrow as possible. Patches of low, dense balsam fir should be left intact or minimally altered, while still allowing the trails to function for their intended recreational purpose. Annual maintenance should ensure that some tree saplings are retained so there is continual recruitment to older age classes. This will help to prevent tree mortality events that could cause the longer-term conversion of gladed trails to completely open trails, degrading special habitat features such as low dense vegetation, vernal pools, or rock ledges.

Concerted efforts should also be made to prohibit any unauthorized gladed trail establishment or maintenance, or unauthorized habitat alteration (cutting) of any kind. The proliferation of trails illicitly cut by recreational, off-trail skiers, and recently documented on some Vermont ski areas, must be actively discouraged.

In instances of habitat removal or alteration for ski trail establishment or expansion, we would recommend a minimum one-to-one mitigation process, such that an area of currently developed habitat equal to (or greater than) that to be altered will be actively restored or passively allowed to recover to conditions suitable for occupancy by wildlife. Further, the timing of vegetation management (including mowing) in areas of high elevation songbird breeding habitat is important and should be delayed until after August first, when the majority of nesting activities are complete.

^{87.} See generally Catherine Kashanski, Vt. Agency of Natural Res., Native Vegetation for Lakeshores, Streamsides and Wetland Buffers (1994).

Disturbance of any kind around key mast areas should be entirely eliminated during the late summer and fall.

VII. THE IMPACT OF SOCIETAL BIASES AND ECONOMIC PRACTICES

Other issues, that are ethical in nature, come into play as well, especially when the charismatic appeal of certain species is taken into account. For example, there may be widespread support for the creation of buffer zones to minimize disturbance to black bears in key mast areas and moderate support for conservation of high elevation Bicknell's thrush habitat. However, societal support may be minimal for preservation of salamander habitat, and nearly nonexistent for ground beetle habitat conservation. As interest and funding levels are often minimal for nongame wildlife management, the best-case scenario might be to integrate the management of keystone species (species whose population or ecological role affects the abundance of numerous other species) or indicator species (species whose presence signifies some measure of habitat quality) into the management of mountain resorts. No matter how strong the supporting scientific evidence, societal values will need to be incorporated into habitat management plans. Consensus will be reached far more easily on charismatic species than on species for which there is little perceived value to society.

One of the ways that ecologists have begun to try to put wildlife and ecosystems on equal footing is to evaluate the economic value that they provide, either through the generation of tourism dollars or through ecosystem services. Although this field is in its infancy, data suggest that these values are anything but trivial. For example, national hunting expenditures were estimated to generate \$20.6 billion in 1996, at least some proportion of which was directly or indirectly returned to local economies. Wildlife watching has also been estimated to provide substantial returns to local economies (greater than \$18 billion per year), with birdwatching generating over 25% of the total. In areas in which there are rare or endemic species, dollars generated for the local economy can be substantial.

^{88.} U.S. FISH & WILDLIFE SERV., U.S. DEP'T OF INTERIOR & BUREAU OF THE CENSUS, U.S. DEP'T OF COMMERCE, 1996 NATIONAL SURVEY OF FISHING, HUNTING, AND WILDLIFE-ASSOCIATED RECREATION, Nov. 1997, at 45, http://www.census.gov/prod/3/97pubs/fhw96nat.pdf.

^{89.} See Curtis H. Freese & David L. Trauger, Wildlife Markets and Biodiversity Conservation in North America, 28 WILDLIFE SOC'Y BULL. 42, 48 (2000).

90. Id.

The benefits that ecosystems provide to humans through nutrient cycling, regulation of disturbances, waste treatment, food production, recreation and other services have been estimated at over \$33 trillion per year. Although the tools that we are using to estimate these services are still being developed, the total estimate in 1997 dollars was 1.8 times greater than the world's gross national product, suggesting that it would be impossible for the world's economies to accurately account for ecosystem goods and services. But, applied to the conservation of biodiversity, some authors have argued that species may still be driven to extinction through optimal behavior in a traditional economic market. 93

In contrast, ecological economics argues that we should limit market substitutions (for example, substituting aquatic systems for aquaculture), maintain minimum stocks of natural capital, and preserve ecosystem function. In this way, the values that ecosystems provide to humans would be explicitly taken into consideration in plans for development of natural areas. At this time, economic incentives are insufficient to favor a shift from a traditional economic paradigm to an ecological economic system. Until the time when we can realistically assess the current impact of human actions on wildlife and their habitat, we will continue to rely on a legal framework that protects the few charismatic species which society deems to have inherent value.

Can a shift in societal values come from within the resort industry and its clientele? Although we frequently look to land managers, biologists, and planners to provide best management practices for these sites, management recommendations are necessarily given in the context of what society deems to be acceptable or appropriate uses. Thus, no matter what the scientific evidence for the persistence of a population, or the healthy functioning of an ecosystem, societal values must be entered into the equation. These demands and decisions will to a large part be dependent upon the information users are given. Assuming price, quality of experience, and ease of access to be equal, we would expect most skiers to prefer to use mountain resorts that leave the least ecologically damaging footprint. However, the way in which these footprints are measured must be standardized so that resort users have the necessary information to make informed decisions. For example, if regional ski reports stated the number

^{91.} Robert Costanza et al., The Value of the World's Ecosystem Services and Natural Capital, 387 NATURE 253, 259 (1997).

^{92.} Id.

^{93.} Colin W. Clark, Profit Maximization and the Extinction of Animal Species, 81 J. Pol. ECON. 950, 950-51 (1973).

^{94.} See generally ROBERT COSTANZA ET AL., AN INTRODUCTION TO ECOLOGICAL ECONOMICS (1997).

of trails open, snow depth, lift ticket price, and a "green index" rating, skiers could use this information to weigh resort land and energy use policies against cost and ski experience. EPA's Sustainable Slopes program was a first step toward this goal, but with no current Federal support for the program and no consistent measurement protocol across resorts, the indices generated will probably be of limited value to resort users. 95

Much of the quality of the ski experience is related to the scenery associated with high elevation ecosystems. As such, mountain resorts have a vested interest in maintaining the quality of these areas. Unfortunately, habitat loss, modification, and fragmentation and their effects on wildlife populations may not be readily apparent to skiers. Armed with information about the ecological impacts of the resort, economic pressures may allow resort users to indirectly effect land use changes that have positive impacts upon wildlife populations.

SUMMARY AND CONCLUSION

The effects of mountain resorts on wildlife habitat and wildlife populations have been poorly studied, despite widespread concern over the ecological effects of development and habitat modification in high elevation ecosystems. Habitat loss, habitat modification, and habitat fragmentation are the three primary means by which mountain resorts affect wildlife populations. Habitat loss will have the greatest effect on species with specialized habitat requirements. For example, Bicknell's thrush (Catharus bicknelli) are restricted by habitat structure and elevation, aquatic salamanders by stream quality, and black bears (Ursus americanus) by loss of key mast areas. The effects of habitat fragmentation are most severe for species that have large area requirements, poor gap-crossing ability, and are intolerant of edge effects.

Our spatial analysis of development at the Stowe and Stratton ski areas suggests that under current management scenarios, populations have theoretically declined by a range of 32% to 41% for species with approximately 1.0 hectare territories, whereas for species with approximately 10.0 hectares territories population declines ranged from 64% to 73%. For a species with a 10.0 hectares territory, edge sensitivity of 25 meters could increase population declines from 75% to 89%. The results of our spatial analysis suggest that species such as Barred Owls (Strix

^{95.} Assessment and Watershed Prot. Division, Office of Wetlands, Oceans & Water, U.S. Envtl. Prot. Agency, Notes on Watershed Management: Ski Resorts Pledge to Protect the Environment, NONPOINT NEWS-NOTES, Dec. 2000, 1, at 23, at http://www.epa.gov/owow/info/NewsNotes/issue 63/63_issue.pdf.

varia) and Northern Goshawks (Accipiter gentilis) may be particularly vulnerable to fragmentation on ski areas because multiple components of their life history make them vulnerable to development on mountain resorts. Other species may be vulnerable to mountain development as well.

Life history traits such as complex life cycles, susceptibility to predation, limited mobility, sensitivity to disturbance, use of humid microclimates, and dependency on leaf litter fauna will also increase species risk. As a fragmenting mechanism, ski trails are relatively benign in comparison to roads, agricultural fields, and urban development. However, most resorts maximize recreational benefits by dispersing trails across the mountain slope, thereby greatly increasing forest fragmentation. Consequently, management practices that minimize disturbance, edge effects, and additional fragmentation will have the fewest negative effects on wildlife populations.

One of the primary concerns regarding high elevation development is the failure to account for long-term cumulative effects of development. Percolation theory predicts that small changes in the amount of forest clearing can have significant impacts on habitat connectivity. Additional losses of 1.0 or 2.0 hectares may cause abrupt declines in habitat quality for a particular species. Cumulative effects of habitat loss can be modeled through existing spatial databases and should be explicitly considered in the planning process for developments in and around mountain resorts. Unfortunately, existing legal and regulatory mechanisms provide little recognition of the importance of key ecological processes (e.g., predation, competition, or herbivory). Therefore, our current species-based approach to conservation may limit our ability to maintain these processes, which are integral to protecting wildlife and their habitat.