Demography and Ecology of Montane Forest Bird Populations in the Green Mountains of Vermont
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INTRODUCTION

"… only a freak ornithologist would think of leaving the trails [on Mt. Mansfield] for more than a few feet. The discouragingly dense tangles in which Bicknell's Thrushes dwell have kept their habits long wrapped in mystery" (Wallace 1939).

Bicknell's Thrush *(Catharus bicknelli)*, recognized as a subspecies of the Gray-cheeked Thrush *(Catharus minimus)* since its discovery in 1881 on Slide Mountain in the Catskills of New York, has recently been given full species status (AOU 1995). Significant differences between the two taxa in morphology, vocalizations, genetics, and breeding and wintering distributions contributed to this designation (Ouellet 1993). This classification has led to the recognition of Bicknell's Thrush as one of the most at-risk passerine species in eastern North America. Rosenberg and Wells (1995) ranked Bicknell's Thrush as number one on a conservation priority list of Neotropical migrant birds in the Northeast. The species has been accorded "vulnerable" status in Canada (Nixon 1999) and is also proposed for "vulnerable" status by BirdLife International for the IUCN 2000 Red List (to be published in October 2000).

The breeding range of Bicknell's Thrush in the United States is limited to subalpine spruce-fir forests of New England and New York (Atwood et al. 1996). In Canada it is found in highland spruce-fir forests in Quebec, Nova Scotia and New Brunswick (Erskine 1992, Ouellet 1993, Gauthier and Aubry 1995). It has also been found in mixed second-growth forest following clear cutting or burning in Quebec (Ouellet 1993) and New Brunswick (Nixon 1996, D. Busby, pers. comm.). As the only breeding songbird endemic to high elevation and maritime spruce-fir forests of the northeastern United States and adjacent Canada, Bicknell's Thrush qualifies as a potentially valuable indicator of the health of montane avian populations and their associated forest habitat. Research aimed at clarifying the distribution, ecology and population status of Bicknell's Thrush in the Northeast have been underway since 1992 (e.g., Atwood et al. 1996, McFarland and Rimmer 1996, Rimmer et al. 1996); similar studies are in progress in New Brunswick (Nixon 1996), Nova Scotia (D. Busby pers. comm.), and Quebec (Rompré et al. 1997).

Decline of high elevation forests in the northeastern U.S. during 1960s and 1970s is a well documented phenomenon (Johnson and Siccama 1983, Eager and Adams 1992). Red spruce (Picea rubra) dieback has been especially pronounced, but mortality of balsam fir (Abies balsamea) has also been extensive and widespread (Miller-Weeks and Smoronk 1993), although most of this has resulted from naturally-occurring fir waves. Atmospheric deposition of acidic ions from industrial sulfur and nitrogen oxides has been strongly, although not conclusively, implicated as a causal factor in red spruce decline (Johnson et al. 1992). Increased winter freezing injury of spruce, possibly mediated through reductions in calcium reserves, may be directly linked to high levels of acidic deposition (DeHayes et al. 1999). Despite declining trends in atmospheric sulfate concentrations resulting from mandates of the 1990 Clean Air Act amend**ments,** acidity

of precipitation in northeastern North America does not appear to be decreasing (Scherbatskoy et al. 1999). Heavy metal toxicity from airborne pollutants has also been implicated as a contributing cause of high elevation forest decline in the northeastern U.S., particularly in the Adirondack and Green Mountains (Gawel et al. 1996), although several recent studies indicate that lead concentrations in the forest floor are rapidly decreasing (Friedland et al. 1992, Miller and Friedland 1994, Wang and Benoit 1997). These documented problems, combined with potential loss of habitat to global climate change (Prasad and Iverson 1999), other atmospheric pollutants (i.e., mercury), ski area development, telecommunication tower construction, and proposed wind power facilities make this restricted habitat one of the most vulnerable in eastern North America.

Many important questions about the ecology and stability of Bicknell's Thrush breeding populations require intensive monitoring of discrete habitat units and studies of known-identity individuals. Baseline data on population densities, territory size, movements, productivity, site fidelity, survivorship, habitat use, and the effects of human activities are needed to evaluate the conservation status of the species across its naturally fragmented, high elevation breeding range. This report summarizes breeding season field studies conducted by the Vermont Institute of Natural Science (VINS) during 1999, in an effort to investigate the effects of ski area-related activities on Bicknell's Thrush and other montane forest birds. Data collected since 1992 are incorporated into many of the analyses presented here.

METHODS

Study areas and focal species.— Bicknell's Thrush (BITH) and Blackpoll Warbler *(Dendroica striata*; BLPW*)* were selected as focal study species because: 1) Bicknell's Thrush is restricted to montane forests and Blackpoll Warbler is a near-obligate resident of this habitat in the Northeast (Atwood et al. 1996, Hunt and Eliason 1999); 2) Bicknell's Thrush has been ranked as the top conservation priority species in the Northeast (Rosenberg and Wells 1995); and 3) these two species and other montane forest breeding birds may be good ecological indicators of the health of this vulnerable habitat. Our intensive study sites were located in Vermont on Mount Mansfield (44º 32' N, 72º 49'W) and Stratton Mountain (43° 05N, 72° 55'W) at 900-1200m. The vegetation at both sites is dominated by balsam fir and white birch (*Betula papyrifera* var. *cordifolia*) and is described in detail by Wallace (1939). Our study sites encompassed areas extensively altered by ski trail development as well as unmanaged natural areas. Focal species nested in both unaltered and altered habitat on each mountain.

Long-term Population Monitoring.— Twelve sites are annually surveyed as part of our long-term population monitoring program (Table 1). At each site, 5 point counts (stations) were established at least 100 m from the nearest forest edge and 200 m apart. Each station was clearly marked and labeled with survey flagging and an aluminum tree tag. Because of park rules in Maine, points were not physically marked but were situated at sites with obvious natural markers and described in detail so as to be easily relocated.

Surveys were conducted by VINS staff biologists and volunteers. Volunteer observers were encouraged to participate in the project if they possessed a high degree of competency in both aural and visual bird identification, and could make a multi-year commitment. Survey methods consisted of unlimited distance point counts, based on the approach described by Blondel et al. (1981) and used in Ontario (Welsh 1995). The count procedure was as follows:

1) Counts began shortly after dawn on days when weather conditions were unlikely to reduce count numbers (i.e., calm winds and very light or no rain). Censusing began shortly (<1 min.) after arriving at a station.

2) Observers recorded all birds seen and heard during a 10-min sampling period, which was divided into 3 time intervals: 3, 2, and 5 mins. Observers noted in which time interval each bird was first encountered and were careful to record individuals only once. To reduce duplicate records, individual birds were mapped on standardized field cards, and known or presumed movements were noted. Different symbols were used to record the status of birds encountered (i.e., singing male, pair observed, calling bird, etc.).
3) Each site was sampled twice during the breeding season (except Maine due to remote locations): once during early June (ca. 1-15 June) and once during late June to early July (ca. 16 June-7 July). Observers were encouraged to space their visits at least 7-10 days apart. For each site visit, all stations were censused in a single morning and in the same sequence.

In preparing the data for population trend and power analyses, we used the higher of the 2 values recorded for each species as the station estimate for each year. Due to differences in the ability of observers to census birds, which can result in biased trend estimates (Sauer et al. 1994), only data from the same observer in consecutive years at the same site were used for trend estimates. To improve the comparability of observations at sites that experienced observer changes, data were divided into subsets corresponding to different observers. Since trends cannot be calculated from subsets of a single year, data were discarded from trend analyses if an observer surveyed a site for only one year. Kendall et al. (1996) recommended that count data from an observer's first year be removed from trend analyses due to a novice effect, which was shown to bias Breeding Bird Survey (BBS) trend results. We chose not to eliminate these data for our analyses in order to avoid further reducing sample sizes. For trend analyses, we used the estimating equations program (ESTEQN), which was generously provided by the Canadian Wildlife Service and was used to produce trend analyses for both the Ontario Forest Bird Monitoring Program and the BBS in Canada (Collins 1997). This program derives an estimate of an overall population trend as a weighted average of the trend seen on individual sites. The approach and methods behind this estimation technique are fully described in Link and Sauer (1994).

We conducted power analyses of the data for 4 species over 4 different time periods using Monitor 6.2 software (Gibbs 1995) specifically designed to estimate the statistical power of population monitoring programs to detect trends. Because the sample size required for statistical significance can be dramatically affected by the magnitude of change and the variance patterns of individual species (Welsh 1995), we calculated power using 4 species with different sample sizes and variability.

Capture-Mark-Recapture.— We used strategically placed mist nets in combination with tape recorded playbacks of Bicknell's Thrush vocalizations to attempt to capture and color band Bicknell's Thrushes. Up to 30 mist nets were used simultaneously to passively capture thrushes as a complement to the use of vocal lures. All passively captured Blackpoll Warblers were color banded. Detailed mensural (e.g., wing chord, weight, tarsus, culmen) and body condition (e.g., subcutaneous fat, molt, feather wear) data were recorded for all captured birds. Age and sex were determined using skull ossification, cloacal protuberance and brood patch (Pyle 1997). We aged Bicknell's Thrushes by outer rectrix shape (Collier and Wallace 1989) and/or the presence of terminal buffy streaks or spots on any greater coverts (Pyle 1997). Each individual was banded with a numbered aluminum band and three color bands to uniquely identify birds for resighting and videography. Both species were opportunistically resighted on study plots during the breeding season, although the secretive nature and occupancy of dense understory vegetation by Bicknell's Thrushes yielded few resights.

Survivorship was estimated and compared using methods described in Lebreton et al. (1992) and Cooch and White (1998) using the program MARK (White and Burnham 1999). We defined a candidate model set that included a fully parameterized global model and all reduced parameter models derived from

the global model for a total of 16 models. Because we used only individuals that were 3 or more years old (ASY) we did not test for age differences. However, we did include sex differences in the global model. For our global model we used sex x time-dependence for both survival and capture estimates. Model notation followed Lebreton et al. (1992). The factorial structure of the models was represented by subscripting the primary parameters survivorship (F) and recapture (*P*) with "g" for sex effects and "t" for time effects. The goodness-of-fit (GOF) of the global model to the data was determined using a parametric bootstrap approach testing 1,000 bootstrap samples. We calculated a quasi-likelihood parameter to adjust for overdispersion in the data by dividing the global model deviance by the mean deviance of the bootstrap GOF samples to calculate the quasi Akaike Information Criteria (QAIC). The model with the lowest QAIC was accepted as the most parsimonious model for the data. Model comparisons within the candidate set were done by deriving an index of plausibility using normalized Akaike weights (Burnham and Anderson 1998). The ratio between weights of any two models indicates the relative degree to which a particular model is better supported by the data. To account for uncertainty in model selection we also report mean parameter estimates and associated standard errors from averaging over all models in the candidate set, weighted by Akaike model weights (Burnham and Anderson 1998, Bertram et al. 2000).

Radio Telemetry. -We placed miniature radio transmitters on Bicknell's Thrush adults on Stratton (1997-1999) and Mansfield (1998-1999). We used radio transmitters from two different manufacturers. All transmitters in 1997 and most (84%) in 1998 were from Wildlife Materials (model SOPB-2012) and weighed 0.9 grams with a battery life of 23 days. Some transmitters in 1998 (16%) and all in 1999 were made by Holohil Systems (model BD-2) and weighed 1.0 grams with a battery life of 60 days. In 1997 and 1998 we attached transmitters to the base of the two central rectrices using dental floss and super glue (Aborn and Moore 1997). Because of an unacceptable rate of transmitter loss in 1998 and the increased battery life available to us in 1999, we attached transmitters using a harness design (Rappole and Tipton 1991). We detected no obvious effects on behavior of radio-tagged birds (see Powell et al. 1998), but we were unable to test this directly via time budgets or movements, due to the species' secretive nature and the dense vegetation and rugged terrain on our study plots.

We relocated radio-tagged individuals with Wildlife Materials TXR-1000 receivers and 3-element, hand-held Yagi antennas using homing or triangulation techniques (White and Garrott 1992). Homing locations were determined by identifying vocalizing birds, quietly approaching individuals to pinpoint locations visually, or by circling the signal area in small habitat islands while walking the surrounding grassy ski trails. Locations were mapped in the field on detailed maps of the study areas, and observers ranked point accuracy on a scale of 0-3 (0=exact, 1=~10m, 2= ~25m, 3= ~50m radius).

Triangulation data were analyzed using LOAS 1.0 software (Ecological Software Solutions 2000). Field tests of bearings to transmitters resulted in a standard deviation of 20^0 which we used to estimate point locations. Transmitter locations with 3 or more bearings were estimated with Maximum Likelihood Estimator (MLE; Lenth 1981) with a 95% confidence ellipse estimated using chi squared method. We used best biangulation when MLE failed or there were only 2 bearings. Best biangulation calculates all intra-bearing angles and selects the bearings whose angles are closest to 90^0 and calculates an error polygon using our 15^0 bearing standard deviation (Ecological Software Solutions 2000).

Nest monitoring and provisioning. -Nests were located by systematic searches, by following radio tagged females during incubation (BITH only), and by observing parental behavior. The chronology and status of all active nests were monitored every 1 to 4 days by checking nest contents, either directly or remotely via binoculars, or by radio telemetry monitoring of females (BITH only). Nest monitoring and vegetation data collection were generally conducted according to guidelines established by the Breeding Biology Research and Monitoring Database Program (BBIRD; Martin and Geupel 1993, Martin et al.

1997).

Because most nests were found after the onset of incubation, nest initiation (day first egg was laid) was calculated from known changes in nesting period (hatching or fledging), assuming one egg per day was laid, and from average values for incubation and fledging periods. When a nest failed during incubation, we calculated the first day of incubation as: date found – ([incubation period – observation days]/2). Nests that fledged at least one young were considered successful.

We evaluated nest success of Bicknell's Thrush and Blackpoll Warbler using Mayfield estimates (Mayfield 1961, 1975) as modified by Johnson (1979) and Hensler and Nichols (1981). Half the number of days between subsequent visits over which a nest was depredated was added to the number of previous days the nest survived to obtain the total number of days the nest survived. We excluded all nests whose status was unknown or undetermined, as well as any nests that we felt may have failed due to research activities. We compared survival probabilities between years and between ski areas and natural areas using CONTRAST (Sauer and Williams 1989). We have not yet calculated Mayfield estimates for additional species monitored.

In 1997 we constructed crude blinds at six Bicknell's Thrush nests to observe adult feeders for a total of 57.4 hours. We did not use these data for chick provisioning analyses because it appeared that some adult behavior was compromised by our presence in the blinds. In 1998 and 1999, nests were videotaped during the nestling stage using a Sony CCD-TR516 Hi-8 Handycam. The camera was mounted on a tripod or a nearby treetop 3-5 m from the nest and usually concealed with camouflage mesh. We taped 96 sessions (one session = 2-4 hours) for a total of 288.8 hours of video tape at 21 nests. Recordings were transferred to VHS video tapes and reviewed on a Sony SLV-679HF video cassette recorder. All tapes were analyzed by one observer (Marc Pickering) who identified adults feeding chicks by observing one or more of the following unique characteristics: colored leg bands, radio transmitter antenna (e.g., if only female had transmitter), unique breast spot patterns, or a behavioral action displayed only by females (e.g., brooding or puffing of breast feathers on the nest rim). A nest was considered to have only one male provisioning if we obtained >6 hours of video tape and < 20% of visits were of unidentified individuals (Table 18). We chose 6 hours because we were able to detect >90% of all provisioning males and 100% of females within that period (Fig. 1). Additionally, we used mist net captures of males in nets placed within 5m of a nest while adults were actively feeding chicks (n= 4 males identified), opportunistic visual observations at the nest (n=2), and observations of fledged chicks shortly after they left the nest (n= 2).

The quality of each recording session was ranked by the reviewer (1=poor, 2=good, 3=excellent). Because poor quality tapes contained many unidentified visits, only quality 2 and 3 tapes (71.9% of tape hours) with >6 total hours of video tape containing < 20% unidentified adult visits were used for chick provisioning analyses (n = 10 nests).

We used the raw feeding rate (total number of trips) to compare among individual males and between total male provisioning rates and female provisioning rates within each brood. To compare each male's and female's overall provisioning rates to those of individuals at other broods, we combined multiple observation samples on each brood. We controlled for variations in brood size, the complex relationship between nestling age and provisioning, and the uneven number of observation days and hours at each brood. Following Westneat (1995), among each sex we separately calculated the deviation of each adult's provisioning rate (number of trips/hour/chick) from the mean provisioning rate for each day of brood age (day 1 = day first egg hatched) using both years of video data. We used the mean deviations for each adult at each brood over all days as the index of provisioning for that nest relative to that of other adults in the population. Negative scores indicated lower than average provisioning rates and positive scores indicated rates above the population mean. We observed some individuals in more than one year of the study and at multiple nests each year. However we considered each brood to be an independent event.

We collected nest site and habitat data using Breeding Biology Research & Monitoring Database

(BBIRD) protocol for all Bicknell's Thrush, Swainson's Thrush (*Catharus ustulatus*) and Blackpoll Warbler nests as well as for some nest sites of other species (Martin et al. 1997). Nest habitat characteristics were measured after the termination of nesting. We measured over 50 variables at each nest site. Using nest data through 1997, we attempted to identify vegetation parameters at both the nest-site (5m radius) and nest-patch (11.3m radius) that characterize Bicknell's Thrush nesting habitat. To do this we used stepwise discriminant function analysis (DFA) with the following 22 variables derived from field data:

A) ground cover ocular estimate in 5m radius:
1) shrubs <50cm tall
2) ferns
3) moss
4) grasses and sedges
5) forbs
6) bare ground
7) leaf litter
8) downed logs

A) number of woody stems >50cm tall and <8cm diameter at 10cm above ground in 5m radius:
1) standing dead stems
2) conifers
3) white birch
4) mountain ash
5) all other deciduous species
6) mean litter depth
7) mean top canopy height

A) small live stems (8-23cm DBH) in 11.3m radius:
1) conifers
2) white birch

A) large live stems (>23cm DBH) in 11.3m radius:
1) conifers
2) white birch

A) total live tree stems >8cm in 11.3m radius:
1) mountain ash
2) all other deciduous species
3) all standing dead trees >12cm DBH

Arcsine and logarithmic transformations were performed to normalize the percentage and non-percentage data, respectively. We compared the microhabitat data at nest sites with three different null data sets from the same montane fir forest used by Bicknell's Thrush (non-use sites >35m from each Bicknell's Thrush nest in random direction but on same contour, nest sites of all other species, and Swainson's Thrush nest sites). Original variables selected by DFA were correlated with the discriminant function to examine their importance. We have not yet analyzed nest habitat features for Blackpoll Warbler.

Artificial nest predation.- We conducted nest experiments on both Mt. Mansfield and Stratton Mountain in 1997 and 1998 to determine the relative effects of a variety of human disturbances upon open-cup songbird nesting. Artificial nests were made of wicker and were similar in size to natural Bicknell's Thrush nests. Nests were left exposed outside for at least 2 weeks before use. We wore gloves and rubber boots while handling and deploying nests and eggs. Each nest was supplied with two Bobwhite *(Colinus virgianus)* eggs. To attempt to identify predators, in 1998 we added one clay egg similar in size to a Bicknell's Thrush egg. We wired it to the nest bottom so that predators would be more likely to leave it after handling. Each basket was placed in a situation that closely approximated actual Bicknell's Thrush nest locations.

In 1997 we deployed 200 nests on each mountain, with 50 nests spaced at least 25m apart in each of 4 treatments, which included: 1) hiking trail edge, 2) ski trail edges adjacent to contiguous forest, 3) edges of forest islands surrounded by ski trails, and 4) natural, relatively undisturbed large forest tracts. In 1998 we placed 250 artificial nests on each mountain, divided equally between the four treatments used in

1997 and an additional treatment of interior areas of large forest islands surrounded by ski trails. Nests were exposed first on Stratton Mountain in mid-June, then on Mt. Mansfield during late June. Rigorous statistical analyses have yet to be completed for these trials.

In 1997 and 1998 we were unable to deploy automatic cameras at artificial nests due to funding constraints. In 1999 we attempted to use four sets of automatic 35mm cameras attached to Trail Master active infrared monitors to determine the identity of predators visiting nests. The infrared beam passed over a natural Bicknell's Thrush nest collected the prior year with a clutch of two House Sparrow (*Passer domesticus*) eggs.

Paternity analysis.- Genetic analyses are being completed by James Goetz for partial fulfillment of a Masters of Science degree in Dr. Therese Donovan's laboratory at SUNY College of Environmental Science and Forestry in Syracuse, New York. DNA was extracted from each blood sample (Chomczynski et al. 1997,) and analyzed using 6 polymorphic microsatellite primers from Swainson's Thrush (T4, T5, T10, T28, T32). For each microsatellite primer set 50 ng of DNA was used in a polymerase chain reaction amplification with forward and reverse primers for a particular locus, one of which is end-labeled with a radioisotope (P-33). The radioactive product is electrophoresed on a polyacrylamide sequencing gel. The radioactive gel is used to expose x-ray film. Using clones of known size as a reference, bands on the developed film are used to visually score allele sizes (L. Gibbs, pers. comm.). The allele scores are used to determine paternity through likelihood-based parentage inference using co-dominant marker data with CERVUS 1.0 software (Marshall et al. 1998).

Home range location, size and movements of Bicknell's Thrush. –Breeding season home ranges were defined as the area used by an individual from 1 June to 31 July each season. We determined home range size and location using the non-parametric kernel method (Worton 1989) calculated with ArcView 3.2 (Environmental Systems Research Institute, Inc.) and Animal Movement Analyst 2.04 (Hooge and Eichenlaub 1997). We used a fixed kernel with the smoothing factor determined by least-squares cross-validation (Seaman and Powell 1996, Seaman et al. 1999). We calculated both the 95% (area the bird actually used) and 50% contours (core area of activity) for individuals with a minimum of 30 locations (Seaman et al. 1999). We used only those locations that were more than 5 min apart based on the general rule that locations t_1 and t_2 can be considered independent if the period between them is sufficient to allow the individual to move from one end of its home range to the other (White and Garrot 1990). Field experience suggested that thrushes could fly from one end to the other in much less time. Locations of individuals known to be on the nest (e.g., brooding females) were excluded.

Home range overlap. –We calculated a static home range interaction of neighboring thrushes from the kernel home range (KHR) using the following equations (White and Garrot 1990): $S_{1,2} = A_{1,2}/A_1$ and $S_{2,1} = A_{1,2}/A_2$ where A_1 and A_2 are the total KHR areas of thrush 1 and 2, $A_{1,2}$ is the area of overlap, yielding the proportion of animal 1's home range overlapped by animal 2 ($S_{1,2}$) and the proportion of animal 2's home range overlapped by animal 1 ($S_{2,1}$). This statistic is limited in that it does not imply any mutual awareness among the tracked thrushes, however a more rigorous dynamic interaction statistic in which individuals are tracked simultaneously was not possible due to logistic and environmental constraints.

RESULTS AND DISCUSSION

Baseline population monitoring.- We have established point count routes on 10 mountains in Vermont, 3 mountains in Maine and 1 mountain in Massachusetts (Table 1). Eleven of these sites (69%) have been

adopted by experienced volunteer birders for long-term monitoring. The remaining five sites are completed each year by VINS staff. We are currently finishing data entry and error checks and will have statistical power estimates and preliminary short term trend results by 31 December 2000. Exploratory power analysis will enable us to identify the number of point count routes necessary to detect population trends over various time periods.

Additionally, we have obtained startup funding from USFWS Region 5 to begin a landscape level citizen science monitoring project in the Green Mountains. Dubbed Mountain Birdwatch, this project will begin in June of 2000. The aim of the project is to use as many volunteers as possible, regardless of their birding expertise. We chose to monitor 5 bird species (Bicknell's Thrush, Blackpoll Warbler, Swainson's Thrush, Winter Wren *[Troglodytes troglodytes]*, White throated Sparrow *[Zonotrichia albicollis]*)and 1 mammalian nest predator (Red Squirrel *[Tamiasciurus hudsonicus]*). A full project description and registration can be found on VINS' web site: http://www.vinsweb.org/conservation/citizenscience/mtnbirdwatch.html.

Survivorship and recruitment.- We captured and marked a total of 48 ASY females and 91 ASY males on 4 intensive study plots from 1992-98 (Tables 2 and 3). On the Mount Mansfield study plots we captured 21 females and 43 males from 1992-98 on MANS, 13 females and 21 males from 1995-98 on RABR. Because the OCTA study plot on Mt. Mansfield has only been used for 2 years, we were unable to analyze those data. On the Stratton Mountain study plots we captured 2 females and 11 males on STRA and 12 females and 16 males on STRB from 1997-98.

The data for the MANS plot adequately fit the global model $\{F_{g*t} P_{g*t}\}$ (P>0.093). We adjusted for overdispersion in the data using 1.7332. The most parsimonious model in the candidate model set was no sex or time dependence for either parameter (Table 4). This model was nearly 2.7 times better supported by the data than a model for which adult survivorship varied by sex (0.49438/0.18573 = 2.67) and over 2.7 times better supported than a model where capture probability varied by sex (0.49438/0.18206 = 2.72). Survivorship was estimated to be 54.7% (± 6.5% SE), with parameter estimates averaged over all the models in the candidate set ranging from 54% to 55.8% (Table 5).

The RABR plot data adequately fit the global model $\{F_{g*t} P_{g*t}\}$ (P>0.13). We adjusted for overdispersion in the data using 1.38572. The most parsimonious model in the candidate model set showed no sex or time dependence for survivorship, but sex dependence for capture (Table 6). This model was over 2.5 times better supported by the data than a model for which for which both parameters varied by sex (0.45579/0.17885 = 2.55), and it was over 2.6 times better supported than a model where neither parameter varied by sex or time (0.45579/0.16987 = 2.68). Survivorship was estimated to be 74.8% (± 8.6% SE), with parameter estimates averaged over all the models in the candidate set ranging from 71.9% to 79.1% (Table 7).

The STRB plot data adequately fit the global model $\{F_{g*t} P_{g*t}\}$ (P>0.78). We adjusted for overdispersion in the data using 2.45. The most parsimonious model in the candidate model set had no sex or time dependence for either parameter (Table 8). However, this model was only slightly better supported by the data than three models in which parameters varied by time (0.15875/0.14451 = 1.1), making model selection difficult. Survivorship was estimated to be 73.9% (± 10.1% SE), with survivorship estimates averaged over all the models in the candidate set ranging from 75.6% to 88.3% (Table 9).

The data for the STRA plot adequately fit the global model $\{F_{g*t} P_{g*t}\}$ (P>0.35). We adjusted for overdispersion in the data using 1.0683. The most parsimonious model in the candidate model set was no sex or time dependence for either parameter (Table 10). This model was over 3 times better supported by the data than a model for which adult survivorship varied by sex (0.38975/0.12527 = 3.11) and a model where capture probability varied by time (0.38975/0.11256 = 3.46). Survivorship was estimated to be 94.6% (± 28.4% SE), with parameter estimates averaged over all the models in the candidate set ranging

from 86.1% to 94% (Table 11). The data from STRA are sparse in both time and individual capture histories, producing very imprecise parameter estimates.

We compared the survivorship of ASY Bicknell's Thrush on STRA (natural area) with STRB (ski area) to begin to explore if adult survivorship may be compromised on impacted areas. The data adequately fit the global model{F $_{g*t}$ P_{g*t} } (P>0.23). We adjusted for overdispersion in the data using 1.5135. The most parsimonious model in the candidate model set was no plot or time dependence for either survivorship or recapture probabilities. Survivorship was estimated to be 80.7% (± 0.12) and recapture was 86.7% (±0.13). This model was 2.9 times better supported than the model were survivorship was group dependent (0.12079/0.04408 = 2.9). Additionally, a likelihood ratio test between the reduced model {F. *P.*}and the more general model {F $_{g}$ *P.*} was not significant (x^2=2.451, df = 1, P=0.1175).

Our intensive mark-recapture study provides the first meaningful estimates of adult Bicknell's Thrush survival. The precision of the estimates are poor on Stratton Mountain because of the scant data in both time and individual capture histories (i.e., recapture probabilities are very high over a short period). As our mark-recapture studies continue, the parameter estimates on each plot will become more robust and modeling will become more sophisticated, including covariables such as age class.

Bicknell's Thrush recruitment, i.e., the number of second year (SY) birds captured each breeding season, was weakly correlated to the previous season's productivity on each mountain. A Pearson correlation of all plots and years yielded no relationship (Bartlett Chi-square statistic: 0.008 df=1 P= 0.929). However, one year on RABR plot was an extreme outlier (1996, 7 SY birds, 0.846 daily nest survival). When we removed this outlier the data were much more strongly correlated (Bartlett Chi-square statistic: 3.892 df=1 P= 0.049). We are currently analyzing Blackpoll Warbler recruitment data.

Nesting parameters and habitat selection.— To our knowledge, there have been only 13 carefully monitored Bicknell's Thrush nests (Wallace 1939) prior to our study. To adequately assess this species' conservation status, we believe that a full understanding of its breeding ecology and nesting biology is necessary.

Nest building commences in early June, with the earliest confirmed date on 1 June 1998, when several pieces of moss were found loosely woven into a circular pattern. Clutch initiation begins shortly thereafter and clutch sizes ranged from 2 (2% of all nests), to 3 (51% of nests), to 4 (47% of nests) eggs. Breeding synchrony peaked during weeks 24 and 25 in each year and declined rapidly thereafter, with a mean of 27 (± 4.6 SD) days between first and last clutch initiation attempts on Mansfield and 27.3 (± 7.8 SD) days on Stratton. Eggs hatched after 11.6 (± 1.4 SD) days of incubation (n = 34 nests), and young fledged 11.6 (± 1.1 SD) days after hatching (n = 41 nests). By 15 July, 71% of broods had fledged. Bicknell's Thrush are single brooded, but may re-nest after early season failures (21% of failed females were known to re-nest, but the actual proportion was likely higher). Clutch size was 2 or 3 eggs in all re-nesting attempts.

Preliminary data analysis indicates that habitat at Bicknell's Thrush nest sites was characterized as young to mid-successional or chronically disturbed montane forest (Table 12), suggesting that Bicknell's Thrush may be a natural disturbance specialist. Disturbances in the montane forest can be both frequent but episodic, or chronic. Areas that receive chronic disturbance include ridgelines exposed to severe weather events and rime ice, both of which often damage trees and slow growth, creating a 2-3m tall krummholtz type forest. Natural disturbances on side slopes include insect damage, debris slides, and fir waves (Marchand 1984, Reiners and Lang 1979, Sprugel 1976). Additionally, anthropogenic disturbances such as ski trail development and maintenance, roads, and hiking trails often mimic natural disturbances. Some disturbed conditions on ski areas can persist for long periods because the trees are exposed to chronic wind damage on some edges (Harrington 1986, Rizzo and Harrington 1988). On the Stratton Mountain ski area plot, most Bicknell's Thrush nests were situated along trail edges (mean distance 7.5 m ± 6.6 SD from edge). Only 2 nests were > 20 m from the edge. It should be noted that these nest locations were not

biased by search effort because they were found by capturing a female and finding her nest with radio telemetry.

Bicknell's and Swainson's thrushes selected different nest site habitats (Table 12). Swainson's Thrush nest sites were located in areas of more mature trees characterized by lower stem densities, larger and taller trees, and more openings with ferns and grasses/sedges. Future data analyses will incorporate all our nest data and will include comparisons of successful nests verses depredated nests, and nest position parameters (e.g., concealment, distance from edge, height of nest).

Like Bicknell's Thrush, Blackpoll Warbler has been remarkably understudied (Hunt and Eliason 1999). We are currently examining nesting parameters and habitat selection for 150 monitored nests of this species. We monitored an additional 241 nests of 18 species (Table 21). We will be examining these nests to determine if there is a relationship between ski trail proximity and nest success.

Productivity.— Probability of nesting success for Bicknell's Thrush varied between 1.1% and 83.9% (Table 13), and for Blackpoll Warbler 5.7% to 79.6% (Table 14). Nest success was strikingly biennial. Field observations indicated to us that large fall cone masts resulted in high Red Squirrel populations on both Mansfield and Stratton the following spring. We reviewed cone production data from a demographic study of balsam fir on Whiteface Mtn. in New York and were struck by this same biennial pattern (M.E. Dodd, pers. com.). We obtained cone estimates for Mt. Mansfield using field notes and photographs, and we ranked each year's cone mast as high, medium or low. A corresponding biennial pattern emerged (Fig. 2). We then compared Blackpoll Warbler and Bicknell's Thrush Mayfield estimates with cone mast data (Fig. 2). Bicknell's Thrush correlated highly with mast data (Spearman correlation = -0.866), but Blackpoll Warbler was much weaker (Spearman correlation = -0.289). These data, while intriguing, require further analysis to more fully understand the complex ecological relationship between cone mast, predator populations and avian nesting success.

We monitored 19 Bicknell's Thrush nests and 38 Blackpoll nests on natural area plots and 38 Bicknell's Thrush nests and 19 Blackpoll nests on ski area plots (Table 14). The overall daily survival rate of Bicknell's Thrush nests on ski areas verses natural areas was not significantly different (x^2=0.4429, df=1, P=0.51), nor was Blackpoll Warbler (x^2=0.0496, df=1, P=0.82).

Artificial nest predation.— Although we have not fully analyzed data from these experiments, results of the trials appear to be inconclusive (Table 15). Patterns of depredation on both mountains led us to suspect that some trap-lining, in which a predator systematically destroys nests placed at regular intervals, occurred.

The automatic camera setup attempted in 1999 was not useful in this habitat because of the extreme difficulty in obtaining line-of-sight across a hidden nest in dense vegetation, combined with wind moving branches and trees into the narrow sight line. A more effective method may involve automatic cameras with a solenoid switch directly attached to an egg in the nest.

We thus have little confidence in the validity of these results, and we do not believe that they can be meaningfully interpreted. We further believe that data collected at real nests give much more robust and relatively unbiased information, and we do not plan to experiment further with artificial nests as a means to evaluate differences in avian nesting success among disturbed and undisturbed areas.

Bicknell's Thrush Home Range.— We have digitized and begun to analyze radio telemetry data for Stratton Mountain. Radio telemetry data on Mt. Mansfield are entered and triangulation calculations are underway. In 1997 we employed radio telemetry to investigate how thrushes move through the ski trail-forest island complex, and to assess their reactions to recreational activities. We quickly discovered that male thrushes were not holding small, discrete territories, as is generally assumed for most Nearctic-Neotropical migrants, but instead broadly overlapped (Table 16). We frequently detected several males singing and calling from the same area within a single hour. The areas of high overlap generally coincided with nest

site locations. However, unlike the Dunnock (*Prunella modularis*), males do not defend exclusive areas that encompass more than one female (Davies 1992), but appear to behave more like male Smith's Longspurs (*Calcarius pictus*), which defend small areas around the female (Briskie 1992). Bicknell's Thrush females tend to occupy home ranges with little or no overlap, and these are much smaller than male home ranges (Table 17). Our field observations suggested that females aggressively protect territories, especially during the brief period of mating and egg laying. Further analyses of our radio telemetry data should better elucidate the dispersion patterns and movements of Bicknell's Thrush, particularly in relation to its complex mating system (below).

Bicknell's Thrush mating system.— We monitored a total of 27 nests in 1997-99 to determine the number of male feeders at each. Of the 21 nests that provided adequate data, 14 (70%) were attended by two provisioning males (Table 18). Four (20%) nests were provisioned by a single male, while one nest was attended by 3 males and another nest by 4 males (Table 18). Only three nests were attended by second-year (SY) males (one each at FORE99.1, OCTA99.2, and STRB97.1) and only three nesting females were SY birds (FORE99.1, RABR99.4 and STRB98.3).

Four males were documented to provision more than one nest during a single breeding season, and three of these individuals simultaneously fed two broods. The nests were located 186-443m apart. In one case a male shared provisioning at a nest (OCTA99.5) until the young fledged, then began to provision simultaneously at another nest 443m away (OCTA99.6) when it hatched (Fig. 3). He left the care of the fledglings from the first nest to the other male for at least the first day. He fed the nestlings in the second nest at nearly the same rate as both of them combined at the first nest (Fig.3).

We documented three instances of males provisioning young at nests of the same female in successive years. Nests were located 45m (STRB97.4 and 98.8), 56m (OCTA98.1 and 99.6) and 115 m (RABR97.4 and 98.2) apart, respectively. At nest OCTA98.1 the male shared provisioning with one other bird, making only 26% of the total male feeding trips. In the following year at OCTA99.6, he was the lone provisioning male and fed at nearly the same rate as the female (Table 18).

Of the 21 video taped nests, ten nests from Mt. Mansfield were sufficiently taped to enable chick provisioning analyses (Table 18). Each nest was recorded for 6-48 hrs with a total of 180.4 hrs of quality 2 and 3 video tape. Four of these nests had one provisioning male and six had =2 males (n = 4 with 2 males, n = 2 with 3 or 4 males).

In seven cases females were found to provision at slightly higher rates than the combined male rate (Fig. 2). However, this difference was not significant (Wilcoxon signed ranks test; Z= -0.969, P=0.33). Females provisioned more at all four nests with a single male and at half of the nests with =2 males, but not significantly so in either case (Wilcoxon signed ranks test with one male: Z= -1.841, P=0.066; with =2 males, Z= 0.105, P=0.9). Only at the four male nest did the female provision at a much lower rate than the males. Three of the six multiple male nests were attended by a male that provisioned at a significantly higher rate than the other males (Fig. 4).

We examined the relationships between the number of males at each nest and the relative provisioning rates of each individual (Fig. 5a). The highest relative provisioning rates were shown by males at 2-male nests. However, these rates did not significantly differ from those of males at single male, 3-male or 4-male nests (Kruskal-Wallis H=7.217, df=3, P=0.065). Likewise, individual female relative provisioning rates did not differ between single male nests and multiple male nests (U-test =9.5, df=1, P=0.59). We found no difference in total relative male provisioning rates between single male nests and =2-male nests (U-test=19, df=1, P=0.13) nor in total relative provisioning rates by both sexes (U-test =13, df=1, P=0.83; Fig. 5b).

We compared nesting success of single male nests (n=4) with multiple male nests (n=17; Table 18) and found no significant differences. At single male nests median clutch size was 3 eggs verses 3.5 for multiple male nests (U-test=24, df=1, P=0.38). The median number of eggs hatching was 3.0 for both groups, and the median number of fledglings was 2.5 for single male nests and 3.0 for multiple male nests (U-test=23.5,

df=1, P=0.4). Larger sample sizes in the future will enable us to more fully explore these differences and calculate Mayfield nest success estimates for each period of the nesting cycle.

We collected blood samples from adults (n=23) and four clutches on Stratton Mountain in 1998. In all four cases paternity was mixed and maternity was unique (Table 19). Unfortunately, none of these nests were sufficiently monitored to correlate paternity results with male visitation and feeding rates. However, at 3 of the nests we documented at least one visit by a male that had no paternal relationship with any of the young (Table 19). We are currently analyzing blood samples from 8 clutches collected on Mt. Mansfield and 2 clutches Stratton Mountain in 1999. Most of these nests were well-monitored by videography and will allow us to compare paternity and feeding visits. Additionally, we are analyzing the sex ratio of each clutch to investigate possible correlations between sex ratio at hatching and the male-biased sex ratio that we have found among adults (see below).

It has been suggested that this type of mating system may be caused by a skewed sex ratio (Davies 1992, Ridpath 1972). Because our capture-mark-recapture sampling employed both active and passive mist netting, which may have caused differential capture probabilities for males and females, estimating sex ratios of populations was not straightforward. To determine if a bias existed, we estimated adult male and female recapture rates from MANS, RABR, and STRB (STRA was not used because of sparse data) and compared them using methods described in Lebreton et al. (1992) and Cooch and White (1999), using the program MARK (White and Burnham 1999). As described above (see *Survivorship and recruitment*), for both MANS and STRB the most parsimonious model did not show sex or time effects for capture probabilities. However, the most parsimonious model for RABR did show a sex effect for capture probabilities. Additionally, a likelihood ratio test (LRT) between the general model {F. *P* }and the reduced model {F. *P*.} was significant (x^2=5.902, df = 1, P=0.0151), indicating a better fit of the general model. Because there does not appear to be a sex bias in capture probabilities for MANS (LRT: x^2= 0.204, df=1, P=0.6515) or for STRB (LRT: x^2= 0.000, df=1, P>0.9), we used the annual male**:**female ratio from breeding season captures on these two plots as an estimate of the sex ratio. The overall mean male **:** female ratio was 1.9 (SD±0.44) with an annual range of 1.4 to 2.8. We are exploring possible causes for this biased sex ratio, which include sexual habitat segregation on the wintering grounds that might lead to differential overwinter survivorship, or sex bias in individual clutches.

The mating system of Bicknell's Thrush appears to be very unusual. About 2.5% of bird species are known to breed in groups, where three or more individuals cooperate to raise a brood (Brown 1987, Stacey and Koenig 1990). Many of these consist of a monogamous breeding pair with *n* helpers who are collateral kin of the brood (Brown 1987, Hartley and Davies 1994, Stacey and Koenig 1990). However, some species' mating associations consist of >1 males that both mate and at least potentially fertilize a female *and* cooperate in provisioning her single brood. This has been described for at least thirteen species representing ten families (Table 20).

This breeding system has generally been termed cooperative polyandry (Faaborg et al. 1980, Faaborg and Patterson 1981), however these species exhibit a diverse array of underlying mechanisms and strategies. In Dunnocks, for example, female promiscuity leads to a variable mating system because dense habitat cover makes it difficult for males to monopolize females, and small prey sizes make more male help valuable for chick provisioning (Davies 1992). Unlike Dunnocks, Smith's Longspur males do not defend individual territories, but are described as female-defense polygynandry (Briskie 1992). This system may be due to low food availability when females arrive and begin egg laying, which causes them to range widely. Coupled with a very short breeding season, this creates conditions where males may be unable to economically defend large territories. Similarly, the cooperative polygynandrous mating system of Alpine Accentors is thought to be due to widely dispersed and patchy food resources combined with asynchrony in female breeding (Davies et al. 1995). However, unlike Smith's Longspurs, male accentors jointly defend a large group home range. Increased survival and enhanced life time reproductive success may drive the formation of cooperative groups of Acorn Woodpeckers and Galapagos Hawks (Koenig and Mumme 1987, Faaborg et al. 1980).

Some of these species exhibit a variable mating system that may include monogamy, polygyny, polyandry, and polygynandry within the same population (Davies 1992, Faaborg et al. 1995, Goldizen et al. 1998,

Koenig and Mumme 1987). Stacey (1982) suggested that mating systems of group-living species occupy a continuum from functional monogamy to complete female promiscuity, in which all males copulate freely and equally with the female. His model suggests that when female promiscuity is beneficial, male-male competition to increase individual reproductive success via monopolization of female(s) will balance with male-male cooperation for survival of young.

Wallace (1939) first detailed the natural history of Bicknell's Thrush *(Catharus bicknelli)* and described two males provisioning young at one nest. He considered the second male to be "extra" and apparently assigned little importance to his keen observation. We confirmed his finding through observations of a color banded population in 1997 and initiated an intensive study of this species' mating system in 1998. We believe that Bicknell's Thrush mating system is best described as cooperative polyandry/polygynandry, because multiple males breed with each female and cooperate in nestling provisioning, occasionally with multiple females.

Management and conservation implications.— Pending full analysis of our existing data, and compilation of more robust data for many aspects of this research, it is premature to provide definitive management recommendations. However, we have worked closely with several ski areas and with the Vermont Fish and Wildlife Department to provide preliminary guidelines for ski area land managers (Appendix A) and to address several site-specific management issues. We developed a mitigation plan with Stratton Mountain for an area of new lift construction in 1999, setting aside for reforestation an area of developed trails equal in size to an area that was removed by construction activities. This exchange also served to connect several small islands of habitat, enhancing their collective value to Bicknell's Thrush and other species. We will continue to develop management guidelines as our data analyses and experience warrant, and to provide advice when requested. A detailed, rangewide conservation assessment and management plan is in the early stages of preparation, but will require additional field data collection and analysis.

Information dissemination and education.— We worked with Stratton Mountain to develop an educational facility on the mountaintop in 1999. This facility features a display on Bicknell's Thrush and other montane forest birds, similar to a display we helped to create at the visitors center on Mt. Mansfield in 1994. We regularly disseminated project information during the summer through informal discussions with hikers, birders, other recreationists, and summer camp groups. Our research was filmed by the Discovery Channel's Animal Planet "All Bird TV" program and aired on 4 and 5 December 1998. We also presented several public slide lectures to local bird and outdoor clubs. We presented a poster paper titled "Home range overlap and movements by male Bicknell's Thrushes during the breeding period: implications for spot-mapping" at the Association of Field Ornithologists annual meeting in October of 1998. We also organized a scientific paper session, titled "Ecology and Conservation of Bicknell's Thrush" at the 117th Stated Meeting of the American Ornithologists' Union in August of 1999. C. Rimmer chaired the session, and project staff contributed 3 papers. We are currently preparing or planning at least 10 scientific papers for submission to refereed professional journals, including the Bicknell's Thrush Birds of North America account, which will be completed in October of 2000. We participated in meetings of the U.S.-Canada Bicknell's Thrush Study Group during September of 1998 in Montreal; May of 1999 in Woodstock; and August of 1999 in Ithaca, NY. This group has an informational web page on Bicknell's Thrush (http://www.ns.ec.gc.ca/wildlife/bicknells_thrush/) in both English and French, with plans for a future Spanish translation. We actively participated in the Partners In Flight Northeast Regional Steering Committee, and we are helping to develop the montane forest habitat sections of 3 physiographic area conservation plans by providing scientific expertise, data and review. The preliminary plans can be reviewed at http://www.partnersinflight.org/pifbcps.htm.

Future study plans.— In 2000 we will continue intensive studies on the Mt. Mansfield RABR and OCTA plots and on Stratton Mountain's STRA and STRB plots. We will suspend research on Mt. Mansfield's MANS plot, due to logistical and funding difficulties. Intensive data collection will include: 1) continued capture-mark-recapture of Bicknell's Thrush and Blackpoll Warbler; 2) nest monitoring of all species, with nest finding for Bicknell's aided by radio tagging females; 3) cone mast and Red Squirrel population monitoring; and 4) a final year of blood sampling and nest videography of Bicknell's Thrush for mating system studies. We will also sample blood and secondary feathers from Bicknell's Thrush, Blackpoll Warbler, Myrtle Warbler *(Dendroica coronata)*, and White-throated Sparrow *(Zonotrichia albicollis)* at several sites in the Northeast to examine mercury body burdens. Finally, we will launch our "Mountain Birdwatch" citizen science project for long term population trend monitoring.

Several components of our 8-year data base have not yet been adequately analyzed or published. This will be a top priority in 2000/2001. We will complete the Birds of North America account during fall 2000 and at least 4 other major peer-reviewed publications by late winter 2001, plus several other shorter papers. We will also begin a comprehensive conservation assessment and management plan for Bicknell's Thrush, using our data from the breeding and wintering grounds, incorporating an extensive data set on migration from banding and museum specimen records, and including data and input from our colleagues in Canada.

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