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

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Kent P. McFarland, Christopher C. Rimmer and James E. Goetz
Vermont Institute of Natural Science
27023 Church Hill Road
Woodstock, VT 05091

## 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)*

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

1997).

Because most nests were found after the onset of incubation, nest initiation (day first egg was laid) was

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 $\{F_{g*t}\ P_{g*t}$

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. $P_g$ }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).

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

*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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