

2001 Report to the Vermont Monitoring Cooperative

Part I. The relationship between cone mast, red squirrel populations and migratory songbird demographics in montane fir forests

Part II. Forest Bird Surveys on Mt. Mansfield and Lye Brook Wilderness Area

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Part I. The relationship between cone mast, red squirrel populations and migratory songbird demographics in montane fir forests

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In the course of demographic research on Bicknell's Thrush (*Catharus bicknelli*) and other montane fir forest bird species on Mt. Mansfield and Stratton Mountain, we documented a biennial pattern of balsam fir (*Abies balsamea*) mast, red squirrel (*Tamiasciurus hudsonicus*) populations, and avian breeding productivity. This report updates information presented in our 2001 VMC report, by examining this cycle and its demographic consequences for Bicknell's Thrush populations.

METHODS

Study Sites.- Our two study sites were located on Mount Mansfield (44° 32' N, 72° 49'W) and Stratton Mountain (43° 05'N, 72° 55'W) in Vermont, USA between 900-1200m elevation in montane fir forest. These sites have a mixed canopy dominated by balsam fir, with lesser amounts of white birch (*Betula papyrifera* var. *cordifolia*) and mountain ash (*Sorbus spp.*) and is described in detail by Wallace (1939) and Rimmer et al. (2001). Both mountains contained areas altered by ski area development and unmanaged, natural areas. Focal species were found in both unaltered and altered habitat on each mountain.

Cone Mast and red squirrel abundance.- From 1994 to 1999 we qualitatively noted a biennial cycle of balsam fir cone production. In July of 2000 we used a technique that enabled us to reliably quantify cone production back to 1992 on both peaks. Cone rachises and scars persist on branches for decades after seeds have been shed, and these can be used to retrospectively estimate when a tree produced cones (Morris 1951, Silvertown and Dodd 1999a and 1999b). We randomly located two 500 m transects on each mountain. At 50m intervals (10 trees per transect) we selected the nearest balsam fir tree greater than 3m tall to ensure it was reproductively active since 1992. We counted the number of rachises, rachis scars and cones on every internode of a branch selected from one of the third to sixth whorls from the top of the main stem. New female cones occur only on the prior season's growth (internode). Year of production for each cone was determined by the internode location on the branch (Morris 1951, Silvertown and Dodd 1999a and 1999b).

A crude index of red squirrel relative abundance during the passerine nesting season (1 June – 1 August) was determined annually from 1998-2001 on Mt. Mansfield and 1997-2001 on Stratton Mountain. We recorded probable territorial locations of squirrels, based on vocalizations and sightings within two subplots on each peak, one on a ski area and one in a natural area. Subplots on each mountain covered approximately 30 ha area.

Avian productivity.- From June to August, nests were located by systematic searches, following radio tagged females during incubation (Bicknell's Thrush only), and by observing parental behavior and other cues. The chronology and status of all active nests were monitored every 1 to 4 days either directly or, when possible, remotely via binoculars, or by radio telemetry of female Bicknell's Thrushes. Nests that fledged at least one young were considered successful. Observations of fledging, fledglings near a nest, parents carrying food nearby, or an empty nest cup with depressed edge and excrement were taken as evidence of a successful nest. Depredation was assumed when the eggs or nestlings (when too young to fledge) disappeared. We assumed that the number of fledglings equalled the number of nestlings observed in the nest on our last visit.

Because most nests were found after the onset of incubation, we evaluated nest success 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. Only open-cup nests of altricial species >25cm above ground were analyzed. We analyzed all nests together, as well as subsets of Bicknell's Thrush and Blackpoll Warbler (*Dendroica striata*), two species that are specialized on montane forest habitat in the region. We compared daily nest survival rates between years with high cone mast and mast failure using the program CONTRAST (Sauer and Williams 1989).

Bicknell's Thrush population dynamics.- 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 on two subplots on each mountain. From 1992-2001 on Mt. Mansfield we captured birds on a 14 ha area on the ridgeline (Ridge subplot) at 1150-1200 m elevation and on a 19 ha area on the east slope (Octagon subplot) at 915-1100 m elevation. Both areas contained a gravel access road, several small buildings, and hiking trails with the addition of ski trail development through the Octagon area. From 1997-2001 on Stratton Mountain we netted a 40 ha subplot on the north end, characterized by extensive ski area development, and a 29 ha subplot on the less impacted south end with only hiking trails.

Up to 30 mist nets were used simultaneously to passively capture thrushes as a complement to the use of vocal lures. 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. Sex was determined by status of cloacal protuberance and brood patch (Pyle 1997). Individuals were aged 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. 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 relatively few resights.

Adult 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. For our global model we used plot * 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 (Φ) and recapture (P) with "g" for plot 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_c). The model with the lowest QAIC_c 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.

We used only after-second year (ASY) individuals in our analysis, because second year (SY) birds tend to range widely and disperse at a high rate the following year making model assumptions difficult to meet. SY individuals may also be less important toward reproduction. During the 1998 and 1999 breeding seasons, we had only one male SY contribute paternity to a clutch ($n = 12$ clutches; Goetz 2001), and only 12 of 79 known-identity females (15.2%) at monitored nests were SY (unpubl. data). We first compared survivorship models with males and females as separate groups. Because the model $\{\Phi, P\}$ was 2.4 times better than the best supported model with group effect $\{\Phi_g, P_g\}$ on Mansfield and >3 times on Stratton, we lumped both sexes and used subplot as the only group effect.

We used our estimates of nest success and number of individuals fledged to calculate per capita annual productivity using the equation $F = p^*y / (2-p)$, where p is the probability that a nest was successful, and y is the mean number of young fledged (Flaspohler et al 2001). This equation assumes that all females that fail in their first attempt will reneest with the same probability of success, but cannot attempt a third nest if the second fails. It also assumes that double-brooding does not occur. We have documented

only one instance of a female attempting a third nest and only one double-brood (Rimmer et al. 2001). Assuming a 1:1 sex ratio at fledging, per capita annual productivity of females was assumed to be one-half per capita annual productivity.

To understand the potential effects of cone mast years on source-sink dynamics, we used the equation $\lambda = Sa + (Sj)(F/2)$ to calculate the finite rate of increase for populations, where Sa is the adult survival rate from one breeding season to the next, Sj is the juvenile survival rate from fledging until following breeding season, and $F/2$ is the mean female per capita annual productivity per female (Pulliam 1988, Budnik et al. 2000, Fauth 2001, Flaspohler et al 2001). We used our own estimates of Sa . No direct estimates of Sj for Bicknell's Thrush exist, so we assumed that Sj was one-half of Sa based on estimates from other passerine species (Ricklefs 1973, May and Robinson 1985, Anders et al. 1997). Assuming closed populations, $\lambda = 1$ would indicate a stable population. We calculated the source-sink threshold (F when $\lambda = 1$) using $(1-Sa)/Sj$. We calculated 95% confidence intervals (CI) around λ using lower and upper CIs for adult survival and fecundity estimates. These yield best-case and worst-case intervals for finite rate of increase.

RESULTS

Balsam fir cone production was strongly biennial (Fig. 1a and b). Both sites were highly synchronized (% trees with cones: $r_s = 0.936$, $n = 10$; mean cones per tree: $r_s = 0.884$, $n = 10$), with mast production occurring in even-numbered years and failing in odd-numbered years. The proportion of trees producing cones in mast years was >75% except in 1996 on Stratton when only 47% of the trees sampled produced cones. All non-mast years were complete reproductive failures with no cones produced. Annual variability in spring populations of red squirrels was strongly correlated to mean number of cones per tree ($r^2 = 0.9899$, $n = 5$ Stratton; $r^2 = 0.7685$, $n = 4$ Mansfield) and the percent of trees bearing cones ($r_s = 0.947$, $n = 5$ Stratton; $r_s = 0.943$, $n = 4$ Mansfield) the previous autumn (Fig. 1a and b).

We monitored a total of 297 nests of 11 species on Mansfield and 210 nests of 10 species on Stratton. Mayfield daily survival rates (DSR) of all open-cup nests were negatively correlated with red squirrel populations ($r^2 = -0.7557$, $n = 5$ Stratton; $r^2 = -0.7705$, $n = 4$ Mansfield) (Fig. 1a and b). There was a significant difference between mean DSR on Mansfield following autumn mast years (0.9408 ± 0.0206 , mean \pm SD) and non-mast years (0.9794 ± 0.0039) (CONTRAST: $x^2 = 24.9855$, $df = 1$, $p < 0.0001$). Despite lower than expected cone production in 1996 on Stratton, there was a significant difference between mean DSR following autumn mast years (0.9378 ± 0.055 SD) and non-mast years (0.9826 ± 0.5674 SD) (CONTRAST: $x^2 = 15.3904$, $df = 1$, $P = 0.0001$). There was no significant difference in annual DSRs between Mansfield and Stratton for all years (CONTRAST: $x^2 = 0.0203$, $df = 1$, $p = 0.89$), mast years (CONTRAST: $x^2 = 0.0725$, $df = 1$, $p = 0.79$), or non-mast years (CONTRAST: $x^2 = 0.02135$, $df = 1$, $p = 0.64$).

The mean clutch size of Blackpoll Warbler nests was nearly equal following mast years (4.29 ± 0.55 SD, $n = 47$) and non-mast years (4.25 ± 0.6 SD, $n = 48$), as was the mean number of chicks fledged per successful nest following mast (3.67 ± 0.9 SD, $n = 39$) and non-mast years (3.49 ± 0.9 SD, $n = 67$). Annual DSR showed an inverse relationship with red squirrel populations ($r^2 = -0.7396$, $n = 5$ Stratton; $r^2 = -0.6836$, $n = 4$ Mansfield) (Fig. 1a and b). The mean DSR of Blackpoll Warbler nests following autumn mast years was lower than non-mast years on both Mansfield (0.944 ± 0.029 SD versus 0.99 ± 0.014 SD) (CONTRAST: $x^2 = 10.9408$, $df = 1$, $p = 0.0009$) and Stratton (0.939 ± 0.056 SD versus 0.99 ± 0.01 SD) (CONTRAST: $x^2 = 4.7859$, $df = 1$, $p = 0.029$). There was no difference in annual DSRs between Mansfield and Stratton for Blackpoll Warbler for all years (CONTRAST: $x^2 = 0.822$, $df = 1$, $p = 0.365$), mast years (CONTRAST: $x^2 = 0.0325$, $df = 1$, $p = 0.86$) or non-mast years (CONTRAST: $x^2 = 0.1626$, $df = 1$, $p = 0.69$).

The mean clutch size of Bicknell's Thrush nests was greater following non-mast years than in mast years ($t = 3.077$, $df = 92$, $p = 0.003$). However, the mean number of chicks fledged per successful nest following mast years versus non-mast years was equal on Mansfield and slightly, but not statistically higher after non-mast years on Stratton (Table 1). Breeding success of Bicknell's Thrush was negatively

correlated to red squirrel populations ($r^2 = -0.9035$, $n = 5$ Stratton; $r^2 = -0.6765$, $n = 4$ Mansfield) (Fig. 1a and b). Mean DSR following autumn mast years compared to non-mast years was lower on both Mansfield (0.902 ± 0.064 SD versus 0.978 ± 0.014 SD) (CONTRAST: $x^2 = 8.017$, $df = 1$, $p = 0.046$), and on Stratton (0.933 ± 0.49 SD versus 0.991 ± 0.007 SD) (CONTRAST: $x^2 = 14.796$, $df = 1$, $p = 0.0001$). There was no difference in annual DSRs between Mansfield and Stratton for Bicknell's Thrush for all years (CONTRAST: $x^2 = 0.3617$, $df = 1$, $p = 0.548$), mast years (CONTRAST: $x^2 = 1.0132$, $df = 1$, $p = 0.31$) or non-mast years (CONTRAST: $x^2 = 1.88$, $df = 1$, $p = 0.17$).

To calculate λ for Bicknell's Thrush on each mountain following mast years versus non-mast years, we estimated mean female per capita annual productivity per female (F), and adult (S_a) and juvenile (S_j) survivorship (Table 1). Female Bicknell's Thrush that nested following autumn mast years produced an average of 0.48 females per nest attempt on Mansfield and 0.31 on Stratton, whereas the number of females produced per nesting attempt after a non-mast autumn was 1.11 and 1.39, respectively. Per capita annual productivity after non-mast years was 2.3 times higher on Mansfield and 4.5 times higher on Stratton than after mast years.

From 1992-2000, we captured and released 98 adults on Mansfield (61 on Ridge subplot and 37 on Octagon subplot), and recaptured 48 of these at least once (32 on Ridge and 16 on Octagon). The data did not fit the global model with sex and subplot * year ($P = 0.024$), apparently due to a sparse dataset. Therefore, we examined sex * year for both subplots combined, but the global model fit poorly ($P = 0.054$). We were reduced to examining subplot * year and ignoring possible differences in survivorship between sexes. The data adequately fit this global model ($P > 0.239$). The quasi-likelihood adjustment for overdispersion in the data (\hat{c}) was 1.135. The model with the lowest QAIC_c in the candidate set was $\{\Phi_g P_g\}$, where survivorship and recapture probabilities were different on each subplot, but did not vary between years. This model was nearly 1.3 times better supported than a model in which survival did not differ between sites. Survivorship was estimated to be 0.57 ± 0.05 SE for Ridge subplot and 0.72 ± 0.073 SE for the lower elevation Octagon subplot.

We captured and released 49 adults on Stratton (18 on south and 31 on north subplot) from 1997-2000. We recaptured 12 on the south subplot and 23 individuals on the north subplot at least once. The data adequately fit the global model ($P = 0.605$). The quasi-likelihood adjustment for overdispersion in the data (\hat{c}) was 0.896. The model with the lowest QAIC_c in the candidate set was $\{\Phi_t P_g\}$, where survivorship varied by each year and recapture probabilities differed by group. The yearly variation in survivorship did not exhibit a biennial cycle (0.89 ± 0.07 , 0.68 ± 0.08 , 0.54 ± 0.09 , 0.80 ± 0.08). This model was more than three times better supported than a model in which survivorship was not time dependent. We used the model with survivorship constant over time as our estimate (0.70 ± 0.04) for overall survivorship during this period to determine λ after mast and non-mast years.

Using our estimated survivorship and fecundity values, λ were < 1.0 after mast years for all study areas and > 1.0 after non-mast years for Stratton and the Octagon subplot on Mansfield, but not the Ridge subplot or all plots combined on Mansfield (Fig. 2). For all years combined, neither Mt. Mansfield nor Stratton Mtn. λ levels were ≥ 1.0 . However, in each case the 95% confidence intervals included 1.0. To maintain a stable population, Bicknell's Thrush would need to produce 1.5 females per breeding female per year on the Ridge subplot, 0.8 on the Octagon subplot (1.26 for Mansfield subplots combined) and 0.84 on Stratton. Alternatively, annual survival rates of adult females and juveniles necessary to maintain a stable population, given observed fecundity for all years combined, would have to be 0.723 and 0.362 on Mansfield and 0.727 and 0.364 on Stratton.

DISCUSSION

Balsam fir mast production, followed by a large increase in red squirrel populations and subsequent depressed passerine nesting success, showed a strong biennial pattern during this study. These patterns were consistent with the hypothesis that cone crops, red squirrel populations, and passerine reproduction were all closely linked.

The correlation between cone, red squirrel and bird reproduction does not necessarily imply causation. There could be unknown factors, such as weather, driving a similar pattern in each of these species, rather than cone mast. However, Gurnell (1983) reviewed many studies showing that squirrel abundance is strongly linked to cone production in the previous year. Red squirrel predation upon bird nests has been widely documented (Martin and Roper 1988, Martin 1993, Wallace 1939, Hatt 1929, Vander Haegen and Degraaf 1996a and 1996b, Bayne and Hobson 1997a, Sloan et al 1998, Degraaf 1995, Boag et al 1984, Tewksbury et al 1998, Sieving and Willson 1998, Hagan et al 1996). We have video-taped red squirrel depredation on a full clutch of Bicknell's Thrush eggs, and we have documented many nest depredations that strongly implicate red squirrels. These studies and our observations lend credence to our hypothesis that balsam fir cone mast is the catalyst for increased red squirrel populations, which lead to depressed songbird productivity.

We believe that strong biennial oscillations in red squirrel numbers are primarily due to immigration from lowland mixed hardwood forests, coupled with high reproductive rates in response to balsam cone mast, followed by emigration to lower elevations after cone crop failure. We do not believe that heavy adult mortality in alternate years produces this pattern. However, this requires further detailed study of both the movements and demographics of red squirrels.

The biennial phenology of balsam fir masting appears to be a spatially and temporally widespread phenomena. Balsam fir trees in Fundy National Park, New Brunswick and in southeastern Newfoundland exhibited the same pattern, with heavy crops in 1998 and 2000 and very small crops in 1999 (K. McFarland, pers. obs.). Cone production on Whiteface Mountain, New York displayed a strong biennial pattern from 1993-1999 (M. Dodd, pers. comm.). Morris (1951) recorded heavy cone production in even years and light to no cone production in odd years from 1920-1950, with only two exceptions occurring in 1927 and 1947. Balsam fir has a two year cycle characterized by a one year interval for replenishment of reserves, with an occasional break in the cycle due to extreme and possibly localized climatic events (Morris 1951). The spatial autocorrelation in cone crops over large areas may be responsible for large-scale population fluctuations in some bird species due to increased red squirrel populations (Hartley 2001).

Wallace (1939) believed that red squirrels were the principal limiting factor for Bicknell's Thrush. However, his work was based on only two years of field work, 1933 and 1935. Nine of 13 nests that he monitored in 1935 failed. He reported that 42% were lost to red squirrels. Being odd-numbered years, we would predict the high squirrel numbers and low avian reproductive success that he recorded. But, was reproductive success in even years enough to offset failure in odd years and perhaps to negate the effects of red squirrels? Our detailed demographic data suggest that Bicknell's Thrush was generally able to mediate low reproductive years in odd years with high reproduction in even years, given relatively high adult survivorship on Stratton and the Octagon area on Mt. Mansfield. However, the low adult survivorship on the ridgeline area of Mt. Mansfield may cause this area to consistently act as a population sink. However, even the ridgeline confidence intervals for λ included 1.0 for all years combined. It appears that a tight balance exists between odd and even years, one that could be easily disrupted by both natural and anthropogenic affects on reproduction or survivorship, leading to a population decline.

We believe that balsam fir mast production sets off a chain reaction that moves throughout the food web and affects functioning of the forest ecosystem. We have developed a simple, conceptual model of this system based on our observations and published studies from other forested systems (Fig. 3). Recognizing the importance of primary producers in ecosystems (Hunter and Price 1992), our model is based on the overwhelmingly dominant tree species, balsam fir. Our conceptual model is meant to highlight the occurrence or strength of interactions between units that depend upon the existence of other interactions in the system (Ostfeld et al. 1996).

Our data clearly indicate changes in red squirrel populations and open-cup nesting passerine productivity, resulting either directly or indirectly from balsam fir mast. As our conceptual model depicts (Fig. 3), our field observations suggested that other species were heavily affected by balsam fir masting. White-winged Crossbills (*Loxia leucoptera*) and Pine Siskins (*Carduelis pinus*) were very abundant during early summer after mast years, but scarce or not present after non-mast years. We occasionally

mist-netted recently fledged young of both species in late May to early June. Adult and juvenile Northern Saw-whet Owls (*Aegolius acadicus*) appeared to be more abundant after masting, presumably in response to increased numbers of small mammals such as red-backed voles (*Clethrionomys gapperi*), which we observed in their bills several times. Red-backed voles are common prey in subalpine and presumably boreal forests (Cannings 1993). Northern Saw-whet Owls may prey upon young birds or adults. We have observed adult Bicknell's Thrushes mobbing both adult and juvenile Northern Saw-whet Owls, indicating that they are perceived as potential predators. We postulate that long-tailed weasels (*Mustela frenata*) may also be more abundant after mast years due to increased populations of small mammals. This may in turn affect bird populations. King (1983) found a strong relationship between beech seedfall, mice populations, and demographic and dietary responses of stoats. Mast years increased mice populations, the primary prey for stoats. Stoat populations increased, but the high mouse populations were apparently not high enough to offset high bird predation by stoats. Dunn (1977) found that weasel predation upon tit species was related to both small mammal and nesting bird density. These studies coupled with our field observations of several adult Bicknell's Thrushes cached with puncture wounds to the skull from canine teeth lead us to postulate a relationship between small mammal populations, weasels and birds in this forest too. Finally, our model showing the cascading events created by fir mast comes full circle to cause indirect herbivorous damage to trees and other plant species in this forest. Several studies have found evidence for decreased Lepidoptera abundance and decreased herbivory levels (Holmes 1990, Marquis and Whelan 1994, Strong et al. 2000), coupled with decreased biomass production of trees the following year (Marquis and Whelan 1994). This effect remains unstudied in montane balsam fir forests, but could be suppressed in years after mast, due to lower bird recruitment following poor breeding years (Hartley 2001).

Balsam fir mast production appears to be a keystone resource in the montane forests of northeastern United States and perhaps similar habitats in highlands of adjacent Canada or other areas in which it is the predominant tree species. We believe we have identified some critical links between key units in the montane fir forest system, increasing our understanding of the importance of indirect multi-trophic-level interactions in this forest system. Further work on aspects of our conceptual model that have been little studied may support the notion of both top-down and bottom-up ecological processes controlling different key functional units in this system as well as the relative strengths of these interactions as mediated by the variation in primary productivity.

LITERATURE CITED

- Anders, A.D., D.C. Dearborn, J. Faaborg, and F.R. Thompson III. 1997. Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11: 698-707.
- Angelstam, P. 1986. Predation of ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47: 365-373.
- Bayne, E. M., and K. A. Hobson. 1997a. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- Bayne, E.M. and K. A. Hobson. 1997b. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. *Ecography* 20:233-239.
- Boag, D. A., S. G. Reeb, and M. A. Schroeder. 1984. Egg loss among spruce grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62:1034-1037.
- Budnik, J.M., M.R. Ryan, and F.R. Thompson III. 2000. Demography of Bell's vireos in Missouri grassland-shrub habitats. *Auk* 117: 925-935.

- Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Canning, R.J. 1993. Northern Saw-whet Owl (*Aegolius acadicus*). No. 42 in A. Poole and F. Gill, editors. The Birds of North America. The Academy of Natural Sciences, Philadelphia, PA.
- Collier, B. and G.E. Wallace. 1989. Aging Catharus thrushes by rectrix shape. J. Field Ornithol. 60: 230-240.
- Cooch, E. and G. White. 2001. Using MARK: a gentle introduction (2nd Edition). <http://www.phidot.org/software/mark/docs/book/>.
- DeGraaf, R. M. 1995. Nest predation rates in managed and reserved extensive northern hardwood forests. Forest Ecology and Management **79**:227-234.
- Dunn, E.K. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. J. Anim. Ecol. 46: 633-652.
- Fauth, P.T. 2001. Wood thrush populations are not all sinks in the agricultural midwestern United States. Conservation Biology 15: 523-527.
- Flaspohler, D.J., S.A. Temple and R.N. Rosenfield. 2001. Effects of forest edges on ovenbird demography in a managed landscape. Conservation Biology 15: 173-183.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammalogy Review **13**:133-148.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology **10**:188-202.
- Hartley, M. 2001. Effects of red squirrel (*Tamiasciurus hudsonicus*) population fluctuations on bird population trends.
- Hatt, R.T. 1929. The Red Squirrel: Its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. Roosevelt Wildlife Annals 2: 11-146.
- Hensler, G.L. and J.D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93: 42-53.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651-661.
- King, C.M. 1983. The relationship between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*) in three New Zealand forests. Journal of Animal Ecology 52: 141-166.
- Lebreton, J-D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.
- Martin, T.E and J.J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90: 51-57.

- Martin, T.E. 1993. Nest predation and nest sites: New perspectives on old patterns. *Bioscience* **43**:523-532.
- May, R.M. and S.K. Robinson. 1985. Population dynamics of avian brood parasitism. *American Naturalist* **126**: 475-494.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255-261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456-466.
- Morris, R.F. 1951. The effects of flowering on the foliage production and growth of balsam fir. *Forestry Chronicle* **27**: 40-57.
- Ostfeld, R.S., C. Jones and J.O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. *Bioscience* **46**: 323-330.
- Pulliam, R.H. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**: 652-661.
- Pyle, P. 1997. Identification guide to North American passerines. Part I: Columbidae to Ploceidae. Slate Creek Press, CA. 732 pp.
- Ricklefs, R.E. 1973. Fecundity, mortality, and avian demography. Pages 366-434 in D.S. Faron, Editor. *Breeding biology of birds*. National Academy of Sciences, Washington, D.C.
- Rimmer, C.C., K.P. McFarland, J.E. Goetz, W. Ellison. 2001. Bicknell's Thrush (*Catharus bicknelli*). In *The Birds of North America*, No. 592 (A. Poole and F. Gill, eds.). The Birds of North America, Philadelphia, PA.
- Sauer, J.R. and B.K. Williams. 1989. Generalized procedure for testing hypotheses about survival and recovery rates. *J. of Wildl. Manage.* **53**: 137-142.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* **79**:2391-2402.
- Sloan, S.S., R.T. Holmes, and T.W. Sherry. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* **62**:529-539.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* **79**:2890-?
- Vander Haegen, W. M. and R. M. DeGraaf. 1996a. Predation on artificial nests in forested riparian buffer strips. *Journal of Wildlife Management* **60**:542-550.
- Vander Haegen, W. M. and R. M. DeGraaf. 1996b. Predation rates on artificial nests in an industrial forest landscape. *Forest Ecology and Management* **86**:171-179.
- Wallace, G.J. 1939. Bicknell's Thrush: Its taxonomy, distribution, and life history. *Proc. Of the Boston Soc. Of Nat. Hist.* **41**: 211-402.
- White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** Supplement: 120-138.

Table 1. Bicknell's Thrush population parameters from Mt. Mansfield and Stratton Mountain, Vermont, USA.

Parameter	Mansfield		Stratton	
	Mast	No Mast	Mast	No Mast
Number of successful/unsuccessful nests	10/17	16/8	6/13	
Exposure days	334.5	391	186.5	3
Daily nest survival rate \pm SE	0.949 \pm 0.012	0.980 \pm 0.0072	0.930 \pm 0.0187	0.992 \pm 0.0
Predicted nest success (%)	24.5	57.2	14.2	
Mean clutch size successful nests \pm SD	3.33 \pm 0.5	3.63 \pm 0.5	3.33 \pm 0.52	3.71 \pm
Mean number fledged successful nests \pm SD	2.7 \pm 1.06	2.71 \pm 1.05	2.33 \pm 0.52	2.88 \pm
Mean per capita annual productivity per female	0.86	1.94	0.36	
Mean female per capita annual productivity per female	0.43	0.97	0.18	
Annual adult survival \pm SE	Ridge: 0.495 \pm 0.057		0.643 \pm 0.074	
	Octa: 0.707 \pm 0.084			
	Mansfield: 0.56 \pm 0.047			
Annual juvenile survival	Ridge: 0.248		0.322	
	Octa: 0.354			
	Mansfield: 0.28			
(λ) finite rate of increase (95% CI)	Ridge: 0.6 (0.45-0.9)	0.8 (0.5-1.1)	0.8 (0.5-1.0)	1.1 (0.8-1.3)
	Octa: 0.9 (0.7-1.3)	1.1 (0.9-1.5)		
(λ) for all years combined	Ridge: 0.8 (0.6-1.0)	Octa: 1.0 (0.8-1.3)	0.99 (0.7-1.3)	

Figure 1. Time series depicting the relationship between autumn balsam fir cone mast followed by summer red squirrel density and daily survival rates of open-cup nesting passerines on, (A) Mt. Mansfield, Vermont and (B) Stratton Mountain, Vermont, USA.

Figure 2. The estimated population growth rate (λ) for Bicknell's thrush populations on Mt. Mansfield and Stratton Mtn., Vermont. Ridge and Octagon subplots were located at separate elevations and are depicted separately due to statistically significant differences in adult survival (S_a). They are also combined under Mt. Mansfield to illustrate λ levels for the entire population on the mountain. Assuming closed populations, solid line indicates stable population level ($\lambda = 1$). Error bars indicate 95% confidence intervals. See Methods for a complete description of the procedure.

Figure 3. Conceptual model of the relationships among key units in the montane fir forests of northeastern North America. Arrows show the predominant influence between units. Solid lines indicate an increase in density or biomass from the donor unit resulting in an increase in the recipient unit, dashed lines indicate a decrease in the recipient level. Heavy lines represent connections well established by observational or experimental data; light lines indicate relationships that are not well documented or are only postulated.