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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only one instance of a female attempting a third nest and only one doublecorrelated to red squirrel populations (

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 documened 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 *(Clethrionymys 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 (MuelowidGamdencl]TJfi. 2000), cou02

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

Parameter	Mansfield		Stratton
	Mast	No Mast	Mast

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 (*Sa*). 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 (λ = 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.