

ALTERNATE YEAR BEECHNUT PRODUCTION AND ITS INFLUENCE ON BEAR AND MARTEN POPULATIONS

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Abstract

Wildlife managers in the northeastern USA are interested in determining the amount of American beech (*Fagus grandifolia*) needed on the landscape to support bear and other wildlife populations. The need to understand the dynamics between beechnut production and wildlife populations is heightened by the impact of beech bark disease and the increased use of intensive forestry practices on commercial forests in the Northeast. Long-term monitoring of Maine's black bear (*Ursus americana*) and marten (*Martes americana*) populations indicate that alternate year patterns in bear reproduction and marten harvest rates may be correlated to beechnut production. In northern Maine, 22% of the female black bears that were reproductively available reproduced following falls when beechnut production was poor. The proportion of reproducing females increased ($P < 0.001$) to 80% following falls when beechnut production was high. After 21 years of a consistent alternate year pattern in bear reproduction, the pattern changed in 2003. In 2003, the proportion of females producing cubs did not increase as expected but rather increased in 2004, after a poor beechnut crop. For marten, trapping harvests rates exhibited a strong alternate year pattern, where harvest rates during odd-numbered years were double that of even-numbered years. Marten harvest patterns were similar ($P < 0.001$; $r^2 = 0.65$) in northern Maine and the Adirondacks of New York, and appeared to be inversely related to beechnut production. Beechnut production in the Adirondacks was cyclical (first order autocorrelation of -0.69) and fluctuated in an alternate year pattern from 1993 to 2003. We propose two hypotheses to explain the

variation in marten harvest rates. (1) Marten harvests decrease during years when beechnut production is good because of the decreased vulnerability of marten to baited traps. (2) Increased energy intake during a good beechnut year increases marten kit production or survival. This results in a large number of juveniles that may be trapped the following fall and increases the overall number of marten taken by trappers.

Introduction

Throughout the range of American beech (*Fagus grandifolia*), beechnuts are an important food for many species of wildlife (e.g., Glover 1949; Nixon et al. 1968; Gysel 1971). However, it is in the northern most part of this tree's range, where other mast producing trees (e.g., oaks [*Quercus* spp.]) are scarce, that beechnuts may have their greatest influence on wildlife populations (McLaughlin et al. 1994, McDonald and Fuller 1994). In Maine, beech trees normally have crop failures every other year (i.e., on odd-numbered years) and good nut production on even-numbered years (Schooley 1990). This alternate year pattern of beechnut production may influence the behavior and population demographics of a number of wildlife species (e.g., McLaughlin 1998).

Wildlife managers in the northeastern USA are interested in determining the amount of American beech needed on the landscape to support black bears (*Ursus americana*) and other wildlife populations. Over the last 10 years, intensive forest management practices have increased the rate at which beech trees are being removed from commercial forests. In addition, beech bark disease remains prevalent in the Northeast, which may decrease the quantity of beechnuts produced over the lifetime of infected trees (but see McNulty and Master this proceedings). To insure that enough mature (40 yr +) beech trees are available for wildlife and that commercial forests remain productive, wildlife managers would like to develop science-based guidelines for foresters to use in managing beech as an important forest component. As a first step towards achieving this goal, we (1) reexamined beechnut production patterns in the Adirondack Mountains of northern New York and Maine, (2) tested the hypothesis that alternate year production of beechnuts influences black bear reproduction in northern Maine, and (3) examined the relationship between beechnut production and American marten (*Martes americana*) trapping harvests in Maine and northern New York.

Bears in the Northeast preferentially feed on high-energy foods, especially hard mast, such as beechnuts and acorns, when they are available (Hugie 1982; Elowe and Dodge 1989; Costello 1992; McDonald and Fuller 1994). Beechnuts have a protein content equivalent to corn (ca 11% dry mass) and a fat content (ca 17.3% dry mass) that is >5 times the fat content of corn (Elowe and Dodge 1989). The fat content of beechnuts may be particularly attractive to black bears. Black bears depend on internal fat deposits for the energy needed for hibernation and reproduction, and hence, feed on foods that maximize their caloric intake (Nelson et al. 1983; Harlow et al. 2002).

Food availability or nutrition is often the factor that limits the growth of black bear populations, with the reproductive success of females, being the most important factor influencing population growth (Garshelis 1994). Females that do not attain a certain mass threshold will not produce offspring (Elowe and Dodge 1989; Samson and Huot 1995), and the percentage of females producing cubs decreases during poor food years (Rogers 1976). Nutrition also influences the age of first reproduction (Rogers 1987). In states like Pennsylvania, where the variety of foods provides bears a high level of nutrition every year, females usually produce cubs by age 4 (Rogers 1987). In contrast, the mean age of first reproduction for female bears in northern Maine is 6 years, because one of their primary fall foods (i.e., beechnuts) is not available every year (McLaughlin et al. 1994). In addition to the effect nutrition can have on reproductive rates, nutrition may also affect cub survival (Rogers 1976, 1987).

The American marten is a forest dwelling species that opportunistically feeds on a variety of small mammals (e.g., red-backed voles [*Clethrionomys gapperi*], snowshoe hare [*Lepus americanus*], and red squirrels [*Tamiasciurus hudsonicus*]), fruits, and nuts (e.g., raspberries [*Rubus* spp.]; Martin 1994; Lachowski 1997). Although the use of beechnuts by marten has not been well described, fisher (*Martes pennanti*), a closely related species, will consume large amounts of beechnuts (Brown and Will 1979). Marten have high energetic requirements and little (5%) body fat (Buskirk and Harlow 1989); therefore, food availability readily influences their behavior and survival. Variation in beechnut production may affect prey abundance and availability, because many of the marten's prey species use beechnuts as a food

source. Beechnut production may also influence the vulnerability of marten to trapping. Marten are trapped for their fur in several jurisdictions in the Northeast using baited traps. In Maine, which has the largest population of marten of any state except Alaska, between 2000-5000 marten are trapped every year. The vulnerability of marten to bait is believed to change with food availability, and marten harvest rates appear to be inversely related to beechnut production.

Methods

Bear Reproduction

Information on black bear reproduction was collected on 3 study areas in Maine from 1982 to 2004. Study areas are described in McLaughlin et al. (1994) and Schooley (1990). The northernmost study area, Spectacle Pond, was located 27 km SW of Ashland, Maine. The area was >95% forested with spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) being the dominant tree species on lowland sites and a complex of sugar maple (*Acer saccharum*), beech, and yellow birch (*Betula alleghaniensis*) dominating the well-drained upland sites. The study area was representative of the region, which was primarily managed as commercial forestland for pulp production. During the fall, bears in this area primarily fed on beechnuts (Hugie 1982, McLaughlin et al. 1994), when they were available, and other hard and soft mast crops (e.g., beaked hazel [*Corylus cornuta*] and wild cherries [*Prunus* spp.]). The Stacyville site was located in north central Maine about 88 km SE of Spectacle Pond. The study area was about 80% forested with agricultural fields adjacent to wooded areas. Fall foods for bears in the Stacyville area included grain crops, soft mast, and hard mast (including beechnuts). The Bradford study area, the southernmost study site, was located in central Maine about 90 km SW of Stacyville. The Bradford study area was about 92% forested and interspersed with a mix of agriculture and residential areas. Bears in this study area primarily fed on grain and apple crops in the fall and some red oak (*Quercus rubra*) acorns in the fall. Beechnuts were uncommon in this area.

Bears were caught in foothold restraints, in late spring to early summer. Body size and mass were measured, and a premolar was extracted for age determination as described in McLaughlin et al. (1994). Female bears were radiocollared and monitored by fixed-wing aircraft throughout the year (McLaughlin et al. 1994). In January and February, crews located the females' dens and

chemically immobilized adult females for collar replacement and collection of morphometric and reproductive data. Cub production was determined from in-den counts of neonates (McLaughlin et al. 1994).

We tested the hypothesis that alternate year beechnut production has no influence on bear reproductive rates by comparing bear reproductive rates from Spectacle Pond, where bears heavily utilized beech, to bear reproductive rates from the Stacyville and Bradford study sites, where beechnuts make up a smaller component of their fall diet. If beechnuts had no influence on bear reproductive rates, we would expect reproductive rates to be equivalent among the three study sites and across years (i.e., no difference in reproductive rates among even- and odd-numbered years). Comparisons among study sites were limited to the period from 1983 to 2000, because 1983 was the first year all study sites had radiocollared bears and by 2000 the number of radiocollared females had declined to only 4 animals at the Stacyville study site (bears were no longer being collared at this site). We tested whether the proportion of reproductively available females (i.e., radiocollared females ≥ 4 yr of age that were not accompanied by offspring when they entered dens in the fall) that produced cubs differed among study sites during even- and odd-years using one-way Analysis of Variance (ANOVA). Female bears ≥ 4 yr of age were chosen for comparison because earliest reproduction occurred at 4 years of age in all three study areas (McLaughlin et al. 1994). Duncan's Multiple Range Test was used to isolate significant differences among means (Ott 1984). Differences in bear reproduction rates within a study site during even- and odd-years were compared using paired t-tests.

Marten Harvest Rates

Marten harvest rates in Maine were determined from pelt tagging records from Wildlife Management Unit (WMU) 2. Maine's WMU 2 encompassed approximately 20,738 km² of northwestern Maine and included portions of Aroostook, Somerset, Penobscot, and Piscataquis counties. This WMU contained the best marten habitat in the state (MDIFW 1990, unpublished data, MDIFW). The landscape in WMU 2 primarily consisted of rolling hills to mountains dominated by spruce-fir forests interspersed with northern hardwoods (similar to the Spectacle Pond study site). Most of this WMU was privately owned and managed as commercial

forest. The marten trapping season, in Maine, ran from approximately November 1 through December 31. Marten trappers were limited to 25 marten/trapper/yr from 1990 until present. Prior to 1990, there was no limit on the number of marten an individual trapper could take in a season.

Marten harvest rates in northern New York were determined from pelt tagging records. Open trapping areas for marten included approximately 15,540 km² of Adirondack Park (WMU 5F, 5H, and 6J) in northern New York. Marten were trapped from the last week of October through mid-December (season length ranged 37-46 days). The marten harvest in New York was restricted to 6 marten/trapper/yr.

Marten trapping records from 1980 to 2004 from Maine's WMU 2 were used to investigate long-term patterns in marten harvest rates. We investigated the relationship between beechnut production and marten harvest rates in New York and Maine using linear regression (Zar 1984). Data from 1990 to 2002 were used for this comparison because Maine initiated a 25 marten harvest limit in 1990, and beechnut production data was not available for the Adirondacks until 1988.

Beechnut Production

Beechnut production in New York was measured at the Huntington Wildlife Forest. The Huntington Wildlife Forest is a 6,000 ha research facility in the central Adirondack Mountains (74° 15' N, 44° 00' W) operated by the State University of New York, College of Environmental Science and Forestry, and is further described in McNulty and Masters (these proceedings). Beechnut production was measured at the stand level from 1988 to 2003 on fifty circular plots (McNulty and Master, this proceedings). From July to November each year, seed traps (13.9 L [5 gal] buckets) were located in the center of each plot. Seed production was estimated from each seed trap for northern hardwood and mixed conifer-hardwood stands (Adirondack Long-Term Ecological Monitoring Program Project #26: Seed Production Survey). We compared beechnut production at Huntington Wildlife Forest to beechnut production in other jurisdictions by characterizing beechnut production using the Durbin Watson statistical test for autocorrelation (SAS Institute 2001) and the first order autocorrelation output. The first order autocorrelation

output is equivalent to the lag 1 autocorrelation function used by Piovesan and Adams (2001) to characterize beechnut production cycles.

Beechnut production in Maine was noted at the Spectacle Pond study site and other sites in northern Maine each fall from 1982 to 2004. Beechnut production was classified as scarce or abundant based on observations by biologists and anecdotal reports.

Results

Bear Reproduction

The proportion of reproductively available females bearing cubs at the Spectacle Pond study site fluctuated in an alternate year pattern from 1982 to 2000 (Fig. 1). In 2001 and 1987, the alternate year pattern of cub production appeared to be attenuated. For both years, the attenuation in the alternate year pattern can be attributed to a large cohort of 4-year old female bears being included in the sample. Although female bears at this study site can reproduce at 4 years of age, they often delayed sexual maturity and first reproduced at 6 years of age (McLaughlin et al. 1994). Therefore, it is likely that most of the 4-year old females were sub-adults and not reproductively available. In 1987, 6 of the 15 reproductively available females ≥ 4 yr of age were 4-year olds. Excluding this cohort from the calculation, 100% ($n=9$) of the available females ≥ 5 yr of age had cubs in 1987. In 2001, 8 of the 15 females that were ≥ 4 yr of age were 4-year old bears. Excluding this cohort from the calculation, 87% ($n=7$) of the available females ≥ 5 yr of age had cubs in 2001, which is in line with the usual alternate year pattern of reproduction (Fig. 1). In 2003, the normal pattern of increased cub production did not occur. This was associated with a lower level of beechnut production than was expected in Maine fall of 2002. The proportion of females bearing cubs in 2004 did not follow the traditional alternate year pattern and was higher than expected (Fig. 1).

The proportion of reproductively available females bearing cubs differed ($F = 6.64$; $df = 2, 24$; $P = 0.005$) among the three Maine study sites during even-years, i.e., years following falls when few beechnuts were produced (Fig 2). Post-hoc tests revealed that fewer ($\bar{X} = 22\% \pm 0.07$ SE) females at the Spectacle Pond study site produced cubs following poor beechnut crops than females at the Stacyville or Bradford sites ($\bar{X} = 58\% \pm 0.17$ SE; $\bar{X} = 76\% \pm 0.05$ SE), respectively.

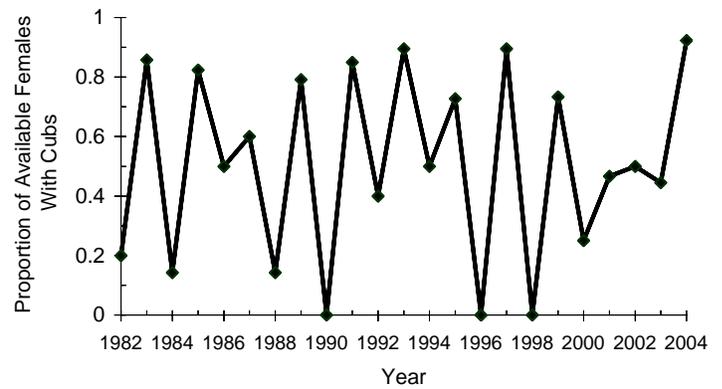


Figure 1.—Proportion of reproductively available female bears (i.e., radiocollared females ≥ 4 yr of age that were not accompanied by offspring when they entered dens in the fall) with cubs at the Spectacle Pond study site in Maine.

The proportion of females with cubs was not significantly different among the Stacyville and Bradford sites for those years.

The proportion of reproductively available females bearing cubs in odd-years, i.e., years following falls when beechnuts were abundant, did not differ ($F = 0.318$; $df = 2, 24$; $P = 0.730$) among the three study sites (Fig. 2). The percentage of reproductively available females producing cubs at the Spectacle Pond, Stacyville, and Bradford study sites was ($\bar{X} = 80\% \pm 0.03$ SE; $\bar{X} = 88\% \pm 0.06$ SE; $\bar{X} = 83\% \pm 0.11$ SE), respectively.

A significant difference in the proportion of reproductively available females bearing cubs from one year to the next was only seen at the Spectacle Pond study site ($P < 0.001$) (Fig. 2). At Stacyville, where beechnuts were less abundant, the year-to-year difference in the proportion of reproductively available females bearing cubs was less evident ($P = 0.116$), and there was no difference ($P = 0.523$) at the Bradford study site where beech is uncommon.

Marten Harvests

In Maine, the marten harvest in WMU 2 fluctuated in an alternate year pattern from 1980 to 2003 (Fig. 3). This alternate year harvest pattern persisted through a period of over-trapping (i.e., 1984 to 1989), appeared to be somewhat attenuated from 1990 to 1994 (in 1990 a trapping limit was imposed of 25 marten / trapper /yr) and resumed a normal pattern until 2002. In 2002, the marten harvest did not decline as much as expected, and

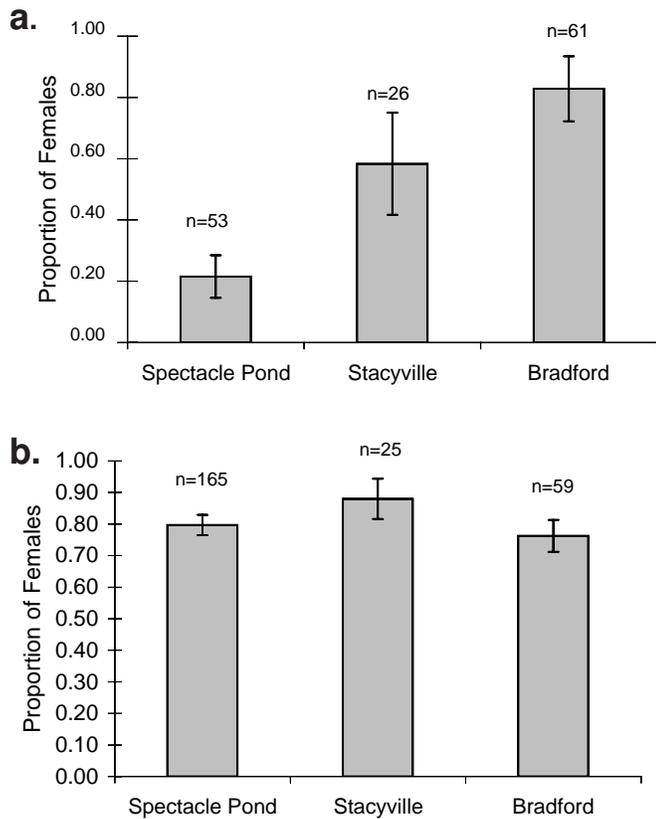


Figure 2.—Proportion of reproductively available female bears (i.e., radiocollared females ≥ 4 yr of age that were not accompanied by offspring when they entered dens in the fall) with cubs at the Spectacle Pond, Stacyville, and Bradford study sites in Maine during (a.) even-years that followed poor beechnut production and (b.) odd-years that followed good beechnut production from 1983 to 2000.

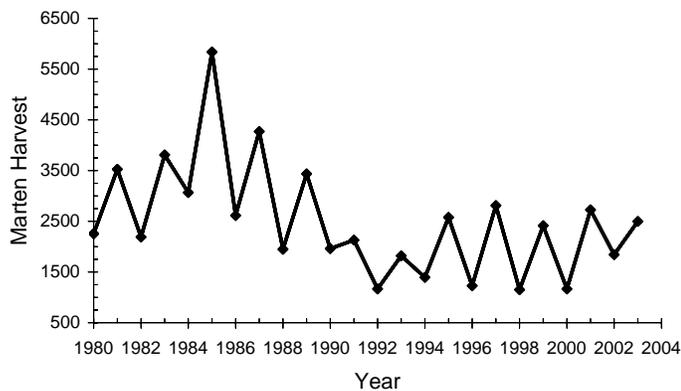


Figure 3.—Marten trapping harvest in Wildlife Management Unit 2 in Maine.

was the highest even-year harvest since the 25 marten limit was imposed. The 2003 harvest was similar ($P = 0.487$, $r^2 = 0.158$) to the past 4 odd-numbered year harvests from (1995 to 2003).

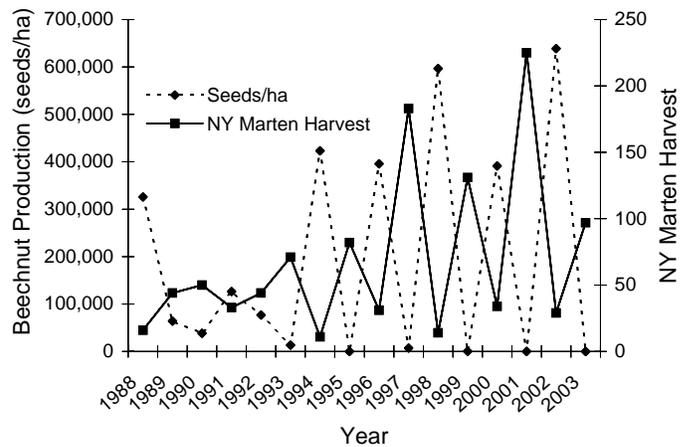


Figure 4.—Marten trapping harvests from Adirondack Park (Wildlife Management Units 5F, 5H, and 6J) in New York compared to beechnut production from the Huntington Wildlife Forest, central Adirondacks. Beechnut production was measured using seed traps on 50 circular plots.

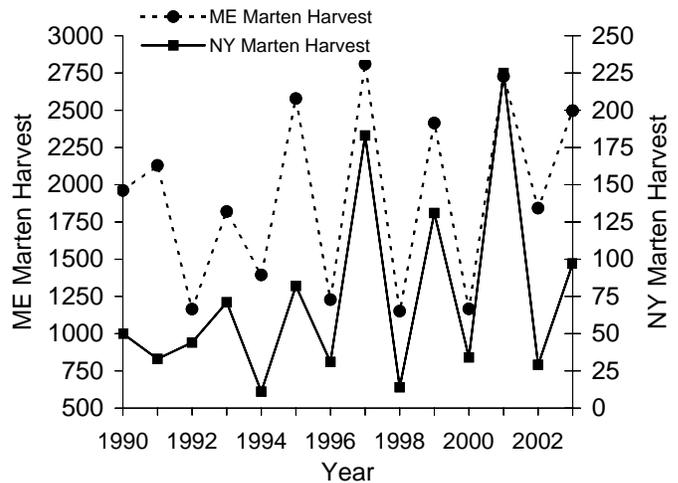


Figure 5.—A comparison of Maine's marten trapping harvests from Wildlife Management Unit 2, to New York's marten trapping harvest from Adirondack Park (Wildlife Management Units 5F, 5H, and 6J).

The New York marten harvest from 1990 to 2003 fluctuated in an alternate pattern from 1993 until 2003. For that period, the marten harvest pattern was inversely related to beechnut production in New York (Fig. 4). From 1988 until 1993, neither beechnut production nor the marten harvest fluctuated in an alternate year pattern. The New York marten harvest was correlated ($P < 0.001$; $r^2 = 0.65$) to the Maine marten harvest (Fig. 5), with the greatest disparity between the data sets occurring from 1990 to 1992, and in 2002 when the Maine harvest rate declined proportionally less.

Beechnut Production

In the Adirondacks, beechnut production in hardwood forests fluctuated in an alternate year pattern starting in 1993, with the heaviest nut production occurring during the fall of even-numbered years (Fig. 4). Nut production ranged from complete mast failures, during 4 years, to an estimated high of 638,712 beechnuts/ha in fall 2002 (Fig. 4). Beechnut production during Fall 2004 was low, breaking the pattern of heavy nut production on even years. Year-to-year beechnut production in the Adirondacks was characterized as having a first order autocorrelation of -0.69 (Durban Watson = 3.26), which is indicative of a negative serial correlation (Ott 1984). That is, beechnut production in a given year was inversely related to beechnut production the following year.

In Maine, beechnut production appeared to fluctuate on an alternate year basis from 1982 to 2001 with abundant crops occurring in even-numbered years and less production in odd-numbered years. In Fall 2002, and through Fall 2004, beechnut production did not appear to follow the alternate year pattern of production observed the previous 20 years. In particular, beechnut production was notably scarce during Fall 2004.

Discussion

We reject the null hypothesis that alternate year beechnut production does not influence black bear reproduction in northern Maine. At the Spectacle Pond study site, where beechnuts were an important fall dietary item for bears, the mean proportion of female bears producing cubs decreased to 22% when a denning period followed a poor beechnut crop. However, during denning periods following good beechnut production, 80% of the reproductively available females produced cubs. The proportion of females producing cubs did not differ among years at the other two study sites where beechnuts were a less important fall food item. At these study sites, bears utilized agricultural crops and soft mast, which are more dependable on a year-to-year basis (McLaughlin et al. 1994). Consequently, cub production at these study areas was more consistent on a year-to-year basis. During years of good beechnut production, the proportion of reproductively available females bearing cubs among the three study areas was equivalent. This indicates that bears at the Spectacle Pond site had the same reproductive potential as bears at the other study sites when food resources were plentiful.

McLaughlin et al. (1994) and McLaughlin (1998) proposed that the differential cub production rates among the study sites might be explained by the mass gain of mature females prior to hibernation. Following good beechnut years, the in-den mass of fully-grown females (i.e., females ≥ 7 yr of age that did not den with yearlings) was similar ($\bar{X} = 67$ kg) among the three study sites (McLaughlin et al. 1994). However, following poor beechnut years, the mass of females ≥ 7 yr of age declined significantly at Spectacle Pond (from 69.8 kg to 53.8 kg) but not at the other study sites. The low mass of females, at Spectacle Pond following a poor beechnut crop, likely indicates that fewer females attained sufficient mass for reproduction.

Beechnut production in Maine appeared to follow a regular alternate year pattern from 1982 until 2001; however, as of Fall 2004, Maine had 3 consecutive years of sparse beechnut production. Despite the scarcity of beechnuts in Maine, a high proportion of reproductively available females produced cubs at the Spectacle Pond study site in 2004. This would appear to indicate that good cub production, in northern Maine, is not necessarily contingent upon good beechnut production the preceding fall. We do not have an explanation for why a high proportion of females produced cubs in absence of a good beechnut crop. Bears are opportunistic feeders and will exploit alternative foods if they are abundant. Since females must receive adequate nutrition for cub production to occur, we have to assume that sufficient alternative foods were available in 2003. The mass of females ≥ 7 yr of age that denned without yearlings was similar (i.e., 65.6 ± 4.7 kg and 64.5 ± 4.0 kg) in 2003 and 2004 at Spectacle Pond. Their mass was somewhat higher than the mass (53.8 ± 12.8 kg) of females (same class and location) that denned following poor beechnut crops from 1982 to 1991 (McLaughlin et al. 1994). The higher mass of denning females in 2003 and 2004 raises the question of whether an alternative food source became more prevalent in recent years. Unfortunately, Maine's Department of Inland Fisheries and Wildlife did not collect enough detailed information on hard and soft mast production to determine whether an alternative food was particularly abundant those years, or whether the distribution of foods has been altered with recent changes in forest harvesting practices. Currently, states in the Northeast are considering a region-wide mast production survey. We strongly support such initiatives and hope this study serves as an example

of how mast production information can be integral to understanding the dynamics of wildlife populations.

The sparse beechnut production in Maine in 2002 and 2004 is not known to be related to any particular climatological event, and may be within the normal variation expected for beechnut production. In other regions (e.g., Michigan; Gysel 1971), beechnut production did not follow the consistent alternate year pattern we observed. High levels of beechnut production are usually associated with a wet period, 2 years prior to the masting event, followed by a hot dry summer, 1 year prior to the masting event (Piovesan and Adams 2001). Maine and other areas in the northeast experienced drought conditions in 2001 and 2002. Although beechnut production at the Huntington Wildlife Forest in New York was the highest in 15 years in 2002, beechnut production was not high in Maine. We do not know why beechnut production in the Adirondacks during the late 1980's and early 1990's differed from the alternate year pattern reported in Maine.

Beechnut production, as measured at the Huntington Wildlife Forest in the Adirondacks, appears to alternate between years in a cyclical pattern similar to other beech populations (e.g., Piovesan and Adams 2001). Beechnut production in the Adirondacks was characterized as having a first order autocorrelation of -0.69. This level of autocorrelation was similar to the level calculated for beechnut production in Michigan (-0.74) from 1959-1968 but higher than what was reported in New Hampshire (0.05 and -0.48) for 1971-1981 and 1976-1981 (Piovesan and Adams 2001). Based on data from New Hampshire (i.e., Graber and Leak 1992) and northern England, Piovesan and Adams (2001) proposed that beech at the northern limits of their range did not cycle, and produced few beechnuts because of the stresses associated with cold climates. We question this conclusion based on beechnut production at the Huntington Wildlife Forest and in Maine. The Adirondacks and northern Maine are well known for cold, severe winters and yet have strong beechnut cycles and abundant nut crops. The disparity between the conclusions of Piovesan and Adams (2001) on beechnut production in northern latitudes and our data emphasizes the need to exercise caution when comparing beechnut production rates among studies. For example, the highest nut production (in 2002) at Huntington Wildlife Forest was 64 nuts/m², which might be

interpreted as evidence of a very low nut production rate as compared to the 658 nuts/m² Gysel (1971) reported in Michigan. However, the measurement of 64 nuts/m² represents beechnut production in northern hardwood and mixed conifer/hardwood stands, while the measurement of 658 nuts/m² represents nut production under individual beech trees (Gysel 1971).

Harvests rates for marten in Maine and the Adirondacks varied in an alternate year pattern and were highly correlated to each other. This year-to-year variation in marten harvest rates appears to be inversely related to alternate year patterns in beechnut production. Similar variations in marten and fisher harvests have been observed for over 100 years, although the periodicity of low and high harvests is not clear. Hardy (1899:526) wrote, "When in the fur trade, I used to buy 175 to 200 [fisher] skins annually. While these were not all taken in Maine, I think, from the best data I could get, that the annual catch of Maine was 150 to 300. The catch varies greatly in different years, just as that of Sables [marten] does, as some years both take bait better than others."

We propose two hypotheses as to why marten harvest rates varies inversely with beechnut production. The first hypothesis is an offshoot of the observations Hardy made 100 years ago, i.e., marten harvests decrease during years when beechnut production is good because their vulnerability to baited traps decreases. We hypothesize that during good beechnut years, small mammals will make heavy use of beechnuts and are easily preyed upon by marten. This increase in prey availability and the consumption of beechnuts by marten lowers the attractiveness of baited traps to marten. Secondly, we hypothesize that increased energy intake during a good beechnut year may increase marten kit production or survival, which results in a large number of juveniles being available for trapping the following fall. This large cohort of juveniles would increase the overall number of marten taken by trappers. We recognize that these two hypotheses may not be mutually exclusive.

The need to understand the dynamics between beechnut production and wildlife populations is heightened by the impact of beech bark disease and increased use of intensive forestry practices on commercial forests in the Northeast. Further work is needed to determine the alternative foods bears rely on when beechnuts are not available, and whether recent changes in forest harvesting

practices have affected the availability of these foods. This work is necessary if wildlife managers are to make recommendations to landowners on the amount of mature beech needed on the landscape. Additional studies are needed to understand how alternate year beechnut production affects the community dynamics of northern forests.

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