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Bottom–up trophic effects on fisher *Pekania pennanti* harvest age structure: associations with mast, voles and owls

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Harvest management quotas for fishers *Pekania pennanti* in some jurisdictions are estimated from the previous year's harvest, and stem from the hypothesis that age ratios in the harvest are largely influenced by 'top–down' trapping pressure. The influence of 'bottom–up' food supply on fisher harvest age ratios might be underappreciated, which could result in a misallocation of quotas in management planning. We assessed a variety of data sources to test the influence of bottom–up processes on fisher populations in Ontario, Canada. We found evidence that bottom–up trophic effects influence the harvested fisher age structure in some regions of Ontario. Evidence also suggests that harvest pressure had little top–down influence on age ratios over the course of our study, and that basing management strategies on this assumption may lead to unintentional overharvest in years of low productivity. We suggest several trophic linkages with potential to facilitate fisher management, including connections among berry and seed crops, small mammals and northern saw-whet owls *Aegolius acadicus*.

Keywords: *Aegolius acadicus*, harvest, mast crop, *Pekania pennanti*, small mammal, trophic levels

All organisms in natural systems are subjected to opposing but often unequal mechanisms of regulation and limitation – 'bottom–up' and 'top–down' (Hunter and Price 1992, Power 1992). The former refers to regulation through the availability of food or other necessities of life, whereas the latter refers to regulation through predation from organisms at higher trophic levels. These processes often occur concurrently, and their relative strengths can vary over space and time (Ostfeld and Keesing 2000, Letnic et al. 2011, Pierce et al. 2012). Understanding these opposing forces can be further complicated in game species, where harvest by humans acts as an additional source of top–down pressure. In these circumstances, the economic benefits of harvest must be balanced with the need for long-term sustainability. In harvested species, a range of possible bottom–up and top–down pressures, including harvest pressure, should be considered by wildlife managers when creating policy or setting harvest limits (e.g. quotas).

The fisher *Pekania pennanti* is a mustelid mesocarnivore endemic to North America that is important to the wild

fur market across much of its range. The fisher is primarily found in the boreal and mixed-wood forests of southern and central Canada and the northeastern United States, as well as some mountainous regions of the western United States and Canada (Gibilisco 1994). In the early 1900s, the fisher was extirpated from many parts of its historic range due to overharvest, habitat loss and persecution by humans (Douglas and Strickland 1987). Fishers have since recolonized or been reintroduced to parts of their former range (de Vos 1951, Thompson 2000, Lancaster et al. 2008), but where trapping is permitted it is still regulated and monitored to ensure sustainability. Fishers are susceptible to overharvest (Buskirk et al. 2012) because they breed only once per year and thus have a limited reproductive output. As a result, there is little opportunity for compensatory reproduction to offset high harvest levels. Douglas and Strickland (1987) found that fishers were susceptible to overharvest if harvest rates exceeded 20–25% of the pre-trapping population.

Fisher harvest limits have often involved quotas set in part through retrospective evaluation of age ratios in the harvest, based on recommendations from Douglas and Strickland (1987) and Strickland (1994). The idea underlying the use of age ratios to allocate harvest is based on the greater susceptibility of male and juvenile fishers to trapping (Strickland and Douglas 1981, Buskirk and Lindstedt 1989, Krohn et al. 1994). Trapping susceptibility might be due

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to the naiveté and greater dispersal of juveniles and to the larger home ranges of males (Strickland and Douglas 1981, Arthur et al. 1989, Krohn et al. 1994, Powell 1994). Such traits cause both juveniles and males to encounter traps more frequently than adult females and make juveniles more likely to enter traps when they are encountered (Powell 1994). Therefore, one would expect adult male and juvenile fishers to be overrepresented if only a small proportion of the population was harvested, but as more animals are harvested, age and sex ratios in the harvest would approach those of the census population (Douglas and Strickland 1987). Douglas and Strickland (1987) recommended the use of the juvenile-to-adult female ratio (J:AF) for assessing harvest because expected ratios can be estimated by considering female fecundity. The J:AF ratio is generated annually in the population when females give birth, unlike the adult male-to-adult female ratio which reflects the effects of multiple years of harvest. Based on counts of corpora lutea in reproductive females (> 2.5 years of age) in the Algonquin region of Ontario, Canada, Douglas and Strickland (1987) determined that an average of three juveniles per reproductive adult female are produced annually. Ratios of 5–7 juveniles per reproductive female are associated with stable harvests (Douglas and Strickland 1987). However, due to the difficulty of aging fishers without expensive cementum annuli counts, Douglas and Strickland (1987) suggested using a J:AF of > 3 juveniles for every adult female > 1.5 years of age. This was suggested because fishers that are at least this age can be identified for less cost via tooth X-ray (Dix and Strickland 1986) and the 3:1 ratio was also a reliable indicator of harvest intensity. Following trapping seasons where age ratios indicate < 3 juveniles for every adult female > 1.5 years of age, harvest quotas may be lowered for the next trapping season, and vice versa.

One criticism of Douglas and Strickland's (1987) suggested approach to fisher harvest management is that the method assumes that changes in the J:AF ratio are due to top-down harvest pressure, rather than bottom-up fluctuations in productivity. If one assumes that fisher productivity is constant, then there is a rationale for changing quotas for the coming trapping season based on an assessment of age ratios in last season's harvest. The idea of stable productivity and top-down pressure driving fisher population trends is not unanimously supported in the literature. For example, Kohn et al. (1993) found that fisher populations in Wisconsin were still increasing during times when the J:AF ratio indicated that an overharvest had occurred. Other studies have found evidence that fisher productivity can be highly variable (Frost and Krohn 1997, Green et al. 2018). One explanation for this may be changes in food availability. Fishers consume a wide variety of prey and seem capable of switching primary food sources (Powell 1979, Kuehn 1989, Bowman et al. 2006, McNeil et al. 2017), but several studies have identified correlations between the abundance of small mammal prey and productivity in mustelids (Thompson and Colgan 1987, Fryxell et al. 1999, Weber et al. 2002, King et al. 2003, Sundell et al. 2013). Fisher abundance has also been linked to productivity of mast crops through the influence of mast seed and fruit production (i.e. masting) on small mammal populations (Jensen et al. 2012). Additionally, there is evidence of a numerical response by fisher

populations to snowshoe hare *Lepus americanus* abundance in some locations (Bulmer 1974, Bowman et al. 2006), but not others (Van Why and Giuliano 2001, Jensen et al. 2012). Taken together, there is reason to expect that fisher J:AF ratios will vary over time, due to bottom-up factors known to influence productivity such as mast crop production and prey abundance.

If J:AF ratios vary due to bottom-up effects of food supply on productivity, and quotas are adjusted using knowledge of the previous harvest's J:AF ratios, this could lead to overharvest during years of low fisher productivity. This would be especially true in situations where productivity fluctuates widely each year, such as in the presence of processes leading to negative temporal autocorrelation at lower trophic levels. For example, Howe et al. (2012) showed that mast production by some berry species in year t and year $t - 1$ were negatively correlated.

There is evidence in some locations in Ontario that fishers may have been overharvested under a quota system informed by harvest age ratios, as fisher harvest was found to be negatively rather than positively related to the current season's J:AF ratio (Fig. 1). For harvest to be sustainable, it should instead be proportional to population growth (Fryxell et al. 2001). Jensen et al. (2012) hypothesized that monitoring of mast abundance or small mammal populations could be used to set harvest limits rather than the retroactive analyses of the previous season's harvest data. If indices of fisher food supply are predictive of fisher population growth and age structure, then these indices could be leading indicators of potential harvest. Such a strategy would reduce the potential for overharvest in populations that are regulated primarily by bottom-up mechanisms.

Another potential indicator of fisher productivity is the abundance or population growth rate of other small-mammal predators. For example, in central Ontario, northern

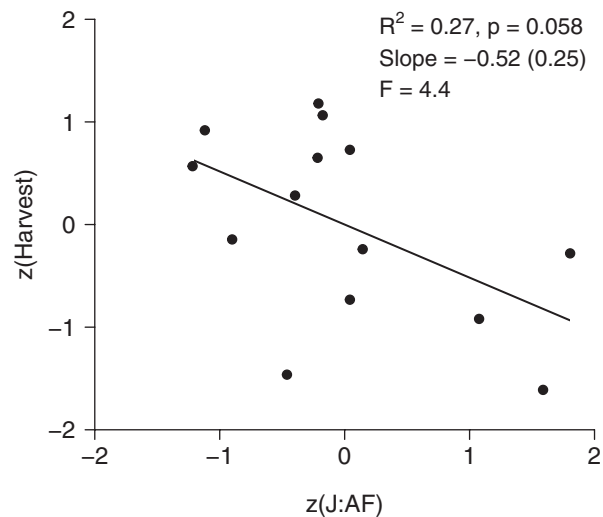


Figure 1. Fisher *Pekania pennanti* harvest juvenile:adult female (J:AF) ratios graphed against total harvest in the Kemptville management district of Ontario (includes the Fur Management Units of Carleton Place, Brockville and Cornwall) prior to 2005, when harvest quotas were removed. Data are z-transformed to a mean of 0 for standardized comparison across Kemptville Fur Management Units (FMUs).

saw-whet owl *Aegolius acadicus* populations are documented to increase in response to small mammal – particularly red-backed vole *Myodes gapperi* – abundance with no time lag (Bowman et al. 2010). This is presumably because owls select a breeding territory based on an assessment of vole abundance and undertake breeding migrations to areas with abundant vole populations (Bowman et al. 2010). Abundance of northern saw-whet owls across central Ontario is estimated every spring with a long-running and well-established volunteer survey organized by Birds Canada. If populations of owls and fishers are correlated, taking advantage of existing northern saw-whet owl data to aid in determining fisher harvest allocation may be a convenient and cost-effective option for wildlife managers.

In this study, we assessed available data in Ontario, Canada to explore relationships between fisher harvest age structure, mast crops, small mammals and another, more easily monitored small-mammal predator – the northern saw-whet owl. We made use of several data sources, including fur harvester submissions and long-term monitoring surveys. We predicted that if top-down harvest is the primary regulator of fisher populations, then J:AF ratios would fluctuate independently between neighboring management units, since harvest quotas are set independently in each unit. Alternatively, we predicted that if bottom-up mechanisms were the primary driver of fisher harvest age-ratios, then closer regions would display greater similarity in age ratios than more distant regions, regardless of harvest management regime. This is because both mast crops and small mammals – possible drivers of bottom-up regulation – display spatial synchrony within Ontario (Bowman et al. 2008, Howe et al. 2012). Further, we expected that if fisher age ratios are influenced by bottom-up mechanisms there should be positive relationships between J:AF age ratio and preceding estimates of small mammal abundance and tree seed production.

Both same year (King et al. 2003) and one-year lagged (Weber et al. 2002) responses to small mammal abundance have been demonstrated in other mustelid populations, and one or both mechanisms may influence fisher harvest age ratios. Increased small mammal abundance in the summer of the year preceding harvest (year $t - 1$) may increase the number of juveniles produced, and thus the J:AF ratio in the harvest, by increasing female fecundity (Thompson and Colgan 1987). Increased small mammal abundance in the summer immediately preceding the fisher harvest (year t) may increase the proportion of juveniles in the harvest by improving juvenile survival through increased food availability and reduced maternal stress (King et al. 2003). Given both of these possibilities, and the ability of mast crop productivity to positively influence small mammal abundance with a one-year time lag (McCracken et al. 1999, Elias et al. 2006, Krebs et al. 2010, Jensen et al. 2012), increased mast crop production also has the potential to positively influence fisher harvest age ratios with a one or two-year time lag ($t - 1, t - 2$; Fig. 2). Similarly, since northern saw-whet owls respond to changes in small mammal populations with no time lag, owl population growth rate may be positively correlated with fisher harvest age ratios later the same year or the following year ($t, t - 1$; Fig. 2).

Methods

Study area

Our study took place in the Great Lakes-St Lawrence East region of Ontario, which encompasses the southern range boundary of fishers within the province. We received fisher harvest data from 11 fur management units (FMUs) within this region (Fig. 3). These FMUs encompassed a vari-

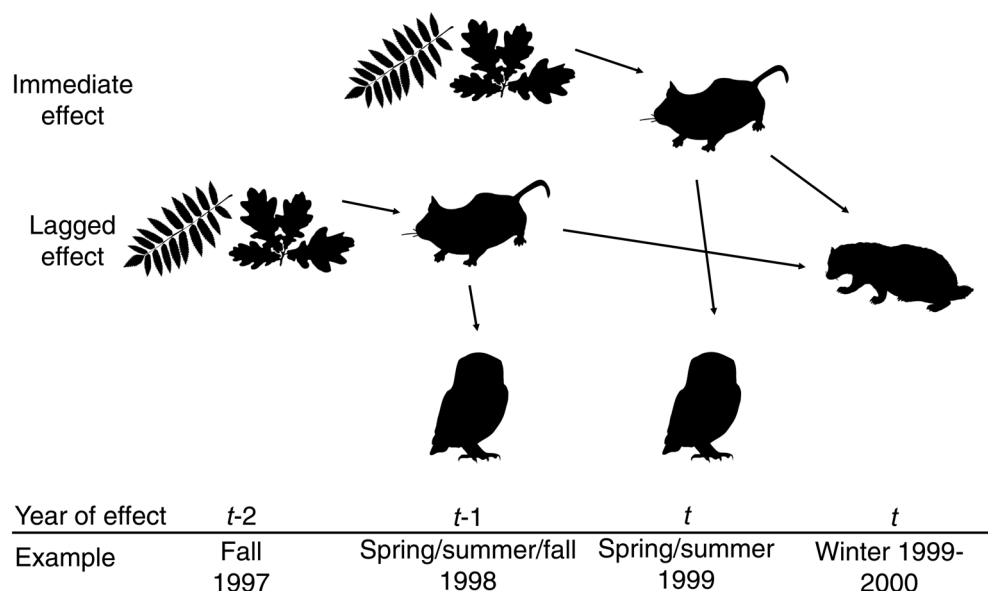


Figure 2. Possible trophic linkages in a Great Lakes-St Lawrence East forest community investigated in this study, including mountain ash *Sorbus* spp. and oak *Quercus* spp. productivity, red-backed vole *Myodes gapperi* abundance and exponential rate of increase, northern saw-whet owl *Aegolius acadicus* exponential rate of increase and fisher *Pekania pennanti* productivity, as represented by age structure in the harvest. We investigated two different frameworks centered on either immediate or one-year lagged effects of changes in small mammal abundance on fisher productivity.

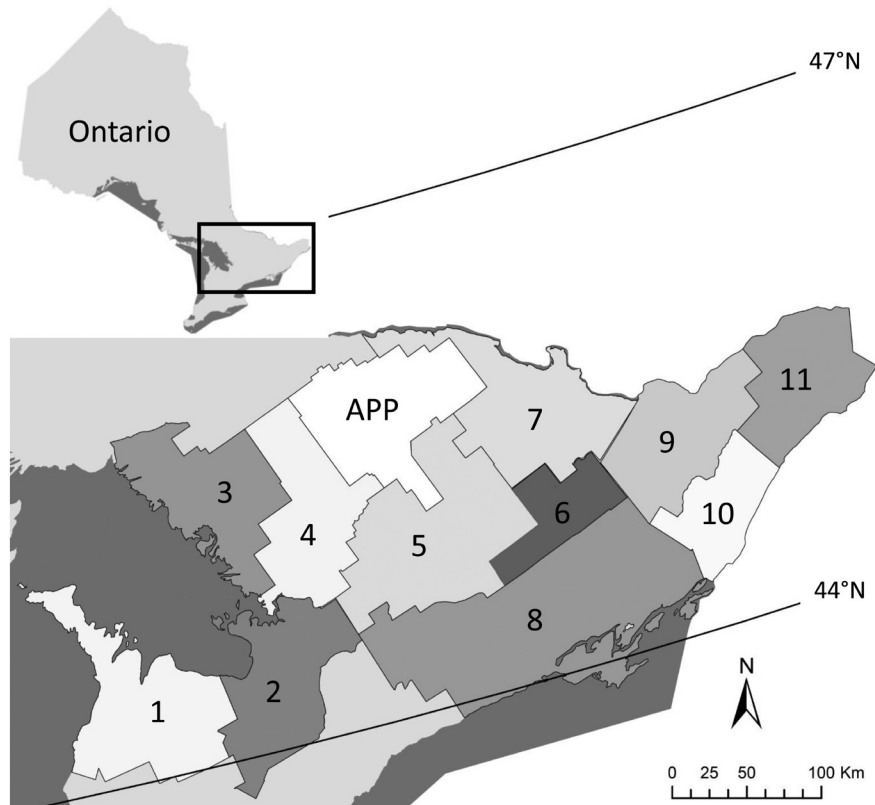


Figure 3. Map of the Great Lakes-St Lawrence East region of Ontario, Canada, showing the locations of 11 fur management units (FMUs) and Algonquin Provincial Park (APP). The 11 FMUs are: 1) Owen Sound, 2) Huronia, 3) Parry Sound, 4) Bracebridge, 5) Bancroft, 6) Mazinaw, 7) Pembroke, 8) Peterborough, 9) Carleton Place, 10) Brockville and 11) Cornwall. The three eastern FMUs (9–11) make up the Kemptville management district. The lines of latitude displayed on the map mark the boundaries of the northern saw-whet owl *Aegolius acadicus* survey region.

ety of landscapes, including units with more agricultural and developed land in the south, to more heavily forested and less populated units in the north. The areas of these FMUs ranged from 3408 km² (Mazinaw) to 15 371 km² (Peterborough). The mean (SD) size of the 11 FMUs was 7192 (\pm 3096) km². Annual home ranges of fishers in Ontario have been estimated to range between 2.1 and 30 km² for females and between 11 and 38.7 km² for males (95% minimum convex polygon; Tully 2006, Koen et al. 2007). Within our study area, the mean (SD) number of fur harvester licenses per FMU over the last two years of our study was 266 (\pm 95).

Fisher age ratio data

Fisher trapping seasons during the first years of our study began in late October and finished at the end of December for all FMUs. The southern part of our study area (FMUs 1, 2, 6, 8–11, and the southern parts of 5 and 7) extended the season end date to the middle of January beginning with 1997–1998 trapping season and the rest of the study area did the same beginning with the 2001–2002 season (Ontario Regulation 670/98). All FMUs in the study area allocated harvest independently and most, but not all, employed quotas to limit harvest. For example, between 2007 and 2012 quotas in the Mazinaw FMU ranged from 1 fisher per 202 ha of trapline area to 1 fisher per 486 ha; these quotas var-

ied by township and were changed annually. On the other hand, the three FMUs in the neighbouring Kemptville District (Carleton Place, Brockville and Cornwall) did not have a limit on fisher harvest over the same time period.

Following the harvest, fisher trappers were invited to submit skulls, jaws or teeth to their local Ontario Ministry of Natural Resources and Forestry (OMNRF) office. Wildlife managers then aged submissions by X-raying the teeth and measuring pulp cavity width (Dix and Strickland 1986). We used these data to determine J:AF ratio for each FMU for each year. Age structure data available for this study spanned 22 years (1995–2016). However, due to the voluntary nature of the sample submission program and changes in data collection methods used by local OMNRF offices, the years of available data varied by FMU (Supporting information).

Small-mammal abundance

Small-mammal abundance was determined from an ongoing annual trapping program in Algonquin Provincial Park, located in the center of our study area (Fig. 3). The Algonquin Small Mammal Project is the longest running continuous mammal survey in North America and has been described in several published articles (Fryxell et al. 1998, 1999, Falls et al. 2007, Denomme-Brown et al. 2020). We used 23 years (1994–2016) of this dataset for the purposes of our study. Small mammals were trapped once or twice a

month, May–August, at 10 trap lines along the Highway 60 corridor of the park. Each trapline was approximately 90 m long and contained 10 trapping stations spaced 10 m apart, each with two small (7.5 × 7.5 × 30.5 cm) Sherman live traps. One Sherman and one Longworth trap (6.4 × 8.4 × 13.8 cm) were used for the years 2013–2016 inclusive. Therefore, each line contained a total of 20 traps. Traps contained a ball of polyester batting for use as bedding and were baited each evening with water-soaked sunflower seeds, oats or peanut butter and checked the following morning. Captured animals were identified to species and marked with a Monel ear tag. We calculated species abundance as the number of captures per 100 trap nights (TN) and exponential rate of increase as the natural logarithm of the ratio of the abundance at time t and the abundance the previous year, at time $t - 1$. The annual mean (SD) trap nights for our 23 years of data was 4678 (\pm 427). Surveys recorded captures of red-backed vole, deer mouse *Peromyscus maniculatus*, eastern chipmunk *Tamias striatus*, red squirrel *Tamiasciurus hudsonicus*, northern flying squirrel *Glaucomys sabrinus*, meadow jumping mouse *Zapus hudsonius*, woodland jumping mouse *Napaeozapus insignis*, short-tailed shrew *Blarina brevicauda*, masked shrew *Sorex cinerius* and other small shrews *Sorex* spp. Not all of these species are fisher prey, were captured in large numbers, or show spatial synchrony over large distances. For this study, we focused specifically on red-backed voles, known fisher prey items (Kuehn 1989, McNeil et al. 2017) with capture rates $> 1/100$ trap nights for all years. Red-backed voles also show spatial synchrony over distances of 200 km in central Ontario, unlike deer mice, which show limited spatial synchrony (Bowman et al. 2008). Therefore, red-backed vole abundance and exponential rate of increase from the Algonquin Small Mammal Project could reasonably be expected to represent abundance and exponential rate of increase in FMUs within 200 km of the park. Additionally, red-backed vole abundance has been linked to northern saw-whet owl productivity (Bowman et al. 2010).

Mast productivity

We collected data on the productivity of seed and berry-producing plants from the OMNRF's annual Ontario Wildlife Food Survey. These are the same reports used by Howe et al. (2012) to demonstrate intrinsic mast seeding processes of berry crops in five OMNRF administrative districts in central Ontario, which overlapped with the northern portion of our study area. Mast seeding (i.e. 'masting') refers to the ability of certain plants to occasionally produce large seed crops. To complete the annual Ontario Wildlife Food Survey, OMNRF field personnel submitted estimated summer and fall fruit/seed productivity scores for a range of plant species from their region on a scale of 0–4, with 0 indicating no or almost no production and 4 indicating a bumper crop. These estimates were based on an annual survey of observations of OMNRF staff. For the purposes of our study we considered only data from the Great Lakes-St Lawrence East region of Ontario. We excluded data from three districts within this region (Sault Ste. Marie, Wawa and Aylmer) because they did not overlap with and were not adjacent to the FMUs included in our study. Mast data

used in our study spanned 17 years (1998–2015), but as was the case with the fisher age ratio data, the voluntary nature of the survey meant that data were not available for all years from all districts or for all species of interest. Additionally, there was variation in reporting strategy within and among districts. For example, some districts submitted multiple observations from specific locations within the district while others provided an overall estimate. For comparability, mean annual productivity scores for each reporting area were weighted equally to calculate a mean overall productivity score for each species of interest over the entire study area.

We initially examined berry and seed production data for 12 species or groups of species: mountain ash *Sorbus* spp., cherries *Prunus* spp., juneberry *Amelanchier* spp., nannyberry *Viburnum lentago*, elderberry *Sambucus* spp., dogwoods *Cornus* spp., red raspberry *Rubus ideaus*, blueberry *Vaccinium* spp., beech *Fagus grandifolia*, maples *Acer* spp., oaks *Quercus* spp. and pines *Pinus* spp. We chose to investigate berry producing mast crops since previous research has suggested they are a good predictor of vole abundance (Krebs et al. 2010). Maple, white pine *Pinus strobus*, beech and oak seedfall have also been linked to small mammal abundance (Schnurr et al. 2002, Elias et al. 2006, Falls et al. 2007, Jensen et al. 2012). The majority of the above berry species and groups of species have been found to display synchrony in productivity across central Ontario (Howe et al. 2012). We found significant, positive correlations in productivity among 39 of our 66 species pairs using Pearson correlation ($r \geq 0.47$, $p \leq 0.05$). Given this, we simplified further analyses by using mountain ash and oak productivity to represent mast productivity across the study area. Mountain ash was one of the most commonly reported species and thus had data available from more districts and years. It also showed significant, positive correlations in productivity with all other berry species ($r \geq 0.49$, $p \leq 0.032$) except blueberries ($r = 0.31$, $p = 0.20$), as well as with beech ($r = 0.86$, $p < 0.001$) and maple ($r = 0.70$, $p < 0.001$). Oak productivity was not correlated with mountain ash ($r = 0.22$, $p = 0.38$), but it was correlated with pine ($r = 0.53$, $p = 0.020$).

Northern saw-whet owl rate of increase

We estimated relative abundance of northern saw-whet owls using data collected during Birds Canada Nocturnal Owl Surveys over 21 years (1996–2016) in the central region of Ontario, which is roughly bordered by the 47°N and 44°N lines of latitude (Fig. 3). Surveys were conducted annually on a single evening in April by volunteers following a predetermined 18 km route. These routes were located along secondary roads and consisted of 10 stops spaced 2 km apart. The protocol at each stop began with 2 min of silent listening for owl calls, followed by the playing of a series of boreal owl *Aegolius funereus* and barred owl *Strix varia* calls interspersed with silent listening periods. Volunteers recorded all owl calls they heard at each station. Birds Canada personnel then estimated an annual index for each owl species, including northern saw-whet owl, using generalized additive models with smoothing terms for geographic location to account for spatial autocorrelation. The response variable was the

number of occupied stations on each route for a given year. Models were created using the binomial version of the ‘gam’ function, which is based on the methods of Hastie (1992) and found in the GAM package for R. Using the indices produced by this calculation (N) we calculated northern saw-whet owl exponential rate of increase in year t using the formula $\ln(N/N_{t-1})$.

Data analysis

Our analysis sought to take advantage of available data sources. We performed several bivariate regression analyses to test for bottom-up effects on fisher harvest age structure. We did not use multivariate models because data were not available consistently for each FMU in each year, and the same mast and small mammal data were used across all FMUs. Due to these limitations we considered our analyses to be exploratory and inductive in nature.

We assessed the relationships in fisher harvest age ratios among FMUs by producing a Pearson correlation matrix. We then used a Spearman’s rank correlation to compare the resulting coefficients to the distance between each pair of FMUs, measured from their geographic centroids. If bottom-up factors were the primary drivers of fisher harvest age structure, we would expect FMUs that were closer geographically to show greater similarity in age ratios. Red-backed voles show spatial synchrony over distances of about 200 km within central Ontario (Bowman et al. 2008), so if vole abundance influences fisher harvest age ratio we would expect to see greater correlation in age ratios among FMUs within about 200 km of each other. If top-down harvest pressure is the primary driver of harvest age structure, we would not expect to see such a relationship since quotas are set independently in each FMU. Instead, age ratios would correspond to indices of harvest rate.

We used linear regression to assess the relationship between red-backed vole abundance in Algonquin Provincial Park and fisher harvest age ratios in the eight FMUs within 200 km of Algonquin Provincial Park (Bracebridge, Bancroft, Pembroke, Mazinaw, Parry Sound, Huronia, Peterborough and Carleton Place). We compared fisher harvest age ratios to vole abundance in the summer immediately preceding winter harvest (t) and in the summer of the previous year ($t - 1$). We also performed a linear regression between mast crop productivity (oak and mountain ash) in year $t - 1$ and red-backed vole exponential rate of increase in year t . To determine if relationships among mast crop productivity, red-backed vole population growth and abundance, and fisher harvest age ratios were maintained across multiple years and trophic levels, we performed linear regressions between mast crop productivity in years $t - 1$ and $t - 2$ and fisher age ratios in each FMU in year t .

Given the synchrony shown between red-backed vole abundance and northern saw-whet owl exponential rate of increase (Bowman et al. 2010), and the potential for both immediate and lagged responses of fishers to small mammals, we used Pearson correlation analyses to assess the relationship between northern saw-whet owl exponential rate of increase in years t and $t - 1$ and fisher harvest age ratios in all FMUs in year t .

Results

There was a negative relationship between J:AF fisher harvest ratios among FMUs and distance between FMUs as measured from the geographic centroids (Fig. 4). In other words, FMUs that were closer together were more likely to show greater, positive correlation in J:AF ratios than FMUs that were farther apart. The largest positive correlations were between three pairs of neighbouring FMUs: Mazinaw-Pembroke, Carleton Place-Brockville and Parry Sound-Bracebridge (Fig. 5). The observed correlations in J:AF harvest ratios were found across management district boundaries and between FMUs subject to differing fisher management regimes (Fig. 5).

Red-backed vole abundance (captures/100 TN) in Algonquin Provincial Park in year $t - 1$ displayed positive relationships with J:AF fisher harvest ratios in the nearby FMUs of Mazinaw and Pembroke in year t (Table 1). Summer red-backed vole abundance was also related to fisher harvest age ratios in the Pembroke FMU later the same year, although the relationship was negative, rather than positive as hypothesized (Table 1).

Red-backed vole exponential rate of increase in Algonquin Provincial Park was positively related to mountain ash productivity in the Great Lakes-St Lawrence East region of Ontario in the previous year (Fig. 6). Oak productivity in the previous year did not have a significant effect on voles. We identified a positive relationship between mountain ash productivity in year $t - 2$ and fisher harvest J:AF ratios in the Pembroke and Parry Sound FMUs in year t (Table 2). In the Cornwall FMU, there was a negative relationship between mountain ash productivity and fisher harvest age ratio over the same time lag (Table 2). Oak productivity in year $t - 2$ was positively related to fisher harvest age ratios in Bracebridge in year t (Table 2). Mountain ash productivity in year $t - 1$ was also related to fisher harvest age ratios in some FMUs. This relationship was positive in Cornwall and negative in Pembroke and Parry Sound (Table 3).

Positive relationships between productivity measures for northern saw-whet owl and fisher were also observed. The exponential rate of increase in owl abundance in central Ontario in year $t - 1$ exhibited positive correlations with fisher harvest age ratios in year t for several FMUs close to

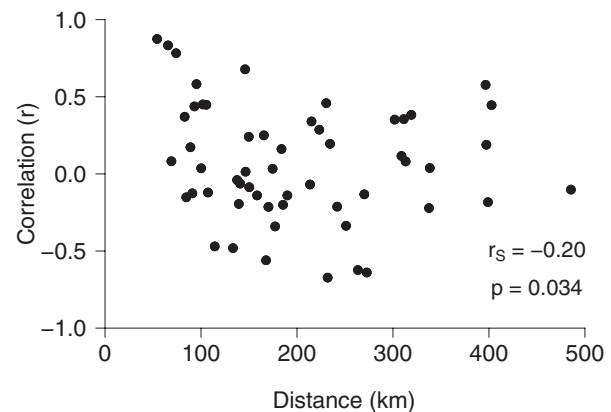


Figure 4. Correlation in fisher *Pekania pennanti* harvest juvenile:adult female (J:AF) ratios among fur management units (FMUs) compared to the distance between geographic centroids of the FMUs.

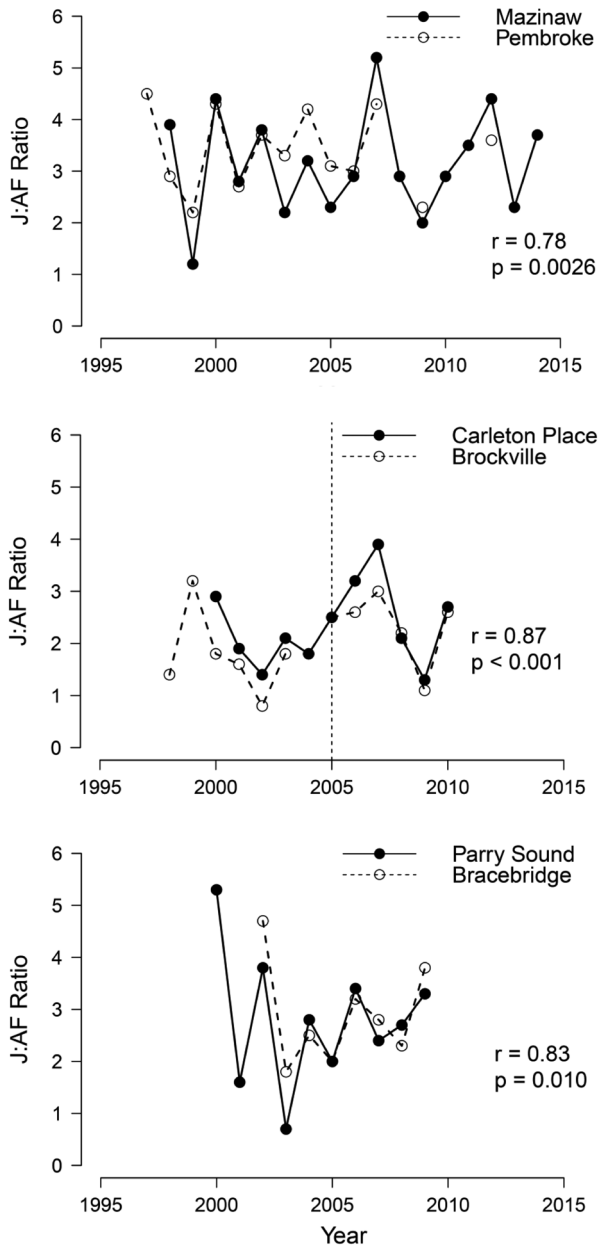


Figure 5. Relationship between fisher *Pekania pennanti* harvest juvenile:adult female (J:AF) ratios in three pairs of fur management units (FMUs) over time. The dashed vertical line in the Carleton Place-Brockville graph indicates the year in which harvest limits (i.e. quotas) were removed in the Kemptville management district.

Algonquin park (e.g. Pembroke, Parry Sound, Mazinaw, Bancroft; Table 4). Exponential rate of increase in owl abundance was correlated with fisher harvest ratios in the Cornwall FMU later within the same year (Table 4).

Discussion

Our findings lend support to the idea of a bottom-up effect of food supply on fisher productivity, and thus harvest age ratios, in some regions of Ontario. This result corroborates previous research showing that fishers exhibit a numerical response to food supply (Bowman et al. 2006), and that age

structure of harvested mustelids can be influenced by food supply (Fryxell et al. 2001, Jensen et al. 2012). Contrary to the suggestions of Douglas and Strickland (1987), our study found little evidence of top-down influences on fisher age ratios in the harvest. Specifically, age ratios display some spatial synchrony, and correlations in J:AF harvest ratios were found across management district boundaries and between FMUs subject to differing management regimes (Fig. 5). For example, quotas in Pembroke ranged from 1 fisher per 154 ha of trapline area to 1 per 277 ha over the course of our study, while quotas in the neighbouring FMU of Mazinaw were generally lower, ranging from 1 fisher per 202 ha to 1 per 486 ha between 2007 and 2012, but harvest age ratios in the two FMUs were strongly correlated (Fig. 5). Correlations in harvest age ratios were also found between two FMUs within the Kemptville management district (Carleton Place and Brockville), despite the removal of harvest quotas in 2005. These examples of synchrony, despite differing management regimes or a lack of active management in recent years, do not preclude the existence of top-down harvest pressure, but they suggest that harvest is not the sole driver of fisher age ratios within our study area. These results are similar to Jensen et al. (2012), who found that total marten and fisher harvest was synchronous across New York, Maine and New Brunswick, despite differences in bag limits and trapping seasons.

In some cases, the synchrony we observed in fisher age ratios between management units may be influenced by spatial synchrony in the abundance of small mammal prey. For example, we found that fisher harvest J:AF ratios in both Mazinaw and Pembroke were influenced by red-backed vole abundance in Algonquin Provincial Park the previous year, which may have resulted in the synchrony in harvest age ratios observed across time in these FMUs. In fact, each of the three pairs of FMUs that displayed synchrony in fisher harvest age ratios across time were located within 200 km of each other (Mazinaw-Pembroke, Carleton Place-Brockville, Parry Sound-Bracebridge), meaning vole population growth in each pair of FMUs may have been synchronized (Bowman et al. 2008).

Synchrony in small mammal population abundances might be caused either by dispersal or by a Moran effect, whereby environmental factors synchronize primary productivity and therefore food supply (Hudson and Cattadori 1999, Bowman et al. 2008). Dispersal seems unlikely to be the cause of red-backed vole synchrony specifically, since previous studies have documented maximum dispersals of only 494–1200 m (Bovet 1980, Bowman et al. 2001), an inconsequential distance at the scale of our study. On the other hand, berry crops are synchronous across central Ontario (Howe et al. 2012), and several researchers have shown mast productivity can predict small mammal population fluctuations the following year (Falls et al. 2007, Krebs et al. 2010, Jensen et al. 2012), which lends support to the Moran effect. Similarly, we observed synchrony in mast production among the majority of the mast species pairs we tested, and further observed a significant influence of mountain ash productivity (which correlated with the productivity of 8 of the 11 other mast species we investigated) on red-backed vole population growth rate in Algonquin Provincial Park the following year.

Table 1. Regression coefficients (R^2), uncorrected p values, slope and intercept values for linear regressions of red-backed vole *Myodes gapperi* abundance in Algonquin Provincial Park (APP), Ontario, Canada, in years $t - 1$ and t and fisher *Pekania pennanti* juvenile:adult female harvest ratios in eight nearby fur management units (FMUs) in year t . The distance of each FMU's geographic centroid from the Algonquin Wildlife Research Station (AWRS), where small mammal sampling took place, is also shown. Regression slope and intercept are displayed with their associated standard errors. Data spans the years 1994–2016 inclusive, however fisher data were not available for all years.

FMU	Distance from AWRS (km)	Year of red-backed vole data	Length of time series (years)	R^2	p-value	Slope (SE)	Intercept (SE)
Huron	169	$t - 1$	17	0.0097	0.71	-0.035 (0.091)	2.5 (0.50)
		t	17	0.031	0.50	0.072 (0.10)	2.0 (0.53)
Parry Sound	117	$t - 1$	10	0.30	0.10	0.23 (0.13)	1.5 (0.77)
		t	10	0.16	0.26	-0.20 (0.16)	3.8 (0.89)
Bracebridge	65	$t - 1$	8	0.086	0.48	0.10 (0.14)	2.3 (0.80)
		t	8	0.0058	0.86	0.031 (0.16)	2.7 (0.86)
Bancroft	67	$t - 1$	18	0.023	0.55	0.047 (0.077)	2.6 (0.40)
		t	18	0.14	0.13	-0.12 (0.074)	3.3 (0.39)
Mazinaw	126	$t - 1$	17	0.38	0.0081	0.24 (0.079)	2.0 (0.43)
		t	17	0.076	0.28	-0.11 (0.096)	3.7 (0.52)
Pembroke	98	$t - 1$	13	0.37	0.026	0.16 (0.063)	2.6 (0.35)
		t	13	0.33	0.042	-0.17 (0.074)	4.3 (0.44)
Peterborough	156	$t - 1$	17	0.040	0.44	-0.044 (0.055)	2.5 (0.30)
		t	17	0.019	0.59	-0.030 (0.056)	2.4 (0.30)
Carleton Place	198	$t - 1$	11	0.10	0.34	0.088 (0.088)	1.9 (0.53)
		t	11	0.032	0.60	0.057 (0.10)	2.1 (0.56)

In some of the FMUs where we observed a positive influence of red-backed vole abundance the previous year on fisher harvest age ratios, we also observed a positive relationship with mast productivity two years previous, providing further evidence of associations between mast and small mammal fluctuations. Mountain ash productivity in year $t - 2$ was positively related to fisher harvest age ratios in the Pembroke and Parry Sound FMUs in year t , while oak productivity was related to fisher harvest age ratios in Bracebridge over the same time span. Furthermore, northern saw-whet owl rate of increase in the central region of Ontario was positively correlated with fisher harvest age ratios in both Pembroke and Parry Sound.

While the relationships outlined above provide evidence of bottom-up influence on fisher productivity in some regions of Ontario, they were not present in all FMUs. The FMUs where positive relationships were observed among

mountain ash and oak productivity, red-backed vole abundance and growth rate, and fisher harvest age ratios tended to be the more northern ones. The southern FMUs (e.g. 1, 2, 8–11) had more agricultural land and thus more edge habitat, which has the potential to support greater small mammal diversity (Osbourne et al. 2005). Fishers in these FMUs may have been relying on different prey sources, or on prey sources that were out of synchrony with events in the Algonquin region.

In some FMUs and for some time lags, mast productivity and red-backed vole abundance were negatively, rather than positively, associated with fisher harvest age ratios. In all but one case these negative associations occurred within the same year for red-backed vole abundance and at a 1-year time lag for mast productivity. Furthermore, these negative associations occurred in FMUs that had displayed a positive association when the greater time lag was used (Pembroke and Parry Sound). For example, fisher harvest age ratios in the Pembroke FMU in year t were negatively associated with red-backed vole abundance earlier the same year and with mountain ash productivity in year $t - 1$, but were positively associated with red-backed vole abundance in year $t - 1$ and with mountain ash productivity in year $t - 2$. This pattern may be explained by Howe et al. (2012)'s finding that prior reproduction influences the productivity of berries, including mountain ash, such that there is a negative correlation between production in year t and year $t - 1$. Based on the linkages observed in our study, this negative temporal autocorrelation may extend to small mammal rate of increase as well. If fisher productivity is primarily influenced by prey abundance the previous year rather than within the same year, and small mammal abundance is similarly influenced by mast productivity the previous year, then comparing harvest age ratios to small mammal abundance within the same year or to mast productivity only one year previously would be comparing across trophic links out of temporal sequence.

If the patterns we observed in some regions of our study area are driven in part by negative temporal autocorrelation in mast productivity and small mammal abundance,

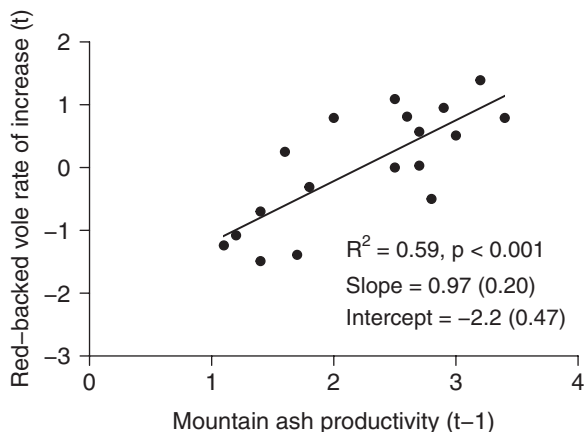


Figure 6. Linear regression of mountain ash *Sorbus* spp. productivity in the Great Lakes-St Lawrence East region of Ontario in year $t - 1$ graphed against red-backed vole *Myodes gapperi* exponential rate of increase in Algonquin Provincial Park in year t . The rate of increase is defined as $\ln(N_t/N_{t-1})$, where N is the number of captures/100 trap nights.

Table 2. Regression coefficients (R^2), uncorrected p values, slope and intercept values for linear regressions of mountain ash *Sorbus* spp. and oak *Quercus* spp. productivity in the Great Lakes-St Lawrence East region of Ontario in year $t - 2$ and fisher *Pekania pennanti* juvenile:adult female harvest ratios in 11 fur management units (FMUs) in year t . Regression slope and intercept are displayed with their associated standard errors. Data spans the years 1998–2016 inclusive, however both fisher and mast data were not available for all years.

District/FMU	Length of time series (years)	Species	R^2	p-value	Slope (SE)	Intercept (SE)
Owen Sound	11	MA	0.0042	0.85	0.090 (0.46)	2.0 (1.0)
		Oak	0.074	0.42	-0.53 (0.62)	3.3 (1.3)
Huronina	17	MA	0.013	0.66	-0.14 (0.31)	2.6 (0.74)
		Oak	0.026	0.54	-0.26 (0.41)	2.8 (0.86)
Parry Sound	10	MA	0.46	0.032	1.1 (0.43)	0.41 (0.97)
		Oak	0.077	0.44	0.77 (0.95)	1.4 (1.8)
Bracebridge	8	MA	0.0085	0.83	0.13 (0.59)	2.6 (1.3)
		Oak	0.67	0.013	1.6 (0.46)	-0.15 (0.89)
Bancroft	13	MA	0.031	0.56	0.18 (0.31)	2.5 (0.69)
		Oak	0.062	0.41	0.32 (0.38)	2.3 (0.77)
Mazinaw	15	MA	0.10	0.24	0.42 (0.34)	2.3 (0.79)
		Oak	0.0052	0.80	0.12 (0.47)	3.0 (0.94)
Pembroke	10	MA	0.55	0.015	0.67 (0.22)	2.0 (0.49)
		Oak	1.2×10^{-5}	0.99	5.4×10^{-3} (0.54)	3.4 (1.0)
Peterborough	15	MA	0.042	0.46	0.13 (0.18)	1.9 (0.41)
		Oak	0.0017	0.88	0.036 (0.24)	2.1 (0.47)
Carleton Place	11	MA	0.072	0.42	0.28 (0.33)	1.7 (0.77)
		Oak	0.089	0.37	-0.45 (0.48)	3.2 (0.97)
Brockville	10	MA	0.069	0.46	0.24 (0.32)	1.5 (0.72)
		Oak	0.083	0.42	-0.38 (0.44)	2.7 (0.88)
Cornwall	9	MA	0.47	0.042	-1.2 (0.49)	4.6 (1.0)
		Oak	0.078	0.47	-0.63 (0.82)	3.4 (1.7)

this has important implications for fisher management. In FMUs where these patterns are present and have a significant effect on fisher productivity, a 'good' fisher age ratio (i.e. a high proportion of juveniles in the harvest) one year is likely to mean a 'bad' age ratio (i.e. a low proportion of juveniles in the harvest) the following year. This relationship could cause overharvest under the current harvest paradigm.

Our study provides exploratory evidence that bottom-up trophic effects influence fisher harvest age structure in some jurisdictions, which has the potential to better facilitate furbearer management and protect vulnerable populations against overharvest. Based on the patterns observed among our linear regressions, a good mast crop (quantified using mean annual mountain ash productivity) will lead to abundant red-backed voles the following year. The increase in red-

Table 3. Regression coefficients (R^2), uncorrected p-values, slope and intercept values for linear regressions of mountain ash *Sorbus* spp. and oak *Quercus* spp. productivity in the Great Lakes-St Lawrence East region of Ontario in year $t - 1$ and fisher *Pekania pennanti* juvenile:adult female harvest ratios in 11 fur management units (FMUs) in year t . Regression slope and intercept are displayed with their associated standard errors. Data spans the years 1998–2016 inclusive, however both fisher and mast data were not available for all years.

District/FMU	Length of time series (years)	Species	R^2	p-value	Slope (SE)	Intercept (SE)
Owen Sound	11	MA	0.023	0.65	0.27 (0.57)	1.6 (1.4)
		Oak	0.13	0.27	-0.63 (0.54)	3.6 (1.2)
Huronina	17	MA	0.0077	0.74	0.11 (0.33)	2.1 (0.76)
		Oak	7.2×10^{-4}	0.92	0.044 (0.42)	2.2 (0.89)
Parry Sound	10	MA	0.48	0.025	-1.2 (0.44)	5.4 (0.98)
		Oak	0.078	0.44	-0.67 (0.82)	4.1 (1.7)
Bracebridge	8	MA	0.078	0.50	-0.38 (0.54)	3.7 (1.2)
		Oak	0.0039	0.88	-0.12 (0.80)	3.1 (1.6)
Bancroft	14	MA	0.0013	0.90	-0.042 (0.34)	2.9 (0.83)
		Oak	0.079	0.33	-0.41 (0.40)	3.6 (0.83)
Mazinaw	16	MA	0.031	0.51	-0.24 (0.36)	3.7 (0.86)
		Oak	0.033	0.50	-0.34 (0.48)	3.8 (0.98)
Pembroke	11	MA	0.36	0.050	-0.65 (0.29)	4.9 (0.71)
		Oak	0.23	0.14	-0.70 (0.43)	4.7 (0.85)
Peterborough	16	MA	0.014	0.66	-0.070 (0.16)	2.3 (0.38)
		Oak	0.0060	0.78	-0.062 (0.21)	2.3 (0.44)
Carleton Place	11	MA	0.0027	0.88	0.058 (0.37)	2.2 (0.82)
		Oak	0.10	0.34	-0.43 (0.43)	3.2 (0.85)
Brockville	11	MA	0.084	0.39	0.29 (0.32)	1.5 (0.75)
		Oak	0.25	0.12	-0.69 (0.40)	3.4 (0.80)
Cornwall	9	MA	0.51	0.030	1.3 (0.49)	-0.84 (1.1)
		Oak	0.36	0.087	1.3 (0.63)	-0.31 (1.3)

Table 4. Correlation coefficients (r) and uncorrected p -values for northern saw-whet owl *Aegolius acadicus* exponential rate of increase in the central region of Ontario and fisher *Pekania pennanti* juvenile:adult female harvest ratios in 11 fur management units (FMUs). Data spans the years 1996–2016 inclusive, however fisher data were not available for all years. Results are shown for the relationship between owl rate of increase the previous year ($t - 1$) and during the spring of the same year (t).

FMU	Year of owl data	Length of time series (years)	r	p -value
Owen Sound	$t - 1$	11	0.094	0.39
	t	11	0.13	0.35
Huronia	$t - 1$	17	-0.19	0.77
	t	17	0.31	0.11
Parry Sound	$t - 1$	10	0.56	0.046
	t	10	-0.73	0.99
Bracebridge	$t - 1$	8	0.28	0.25
	t	8	-0.16	0.65
Bancroft	$t - 1$	16	0.26	0.16
	t	17	0.014	0.48
Mazinaw	$t - 1$	17	0.38	0.064
	t	17	-0.10	0.66
Pembroke	$t - 1$	13	0.56	0.022
	t	13	-0.41	0.92
Peterborough	$t - 1$	17	0.031	0.45
	t	17	-0.12	0.68
Carleton Place	$t - 1$	11	0.24	0.24
	t	11	0.10	0.38
Brockville	$t - 1$	12	0.024	0.47
	t	12	0.32	0.15
Cornwall	$t - 1$	9	-0.58	0.95
	t	9	0.70	0.017

backed voles results in an increase in northern saw-whet owl population growth rate within the same year (Bowman et al. 2010). This increase in prey availability may help to increase female fisher fecundity, and in some regions we see a large proportion of juvenile fishers in the harvest the following year. This process is linked across three trophic levels and is

played out over three years in some regions – most clearly in the Pembroke FMU (Fig. 7).

Knowledge of these linkages, combined with in-year information on fisher population growth, may be a preferable basis for estimating sustainable harvest levels, and may be less likely to lead to unintentional overharvest than a retrospective assessment of J:AF harvest ratios. Wildlife managers may have some leeway to use the monitoring program most feasible for their jurisdiction. For example, in regions without small mammal monitoring the use of mast productivity or owl abundance as an indicator of fisher productivity may be preferable. Mast crop and owl abundance estimates rely on existing volunteer surveys and are readily available. Another benefit of both of these surveys is that they already cover a wide geographic area. However, we caution that data on mast, small mammals or owls used in fisher harvest management planning for a particular region should be assessed locally for linkages with fisher productivity, since the patterns we identified in our study varied by FMU and were not synchronous across the whole study area. In general, we recommend establishing a local understanding of trophic linkages affecting fisher population growth, and where possible, using leading indicators of population growth as an aid in harvest management. In some cases, or at some times, fisher abundance can also be assessed to ensure sustainability. Recent advances have made the estimation of abundance more efficient through the use of remote detectors (e.g. cameras; Rowcliffe et al. 2008).

We also encourage continued efforts to understand the trophic dynamics within the Great Lakes-St Lawrence East forest community. Studies comparing fisher populations with prey populations from locations outside Algonquin Provincial Park may reveal additional relationships that could help to further inform fisher harvest management and would be particularly useful near the edges of the fisher's range in Ontario, where we did not test the influence of Algonquin Provincial Park small mammal abundance. Our study would

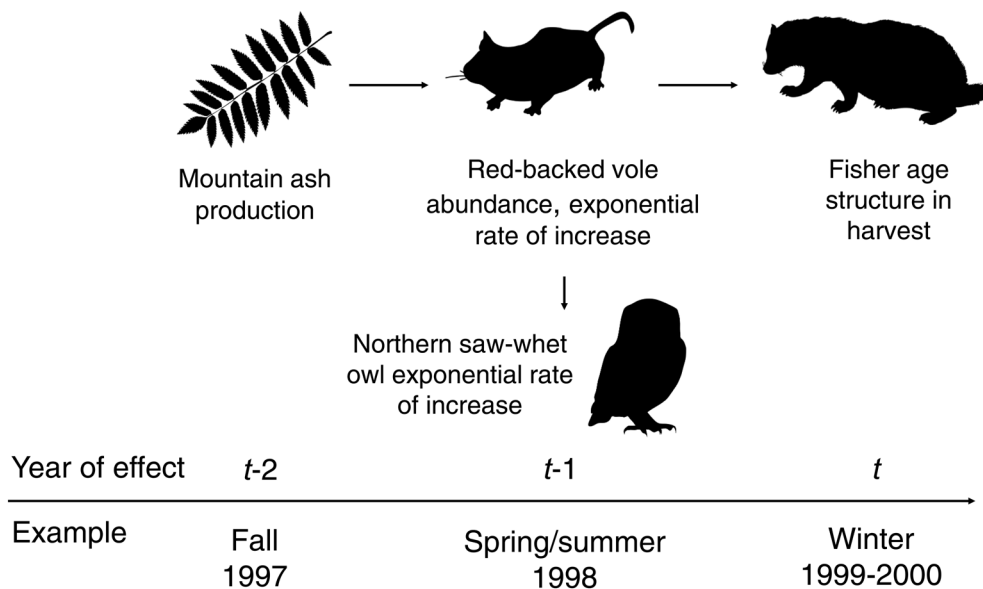


Figure 7. Summary of trophic relationships identified in the Pembroke Fur Management Unit (FMU) including mountain ash *Sorbus* spp. production, red-backed vole *Myodes gapperi* abundance and exponential rate of increase, northern saw-whet owl exponential rate of increase *Aegolius acadicus* and fisher *Pekania pennanti* productivity, as represented by age structure in the harvest.

not have been possible without long-term monitoring of small mammals, and implementing additional small-mammal studies in other regions would provide valuable data for future management planning. We recognize that these surveys are labour intensive and require an appropriate and regularly accessible location for setting traps, but the Algonquin Small Mammal Project provides a useful template and some aspects of the project could be incorporated by other jurisdictions.

It is worth revisiting here the lows experienced by fisher populations in the early 1900s and their continued vulnerability. Fishers have a relatively fixed reproductive output and are thus susceptible to overharvest (Buskirk et al. 2012), and recent genetic monitoring has suggested a decrease in either population density or dispersal in Ontario since the early 2000s (Greenhorn et al. 2018). Greenhorn et al. (2018) also found that immigration from the Adirondack region of New York – an important refuge for fishers during times of high harvest pressure – has slowed or ceased in recent years. For these reasons, and despite our findings regarding the importance of bottom-up effects, we would encourage continued monitoring and evaluation of harvest and age ratio trends, especially in the context of an adaptive management program where we can continue to learn about the place of fishers in the ecosystem and the top-down and bottom-up pressures that act on them. Although we have argued that top-down factors should not be treated as the sole source of variation in fisher harvest age ratios, and we failed to find evidence of their influence in our study, more information is needed before we can discount them entirely. It is likely that top-down factors act simultaneously with bottom-up factors and may modulate their influence, and that the relative strength of these factors varies over space and time. Furthermore, although we are suggesting that harvest age ratios by themselves are not informative for setting future quotas, we nevertheless consider that age ratios have management value insofar as they appear indicative of population growth.

In addition, factors influencing the potential strength of top-down pressure merit further investigation. It is possible that the apparent lack of harvest impact on fisher age ratios we observed in the Great Lakes-St Lawrence East region of Ontario may be due in part to limitations in trapper access. Private land, where trapping is prohibited, may create de facto refuges. The extent of such refuges is unknown, and jurisdictions should consider the proportion of the land base excluded from trapping activities when assessing harvest pressure. If extensive, this land could serve to limit trapper impact on fisher (or other furbearer) population dynamics. An assessment of trapper effort (e.g. number of nights trapped and number of traps deployed, area covered by fur harvest) would also provide a more detailed picture of top-down pressure.

Our study reinforces previous findings suggesting that knowledge of bottom-up factors is important for fur harvest management (Fryxell et al. 2001, Haydon and Fryxell 2004). This may include having knowledge of small-mammal population trends and variation in mast crop productivity (Howe et al. 2012, Jensen et al. 2012). The associations we found between two different small mammal predators – fishers and northern saw-whet owls – in some FMUs further underscores the connected nature of trophic relations in

the system, and we suggest that harvest management can be facilitated by an improved understanding of these community-level interactions.

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Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.dbrv15f1w>> (Greenhorn et al. 2021).

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