

NUMERICAL RESPONSE OF FISHERS TO SYNCHRONOUS PREY DYNAMICS

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Fisher (*Martes pennanti*) populations may respond numerically to fluctuating hare populations, although uncertainty remains about this contention. We analyzed livetrapping data from Ontario (448,654 trap nights) that contained trend information for fishers, lagomorphs (snowshoe hares [*Lepus americanus*] and eastern cottontails [*Sylvilagus floridanus*]), and North American porcupines (*Erethizon dorsatum*) for 1995–2004. The data encompassed a synchronous fluctuation of lagomorphs and porcupines. Fisher populations appeared to have a delayed, positive numerical response with a lag of 2 years to changing lagomorph abundance, but they also appeared to switch to an unmeasured, alternate prey during the lagomorph low. This finding suggests that fishers are generalist predators that should have a stabilizing effect on the predator–prey system.

Key words: delayed density dependence, *Erethizon dorsatum*, fur harvest, *Lepus americanus*, limit cycle, *Martes pennanti*, numerical response, predation, stability, time series

The most thorough empirical study of the numerical response of fishers (*Martes pennanti*) to changing prey density was conducted by Bulmer (1974, 1975). He looked at trends of fisher populations from Canadian fur harvest records for the periods 1751–1847, 1848–1909, and 1920–1969. He concluded that during those years, fisher populations exhibited a 10-year cycle in abundance that was caused by fluctuating densities of snowshoe hares (*Lepus americanus*—Bulmer 1974). Bulmer (1975) further concluded that in the absence of density-dependent population growth, the fisher numerical response to hares should be lagged by 2.6 years, and that this phase lag is caused mainly by mortality among both juveniles and adults. He suggested that density dependence would shorten the phase lag. Other authors also have demonstrated that fisher harvest returns have historically tended to be cyclic (e.g., Butler 1953; Rand 1944). In contrast are studies that have either found no evidence of cyclicity in fisher populations (Coulter 1960; Hamilton and Cook 1955; Leonard 1986) or that have been ambiguous in this regard (Kuehn 1989; Strickland 1994). These different conclusions may result from continental variation in the amplitude of hare cycles (e.g., Murray 2000) or from anthropogenic effects,

such as habitat fragmentation, altering the cyclic dynamics of hares and their predators (Voigt et al. 2000). In any case, uncertainty over the cyclicity of fisher populations leads to difficulty in managing harvests, and caused Douglas and Strickland (1987:519) to state that the “whole question as to whether or not fisher populations are cyclic, and if so why, requires further investigation.”

The relationship between fishers and snowshoe hares is complicated by the unique potential for fishers to prey extensively on North American porcupines (*Erethizon dorsatum*). Although it has long been known that fishers prey on porcupines (Schoonmaker 1938), the extent to which fishers have a numerical response to these rodents is unknown. Only 2 investigations have simultaneously studied fisher and porcupine populations (Earle and Kramm 1982; Powell and Brander 1977). Powell and Brander (1977) found that porcupines on their 178-ha study area declined from 21 to 5 during 13 years after the restoration of fishers to the Upper Peninsula of Michigan. Similarly, Earle and Kramm (1982) found that porcupine population densities were lower where they overlapped with fishers than where they did not overlap. Neither study suggested a numerical response of fishers to changing porcupine numbers, although Powell and Brander (1977) suggested that there should be long-term stability between populations of these 2 species. Powell (1980) demonstrated in a 1-predator–1-prey simulation model that this stability could be achieved in part through a numerical response of fishers to changing porcupine population densities. Powell (1980) also modeled a system with

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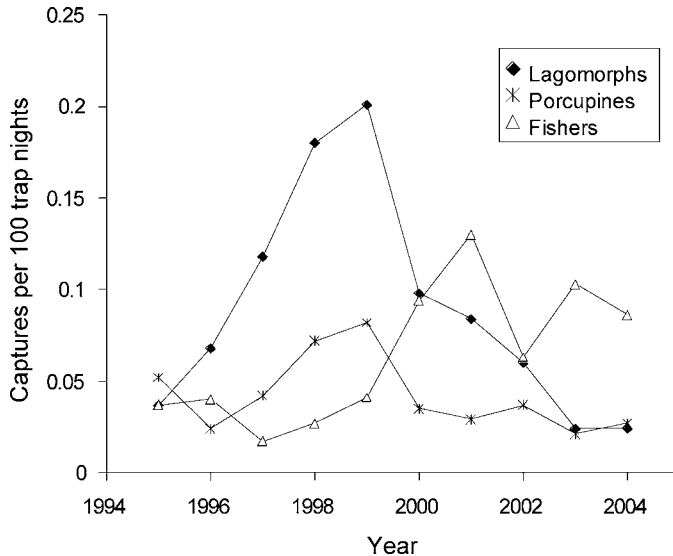


FIG. 1.—Fluctuations in abundance of fishers (*Martes pennanti*), lagomorphs (*Lepus americanus* and *Sylvilagus floridanus*), and North American porcupines (*Erethizon dorsatum*) captured in eastern Ontario during June–October, 1995–2004. Total trap nights during the 10 years was 448,654.

fishers, hares, porcupines, and white-tailed deer (*Odocoileus virginianus*) carrion, and found that cyclic hare populations created stable limit cycles. No published empirical studies contain concurrent time-series information for fishers, hares, and porcupines.

As 1 tool for fighting the northward spread of raccoon (*Procyon lotor*) rabies, the Ontario Ministry of Natural Resources has an intensive livetrapping program in southeastern Ontario, Canada (Rosatte et al. 1992, 2001), the objective of which is to vaccinate potential rabies vectors. Ancillary captures of fishers, hares, and porcupines during 10 years provided us with a unique opportunity to study this predator–prey system. We expected that fisher populations would exhibit a numerical response to changing hare population densities with a lag of 2–3 years (Bulmer 1974).

MATERIALS AND METHODS

The study encompassed an approximate area of 950 km², bordered to the south by the St. Lawrence River, to the north by latitude 45°00'N, to the east by longitude 75°15'W, and to the west by longitude 76°00'W. This area was within the Great Lakes–St. Lawrence forest region (Rowe 1972), a temperate–boreal ecotone. Historically, the area was dominated by deciduous and mixed forests containing sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), basswood (*Tilia americana*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), white pine (*Pinus strobus*), white spruce (*Picea glauca*), hemlock (*Tsuga canadensis*), eastern white cedar (*Thuja occidentalis*), and balsam fir (*Abies balsamea*—Keddy 1994). The western half of the area was bisected by the Frontenac axis, a southern extension of the Canadian Shield, a geological formation that has remained largely forested. The eastern half of the area was off-shield and heavily settled by humans, with extensive agricultural and road developments. Agricultural fields include both pastures and row crops, which were dominated by corn and soybeans.

During June–October, 1995–2004 inclusive, an extensive live-trapping program (trap–vaccinate–release) was carried out in the study area, with the main objective of vaccinating potential vectors of raccoon rabies (Rosatte et al. 1992, 2001). The 950-km² area was divided into 121 cells, the average size of which was 12 km². The extent of the trapped area increased somewhat over the years, as did the trapping effort, as rabies entered the province. During 1995 and 1996, 300–400 trap nights were conducted per cell. From 1997 to 1999, 700–800 trap nights per cell were conducted, and since 2000, 600–1,600 trap nights per cell were carried out. Trapping took place over 2–3 consecutive weeks per cell. Not all cells were trapped every year, depending on management objectives.

The trapping protocol involved setting 100 Tomahawk model 106 and 108 (Tomahawk Traps and Equipment, Tomahawk, Wisconsin) live traps per night per cell. Traps were stratified across habitat types within each cell, baited with canned sardines, and checked once daily. Captures of snowshoe hares, cottontail rabbits (*Sylvilagus floridanus*), and porcupines were noted by workers, but these animals were released unmarked after capture. However, the trappers did not generally make a distinction between captured hares and rabbits, and so these were grouped as lagomorphs for the purposes of the present study. Captured fishers were released unmarked during the 1st years of the trap–vaccinate–release program but were marked during the later years using Monel ear tags (National Band and Tag Co., Newport, Kentucky). No sedatives were used when fishers were handled. All animal handling procedures were approved by the Ontario Ministry of Natural Resources Animal Care Committee and followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

We analyzed the numerical response of fishers to changing lagomorph and porcupine abundance. For all groups, our index of annual population size was captures per 100 trap nights. Therefore, we assumed that detection probabilities did not vary among years, meaning that changes in our index of population size should be directly related to changes in the population within the study area as a whole. Further, because individuals of all species were not regularly marked, we were not able to generate meaningful confidence intervals for our abundance estimates. The trapping effort (see “Results”) suggests that our assumption of unbiased detection probabilities was reasonable, and the lack of confidence intervals was negligible because we would expect them to be small. We used phase-space plots (Rosenzweig and MacArthur 1963) to depict potential predator–prey relationships, and Pearson correlations to compare fisher abundance at time *t* (where *t* = year) with prey abundance at times *t* – 1, and *t* – 2. Statistical analyses were carried out with S-PLUS 6.0 (Insightful Corp., Seattle, Washington).

RESULTS

Between 1995 and 2004 inclusive, trapping was carried out for 448,654 trap nights (\bar{X} per year = 44,865 trap nights, range = 25,075–72,699 trap nights), which were conducted between June and October in the study area to vaccinate potential rabies vectors (Rosatte et al. 2001).

During the study period, lagomorph populations increased to a peak in 1999, and subsequently declined (Fig. 1). From a low of 0.037 captures per 100 trap nights in 1995 to a high of 0.201 captures per 100 trap nights, hares and rabbits exhibited a 5.4-fold increase. They subsequently declined in 2003 to a new low of 0.024 captures per 100 trap nights. Porcupine populations also peaked during 1999, increasing 3.4-fold from

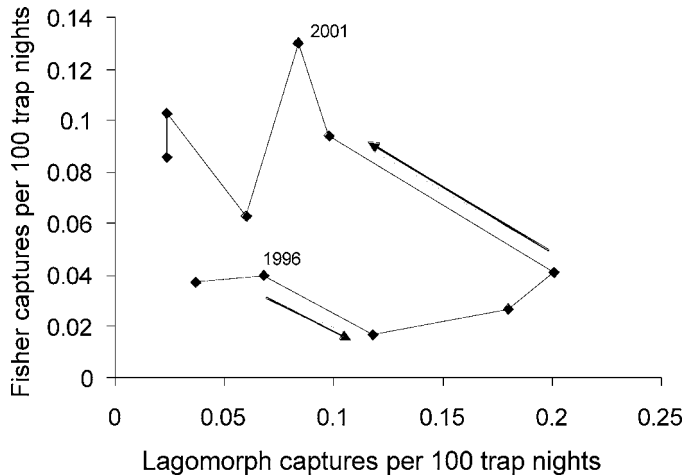


FIG. 2.—A phase-space plot depicting numerical response of fishers (*Martes pennanti*) to fluctuating lagomorph abundance during 1995–2004 in eastern Ontario. Lagomorphs are *Lepus americanus* and *Sylvilagus floridanus*.

a low of 0.024 captures per 100 trap nights in 1996 to a high of 0.082 captures per 100 trap nights (Fig. 1). Finally, fisher populations peaked 2 years after the porcupines and lagomorphs, in 2001 (Fig. 1). Fisher populations exhibited a 7.7-fold increase from a low of 0.017 captures per 100 trap nights to a high of 0.130 captures per 100 trap nights. Fishers declined for a year in 2002; however, we were surprised to see an increase to 0.103 fishers per 100 trap nights in 2003.

During 1995–2002, the phase-space plot of fisher abundance versus lagomorph abundance formed a nearly closed loop, spiraling in a counterclockwise direction (Fig. 2). This pattern is indicative of an interactive relationship between predator (fisher) and prey (lagomorph) with delayed density dependence. The time series (Fig. 1) suggests that delayed density dependence, or negative feedback, might have been caused by a 2-year lag in the numerical response of fishers to changing lagomorph abundance. This notion is supported by Pearson correlations: the strongest relationship between fisher and lagomorph abundance during 1995–2004 occurred where lagomorph numbers were lagged by 2 years ($r = 0.68$, $n = 8$, $P = 0.06$; compared to a 1-year lag, $r = 0.01$, $n = 9$, $P = 0.97$; compared to no lag, $r = -0.45$, $n = 10$, $P = 0.19$). However, during 2003, fishers appeared to respond to some alternative food source, and this shift is apparent in the phase-space plot (Fig. 2). Parameters for the relationship between the fisher rate of increase and lagomorph abundance lagged by 2 years are shown in Fig. 3.

A phase-space plot of fisher abundance versus porcupine abundance also formed a nearly closed, counterclockwise loop during 1995–2002 (Fig. 4), although this loop appeared noisier than that between fishers and lagomorphs. Because porcupines peaked in 1999, during the same year as lagomorphs, it was expected that some delayed density dependence should be apparent between fishers and porcupines. Pearson correlations demonstrated that the strongest positive relationship between fisher and porcupine abundance during 1995–2004 occurred where porcupine abundance was lagged by

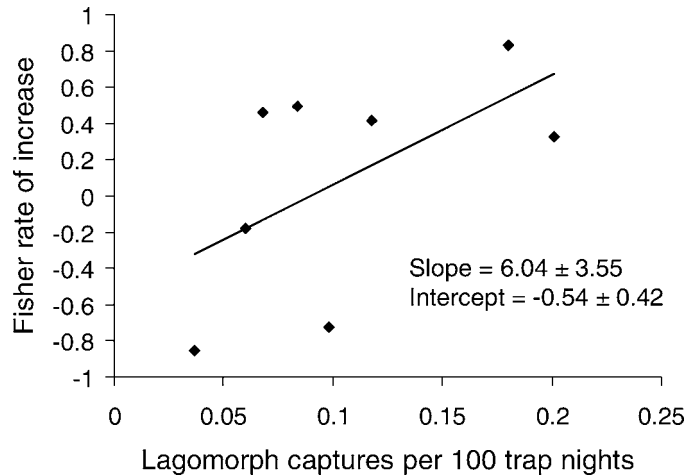


FIG. 3.—Fisher (*Martes pennanti*) rate of increase ($r = \ln(N_t/N_{t-1})$) and lagomorph abundance (captures per 100 trap nights) lagged by 2 years (N_{t-2}) during 1995–2004 in eastern Ontario ($F = 2.89$, $R^2 = 0.33$, $n = 8$, $P = 0.13$).

2 years ($r = 0.50$, $n = 8$, $P = 0.20$; compared to a 1-year lag, $r = -0.005$, $n = 9$, $P = 0.98$; compared to no lag, $r = -0.58$, $n = 10$, $P = 0.08$).

DISCUSSION

Fisher populations in the study area appeared to have a delayed, positive numerical response to lagomorph abundance. Bulmer (1975) suggested that the phase lag of fishers in response to changing hare densities should be 2.6 years, and less in the presence of density dependence. We found a phase lag of 2 years. According to Bulmer (1975), the cause of the lagged decline of fishers is mortality acting on both juveniles and adults. Others (Douglas and Strickland 1987; Kuehn 1989; Leonard 1986) have indirectly supported this putative cause by demonstrating that fisher productivity, as indexed by counts of corpora lutea, does not change as hare populations fluctuate. However, no studies have been conducted on the effect of food

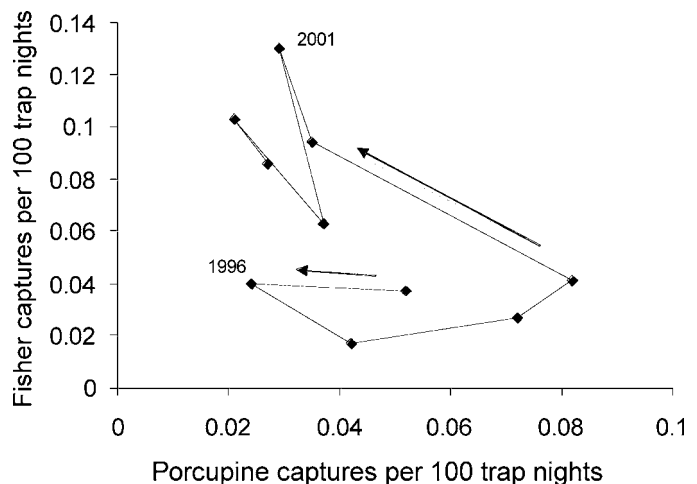


FIG. 4.—A phase-space plot depicting numerical response of fishers (*Martes pennanti*) to fluctuating North American porcupine (*Erethizon dorsatum*) abundance during 1995–2004 in eastern Ontario.

supply on the litter size, survival, or movement of fishers. It remains an open question how much productivity, mortality, and emigration each contributed to the decline, but we suspect that all played a role, as has been demonstrated for Canadian lynx (*Lynx canadensis*—O'Donoghue et al. 1997).

Fishers have recently recolonized southern Ontario, including our study area, after having been extirpated for several decades. Genetic evidence has demonstrated that the fishers in this area have immigrated from the south—particularly the Adirondack region of New York (Carr 2005). This recolonization suggests a nonexclusive alternative hypothesis for the numerical response we have observed. High fisher densities along the front of the expanding population are expected because of the availability of naïve prey (e.g., Caughley 1970), and the peak observed in our data may have been associated with this front. However, it is unclear when an expansion peak ought to have occurred, and the simplest explanation is a delayed numerical response to lagomorphs. Nevertheless, future data collection will be required to distinguish with certainty between the numerical response and expanding front hypotheses.

Fishers may have switched to alternative food sources during the lagomorph decline, because fisher abundance increased during 2003. This is consistent with their being generalist predators, and is different from the response of hare specialists such as lynx to cyclical dynamics (e.g., O'Donoghue et al. 1997). Rather than contributing to cycles, predation by generalist predators can often be stabilizing (Hanski et al. 1991; Oksanen et al. 2001). The conclusion that fishers are generalist predators is supported by numerous diet studies (see Martin [1994] for a review), including 1 in our study area that took place during the lagomorph decline of 2000–2001. Remains of >14 mammalian species were detected in 97 fisher gastrointestinal tracts, and 6 different food categories (birds, cottontail rabbits, fruit and other vegetation, raccoons, snakes, and white-tailed deer) each occurred in >15% of the fishers sampled. Hare and porcupine remains occurred in only 7% and 4% of the fisher gastrointestinal tracts, respectively (D. Bland, K. Coleman, and A. Bendig, in litt.).

Although a numerical response often is associated with specialist predators, several studies have demonstrated such responses by generalists including bobcats (*Lynx rufus*—Knick 1990), red foxes (*Vulpes vulpes*—Small et al. 1993), and coyotes (*Canis latrans*—O'Donoghue et al. 1997). However, generalist predators should have a stabilizing functional response (Murdoch and Oaten 1975); thus, we predict that this should be the case for fishers in our study area if they are indeed generalists.

Lagomorphs and porcupine populations fluctuated synchronously over time during our study. Without a longer time series, it is unclear whether the fluctuation was part of a cyclical system, but it is reasonable to speculate that fluctuating lagomorph numbers were driving fluctuating community dynamics, resulting in changing densities of both fisher and porcupine populations (e.g., Powell 1980). Porcupine densities could have increased if fisher predation on porcupines was buffered during the lagomorph increase, and the subsequent porcupine decline could be explained by increased predation during the fisher

peak. Powell and Brander (1977) suggested that fisher predation can regulate porcupine populations. Although porcupines are known to be an important prey item for fishers (Powell 1979), both our correlation analyses and visual inspection of the phase-space plots suggest that lagomorphs in our study area were more closely related to the fisher numerical response than were porcupines. Nevertheless, the large amplitude of the fisher fluctuation compared to the prey fluctuations suggests that both prey species contributed to the fisher response (e.g., Boutin 1995).

Our research is consistent with 2 conclusions. First, it appears that where lagomorph populations fluctuate widely in abundance, fisher populations will have a numerical response that is delayed by 2 years. This is an important consideration for allocation of fisher trapping quotas and suggests that hare trends be used as a component of fisher harvest management. Second, fishers appeared able to switch to an alternative prey during a low phase of 2 major prey groups, lagomorphs and porcupines. This suggests that fishers are generalist predators that will likely play a stabilizing role in the predator–prey system we studied.

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