

Habitat suitability and source–sink dynamics of beavers

JOHN M. FRYXELL

Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Summary

1. Theory suggests that territorial species should share many of the same dynamical characteristics as metapopulations, including asynchronous local dynamics, potential for stochastic extinction of the population when rates of successful dispersal fall below mortality risk, and critical importance of the ratio of suitable to unsuitable habitat for long-term persistence. These propositions were tested on a population of beavers (*Castor canadensis* Kuhl) in Algonquin Provincial Park, Ontario, which has been continuously monitored over 11 years.

2. Results showed that the total population was considerably less variable than local abundance at 14 beaver colonies, due to asynchrony among local populations. This suggests that local ecological interactions were more important in determining year-to-year variation in beaver numbers than broad-scale environmental processes, such as weather.

3. Of the local colonies, 20% were never abandoned over 11 years, although there was considerable turnover among adults. Offspring production exceeded adult abundance at five source colonies, which did not quite compensate for negative net production at nine sink colonies. These observations were consistent with predictions of spatially structured models of territoriality incorporating local variation in habitat suitability. Mean colony size and probability of recurrence from year-to-year were associated with local food availability, indicating that trophic interactions were important in determining local population dynamics.

4. The beaver population in Algonquin declined steadily over the study period, however, suggesting that spatial and demographic processes were insufficient to stabilize abundance over time. This is consistent with predictions of spatially structured models of territoriality in which suitable and unsuitable habitats are interspersed. It is hypothesized that long-term decline in habitat suitability is induced by acceleration of woody plant succession due to selective foraging by beavers.

Key-words: beaver, demography, source, sink, territory.

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Introduction

An important body of recent ecological theory focuses on the importance of spatial considerations on the population dynamics and conservation of territorial species (Lande 1987, 1988; Lamberson *et al.* 1992, 1994; Noon & McKelvey 1996). According to these models, dispersers visit a number of potential territory sites before settling down to rear offspring. The probability of successful dispersal depends strongly on the habitat suitability of sites and the degree to which sites are already saturated by resident territory-holders. Moreover, there is a chance that dispersers will fail to

locate patches of suitable habitat that are interspersed among unsuitable habitat patches, leading to a meaningful risk of population extinction when dispersal success falls below the average risk of mortality for territory-holders.

Noon & McKelvey (1996) demonstrated that spatially structured models for territorial species have identical dynamic characteristics as classic metapopulation models, despite obvious differences in the biological meaning of their respective parameters. In classic metapopulation models, stochastic extinction of local populations is balanced against recolonization via occasional dispersal events (Andrewartha & Birch 1954; den Boer 1968; Levins 1969; Lande 1987, 1988; Noon & McKelvey 1996; Hanski 1997; Hanski & Simberloff 1997). Hence, recolonization in metapopulation models is recast as dispersal in spatially structured models of territorial

Correspondence: John M. Fryxell, Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1. Tel: 519 824 4120 ext 3630. E-mail: jfryxell@uoguelph.ca

species, whereas local extinction events are mathematically analogous to mortality of territory-holders.

The dynamic similarity of spatially explicit territoriality models and metapopulation models suggests the following predictions. First, temporal variability of the entire population should be less than that within individual territories (the so-called portfolio effect), provided that regional forcing processes such as weather are less important than local ecological interactions. Secondly, a critical demographic characteristic determining sustainability of the overall population is the ratio of the expected rate of dispersal success relative to the expected mortality rate of territory-holders. Thirdly, interspersed of suitable and unsuitable patches of habitat can create a threshold effect, such that the population might not be able to persist should the proportion of suitable habitat fall below a critical threshold (Lande 1987).

Habitat suitability in spatially structured models of territoriality is in many ways analogous to source–sink comparisons in metapopulation models. A metapopulation might be composed of a mixture of self-sustaining source colonies, which are permanently occupied, as well as a number of sink colonies that cannot sustain themselves and are consequently transient in nature (Pulliam 1988; Pulliam & Danielson 1991; Pulliam, Dunning, & Liu 1992). In a territorial population, source colonies would be territories in habitat suitable for production of dispersing offspring, whereas sinks would be territories falling in habitat patches in which the expected rate of reproduction is insufficient to replace the parents.

Over the past 11 years, my co-workers and I have studied a spatially structured population of beavers in Algonquin Provincial Park, Ontario. The research programme includes studies of beaver behaviour, population dynamics and community structure. As part of this larger programme, we monitored annual variation in abundance at 14 beaver colonies as well as recording presence and absence of beavers at a larger sample of 60–70 colonies. Here, the variability of local beaver colonies vs. that of the overall population over time is compared and ecological correlates of local beaver demography are considered, to test whether the Algonquin system is consistent with these features of spatially structured models of territoriality.

Methods

Basic demographic data were obtained from annual sampling of 14 beaver ponds in southern Algonquin Provincial Park, centred at 45°35'N and 78°25'W. Study sites were chosen that had relatively small ponds, to facilitate measurement of resource availability, and which were within walking distance of a road bisecting the southern part of Algonquin Park. Such features were common among a larger set of study sites < 2 km from the road, all of which had extant beaver dams and lodges at the beginning of the study. Colonies at which local abundance was estimated were separated by 2–21 km from each other. During September to October,

beavers were captured at each pond using three Hancock traps set around the perimeter of the pond, particularly near feeding stations or the lodge. Trapping at each site was conducted over 1 week, comprising a prebaiting interval of three nights followed by four nights during which traps could actually be sprung. Traps were baited with leafy aspen branches and liberal doses of pulverized castor gland, using the number of different individuals captured per 4 days as the index of local population abundance. The social system of beavers is such that local populations are kin groups (Novak 1987).

Captured individuals were weighed in the trap, tagged in both ears using aluminium or monel ear tags, and immediately released at the point of capture. All individuals < 8 kg were classified as being young of the year (Novak 1987). Although some marked individuals were recaptured as long as 4 years after initial tagging, recaptures across years were fairly uncommon, averaging 30.3% for 76 young of the year and 12.6% for 111 older individuals captured over the entire study period. Given the low frequency of recaptures, we did not feel the data justified site- or age-specific estimates of survivorship.

At the end of October every year, we visited a further set of 60–70 sites with extant beaver dams and lodges, interspersed with our trapping sites. At this larger set of sites, we assessed whether the beaver lodge or dam had been recently maintained, as evidenced by freshly cut sticks, whether food cuttings were present at feeding stations or in the water, and whether a winter food pile had been constructed. Positive scores in any two of these three categories were taken to indicate that the beaver colony was currently active.

Food abundance was measured at all 14 study sites during 1988–90. These ponds were all < 4 ha in area and had well-defined shorelines. All deciduous woody plants were counted that occurred within transects placed perpendicularly to the pond shoreline. Each transect was 2 m wide and extended 60 m perpendicularly to the shoreline. Transects were marked by flagging tape and wooden stakes at 10-m intervals. Between eight and 16 transects were sampled at each site, spaced 50 m apart along the shoreline closest to the lodge. Data for each transect were lumped into 2 m × 10 m sections extending outward from the shoreline. Working systematically along each transect section, we noted the plant species, measured stem diameter 20 cm above ground, and noted whether or not the stem had been cut by beavers. Deciduous woody trees and shrubs were concentrated on solely, because conifers are rarely cut for food by beavers at the study sites (Donkor & Fryxell 1999). The choice to limit transects to 60 m length was based on earlier observation of the limits of feeding forays by beavers (Donkor & Fryxell 1999). The edible biomass of the 10 most common food plants (Donkor & Fryxell 1999) was calculated using Fryxell & Doucet's (1993) allometric equation relating g dry mass of leaves, bark and twigs to stem diameter measured in cm ($y = 16.93x^{2.50}$).

Aquatic food abundance was also sampled at all the long-term study sites by counting all floating water

plants, mainly white water lilies (*Nymphaea odorata* Aiton), within 1-m-wide transects laid using floating nylon rope across the ponds. Subsequently, these counts were multiplied by the average wet mass of individual ramets (Doucet & Fryxell 1993) to estimate biomass per unit surface area of ponds. Ten aquatic transects were counted at each pond, spaced evenly by eye. Coefficients to convert wet mass of water lilies to their dry mass equivalent came from Doucet & Fryxell (1993).

Results

The mean abundance of beavers at the trapped study sites dropped over 50% over the course of 11 years (Fig. 1), ranging from a maximum of 2.3 animals captured per trapping session in 1988 to a minimum of 0.9 animals in 1998. Linear regression indicated that this decline was statistically significant ($F_{1,9} = 60.61, r^2 = 0.87, P < 0.001$). The larger sample of sites monitored for signs of colony activity exhibited an identical trend over time, declining from 73% active colonies in 1988 to 38% active in 1998. Linear regression indicated that this steady decline was also highly significant ($F_{1,9} = 12.53, r^2 = 0.58, P < 0.006$). On the basis of these two estimators, it seems clear that the population of beavers in our study area was not at equilibrium over the past 11 years of study.

The proportion of young of the year among total captures averaged 32.5%, and was apparently unrelated to either year ($F_{1,9} = 0.067, P = 0.801$) or population density ($F_{1,9} = 0.007, P = 0.933$). This suggests that decline in Algonquin beavers was not tempered by density-dependent compensation in offspring recruitment, nor was there evidence that changes in recruitment of offspring were responsible for the decline in the mean population density of beavers over time.

All the local sites varied considerably in abundance over time (Fig. 2). Spatial autocorrelation was tested for by first calculating the degree of correlation between

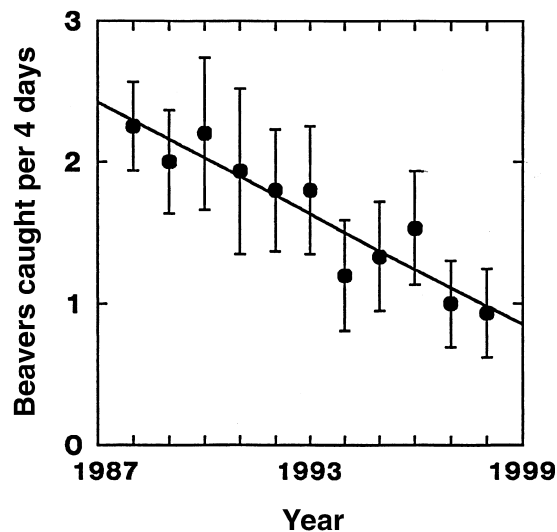


Fig. 1. Annual changes in beaver density averaged over 14 sites in Algonquin Provincial Park, Ontario during 1988–98.

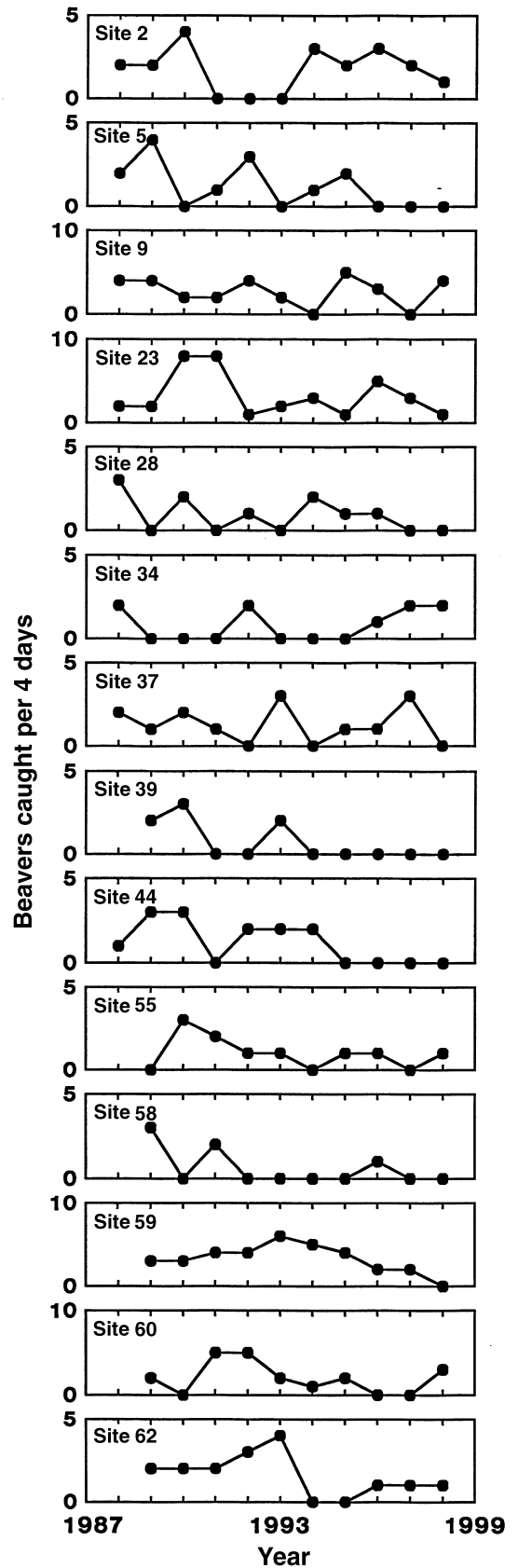


Fig. 2. Annual changes in beaver density at 14 sites in Algonquin Provincial Park, Ontario during 1988–98.

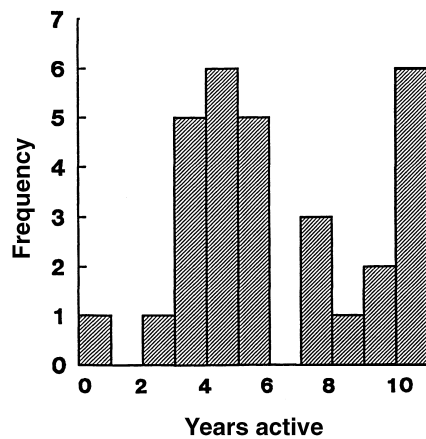


Fig. 3. Frequency distribution of years of occupation of 30 beaver colonies in Algonquin Provincial Park, during 1988–98.

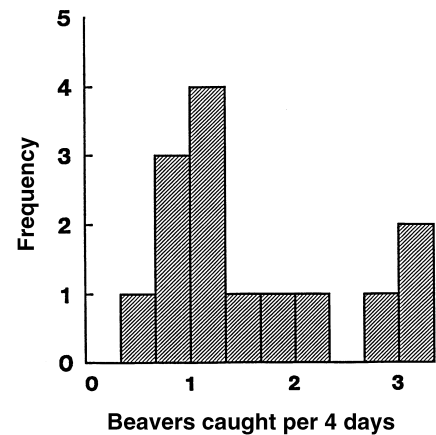


Fig. 4. Frequency distribution of mean density of beavers at 14 beaver colonies in Algonquin Provincial Park, Ontario, during 1988–98.

annual abundance at each pair of sites estimated over the last 10 years. Although the degree of correlation between sites was generally low (mean $r = 0.032$), there were some pairs of sites which covaried strongly (range = -0.83 – 0.77). Regression of pair-wise correlation coefficients against the distance between sites showed no statistically significant relationship that we could discern ($F_{1,89} = 0.982$, $P = 0.325$). This suggests that individual colonies varied independently of one another, irrespective of distance separating them (i.e. local territories were dynamically asynchronous).

Because population variation is commonly correlated with mean abundance (Taylor 1961), the magnitude of variability at the population level vs. that at the colony level was assessed by comparing coefficients of variation (SD/mean). The coefficient of variation at the population level was 0.284, whereas the average coefficient of variation among sites was 1.009, suggesting that population variability at the local colony level was several times that exhibited by the overall population.

Reduction in variability necessarily stems from spatial independence among sites. Hence, low abundance in any given year in some beaver colonies in Algonquin tended to be compensated for by high abundance at other sites. Because individual colonies did not fluctuate in unison, variability of the overall population was therefore smaller than that of its component colonies (the so-called portfolio effect).

There was considerable variation among sites, however, in the degree of population persistence over time. Of 30 sites monitored continuously for all 11 years of the study, only 20% were occupied continuously (Fig. 3). The other 80% of sites were abandoned at least once during the study period, often repeatedly. By abandon, it is simply meant that once-resident animals disappeared for one reason or another, not that animals made a conscious decision to move away. Sometimes sites were abandoned for only a single year (e.g. site 9 in Fig. 2), but longer stretches of abandonment were also observed (e.g. site 44 in Fig. 2). The frequency

distribution of colony occupation had two modes, one at 100% occupancy, the other at 50% occupancy over time.

Similar variation in demographic characteristics was detected across study sites. Two of the closely monitored sites had high levels of abundance (averaging over three animals per 4 days of trapping), whereas the other 12 sites had 50% lower trapping success (Fig. 4). Most of the variability in numbers across sites stemmed from differences in offspring production. The two sites with highest average abundance produced nearly as many offspring as the other 12 sites combined (Table 1). Examination of the numbers of different individuals captured at study ponds showed that offspring outnumbered adults and subadults (animals > 8 kg in body weight) at five of 14 colonies (Fig. 5). These results suggest that few of the Algonquin study sites showed sufficient recruitment of offspring to match adult numbers, perhaps due to variation in habitat suitability.

One of the most important components of habitat suitability is resource abundance. Local beaver abundance

Table 1. Demographic characteristics of beavers captured over 11 years at Algonquin Provincial Park, Ontario

Site number	Adult captures	Adult recaptures	Juvenile captures	Juvenile recaptures
2	13	3	2	1
5	10	1	2	0
9	13	3	8	6
23	9	0	19	6
28	9	0	1	0
34	9	0	0	0
37	5	1	8	0
39	3	1	2	0
44	4	0	6	2
55	9	0	0	0
58	5	0	1	0
59	6	2	15	6
60	12	1	5	2
62	4	2	7	0
Total	111	14	76	23

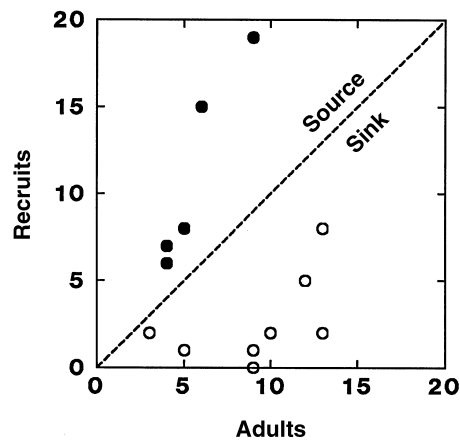


Fig. 5. Cumulative offspring recruitment in relation to cumulative adult abundance at 14 beaver colonies in Algonquin Provincial Park, Ontario, during 1988–98. The dotted diagonal line indicates the demarcation between source and sink colonies.

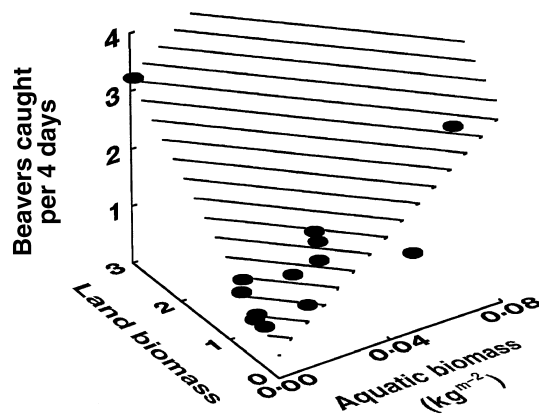


Fig. 6. Mean beaver density at 14 beaver colonies in Algonquin Provincial Park, Ontario, in relation to food availability in aquatic and terrestrial habitats (measured in kg m^{-2}). See text for statistical evaluation of multiple regression equation.

was apparently related to food availability (Fig. 6). Regression analysis of data covering all 14 local populations indicated that beaver density was positively associated with aquatic biomass ($y = 1.23 + 16.25x$, $R^2 = 0.31$, $F_{1,12} = 5.33$, $P = 0.040$). The most prominent outlier from the aquatic regression line (Fig. 6) was a recently colonized site, judging by numerous recently killed trees in the centre of the pond and sparse aquatic vegetation, whereas the other study sites had been obviously occupied by beavers for longer periods. Including terrestrial biomass (z) as a second explanatory variable in a multiple regression analysis substantially improved the predictive power ($y = 0.67 + 20.63x + 0.77z$; $R^2 = 0.64$; $F_{2,11} = 9.90$; $P = 0.004$). Both variables had slopes significantly different from 0 (aquatic biomass: $t = 5.455$, $P = 0.003$; terrestrial biomass: $t = 3.213$, $P = 0.008$). Although sample sizes were small, these results are consistent with the notion that food

availability in both the aquatic or terrestrial realms was positively related to local beaver abundance.

Discussion

These results provide evidence that spatial processes are important in determining temporal dynamics of beavers. In the Algonquin landscape, beavers live in discrete colonies that occur mainly in small, shallow lakes. Consistent with this spatial isolation, no correlation was detected in local dynamics even among close sites. One possible weakness in this analysis was that no information was available regarding intercolony distance via waterbodies, which might arguably be a better measure of spacing than straight-line distance. On the other hand, the topography of the region, with small pothole lakes often isolated from any other waterbodies, might suggest that straight-line distance is a perfectly suitable measure of ecological separation.

Isolated units displayed frequent episodes of abandonment and re-colonization. It was obvious from the number of different adults recorded at each site that adult populations turned over rapidly, which could only occur via immigration. Only one instance was observed of site colonization by an individual marked initially at another site, so no comment can be made on the frequency of dispersal or the distance that dispersing individuals may travel.

A scattering of previous studies have measured dispersal distance in beavers. Leege (1968) found that 20% of 10 marked youngsters in Idaho dispersed between the ages of 12 months and 16 months, whereas 70% of 10 yearlings dispersed successfully between the ages of 20 months and 28 months of age. Mean dispersal distance was 8 km, with a maximum of 18 km. Svendsen (1980) also found that dispersal in Ohio occurred predominantly when beavers were in their second year, with over 90% of marked individuals moving beyond the drainage of the local study area when they dispersed. Van Deelen & Pletscher (1996) found that survival of 10 dispersing 2-year-olds in a montane ecosystem was 70%, with a mean dispersal distance of 8 km. Interestingly, 12 of 22 2-year-olds did not move away from natal sites, suggesting that dispersal probability can be highly variable across systems.

Algonquin beavers are perhaps best characterized as a population in which some territories are sources, but most territories are sinks, presumably due to habitat differences (Pulliam 1988; Pulliam & Danielson 1991; Pulliam, Dunning, & Liu 1992; Smith *et al.* 1996; Sæther *et al.* 1999). A small fraction of the Algonquin colonies were persistent from year to year, and a smaller fraction still permitted offspring production of sufficient magnitude to replace parents. For these supersites, local extinction was a rare event.

Pulliam (1988) characterized source populations as having more emigrants than immigrants, a field metric that has been useful in understanding other source–sink systems (Smith *et al.* 1996; Sæther *et al.* 1999). Beavers

typically disperse from their natal colony in their second or third year of life before breeding (Leege 1968; Svendsen 1980; Van Deelen & Pletscher 1996), so any adults found at a pond are usually immigrants that have arrived from another colony. Following this reasoning, five of the Algonquin study sites were sources at which offspring outnumbered immigrants, whereas the other nine sites were sinks. Interestingly, observations summed across all 14 study sites indicated that adults exceeded offspring production (Table 1), which is consistent with the observed decline in total population abundance (Fig. 1).

Watkinson & Sutherland (1995) have demonstrated elegantly that simple comparisons of mortality and recruitment within local populations in a metapopulation context can produce misleading impressions about whether those local populations are sources or sinks. They argue that density-dependent effects on local demography induced by augmenting the local population with immigrants from other sites could imply falsely that a local population is a sink, even though the local population would be perfectly capable of sustaining itself in isolation. This obviously complicates assessment of source–sink status in many species. There are no published accounts, however, of immigrants augmenting beaver colonies in which adults have survived from the previous breeding season. As a consequence, simple comparison of local recruitment to adult numbers should be sufficient to assess source–sink status.

The vegetation measurements suggest that the most productive source colonies had either an abundant supply of emergent aquatic plants or an abundant supply of terrestrial vegetation comprising highly nutritious species. Trembling aspen (*Populus tremuloides* Michx), willows (*Salix bebbiana* L.), beaked hazel (*Corylus cornuta* Marsh), speckled alder (*Alnus rugosa* [L.] Moench), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh) and white birch (*Betula papyrifera* Marsh) are the woody plant species that are most commonly eaten by beavers in Algonquin (Donkor & Fryxell 1999). Many of the deciduous plants favoured by beavers are early successional species that best regenerate under well-lit conditions. Their current presence in Algonquin forest stands arises from disturbance due to fires and/or logging, events that last occurred several decades ago at our study sites. Every time a beaver consumes a sizeable woody plant, it creates an opportunity for replacement by either a shade-intolerant or a shade-tolerant species (Naiman, Johnston & Kelley 1988; Johnston & Naiman 1990; Pastor & Naiman 1992). If the probability of attack on a particular plant species exceeds the probability of replacement, then forest composition should change over time.

One of the key factors influencing the outcome of selective foraging is the likelihood of replacement by young saplings in the understory following removal of a taller tree via herbivory. Removal of large trees opens large gaps in which shade-intolerant plants probably recruit more readily than shade-tolerant plants, which

would probably retard succession (Pastor & Naiman 1992). On the other hand, if smaller saplings are at greater risk of attack than mature trees, the small gaps created by herbivory by beavers may not enhance recruitment by shade-intolerant species but rather enhance the release of shade-tolerant plants from the understory. If this were the case, beaver foraging over time could conceivably accelerate succession from forest predominated by nutritious shade-intolerant plants to a forest that is predominated by shade-tolerant, less-nutritious plants.

Earlier empirical work showed that recruitment rates by several key forage species in Algonquin were inversely related to distance-dependent risk of foraging by beavers, whereas the opposite pattern was seen in non-preferred plants, such as conifers (Donkor & Fryxell 1999). This pattern is most consistent with the accelerated succession hypothesis. On the other hand, recruitment of mesic species, such as alders and willows, was positively related to the risk of beaver foraging, which is most consistent with the retarded succession hypothesis outlined by Pastor & Naiman (1992). No firm conclusion can be reached on the basis of such conflicting observational data. A better approach would be to actually measure rates of sapling recruitment in response to experimental removal of stems.

The accelerated succession hypothesis predicts that local source populations of beavers cannot sustain themselves indefinitely on terrestrial vegetation. Eventually degraded sites can only support sink populations of beavers. This decline in fortunes might be reversed, however, by disturbance due to forest fires or if local conditions supported ample production of aquatic plants. Forest fires are largely irrelevant for our study beaver population, because of an aggressive fire suppression programme in Algonquin Provincial Park. For some of the study sites, aquatic vegetation sustained high levels of occupancy by beavers as well as substantial production of offspring. Dam creation, followed by siltation and high rates of nitrogen transfer to beaver ponds, should favour improvement in aquatic plant life (Naiman, Johnston, & Kelley 1988). Such improvement in resource availability could provide a plausible alternate pathway to ecological sustainability of local colonies. The fact that few such sites were identifiable among the long-term study populations suggests, however, that this positive feedback may be infrequent in Algonquin.

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