

## Special section

# Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population

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### Abstract

We conducted a 4-year study of beavers *Castor canadensis* to compare the movements, survival and habitat of adults established in existing colonies to juveniles dispersing to new sites in a region with high beaver densities along a suburban–rural gradient. Estimates of annual survival were high for adult and juvenile beavers. Of nine known mortalities, seven (78%) were juveniles. Mortalities occurred during spring–summer, and none during fall–winter. There was a trend toward higher-to-lower survival along the suburban–rural gradient, respectively. Human-induced mortality (e.g. trapping and shooting) was higher in rural areas, whereas nonhuman-induced mortality (e.g. disease, accidents) was higher in suburban areas. Fifteen (14 subadults and one adult) beavers moved from natal colonies to other areas. The average dispersal distance for subadults was 4.5 km (SE = 1.0) along streams or rivers, or 3.5 km (SE = 0.7) straight-line point-to-point. Most dispersal movements were made in spring (April–June). In two cases, individual subadults made return movements from their dispersal sites back to their natal colonies. Dispersal sites tended to be in smaller, shallower wetlands or streams and in areas with higher overstorey canopy closure compared with natal colonies. Woody vegetation usually preferred by beavers for food tended to be less common at dispersal sites than at natal colonies. In regions with high densities of beaver, dispersing juveniles are likely to attempt to colonize lower quality sites. High densities of beavers also lead to more human–beaver conflicts and, in Massachusetts, the pest control management options in place during the past decade have been ineffectual at controlling population levels. Alternately, in regions with no beavers or very low densities and where reintroductions are being attempted, the landscape matrix surrounding release sites should include suitable sites for dispersing young to establish colonies.

### Introduction

Examination of all phases of a species' life history is important to advance ecological understanding, manage populations and conserve biodiversity. The transition from parental provisioning to independence is perhaps the least studied phase in a species' life history, often because it is difficult to keep track of these young, dispersing individuals. Dispersal behavior is highly variable within and among species (Forsman *et al.*, 2002), yet is a critical component in determining the distribution, resource allocation and demographic characteristics of populations (Mathias, Kisdí & Olivieri, 2001). As young animals disperse and become

established on new territories, the quality of the habitat can be a key determinant in their survival and subsequent fitness (Oli & Dobson, 1999). Likewise, other aspects of life history during the early phase of life, such as growth, development, nutrition, and environmental effects and constraints, can be great influences on the optimization of life histories and on population dynamics (Lindström, 1999; Kokko & Ekman, 2002).

North American beavers *Castor canadensis* and European beavers *Castor fiber* greatly modify the landscape through their dam-building behavior; thus they are called 'ecosystem engineers' and 'keystone species' (Naiman, Melillo & Hobbie, 1986; Gurney & Lawton, 1996). Beavers

show well-formed family group behavior, with relatively long periods of juvenile dependency upon parents, long lives (generally up to 10–12 years in the wild and up to 21 years in captivity; Müller-Schwarze & Sun, 2003), prolonged development periods, normally somewhat delayed sexual maturity (1.5–3 years of age) and high survival of both adults and young (Baker & Hill, 2003), especially for *Rodentia*. Typical colony structure (where the term colony has been used to describe one extended-family group) includes a mated adult female and male pair with two to four (sometimes up to six or more) offspring, called kits, which are <12 months old, and young of the previous year, called yearlings, which are 12–24 months old (Svendsen, 1980; Baker & Hill, 2003). Adult pairs have one litter per year, but juveniles from the previous year usually stay associated with their natal colony for 1–2 years after birth. Occasionally, pre-dispersal subadults (>24 months old) and additional adults may remain as part of the colony (Busher, 1987). The subadult phase, however, is when most young beavers make the transition to independence. They travel out from their natal colonies, seeking new areas to build dams, lodges and food caches, and ultimately to mate and reproduce. The time invested in establishing territories and raising young, their ability to so greatly alter their environment and, more recently in places like southern New England, their exponentially rising populations make beavers an interesting species to study for a variety of reasons, including their survival, movement and habitat relationships during the transition phase from parental dependency to independence.

Predation by wolves *Canis lupus*, coyotes *Canis latrans*, bobcats *Lynx rufus* and black bears *Ursus americanus* can be important sources of mortality in some beaver populations, but mortality due to these and other carnivores is often opportunistic and likely not often a limiting factor on beaver populations (Baker & Hill, 2003). Disease, starvation, drownings and accidents can also occur. However, trapping by humans for fur is historically and arguably the major source of mortality for beaver populations in the last two to three centuries (Novak, 1987). Beaver populations in both North America and Europe have been greatly influenced by human exploitation and land-use changes, so that by the end of the 19th century both beaver species had been extirpated from large portions of their ranges (Busher & Dzieciolowski, 1999). Alternatively, beaver populations in some parts of North America have recently been increasing because of new restrictions on fur trapping (Deblinger, Woytek & Zwick, 1999). In Massachusetts, beaver populations subsequently increased exponentially, from an estimated 20–30 000 to perhaps as high as 50–70 000 individuals [Massachusetts Division of Fisheries & Wildlife (MDFW), unpubl. data].

During 2001–2004, we studied beaver populations along an urban–rural gradient in Massachusetts. In general, our focus was on demographic performance, movements and habitat use, with interest in two overriding variables: variation of human dominance (notably suburban development) on the landscape and the lack of fur harvest (i.e. an unexploited population). Both are relatively new but grow-

ing phenomena facing beaver and other wildlife species in North America, and have important implications for understanding and managing populations. In this paper, we compare how these anthropogenic influences affect beaver populations in general, but particularly juvenile animals as they make the transition from a relatively long and normally stable existence in the natal colony to dispersal, independence and establishment of their own colonies. We hypothesized that changes in management regimes and land use would shift the timing and source of mortality in beavers, and that juvenile beavers transitioning from parental care to independence would attempt to establish home ranges in suboptimal areas because of near-saturated habitat.

## Methods

### Study areas

In 2001, three 870-km<sup>2</sup> study areas were established in north-eastern, central and western Massachusetts to represent different degrees of human development, from heavy suburban in the north-east, to mixed rural and light suburban in central, to rural in the west. The north-eastern study area was located within two forest vegetation zones, transition hardwoods–white pine *Pinus strobus*–eastern hemlock *Tsuga canadensis* and central hardwoods–eastern hemlock–white pine (Westveld *et al.*, 1956), and ranged from 36 to 207 m in elevation. The area was 44% forested, 38% residential, 9% agricultural and 7% water/wetland (MacConnell, Goodwin & Jones, 1991). The density of roads, including Interstate, US, and state highway systems and town paved and unimproved roads, was 0.83 km km<sup>-2</sup> (MassGIS, Executive Office of Environmental Affairs, Boston, MA, USA; www.mass.gov/mgis). Human population density was 336 people km<sup>-2</sup> (Massachusetts Municipal Association, 1995). Beaver surveys conducted in 2001 estimated beaver densities at 0.70 active colonies km<sup>-2</sup> (MDFW, unpubl. data). The central study area was located within the transition hardwoods–white pine–eastern hemlock forest vegetation zone (Westveld *et al.*, 1956), and ranged from 225 to 438 m in elevation. The area was 67% forested, 15% residential, 11% agricultural and 7% water/wetland (MacConnell *et al.*, 1991). The density of roads was 0.48 km km<sup>-2</sup> (MassGIS, Executive Office of Environmental Affairs, Boston, MA, USA; www.mass.gov/mgis). Human population density was 64 people km<sup>-2</sup> (Massachusetts Municipal Association, 1995). Beaver surveys conducted in 2001 estimated beaver densities at 0.83 active colonies km<sup>-2</sup> (MDFW, unpubl. data). The western study area was located within two forest vegetation zones, northern hardwood–eastern hemlock–white pine and transition hardwoods–white pine–eastern hemlock (Westveld *et al.*, 1956), and ranged from 207 to 650 m in elevation. The area was 76% forest, 8% residential, 12% agricultural and 4% water/wetland (MacConnell *et al.*, 1991). The density of roads was 0.28 km km<sup>-2</sup> (MassGIS, Executive Office of Environmental Affairs, Boston, MA, USA; www.mass.gov/mgis). Human population density was 17 people km<sup>-2</sup>

(Massachusetts Municipal Association, 1995). Beaver surveys conducted in 2001 estimated beaver densities at 0.43 active colonies km<sup>-2</sup> (MDFW, unpubl. data).

### Demography and movements

We used box and Bailey traps to capture beavers in April–October 2001–2003. Box traps were baited with aspen *Populus* and scent lure to attract beavers (Koenen *et al.*, 2005), whereas Bailey traps were not baited and used to intercept moving beavers. Captured beavers were immobilized with an intramuscular injection of ketamine hydrochloride (10–13 mg kg<sup>-1</sup> body mass) and acepromazine maleate (2.5 mg) to calm the animal and facilitate handling (Lancia, Brooks & Fleming, 1978). We determined sex by the presence or absence of a baculum (Osborn, 1955), nipples on lactating females, and color and viscosity of anal gland secretions (Schulte, Müller-Schwarze & Sun, 1995). We determined age by physical size and weights: individuals > 15 kg were classified as adults (≥ 36 months), those between 10 and 15 kg were yearlings (12–24 months) or subadults (≥ 24 months), and those < 10 kg were kits (< 12 months; i.e. captured within 8 months of birth) (Patric & Webb, 1960; Svendsen, 1980). We were able to confirm the age and sex of several individuals over time through recaptures. We used sterile ointment to prevent the beaver's eyes from drying out and a wet towel wrapped around the tail to keep the beaver cool. Beavers were fitted with metal and colored plastic ear tags (Miller, 1964; Wheatley, 1997) and a tail-mounted radio transmitter, equipped with a mortality sensor that marked double time when the transmitter was motionless > 8 h (Rothmeyer, McKinstry & Anderson, 2002). All marked beavers were placed back into box traps in a shady protected area near the water, and the individuals were not released until they fully recovered from anesthesia, which was judged based on alertness, mobility and ability to hold up the head and move within the box trap. Our research protocol, No. 23-02-02, was approved by the University of Massachusetts at Amherst Institutional Animal Care and Use Committee and by the Massachusetts Division of Fisheries and Wildlife, Permit No. 062.01-3LP.

We monitored beavers with radio transmitters from the ground 1–5 times a week during 2001–2004. Occasionally (4–6 times per year), we flew in fixed-winged aircraft to locate beavers from the air, especially if we lost track of a signal. Locations of beavers were noted when they remained in the original colony or wetland where they were trapped, and marked on topographic maps along with a global positioning system (GPS) point when movements occurred away from the original colony. When a mortality signal was detected, an intensive search was conducted until we located the transmitter. Thorough examinations often led to clues or evidence indicating the cause of death (e.g. carnivore tracks or scats). Carcasses were collected and necropsies were conducted by staff at Tufts Wildlife Clinic, School of Veterinary Medicine, North Grafton, MA, USA. We also noted when and where beavers were killed on roads in the three study areas; date, location, age, and whether marked

or unmarked were recorded. We censored capture histories for beavers with radio transmitters when the animal died and was recovered or when the signal or radio was lost (White & Garrott, 1990). We used program MICROMORT (Heisey & Fuller, 1985) to estimate survival and cause-specific mortality. We estimated survival by study area and season, with spring–summer being the ice-free months of April–September and fall–winter being October–March.

### Habitat use

We divided beaver colonies into two categories: natal colonies were those colonies with established family groups where we captured and marked adults and juveniles, whereas dispersal colonies were those sites that were newly established by marked, dispersing subadults, and had evidence of newly made or refurbished lodges, bank dens and dams. At each colony, we located the main active lodge based on telemetry locations and noted its position with GPS. A map layer for all colonies was created in ArcMap (ESRI ArcView, Redlands, CA, USA) based on data available in a state-maintained geographic information system (GIS) (MassGIS, Executive Office of Environmental Affairs, Boston, MA, USA; [www.mass.gov/mgis](http://www.mass.gov/mgis)). We based wetland type on the wetland classification system used by the Massachusetts Department of Environmental Management and hydrography data available through MassGIS. Primary wetland type was where the lodge was located; secondary types were any surrounding wetland types. We calculated wetland size by adding areas of primary and secondary wetlands around the lodge, based on the coverage provided in the MassGIS database. Stream gradient was determined from the US Geological Survey National Elevation Data digital elevation model overlaying the hydrography layer. Per cent slope was calculated as the difference in elevation between two points, one 200 m above and one 200 m below the lodge.

We chose 10 natal colonies and 10 dispersal colonies for field vegetation sampling based on accessibility or at random from across the three study areas. In the field at each of these colonies, we established 2–4 transect lines, 50–100 m in length, at random points on the north, east, south and/or west edges of the wetland. Transect lines started at the water's edge and continued away from the water into the uplands. Along each line, we noted the woody plant species within 2 m on either side of the line. The species, whether it was tree [> 3 m in height and > 2.5 cm diameter at breast height (DBH)] or shrub form (0.5–3 m in height), was recorded along with DBH for trees. At 0, 25, 50, 75 and 100 m intervals on each line, overhead canopy cover was estimated by averaging concave densiometer measurements in four directions around each point. Concave densiometers can overestimate true canopy coverage, but our goal was a simple comparison of canopy coverage (Cook *et al.*, 1995) between natal and dispersal sites. Woody plant species were categorized as preferred, not preferred, or moderately preferred or used seasonally by beavers for food, based on our observations in the field and data summarized by Allen

**Table 1** Woody plant species utilized by beavers *Castor canadensis* as food, listed as preferred species (those that beavers select when available), occasional or seasonal, and not preferred

Preferred	Occasional or seasonal	Not preferred
Alder <i>Alnus</i> spp. Mill.	Apple <i>Malus</i> spp. Mill.	Eastern hemlock <i>Tsuga canadensis</i> (L.) Carr.
Aspen <i>Populus</i> spp. P.	Ash <i>Fraxinus</i> spp. L.	Eastern white pine <i>Pinus strobus</i> L.
Birch <i>Betula</i> spp. L.	American beech <i>Fagus grandifolia</i> Ehrh.	Other conifers
Dogwood <i>Cornus</i> spp. L.	Blueberry <i>Vaccinium</i> spp. L.	Red maple <i>Acer rubrum</i> L.
Willow <i>Salix</i> spp. L.	Cherry <i>Prunus</i> spp. L.	Elder <i>Sambucus</i> spp. L.
	Hazelnut <i>Corylus</i> spp. L.	
	Maples (other than red) <i>Acer</i> spp. L.	
	Oak <i>Quercus</i> spp. L.	
	Witch hazel <i>Hamamelis virginiana</i> L.	
	Viburnum <i>Viburnum</i> spp. L.	

**Table 2** Annual mean survival (*S*) of beavers *Castor canadensis* marked with telemetry radios in Massachusetts

	<i>n</i>	<i>S</i>	SE	95% CI
All beavers	63	0.84	0.002	0.75, 0.95
Adults	24	0.88	0.006	0.75, 1.00
Juveniles	39	0.82	0.004	0.71, 0.96
Males	33	0.81	0.005	0.68, 0.98
Females	27	0.90	0.004	0.79, 1.00

CI, confidence interval.

(1983), Novak (1987), Baker & Hill (2003) and Müller-Schwarze & Sun (2003) (Table 1).

## Results

### Survival and cause-specific mortality

During 2001–2003, we captured and fitted 63 individual beavers (39 juveniles and 24 adults) with radio transmitters and ear tags. Seventeen of these animals were captured in the suburban north-east, 32 in the suburban–rural mix central and 14 in the rural west study areas. Annual survival was 0.84 (0.75–0.95 95% confidence interval) for all beavers, and 0.88 (0.75–1.00) for adults and 0.82 (0.71–0.96) for juveniles (Table 2). No mortalities were recorded during the fall and winter seasons (October–March).

A decline in survival was noted along the suburban–rural gradient, from eastern to western Massachusetts (Table 3). No mortality occurred in the suburban north-eastern part of the state; survival for adults and juveniles combined was

**Table 3** Annual mean survival (*S*) of beavers *Castor canadensis* marked with telemetry radios along a suburban–rural gradient in Massachusetts

Area	Development	<i>n</i>	<i>S</i>	SE	95% CI
North-east	Suburban	17	1.00	–	–
Central	Suburban–rural	32	0.85	0.005	0.73, 0.99
West	Rural	14	0.66	0.02	0.46, 0.99

CI, confidence interval.

0.85 (0.73, 0.99) in the suburban–rural mix study area in central Massachusetts and 0.66 (0.46, 0.99) in the rural western part of the state. Cause-specific mortality rates from natural causes (e.g. accident, disease) were 0.11 (0.00, 0.23) in the central suburban–rural mix area and 0.8 (0.00, 0.23) in the western rural area. For human-caused mortality (e.g. animal control, shooting) the rates were 0.04 (0.00, 0.11) in the central suburban–rural mix and 0.24 (0.01, 0.48) in the western rural area.

Nine dead beavers were recovered in the field; seven (78%) were juveniles, four in dispersal sites and three at natal colonies. Both adult carcasses were retrieved from natal colonies. Specifically, three beavers were trapped (two subadult males by an animal control agent in September 2002 and August 2003, and one subadult of unknown sex by a fur trapper using cage traps in March 2002), two were killed by predators (a male kit killed by a bobcat in September 2001 and a dispersing subadult female killed or scavenged by a coyote in May 2003), one adult male was shot in September 2001, one adult female died of intestinal rupture and adhesions associated with the reproductive tract in May 2001, one subadult female died of apparent infection in wounds possibly caused by intraspecific fighting in June 2004, and one subadult male was crushed by a tree that had fallen in May 2003.

### Dispersal and movements

We recorded > 2000 telemetry locations during 2001–2004. Fifteen beavers moved from the colony where they were originally captured to other sites. Only one (7%) of these individuals was an adult; the other 14 (93%) were subadults. One subadult died en route on an upland area between wetlands, apparently killed or scavenged by a coyote. It had traveled 2.9 km from the wetland where it was marked. The average dispersal distance for subadults was 4.6 km (SE = 1.0, range 0.4–11.4 km) along streams or rivers, or 3.5 km (SE = 0.7, range 0.1–8.0 km) straight-line point-to-point. The single adult had traveled 0.7 km. In two cases, individual subadult beavers made return movements from their dispersal sites back to their natal colonies. Dispersal movements by marked subadult beavers were usually made in spring (April–June). Of 46 beavers documented killed on roads and highways, 32 (72%) occurred in April–May, which is concurrent with a time of high dispersal activity, with the remainder occurring throughout the year. None of the road-killed beavers were marked.

## Characteristics of natal and dispersal colonies

Most of the wetlands associated with natal colonies were categorized as shrub swamp (eight of 19, 42%), wooded deciduous swamp (four, 21%) or deep marsh (four, 21%). Only two colonies were classified as stream (streams with steeper banks and little or no associated streamside wetlands; 8%) and one as shallow marsh (8%). Most of the wetlands associated with dispersal colonies were classified as shrub swamp (three of 13, 23%), open water (three, 23%) or stream (three, 23%); two were wooded deciduous or mixed conifer–deciduous swamp (15.5%) and two were shallow marsh (15.5%).

The size of primary wetland (i.e. where the main active lodge was located) was greater in natal colonies than in dispersal sites ( $\bar{x}$  = 17.6 ha,  $SE$  = 3.3,  $n$  = 19 and  $\bar{x}$  = 2.0 ha,  $SE$  = 0.6,  $n$  = 13, respectively;  $t$  = 4.6,  $P$  < 0.001). The mean per cent slope of streams in dispersal colonies was greater than streams in natal colonies ( $\bar{x}$  = 0.80%,  $SE$  = 0.14%,  $n$  = 13 and  $\bar{x}$  = 0.43%,  $SE$  = 0.12%,  $n$  = 19, respectively;  $t$  = 2.05,  $P$  = 0.049).

Vegetation sampled along transects was predominantly shrubs for both natal and dispersal sites (80% shrubs and 20% trees at natal sites; 78% shrubs and 22% trees at dispersal sites). Deciduous tree species were more common than coniferous trees at both natal and dispersal colonies [63% ( $SE$  = 8%) deciduous at natal sites, 74% (8%) at dispersal sites], as were deciduous shrub species [86% (5%) deciduous at natal sites, 78% (9%) at dispersal sites]. At natal sites, 16 species of shrubs and nine species of trees made up  $\geq 50\%$  of the species. High-bush blueberry and viburnum species were the most common shrubs; red maple, white pine, alders and cherries were the most common trees (see Table 1 for scientific names). At dispersal sites, 15 species of shrubs and eight species of trees made up  $\geq 50\%$  of the species present. Shrub species were diverse with no species dominating dispersal sites; red maple, eastern hemlock and white pine were the most common trees. The mean DBH for trees was 13.5 cm (1.3) for natal colonies and 15.3 cm (0.8) for dispersal sites ( $t$  = 1.16,  $P$  = 0.26). Canopy closure was 64% (9%) at natal colonies and 87% (2%) at dispersal sites ( $t$  = 2.54,  $P$  = 0.03).

Abundances of the five species of woody plants preferred by beavers as food were equal for dispersal and natal sites in shrub form [9% (3%)], but present in higher proportion in tree form at natal sites [13% (6%)] than at dispersal sites [6% (3%)]. Abundances of the species of woody plants not preferred by beavers as food were present in slightly higher proportion in shrub form at dispersal sites [20% (7%)] than at natal sites [14% (5%)] and were higher in tree form at dispersal sites [53% (5%)] than at natal sites [40% (10%)].

## Discussion

Estimates of beaver survival are not widely available in the scientific literature. Van Deelen & Pletscher (1996) reported

a survival rate of 70% for dispersing subadults in Montana. McNew (2001) reported survival rates of 43% ( $n$  = 18) and 80% ( $n$  = 14) for juvenile beavers and 78% ( $n$  = 9) and 100% ( $n$  = 3) for adults in two study areas in Illinois. McKinstry & Anderson (2002) reported a survival of 43% ( $n$  = 114) in Wyoming. In our study, survival of both adults and juveniles was high (about 84%), and juvenile survival was not significantly lower than adult survival. Of the mortality that did occur, all was during the spring and summer months; no mortalities were recorded during the fall and winter. This may be indicative of fall and winter being relatively stable periods for most beavers. Beavers may be more at risk to mortality during spring and summer because of increased movements of inexperienced young in states like Massachusetts, where mortality due to pest control activity is likely greater than fur harvest. Those individuals that are in established colonies, or those subadults that have established new colonies, have done so by fall and thus have likely increased their chances for over-winter survival. There was an interesting trend in survival along the suburban–rural gradient, with highest survival (essentially no mortality) occurring in the heavy suburban areas in eastern Massachusetts and lowest survival occurring in the more rural western part of the state. Human-caused mortality, such as that from trapping and shooting, appeared to be higher in rural areas, where these methods of removal are traditional and therefore more culturally established than in urban areas.

For a variety of vertebrate taxa, it is often assumed that dispersal of young animals is associated with increased mortality, particularly because of the inexperience of juveniles, unfamiliarity with new areas and increased risk of predation (Smith, 1974; Jones, 1988; Small, Holzward & Rusch, 1993; Bjurlin & Bissonette, 2004; Kershner, Walk & Warner, 2004). Most studies have indeed found that dispersers experience higher mortality than nondispersers or resident animals for both birds and mammals (Jones, 1986; Rappole, Ramos & Winker, 1989; Woollard & Harris, 1990), but at least a few have found no evidence of increased mortality (Keith *et al.*, 1984; Kershner *et al.*, 2004; see Small *et al.*, 1993 for a review and additional citations). Newly independent beavers, forced to establish their first colony site in suboptimum habitat, probably have lower chances of survival (Bradt, 1938; Townsend, 1953; Aleksuk, 1968; Lande, 1987; Campbell *et al.*, 2005). Although juvenile survival was not substantially lower than adult survival in this study, sample sizes were not large enough to allow for further subdivision of the data (e.g. for subadults in marginal versus optimum dispersal sites). However, subadults that have dispersed to smaller, shallower wetlands, or that have modified small streams with little terrestrial and no aquatic food, are probably less likely to survive or more likely to move to another site. Important stochastic events would also alter the outcome (Haughland & Larsen, 2004). For example, particularly cold winters in southern New England would cause smaller wetlands and streams to freeze to the bottom, thus destroying the winter quarters and food caches of the resident beavers. Although we did not observe

extreme winter temperatures during the 4 years of this study, there are certainly winters in the northern portions of the beavers' geographic range that would be subjected to these conditions periodically.

The initiation of independence among subadult beavers probably starts with their dispersal from the natal colony. Although there is some evidence that >50% of kits die in their first 6 months of life (McTaggart & Nelson, 2003), the dispersal period may be the time of highest risk of mortality in the beaver's life history as dispersing subadults are more likely to be subjected to mortality as they travel to new sites. The risk of mortality may increase as dispersers visit a number of potential territory sites before settling down to rear offspring (Fryxell, 2001). The probability of successful dispersal also depends on habitat quality and the degree to which sites are already saturated by resident territory holders, as dispersers will fail to locate patches of suitable habitat that are interspersed among unsuitable patches (Fryxell, 2001).

The habitat saturation hypothesis (Jones, 1988) predicts that dispersers will be less successful (i.e. either die or fail to find a breeding site) in high-density populations. Dispersal will be less common, philopatry more common and distances moved by those individuals that do disperse will be shorter. In Massachusetts, where the beaver population has been growing exponentially and densities are high, the mean straight-line dispersal distance of 3.5 km (SE = 0.7) was less than other studies [9.9 km (Leege, 1968); 8.0 km (Van Deelen & Pletscher, 1996); 10.2 km for females and 3.5 km for males (Sun, Müller-Schwarze & Schulte, 2000)]. The ability for dispersing juveniles to find good quality, vacant habitat has probably been reduced since the mid-1990s, when traditional trapping methods were made illegal and the number of beavers has increased. Although colony surveys indicate that current available habitat is not yet saturated in Massachusetts (MDFW, unpubl. data), densities are high and habitat is nearly saturated. We observed anecdotal evidence of intraspecific strife among beavers seen in the field, such as scarring on tails and body wounds, during our study. In addition, one of nine known mortalities was thought to be due to infection resulting from wounds.

Compared with natal colonies, dispersal sites established by subadults independent of their parents were smaller in size and tended to be in shallower wetlands with more closed canopy conditions. Dispersal sites were along streams of higher gradient than natal sites, but still well within below maximum gradient levels used by beavers (15%; Allen, 1983). Although preferred woody plant foods such as aspen, alder and willow were rarely available on the landscape overall, largely because early successional stage forest is less common throughout southern New England because of decreased cutting and a resurgence of second-growth forest (Trani *et al.*, 2001), presence of these species was even less around dispersal sites than natal colonies. Nonpreferred woody species, such as conifers and red maples, tended to be more common around dispersal sites. Our observations in the field also led us to believe that aquatic plants, which

are a critical source of food for beavers during summer (Jenkins, 1979), were often more abundant at natal colonies than dispersal sites. Conifers are rarely cut by beavers for food, and the most productive colonies in Canada had either an abundant supply of emergent aquatic plants or an abundant supply of terrestrial vegetation such as aspen, willows, alder and birch (Donker & Fryxell, 1999). This combination of habitat variables indicates that, on average, dispersal sites chosen by juvenile beavers are of lower overall quality than the natal colonies where they originated (Allen, 1983).

Massachusetts has one of the highest human populations of any state in the US, accompanied by rapid and extensive urbanization. The process of urbanization involves both changes to the landscape and changes in human attitudes and perception of nature. In Massachusetts, widespread development and changes in traditional wildlife management laws and regulations are having a direct influence on the population dynamics and life-history consequences of wildlife, as evident from the population of beavers. Beavers, in turn, act as agents of change, altering ecosystems with their dam-building activities on a scale large enough to be considered keystone species (Naiman *et al.*, 1986). As human development takes on a larger role in terms of altering ecosystems, beaver-human conflicts will likely increase. Dispersing subadults, seeking new sites to settle and colonize, will likely be the component of the population most affected.

Management of overabundant species is usually spatially and temporally specific, and involves manipulations of populations often more than manipulation of habitat (e.g. vegetation management). Recent restrictions on trapping regulations have resulted in a high survival of both juvenile and adult beavers and subsequent exponential population growth. Because pest control management is very time and area specific and beavers are now so numerous, effects to remove beavers from specific locations are often temporary, as juveniles and other dispersers move quickly into vacated territories.

Attempts to reestablish beaver populations into former range where they have been extirpated by overharvest and land-use changes are widespread across Europe and occur in parts of North America (Dijkstra, 1999; Macdonald & Tattersall, 1999; Sieber, 1999; Fustec *et al.*, 2001; McKinstry & Anderson, 2002). Our research has shown that a landscape perspective should be considered when reintroducing beavers to an area. The matrix of land around release sites should contain suitable potential habitat for dispersing juveniles, with conditions (e.g. adequate water, gentle stream gradients, abundant woody and aquatic vegetation) that will allow juveniles to establish their own colonies and promote survival and reproduction (Fustec *et al.*, 2001; Campbell *et al.*, 2005). Successful reintroduction programs and the restoration of the aquatic habitats that beavers create to enhance biodiversity will occur when habitat is provided for dispersing juveniles within a few kilometers of the target release sites.

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