POPULATION ECOLOGY OF BEAVERS IN ILLINOIS

Thomas A. Nelson and Clayton K. Nielsen

Department of Biological Sciences at Eastern Illinois University
Cooperative Wildlife Research Laboratory at Southern Illinois University Carbondale
State Furbearer Fund, Illinois Department of Natural Resources

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This publication is dedicated to the memory of Dr. Alan Woolf — biologist, mentor, friend.

Cover photo: Beaver tagged for study of beaver population ecology in Illinois.

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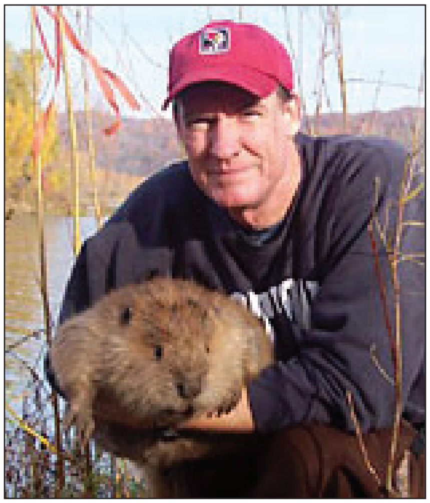
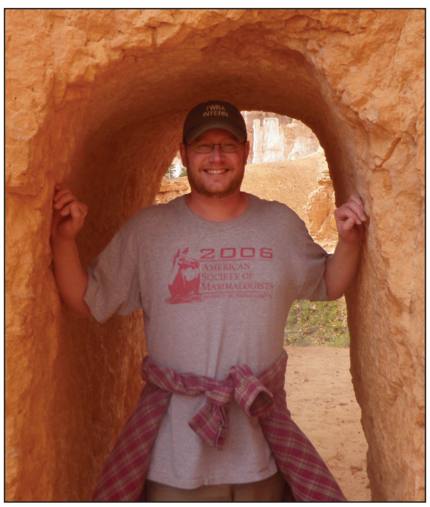


Dr. Tom Nelson

Dr. Tom Nelson is currently a Professor and Department Head in the Biology Department at North Georgia College and State University in Dahlonega. He received a B.S. in Biological Sciences from Illinois State University and M.A and PhD degrees in Zoology from Southern Illinois University Carbondale. He has served as president of both the Arkansas and Illinois chapters of The Wildlife Society. Tom is the former director of the Fisheries and Wildlife program at Arkansas Tech University. He subsequently served as professor and director of the Environmental Biology program at Eastern Illinois University. During this period, he was appointed by the governor to serve on the Illinois Endangered Species Protection Board. He is the recipient of numerous awards for teaching and research in the field of mammalian ecology. From 1994-2006, he directed the M.S. research of 23 graduate students. Tom's research centers on the relationships between man-made habitat alteration (forestry, agriculture, urbanization) and resident mammal species.



Dr. Clayton K. Nielsen

Dr. Clayton K. Nielsen is Assistant Professor of Forest Wildlife in the Cooperative Wildlife Research Laboratory and Department of Forestry at Southern Illinois University Carbondale (SIUC). He teaches undergraduate/graduate courses in forest management for wildlife, research methods, and tropical ecology. Clay is active with The Wildlife Society (TWS) as the Past President of both the North Central Section and Illinois State Chapters. He is a Certified Wildlife Biologist® and the advisor of the SIUC Student Chapter of TWS and Zoology Club. Clay serves as the Director of Scientific Research for the non-profit Cougar Network, is a member of the IUCN Species Survival Commission Cat Specialist Group, and is a Research Associate with the Northern Rockies Conservation Cooperative. In addition to having published >100 scholarly works and having given >280 guest lectures and presentations at professional meetings, his research has been showcased by major media outlets such as TIME magazine, National Geographic magazine, NPR, the History Channel, and the Discovery Channel. Clay and his graduate students study ecology and management of mammalian wildlife species.

INTRODUCTION

Beavers (*Castor canadensis*) are native to North America and have a long history of importance to explorers and settlers (Baker and Hill 2003). Historically, beavers were found throughout North America with a population estimated at 60–400 million animals prior to European settlement (Baker and Hill 2003). During the 17th and 18th centuries, beavers were exploited by fur trappers primarily for European markets, where pelts were used to manufacture felt hats. By 1850, beaver populations had declined substantially due to a combination of market trapping, habitat loss, and harvest by Native Americans for food (Novak 1987). Reintroduction efforts in Illinois began in 1929 and were successful (Pietsch 1956). Populations increased, and Illinois had its first legislated trapping season for beavers in 1951, with a harvest of 659 animals.


Beaver dam across an Illinois stream.

Beavers are important in ecosystems as a keystone species uniquely capable of modifying wetland habitats via dam building and vegetation cutting activities (Baker and Hill 2003). Beaver dams alter hydrology, plant species composition, and sediment balance of forested wetlands (Naiman et al. 1994). Beaver cuttings of larger individual trees for dam-building purposes can initiate gap-phase regeneration in wetland forests; these activities and beaver cuttings of young woody vegetation for food result in a shifting mosaic of successional stages on the landscape (Johnston and Naiman 1990). These influences of beavers on wetland fish and wildlife species range from highly beneficial (e.g., for waterfowl; McCall et al. 1996) to detrimental (e.g., for trout and salmon whose movements are blocked by dams; Olson and Hubert 1994). Beavers are also of great economic concern to humans, valued positively as a furbearing species providing income and recreational opportunities for trappers, but reviled as a nuisance species that can damage timber stands, roads, agricultural crops, and ornamental trees (Baker and Hill 2003).


Beaver swimming following capture and handling. Note ear tag in left ear.

Beaver populations have increased considerably in much of North America since 1850 when populations had been overharvested. Few effective predators exist for beavers (Novak 1987, Baker and Hill 2003), and tularemia (*Francisella tularensis*) is the only disease known to potentially decimate beaver populations (Novak 1987). Human harvest of beavers has decreased due to declining trends in trapper numbers (International Association of Fish and Wildlife Agencies 2005) and local and statewide ordinances banning beaver trapping (Baker and Hill 2003, DeStefano et al. 2006). Furthermore, beaver populations have expanded into urban settings where they are protected from harvest (Busher and Lyons 1999). Given these changes in beaver abundance and increased restrictions on trapping, demographic information about unexploited beaver populations is needed to support management of populations and habitat.

The purpose of our research was to investigate the current status and ecology of beavers in Illinois and to provide useful information to wildlife biologists to better define management options and strategies. Beavers exhibit wide variations in colony composition, demographics, and behavior over their broad geographic range, so regional population studies are important for sound management of this species. To accomplish this we established a partnership among the Illinois Department of Natural Resources, Cooperative Wildlife Research Laboratory at Southern Illinois University Carbondale, and the Department of Biological Sciences at Eastern Illinois University. This collaboration allowed us to compare and contrast Illinois beavers inhabiting diverse ecosystems. We focused on 4 primary areas of interest: (1) population densities and demographics, including age-specific natality and mortality rates; (2) daily movements and dispersal of juveniles; (3) source-sink dynamics in rivers and streams; and (4) genetic relationships within individual colonies and between populations. Beaver ecology was studied in Illinois during 1999–2008.

STUDY AREAS

One of the important advantages of the regional collaboration that occurred throughout this study was the need to study beavers occupying very different landscapes. Much of central and northern Illinois is defined by extensive row-crop agriculture and flat terrain. Here, the habitat available to beavers tends to be long, narrow stream corridors and drainage ditches traversing large corn and soybean fields. In contrast, the landscape of southern Illinois is more forested, less easily drained and characterized by the presence of extensive wetland complexes in certain areas.

Southern Illinois

In southern Illinois, we conducted research primarily on the Union County Conservation Area (UCCA), located in the lower Mississippi River bottomlands (Figure 1). The UCCA encompasses 2,510 hectares primarily managed as an overwintering site for waterfowl and flooded annually by managers during October–February. The UCCA contains a network of connected wetlands and drainage ditches, with 2 drainage ditches connected to the Mississippi River. Wetlands are interspersed by agricultural fields and bottomland hardwood forests. The UCCA consists of 550 hectares of lakes and permanent and seasonal wetlands, with sloughs persistent. Dominant aquatic vegetation is buttonbush (*Cephalanthus occidentalis*), elodea (*Elodea* spp.), and water lily (*Nymphaea* spp.). The UCCA also contains 770 hectares of bottomland hardwood forest. Portions of the forest were flooded seasonally, either naturally or by managers. Dominant tree species include green ash (*Fraxinus pennsylvanica*), black willow (*Salix nigra*), and cottonwood (*Populus deltoides*) in wet areas, with sweetgum (*Liquidambar styraciflua*), pecan (*Carya illinoensis*), and pin oak (*Quercus palustris*) in drier areas. The UCCA is actively farmed, and agriculture fields (i.e., corn, soybeans, winter wheat, and milo) comprise 81% of the 1,195 hectares of open fields. Beavers were protected from legal harvest on the UCCA during our study.

Aerial view of the Union County Conservation Area, southern Illinois.

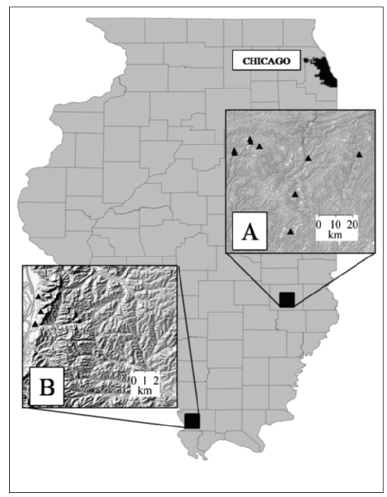


Figure 1. Locations of study areas in central Illinois (A) and southern Illinois (B) where beavers were studied from 1999 to 2008. Triangles indicate the locations of colonies that were intensively studied to assess population ecology and genetics.

The climate of southern Illinois is temperate and mid-continental with cool winters; wet springs; and hot, humid summers. The average annual temperature is 14°C, with temperatures ranging from 27°C in July and

0°C in January (Evans 1981). On average there are 206 frost-free days in Union County (Miles et al. 1979). Annual precipitation is 114 centimeters of rainfall, and April and May are the wettest months (Evans 1981).

Central Illinois

Research in central Illinois was conducted in the Embarras River watershed, 1 of 9 major watersheds in the state (Figures 1 and 2). The 6,800 square kilometer watershed is almost entirely rural, encompassing a mix of farmland and small towns in portions of 12 counties. Approximately 75% of the area is cropland, 11% grassland, 11% forests, and 2% urban. Loss of natural habitats in this area has exceeded rates statewide. Only 30% of the pre-settlement area of forests and 11% of wetlands remain. Non-forested wetlands cover only 0.3% and native prairies <0.01% of the watershed. Corn and soybeans are the predominant crops in the northern half of this area; small grains and hay complement row crops in the southern half (Wiggers 1998).

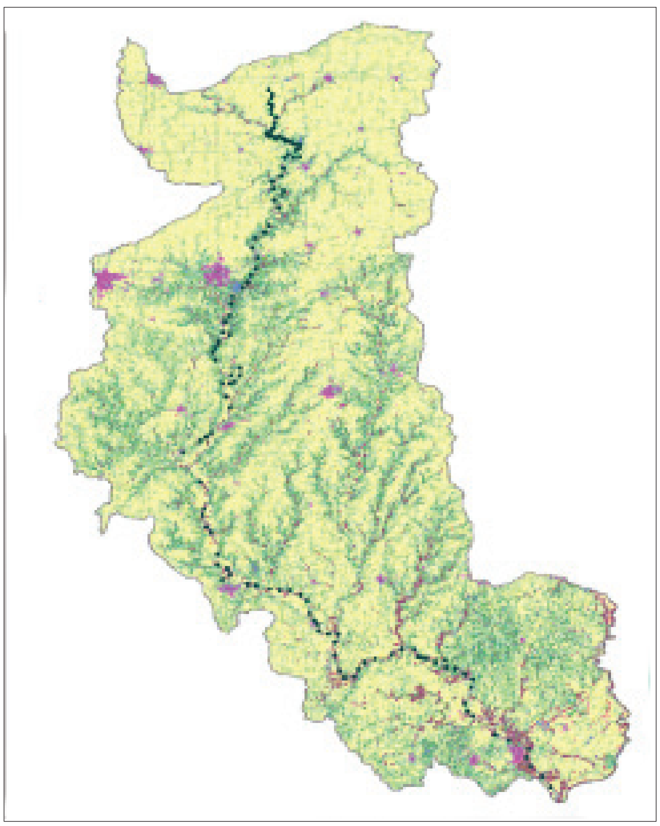


Figure 2. Distribution of 125 beaver colonies observed along a 315-km stretch of the Embarras River in southeastern Illinois during 2001–02. Each dot represents 1 colony.

The Embarras River is 315 kilometers in length, extending from Champaign County in the north to its confluence with the Wabash River in Lawrence County. Over this distance, the river channel increases from 5 to 28 meters in width. The Embarras and its tributaries were selected for this study because they are moderate-sized, low-gradient streams, typical of many in the cornbelt, draining a large, relatively flat watershed. Forested riparian zones are dominated by green ash, maples (*Acer saccharinum, A. saccharum, A. negundo*), cottonwoods, sycamore (*Platanus* spp.) and black willow.

Most stream banks have been impacted by agriculture and development. The large watershed and seasonal changes in precipitation cause water levels to fluctuate dramatically. Tiling of cropfields and channelization of the lower river have increased the volume and velocity of water in the main channel, aggravating bank erosion and sedimentation. In spite of these impacts, water quality in the river is good: 45% of the river meets all Illinois water standards, 46% is considered degraded to a minor extent, and 2% is severely degraded (Wiggers 1998).

Central Illinois has a temperate, mid-continental climate with colder winters and milder summers than the southern part of the state. Average annual temperature is 12°C, with warmest temperatures (25°C) in July and coldest (-1°C) in January. There are typically 180 frost-free days in this region. Annual precipitation averages 94 centimeters; the wettest month is May (Hamilton 1993).

METHODS

Colony Density

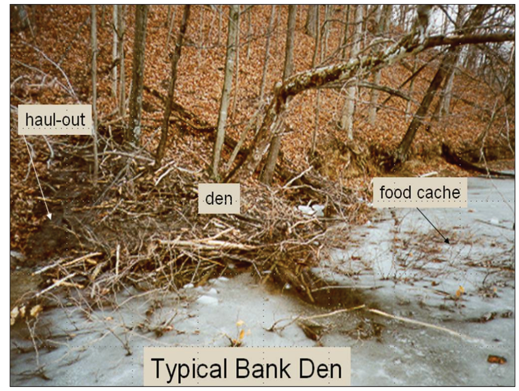
In southern Illinois, we used a combination of spatial organization data and ground searches of wetlands to estimate colony density (colonies/square kilometer) of beavers. Because the study area here consisted of a series of interconnected wetlands, sloughs, and ponds, colony density was calculated as an areal metric (colonies/square kilometer). We quantified the number of active beaver colonies, which we distinguished by apparent or known use and fresh vegetation cuttings, within these areas following complete ground searches of all wetlands.

In central Illinois, the number and location of beaver colonies were mapped during November 2001–February 2002 when bank dens, food caches, and chewed trees were most evident. The entire river was searched during this time frame and searches were conducted on foot or by boat. We followed the guidelines of Robel and Fox (1993) in defining a beaver colony. Most colonies were identifiable based on the presence of a den or set of dens in close proximity and a food cache. However, when dens were not visible because of water levels, a colony was considered to be present wherever there was an area ≥0.3 kilometer in length with fresh sign including food caches, dams, and fresh cuttings.

Typical beaver dam across stream in southern Illinois.

During the first 2 years of the study, more extensive aerial surveys of beaver lodges and dens were conducted using helicopters (Woolf et al. 2003). Eight watersheds in central and southern Illinois (including the Embarras and Big Muddy watersheds) were sampled. Twenty randomly-selected landscape blocks containing beaver habitat were surveyed in each watershed, except 30 were sampled in the Kaskaskia, the largest watershed. Suitable habitat in each block was classified into 1 of 3 categories: streams, permanent wetlands, and intermittent wetlands. Streams included perennial waterways, ditches and the shorelines of large rivers. Permanent wetlands included riparian and palustrine forested wetlands, ponds >1 hectare, and lakes. Intermittent wetlands consisted of wooded and non-wooded seasonal wetlands >5 hectares in size.

Helicopter surveys were conducted at low altitude (<100 meters above the ground) and slow speeds (<50 knots) to optimize observations consistent with safety. Sign of beaver presence was classified as cuttings, food cache, lodge/bank den, or dams and recorded on 7.5-minute topographic maps. Each observation of sign was assigned to 1 of the 3 habitat categories. We calculated the density of sign associated with each wetland type by summing the amount of sign in each wetland type and dividing by the total area of that category surveyed. Total sign in the watershed was then extrapolated based on the amount of each habitat category in the watershed. Aerial survey methods are described in detail by Woolf et al. (2003). Based on these surveys, we could estimate and rank both the quantity and relative quality of beaver habitat among watersheds and between regions of the state.



Typical bank den for beavers in central Illinois.

Population Density and Colony Size

To investigate the size and sex-age structure of each colony, we trapped out a total of 151 colonies on both study areas. Trapping was conducted from December to March each year. Colonies were located by searching streams, lakes, and wetlands by boat and on foot. Most beavers were trapped using #330 conibear traps set near the entrances of bank dens and lodges or around food caches using castoreum-based lures and food lures. Additional beavers were trapped and euthanized using snares at targeted lodges by administering an intravenous injection of Nembutal (pentobarbital sodium; 1 milligram/2.5 kilograms). We also solicited

Conibear set for capturing beavers at the dam.

whole carcasses from cooperating trappers in both central and southern Illinois. Because trappers provided animals taken from colonies that were not completely trapped out, the sex-age composition of this sample was not necessarily representative of the whole population. Consequently, we used the data from these animals to assess age-specific reproductive rates, but excluded them when estimating the mean size and sex-age composition of colonies.

Most beavers were aged based on the eruption, degree of basal closure, and deposition of cementum annuli on the cheek teeth (Larson and van Nostrand 1968). When this was not practical, we weighed individuals on a spring scale (accurate to 0.3 kilograms), and assigned them to 1 of 4 age classes (kits, yearlings, subadults, and adults) based on weight (McTaggart 2002). Sexing was conducted during necropsy based on primary sex organs. Based on this information, we estimated the sex-age composition of each colony and of the regional populations.

To provide a second estimate of the number of beavers in each colony, we conducted night censuses at numerous colonies in central Illinois before removal trapping was conducted. Censuses were conducted using second-generation night-vision goggles, an infrared (IR) headlamp, and IR spotlight to enhance vision after dark. Each colony was censused twice by an experienced observer. Censuses were initiated at sunset and conducted for 2.5 hours. Observers sat 10-20 meters downwind from the den and counted each beaver as it emerged from the lodge and moved about the area. Only beavers that could be positively identified as unique individuals were counted to avoid overestimating colony size. When 2 censuses resulted in different estimates of colony size, the highest count was used as the estimate. After removal trapping was completed, we conducted a final observation at each colony to ensure that no beavers remained.

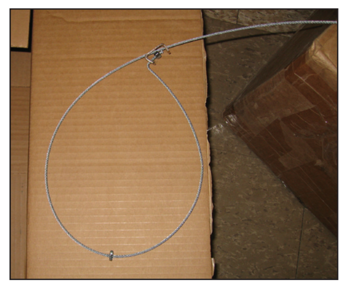
Reproductive Rates

Complete reproductive tracts were removed from all kill-trapped females. Ovaries were stored in Mossman's AFA solution and uteri were stored frozen until the end of each trapping season (Provost 1962, Henry and Bookhout 1969). Subsequently, we thawed each uterus, split it lengthwise with scissors, and examined each uterine horn for placental scars. Scars generally were evident when a light was held behind the uterus to illuminate them, but it was helpful to palpate for scars by passing the tissue of each uterine horn between the fingers, feeling for thicker sections of tissue (Hodgdon 1949, Brenner 1964). Visible embryos also were counted. Placental scar counts and embryo counts were used to estimate the past and current year's fetal rates, respectively (Bond 1956, Brenner 1964).

Ovaries were examined macroscopically by slicing each ovary into 1 millimeter cross-sections. Corpora lutea were distinguishable as light bodies against the gray background of the ovary. Age-specific ovulation rates were estimated as the mean number of corpora lutea/female in each age-class. We subtracted the number of embryos (when these were visible) from the number of corpora lutea to estimate *in utero* losses (Provost 1962, Brenner 1964, Henry and Bookhout 1969).

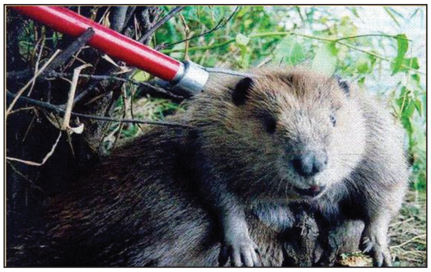
Live-trapping and Radiotelemetry

Increasingly, snares are recognized as a cost-effective, efficient, and safe alternative to large, bulky Hancock, Bailey, or box traps (Weaver et al. 1985, McKinstry and Anderson 1998, McNew et al. 2007). Snares enable beavers to be trapped without inflicting physical injury to the animal. We live-captured beavers during this study with commercially available snares made of 7x7 stranded aircraft cable. Snares were equipped with a stop crimped ~15 centimeters from full closure to minimize the accidental capture of white-tailed deer (*Odocoileus virginianus*) and set with a 25 centimeter loop to avoid capturing non-target species such as river otters (*Lontra canadensis*) or raccoons (*Procyon lotor*) and labeled with metal identification tags as required by Illinois law (McNew et al. 2007). Snares were anchored in position along haulouts, feeding locations, and in shallow channels by



Cable snare used to live-capture beavers.

Cable snare at a haulout set.



Beaver restrained by catch pole.

Restrained beaver being injected with hand syringe.

Beaver being weighed by spring scale.

driving a 1.5 meter length of rebar into the stream substrate and attaching the snare by its swivel base to the post. We checked all snares each morning to minimize the time any animal was restrained.

Snared beavers were brought under control by placing the loop of a catchpole (Tomahawk ™, Tomahawk, WI) around its neck and 1 foreleg. We then anesthetized each by hand-injecting a combination of ketamine and xylazine (Kreeger et al. 1987) with excellent success. Each beaver was marked for individual identification with #16 Monel metal ear tags and a PIT tag (Biomark, Boise, ID) with a unique alphanumeric code that was injected subcutaneously between the scapulae (Nietfeld et al. 1996).

Anesthetized beavers were weighed using a spring scale and age was assigned based on weight as described earlier. Individuals were classified as kits when <1 year old, yearlings in the second year of life, 2 year olds in the third year, and as adults beyond 3 years of age (Patric and Webb 1960). The sex of live animals was determined by palpating for the presence of a baculum through the cloaca, just anterior of the pelvic girdle (Osborn 1955). Females were identified by enlarged mammaries when lactating or inferred from the absence of a baculum (Svendsen 1980). In the final 2 years of the study, tail tissue was saved in a vial of alcohol and molecular methods were used to verify sex (Crawford et al. 2007).

The beaver's fusiform body presents special problems for attaching radiotransmitters. Typical radiocollars can slip over the head if attached too loosely and cause abrasions if attached to tightly (Weaver 1986, Rothmeyer et al. 2002). Surgically-implanted intraperitoneal transmitters have been used successfully in a number of studies. Although animals are usually transferred to a clinical setting for surgery, prolonging restraint and surgery exposes them to increased risk of death from the operation (Wheatley 1997, Rothmeyer et al. 2002). Furthermore, the range of reception for intraperitoneal transmitters is limited by enclosure in the body cavity and can be less than reception distances for externally-mounted transmitters (Wheatley 1997, Rothmeyer et al. 2002).

Tags placed in beaver tails for research. Rectangular tag with transmitter used for radiotelemetry; other tag used for identification via remote videography.

Consequently, we elected to use tail-mounted transmitters designed specifically for beavers (ET-7 transmitter, Telonics, Mesa, AZ). The transmitters are mounted on a modified plastic cattle tag containing an integrated, threaded post and nut assembly that weighs less than 1% of the beaver's body weight. Transmitters were equipped with mortality sensors that increased the signal rate after 8 hours of inactivity.

Once animals reached a surgical plane of anesthesia, we drilled an 8 millimeter hole in the tail approximately 5–8 centimeters from the base and 2–3 centimeters off of the midline using a battery-powered hand drill and bit cold sterilized with a 15% bleach or 10% iodine solution. The radiotag was installed through the hole and secured in place with a washer and nut (Rothmeyer et al. 2002, McNew 2003). This method proved to be simple and quick. The tags imposed little stress on the animals, provided a solid attachment for the transmitter, and resulted in an acceptable reception distance averaging 400 meters over a range of conditions (McNew and Woolf 2005).

After processing, each beaver was secured in a plastic bin to keep it cool, shaded and protected during recovery. After 2 hours, the beaver was checked for signs of alertness. If the animal was sitting up or

Recovered beaver being released from holding tub.

moving in the container, it was restrained with a catchpole and led to water. If the animal demonstrated an ability to walk and swim while maintaining equilibrium and orientation, it was released (McNew 2003). Recovery bins were sterilized with a 15% bleach solution between uses.

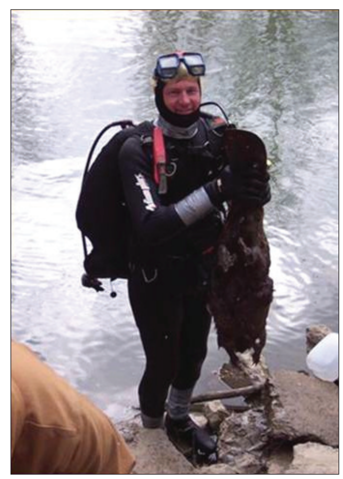
Tracking beavers using radiotelemetry.

After release each beaver was monitored regularly to establish survival and movement patterns until death or exhaustion of the transmitter's battery, usually 10–12 months later. Radiolocations were recorded 2–3 times/week and more often as indicated by movement patterns during the peak period of dispersal. We located radiomarked beavers by taking ≥2 bearings using a receiver; a handheld, 4-element Yagi antenna; and compass (White and Garrott 1990). We allowed ≤20 minutes between the first and last bearing. Beavers have a crepuscular and nocturnal activity period (Hodgdon and Lancia 1983); therefore we collected locations throughout the 24-hour diel period. At least once monthly, we obtained a visual sighting of each animal by homing in on the transmitter. Visual confirmations of location also were made whenever an animal made an unusual movement or when a triangulated location seemed improbable. If we were not able to locate a beaver for >10 days, we searched for the animal and located it using a Cessna 172 aircraft with 2 H-Adcock antennas mounted to the wing struts.

We entered radiotelemetry data into LOCATE II or LOAS to transform bearings into an estimated beaver location expressed in universal transverse mercator (UTM) coordinates (Nams 1990). Movements and distances were mapped and analyzed using ArcView 3.3 with the Spatial Analyst, X-Tools, Animal Movements (Hoodge and Eichenlaub 1997), and MrSid (LizardTech, Inc., Seattle, WA) extensions. The accuracy of locations was tested using a procedure modified from White and Garrott (1990). Based on these tests, the mean distance error was 11.0 ± 1.2 meters (standard error throughout).

Survival Rates and Causes of Mortality

Extensive radiomonitoring was used to monitor survival on both regional study areas. Subsequently, rates were calculated separately for each study area and for beavers inhabiting the river versus tributaries in central Illinois. Beavers that did not survive the first week after capture were censored from the analyses.



Using SCUBA gear to retrieve a dead beaver.

When we detected a mortality signal during radiomonitoring, we retrieved the carcass. A field investigation was conducted immediately at each recovery site and carcasses were returned to the laboratory for a complete necropsy within hours. Cause of death was assigned based on these necropsies. We classified mortalities into 5 categories: predator, capture-related, disease, harvested, and unknown. We sent tissues or whole fresh carcasses of potentially diseased animals to the University of Illinois Veterinary Diagnostic Laboratory for analysis.

We used the known fates model in program MARK to estimate annual and seasonal survival rates for juvenile (i.e., pooled yearling and subadult age-classes) and adult beavers at monthly intervals (White and Burnham 1999). We right-censored survival data for analysis, and we censored data from dispersing animals. We divided the year into 4 seasons: spring (1 Mar–31 May), summer (1 Jun–14 Sep), fall (15 Sep–15 Dec), and winter (16 Dec–28 Feb). For the southern Illinois population, we constructed 16 a priori models using sex, age, and season as covariates (Table 1), and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank and select models (Burnham and Anderson 2002, Bloomquist and Nielsen 2010). In central Illinois, differences in survival rates between beavers inhabiting the river versus tributaries and between age-classes were tested using Contrast software (Hines and Sauer 1989, Sauer and Williams 1989).

Videorecording the Survival of Kits in the Den

We investigated natality and kit survival in the den using remote video-recording systems during April–June 2005 and 2006 (for a detailed description see Bloomquist and Nielsen 2009). Briefly, we used 4 burrow probe systems consisting of a fiber optic camera, infrared light, and videocassette recorder (VCR) powered by 2 marine batteries to videotape beavers inside their lodges or bank dens. Eighteen lodges were observed using this system in southern Illinois and 13 bank dens were monitored in central Illinois.

Video camera installed in a beaver lodge.

We programmed the VCR to tape for 4-hour activity periods with a 1-hour break between activity periods, thereby sampling active and inactive times for beavers for 24–30 hours (i.e., the maximum time possible), after which we replaced the batteries and tape. We video monitored each lodge for 90 hours, and then we moved the equipment to a different lodge. We determined the number of kits per lodge in spring and video monitored them weekly. We recorded the number of kits that we observed on video tape, and we considered the litter count to be complete when we saw the kits nursing. Based on the number born and the apparent loss of kits during the spring and summer we estimated apparent survival and recruitment rates.

Video-recording in traditional stick lodges was relatively easy, but camera installation in bank dens proved to be problematic. The approximate location of the den underground was located by homing on the signal of the resting radiotagged beaver inside. However, finding a point of access for the camera into the den was difficult because dens were often >1 meter underground. In these situations, careful digging using a soil auger and careful placement of the camera was necessary to avoid disturbing the den. However, some dens had a ventilation hole on the surface through which the video camera could be positioned. If the camera was not installed directly into the den, the chances of obtaining useful images declined dramatically.

Installing a video camera inside a bank den.

Home Range, Dispersal, and Movements

A total of 163 radio-tagged beavers were monitored over a 5-year period on both study areas. Each animal was located at 1–3 day intervals using radiotelemetry and triangulation techniques. We calculated 50% and 95% fixed kernel home ranges using the Animal Movements Extension in ArcView 3.3 based upon a minimum of 30 locations each season.

Kernel home range estimates provide a reliable contouring method that accommodates multiple centers of activity, excludes unused areas, and reduces the influence of outliers. The 95% kernel home range incorporates most of the area used by the animal while excluding outliers (White and Garrott 1990). The 50% kernel home range represents the core area of use within the home range (Blundell et al. 2001, Vokoun 2003, Herr and Rosell 2004).

However, kernel home ranges proved to be problematic in central Illinois, where beavers occupy and move along linear features such as rivers because they incorporated adjacent land rarely (if ever) used by the animal, resulting in an overestimation of range size. Therefore, we calculated home range lengths for each animal by measuring the length of the stream channel within each 50% and 95% kernel boundary. Seasons were defined by the equinoxes and solstices. Seasonal home ranges were calculated using all locations for a given animal collected during each season. Locations from all seasons were combined to estimate annual home ranges. In addition, pre- and post-dispersal ranges were calculated for individuals that dispersed during the study. Several individuals did not settle into a stable home range and were classified as 'floaters' and were not included in home range calculations.

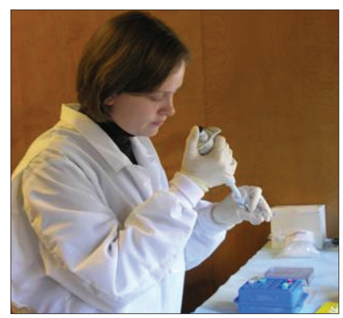
Beaver tagged for study of beaver population ecology in Illinois.

Comparisons of median seasonal home ranges, and pre- and post-dispersal ranges were conducted with non-parametric tests; all statistical tests with $P < 0.05$ were considered statistically significant. Differences in home range size between males and females were tested using the Mann-Whitney U-test. A Wilcoxon signed rank test was used to compare matched seasonal home ranges for differences.

Kinship and Genetic Structure

When we trapped out colonies to assess their size and composition, we removed a small section of muscle tissue from each beaver to elucidate the genetic relationships among individuals within a colony, among neighboring colonies, and between populations in central versus southern Illinois. Colonies were all separated by ≥1 kilometer and data collected from radiomarked individuals confirmed that these were in fact distinct colonies. Tissue samples were stored in 95% ethanol or aluminum foil at -20° C. When possible, tissues were collected from pregnant females and their fetuses. During the 2005–06 trapping season, additional tissue samples were collected from live-trapped and anesthetized animals using a 2-millimeter biopsy punch of ear tissue was collected for genetic analysis. All DNA samples used in this study were archived at Eastern Illinois University.

DNA was extracted and amplified using a polymerase chain reaction (PCR) for each of 7 microsatellite loci isolated during the study. Methods are described in detail by Crawford et al. (2008, 2009). PCR products were screened by capillary electrophoresis and scored using Fragment Analysis. Deviations from Hardy–Weinberg equilibrium and the presence of null alleles were tested in both populations using CERVUS 3.0 software. Linkage disequilibrium tests with Bonferroni correction were conducted using GENEPOP 3.4.



DNA analysis of beaver populations.

The average relatedness (R) within each colony was calculated with jackknife resampling over all loci using the program RELATEDNESS 5.0.8. For colonies containing ≥3 young, we calculated average relatedness among young within each colony. In addition, we tested the average relatedness of adult females within colonies to examine female philopatry. The likelihood-based software KINSHIP 1.3.1 was used to test hypotheses of kinship among colonies. We attempted to assign parentage to all fetal samples, young, yearlings, and subadults within colonies; however, candidate parents could not be identified for several individuals.

In total, we examined the occurrence of extrapair mating in 9 litters. For males, extrapair mating was identified when a male sired the offspring of >1 female in the same breeding season. Extrapair mating was identified for females that produced offspring sired by >1 male within the same litter. Parentage was assigned by a likelihood approach using CERVUS. Candidate parents were determined for both the 80% and 95% confidence levels after a parentage simulation. Occurrences of extrapair mating within the same litter and breeding season were investigated using CERVUS and confirmed, when possible, by examining allelic variation among offspring. The computer program SPAGeDi 1.2 was used to examine the relationship between geographic distance and genetic relatedness.

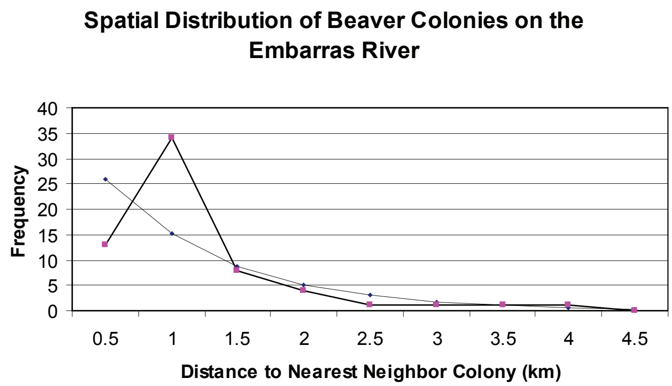


Figure 3. Observed and expected distributions of nearest neighbor distances between beaver colonies on the Embarras River, 2001–02. The expected distribution is an exponential distribution that would occur if colonies were distributed randomly along a river. The spatial distribution of colonies was more uniform than would be expected by chance.

RESULTS

Population Density and Colony Size

During fall 2004 and 2005, we live-captured 92 individuals at 10 colonies on the southern Illinois study area and in March 2006, we captured and euthanized another 79 beavers from 8 colonies, a total of 171 beavers in 18 colonies. The sex ratio of this sample (79 males: 81 females: 11 of unknown gender) did not differ from 1:1 ($P = 0.874$). On our 5.5-square kilometer study area, colony density was 3.3 colonies/square kilometer. Colonies averaged 9.5 ± 1.5 beavers/colony, so the density of beavers on the southern Illinois study area was 31.1 beavers/square kilometer (Bloomquist and Nielsen 2010).

In contrast, densities were lower and colonies were smaller in central Illinois. Because colonies were located linearly along the Embarras River and its tributaries, it was appropriate to calculate colony density as colonies/kilometer rather than colonies/square kilometer as was done in southern Illinois. We located and mapped 125 colonies on the Embarras River, a mean of 0.40 colonies/kilometer or ~0.8 colonies/square kilometer. Colonies tended to be uniformly distributed (Figures 2 and 3), likely a result of inter-colony territoriality.

A total of 239 beavers were harvested on the central Illinois study area, including 169 that we trapped and 70 supplied by cooperating trappers. The sex ratio of this sample (128 males: 111 females) did not differ from unity ($P = 0.300$). Males composed 53-55% of the kit and yearling classes. Ages ranged from kits to 15 years old; 74% were ≤2 years old. The age distribution of beavers harvested from our trapped-out research colonies differed from those supplied by cooperating trappers ($P = 0.040$). Cooperators harvested relatively more yearling and 2-year-old beavers (58.6%) and fewer older beavers (10.0%), whereas these classes comprised 34.3% and 33.1%, respectively, of the beavers in our research colonies.

Harvested beaver.

We trapped-out 28 colonies in central Illinois during the first 2 years of the study. Colonies ranged in size from 2 to 11 beavers (mean = 5.6 ± 2.5). A typical colony was composed of 2 breeding adults, 1–2 yearlings, and 2 kits. However, 43% of the colonies had ≥1 adult (>2 years old) resident in addition to the breeding pair. We found no correlation between the number of yearlings and adult "helpers" in a colony and the number of kits raised ($P = 0.400$). Given the mean density and size of colonies, central Illinois averaged

2.2 beavers/kilometer of river or ~11 beavers/square kilometer of riparian habitat, approximately one third the density found in southern Illinois. Notable was the difference in the sex-age composition of the colonies in southern and central Illinois (Table 1). Whereas colonies on the southern site averaged 9.5 beavers/colony, including >6 adults, those in central Illinois were smaller, averaging only 2.8 adults. In contrast, central Illinois colonies tended to have more kits (1.7 versus 1.1, respectively).

Reproductive Rates

In southern Illinois, 9 of 25 (36%) adult females were bred and no juvenile females were bred (Bloomquist and Nielsen 2010). Reproductive tracts from the 9 adult females contained 33 fetuses, an average of 3.7 ± 1.2 offspring/breeding adult. From remote videography, we observed 8 females with 28 kits and saw no loss of kits or direct mortalities during the neonatal period (Apr–Jun). Combining methods, we observed 61 offspring from 17 adult females, a natality rate of 3.6 ± 0.3 offspring/breeding adult. Extrapolating these estimates to our euthanized sample, we would have expected to find 32.4 kits in these colonies, but only 9 were observed. Hence, kit survival to 11 months was only 28% (9/32.4).

Table 1. Typical age composition of beaver colonies in southern and central Illinois, 2001–06. Listed are mean number of beavers per age class.

Age class	Southern Illinois (*n* = 18 colonies)	Central Illinois (*n* = 28 colonies)
Adult males	3.3	1.5
Adult females	3.2	1.3
Yearlings	1.9	1.1
Kits	1.1	1.7
Total	**9.5**	**5.6**

Reproductive rates were higher in the harvested central Illinois study area where we examined the reproductive tracts of 111 females. Only 2 of 27 (7.4%) yearling females had ovulated and 1 of these carried 3 fetuses. The percentage of females ovulating increased to 52.6% among 2-year-olds and 76.6% among beavers ≥3 years old (Table 2). Ovulation rates for those females that ovulated did not differ significantly among age classes (P = 0.280), but the tendency was for older females to produce more ova, averaging 2.5 ova/female among yearlings, 3.6 among 2-year-olds and 4.4 among older females (Table 2). Twenty-two females were captured late enough in the breeding season to carry fetuses. Of those, the mean number of fetuses was 3.0 for yearlings, 3.4 for 2-year-olds, and 4.3 for older beavers (Table 2). The number of placental scars/female also was influenced by age (P = 0.001). Females that were 2 years old averaged 1.3 scars, 3-year-old females averaged 2.0 scars, and older females averaged 3.3 scars. There was a positive correlation between the weight of the mother and the number of ova shed (P = 0.001).

Table 2. Reproductive rates of female beavers harvested in central Illinois, January 2000–01.

Age-class (y)	*n*	Proportion breeding (*n*)	Ova per ovulating female	Percent with fetuses	Fetuses per breeding female	Daughters born per female/y[1]
Kits	35	0.00 (0)	--	0.0	--	0.00
Yearlings	27	0.07 (2)	2.5	3.7	3.0	0.11
2-y old	19	0.53 (10)	3.6	26.3	3.4	0.90
≥3-y old	30	0.77 (23)	4.4	53.3	4.3	1.62

[1] Calculated as the proportion of females breeding x the number of fetuses/female x 0.5 female offspring.

We estimated the percentage of ova that were fertilized and underwent early development using age-specific ovulation rates and fetal rates. Twenty-two adult females produced 97 ova and carried 88 fetuses, suggesting that 9% of the ova were not fertilized or did not develop to the visible stage. Of the fetuses we examined, 4% were in the process of being resorbed. Consequently, the loss of ova and early embryos was approximately 13%.

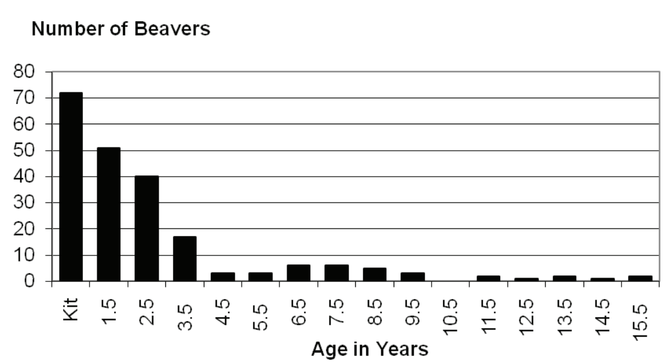


Figure 4. Age distribution of 215 beavers captured and aged in central Illinois, 2001–06.

Survival Rates and Causes of Mortality

Based on a trapped sample of 215 individuals in central Illinois, beavers ranged up to 15 years of age, but survival past 4 years old was uncommon (Figure 4). On the southern study area where beavers were not harvested, annual survival for females was 76%, while adult males survived best (87%) and juvenile males had the lowest survival (55%)(Table 3). In contrast, in the harvested central Illinois population, survival was lower as might be expected and varied between years and habitats. The average adult survival rate was 48% and only 36% of juveniles survived. However, combined survival rates were as low as 35% in 2005 when a tularemia outbreak claimed a high number of individuals and as high as 68% the following year when the population rebounded. We also found that beavers inhabiting the main river channels had somewhat higher survival rates (57%) than those inhabiting

Table 3. Seasonal survival rates of unexploited beavers in southern Illinois, 2004–06.

	Juvenile male			Pooled female			Adult male		
Season	**S**	**SE**	***n***	**S**	**SE**	***n***	**S**	**SE**	***n***
Fall	0.63	0.06	18	0.87	0.01	35	1.00	---	9
Winter	0.87	0.01	14	0.87	0.01	28	0.87	0.01	9
Spring	1.00	---	12	1.00	---	28	1.00	---	10
Summer	1.00		6	1.00		21	1.00		12

smaller tributaries (48%) where fluctuating water levels contributed to mortalities. On both study areas, survival was highest during the spring and summer and lowest during the fall and winter.

As mentioned earlier, the survival of neonatal kits in the den was high. Of the 8 videotaped colonies with neonates in southern Illinois and 13 colonies in central Illinois, we recorded no deaths among neonates during the first 3 months of life. However, survival decreased once the kits left the den and began actively swimming by mid-summer. In central Illinois, kit survival to 6 months of age was estimated to be 43% and survival to 11 months in southern Illinois was only 28%. So, although birth rates were quite high on both study areas, recruitment (survival of young to sexual maturity) averaged 1.1 and 1.7 kits/colony on the southern and central Illinois sites, respectively.

Of 54 radiotagged beavers that died and were recovered, the primary cause of death in the harvested central Illinois population was legal trapping (Table 4). Disease, another important cause of death, hit both study populations hard during the winter and spring of 2004–05. Tularemia was the confirmed cause of death of 6 individuals. Four additional beavers that died during the same period were too decomposed to confirm, but also likely victims of this disease. One beaver was diagnosed with bacterial bronchopneumonia (*Haemophilus spp*. and *Klebsiella pneumoniae*) after

Table 4. Causes of mortality among 54 beavers radiomarked and recovered on the central and southern Illinois study areas during 2002–06.

Cause of death	Central Illinois % (*n* = 27)	Southern Illinois % (*n* = 27)
Trapping	51.9	7.4
Disease	29.6	22.2
Predation	3.7	25.9
Accident	3.7	3.7
Drowning	3.7	3.7
Poison	0.0	3.7
Unknown	7.4	33.3

drowning under the ice on Lake Charleston. Another died unexpectedly during anesthesia. The subsequent necropsy revealed the presence of raccoon roundworm (*Baylisascaris procyonis*) in the heart muscle, making this animal susceptible to the stress of capture. One individual was killed by a dog and 1 was road-killed while crossing a state highway.

In southern Illinois, where the study area was not open to trapping, 2 individuals were legally harvested by a trapper just outside the area. Predation by canids (domestic dogs or coyotes [*Canis latrans*]) was relatively more important here. One individual died from poisoning after ingesting anti-freeze. Of the unknown mortalities, 3 died inside the den and cause of death could not be determined.

Home Range Size

The home ranges of males and females did not differ in size on either study area. Ranges tended to be largest in the winter when resources were more scarce and smallest in the summer when food was abundant and kits were in the dens. However, we found substantial differences in home range sizes between the 2 study areas. In southern Illinois, home ranges averaged 26 hectares and the mean core area (usually centered on the lodge) was 4 hectares. In contrast, home ranges were much larger in central Illinois, averaging 105 ± 30 hectares, as were core areas (28 ± 12 hectares). Because beavers in central Illinois primarily occupy linear rivers and streams, we also calculated mean home range and core area lengths which were 2.3 kilometers and 0.9 kilometers, respectively. Ranges tended to be larger in deep and wide sections of the river, also increasing in size as the distance to the nearest crop fields increased. Home ranges and core areas on tributary streams were smaller than those on the river.

Dispersal

For 4 years (2002–06), we monitored the movements of 130 juvenile and subadult beavers on the 2 study areas (70 in southern and 60 in central Illinois) for 30,511 radiodays (mean = 235 days/beaver). In southern Illinois, 47% of juveniles dispersed, as did 66% of subadults. Males comprised 66% of the dispersing beavers. Dispersal was initiated over a broad period from 1 October to 23 March, but most occurred during January and early February. In turn, most dispersers had settled into their new territories by late-April, but juveniles sometimes remained transient through late-June and 2 individuals never settled permanently in a new location. Dispersers traveled an average distance of 4.0 ± 0.8 kilometers before settling and dispersal distances were similar between the sexes. The longest movement was by an individual that traveled 14 kilometers to its new home range. Beavers that had access to streams and rivers tended to disperse farther from their natal colonies (mean = 5.9 kilometers) than those that were landlocked (mean = 1.7 kilometers). The survival rate for dispersers was 62% and did not differ from that of non-dispersers.

Beaver entering the water.

In central Illinois, beavers dispersed solely up and down the relatively narrow river and stream corridors. We found no evidence of overland travel, although beavers must do this from time-to-time as isolated farm ponds and borrow pits are often colonized in this region. For example, a thorough survey of borrow pits along Interstate 57 between Champaign and Marion found that 5 of 21 (23.8%) of these pits were occupied by beavers. Dispersal rates were lower in central Illinois, with 28.5% of juveniles and 27.3% of subadults dispersing, approximately half the rate as in southern Illinois. Males comprised 84.6% of the dispersers. Dispersal movements did not start until late-January in central Illinois and culminated by 5 July. The median date of dispersal was 25 February, about 2–4 weeks later than in southern Illinois. Dispersal movements tended to be much longer in central Illinois, averaging 14 kilometers. The longest movement by a female was 47 kilometers (crossing the territories of ≥6 other colonies) and 1 male moved 247 kilometers downstream, including 30 kilometers in a single day. Survival during the pre-dispersal, dispersal, and post-dispersal periods were 62%, 58%, and 100%, respectively. The post-dispersal survival rate was significantly higher than the pre-dispersal and dispersal survival rates. In addition, dispersing individuals had a higher survival rate (58%) than non-dispersers (23%) during the study.

Exploratory forays by individuals (defined as repeated movements away from the natal territory) prior to dispersal were common by both males and females in central Illinois. Both juveniles and subadults moved upstream and downstream for a period of days or weeks. Some of these individuals subsequently dispersed, but others settled back into their natal colonies for another year. Because neighboring colonies usually occupied territories both upstream and downstream from the natal colonies, these exploratory forays often crossed through others' territories.

Beaver swimming in small lake.

Source-sink Dynamics

In central Illinois, we hypothesized that colonies might show source-sink dynamics with colonies inhabiting the main river acting as population sources, whereas those on tributary streams were sinks. Thirteen colonies were intensively monitored during 2004–05 to count the number of kits produced, estimate survival rates, and quantify dispersal rates and directions of beavers. Rates were compared for river versus stream beavers.

The mean number of young observed in colonies on the Embarras River was 2.8 ± 1.3. The mean number of young observed in colonies on tributary streams was 0.7 ± 0.2. In spite of the apparent biological difference, the high variability of the reproductive success of river colonies resulted in a lack of statistical significance (P = 0.260). Generally, colonies on the main river produced the largest number of kits and our 2 most productive colonies were there. One contained 2 adults, 1 subadult, and 5 kits and a second consisted of 2 adults and 5 kits. Together, these 2 colonies produced a total of 10 kits, 59% of the total number of kits observed in all 13 colonies. On tributaries, colonies tended to be smaller. One colony on Kickapoo Creek contained 2 adults and 2 kits, however, it was most common to see 2 adults and 1 kit or 2 adults with no young on the tributaries.

Survival rates were higher for river colonies throughout most of the 2-year period (Figure 5), however patterns differed between years and by August of the first year, such that survival was somewhat lower on the river. Tularemia and trapping, the primary sources of mortality, impacted survival rates in both the river and tributaries. However, in the absence of trapping, only 1 beaver originating from a river colony would have died. Among surviving juveniles and subadults, 3/8 (38%) of the individuals from river colonies dispersed, while 6/13 (46%) of beavers born on tributaries dispersed. Dispersal rates were somewhat higher on the river, but the difference was not significant (P = 0.083). Generally, beavers dispersing from river colonies tended to settle on the river and those dispersing along tributaries settled elsewhere along the tributary. We found no clear pattern of dispersal from the source (river) habitat to the sink (tributary) habitat as we hypothesized.

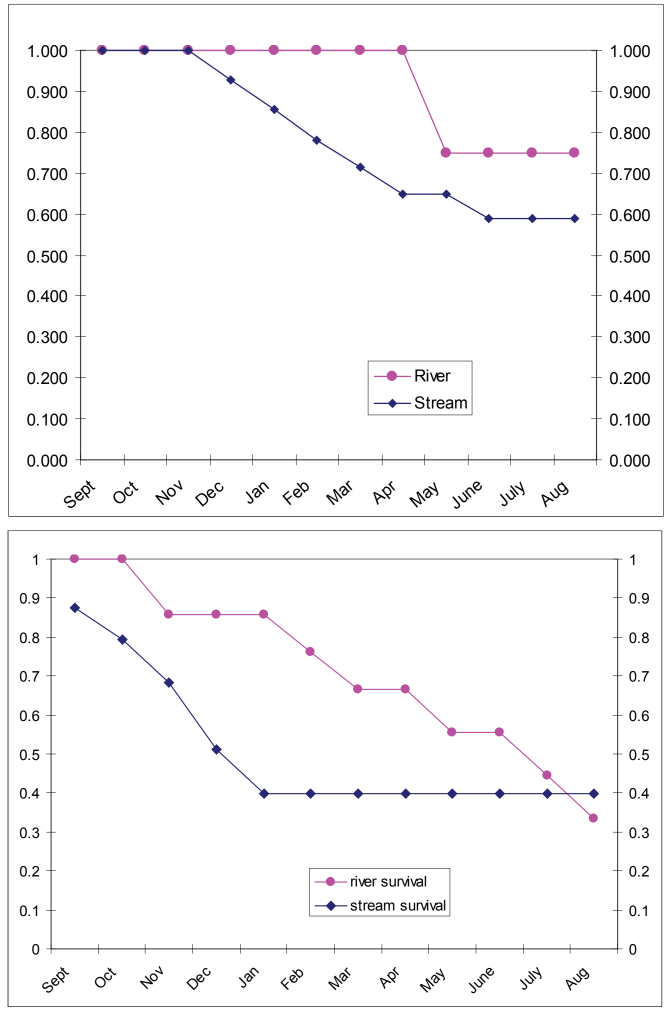


Figure 5. Survival curves for beavers inhabiting the Embarras River and its tributaries during 2004–05 (upper graph) and 2005–06 (lower graph). Survival tended to be higher in the river compared to tributaries.

Kinship and Genetic Structure

Based on the number of colonies that we found with >2 adults, we questioned whether the monogamous pairing, generally thought to be the primary mating pattern in beavers, was typical in Illinois. Since there had been no genetic studies on beavers to investigate parentage or family relationships within colonies, we used microsatellite loci to describe genetic relationships within the 2 Illinois populations. Specifically, we measured the extent of relatedness (R) within members of a colony, prevalence of "cheating" among paired partners, and whether neighboring colonies tended to be more related than distant colonies.

Tissues were collected from 49 beavers in southern Illinois and 46 in central Illinois for genetic analysis. Beavers in this portion of the study came from 3 colonies in southern Illinois that averaged 9.0 ± 2.0 beavers/colony and 12 colonies in central Illinois that averaged 3.8 ± 2.4 beavers/colony. Each colony in southern Illinois had ≥1 pregnant female, providing additional samples from 22 fetuses in 6 litters. All microsatellite loci were moderately polymorphic in both populations and none was identified as linked.

Colonies in both study areas varied widely in average relatedness (Table 5), ranging from 0.04 to 0.64 in central Illinois and from 0.16 to 0.41 in southern Illinois. Of 6 fetal litters collected in southern Illinois, 2 (33%) were composed of half-siblings, although the most-likely fathers could not be identified. In central Illinois, young occupying the same colony were identified as full-siblings in 4 (67%) of 6 colonies with R-values near 0.50. In the 4 largest colonies (≥7 individuals), adult females were shown to be first-order relatives; however, mother–daughter pairs could not be distinguished from full-sibling pairs because all shared 1 allele at each locus. Our sample included 3 colonies with ≥2 adult males. In each case, these males were either unrelated or second-order relatives.

Table 5. Average relatedness values for age and sex classes within beaver colonies in central and southern Illinois, 2005–07.

	Average pairwise relatedness (R + 1 SE)	No. pairwise comparisons (no. colonies)
All members		
Central Illinois	0.33 ± 0.19	97 (12)
Southern Illinois	0.24 ± 0.14	420 (3)
Fetal littermates		
Southern Illinois	0.45 ± 0.13	33 (3)
Young		
Central Illinois	0.50 ± 0.19	19 (6)
Adult females		
Central Illinois	0.55	1 (1)
Southern Illinois	0.45 ± 0.09	30 (3)
Adult males		
Southern Illinois	0.03 ± 0.31	10 (3)

Microsatellite loci showed moderate levels of polymorphism in both populations, giving a combined total exclusionary power of 0.987 for the first parent and 0.917 for the second parent in central Illinois and 0.990 and 0.933, respectively, in southern Illinois. In central Illinois, our analysis identified ≥1 parent with 95% confidence in 23 (74%) of 31 young, yearlings, and subadults, including parental pairs (16%) for 3 young. Because of these results, extrapair mating could only be assessed for 2 litters. We found 1 colony in which 1 male sired the young of 2 females. In another colony containing 3 young, 2 were full-siblings and the other a half-sibling.

In southern Illinois, 16 (61%) of 26 offspring (from 7 litters) were assigned to 10 parental pairs and extrapair mating was assessed for all litters. All fetal specimens were correctly assigned to their mothers. Six males were identified as the sires of 13 (59%) of 22 fetuses. Males from different colonies were identified as the most-likely fathers for 6 (46%) of these 13 fetuses. Two litters contained half-siblings and subsequent analysis revealed these had been sired by ≥2 different males. A half-sibling pair was found living in the father's colony, whereas the mother of both of these kits occupied a separate colony with another mate. The latter was identified as the father of her 2-year-old offspring still occupying the natal colony, as well as the sire of her current unborn litter. None of the adult females from the paternal colony were identified as possible mothers of these young. In total, we found 3 occurrences of within-season extrapair mating and 7 instances of intercolony mating in southern Illinois. When combining results from both study areas, a total of 5 (56%) of 9 litters showed evidence of within-season extrapair mating.

We found no relationship between genetic relatedness and distance between colonies in central Illinois (n = 1,380 pairs; P = 0.283). Pairwise distances ranged from 1 to 68 kilometers, consistent with dispersal data showing that individual beavers may move over long distances from their place of birth to their eventual place of reproduction. Relatedness was weakly correlated with distance in southern Illinois (n = 2,120 pairs; P = 0.060). Distance between relatives spanned a smaller range here, with pairwise distances from 1 to 5 kilometers.

We also used genetic analysis to investigate the extent of genetic differences within and between the southern and central Illinois populations. Polymorphism was moderate at all loci in both populations. We found no significant genetic differences between the sexes with F_{ST} values of -0.004 (P = 0.670) and -0.006 (P = 0.600) in central and southern Illinois, respectively. Similarly, we found no genetic differences among age-classes in central Illinois (F_{ST} = -0.006; P = 0.702), but a low level of subdivision in southern Illinois (F_{ST} = 0.021; $P < 0.050$). A moderate level of genetic subdivision was evident in the 3 large beaver colonies in southern Illinois (F_{ST} = 0.086; $P < 0.001$).

Although "within population" genetic structure was low in each population, the central and southern Illinois populations differed genetically from each other. For example, allele frequencies differed at 6 of 7 loci ($P < 0.001$). F_{ST} values for each of these 6 loci differed significantly from 0, ranging from 0.05 to 0.15 ($P < 0.001$). The overall F_{ST} value (0.07 ± 0.01) between populations also differed significantly from 0 ($P < 0.001$). Our analyses suggest that southern and central Illinois populations are 2 genetically distinct clusters. Individual animals could be assigned to 1 of the 2 populations with a high level of certainty (mean = 0.82 ± 0.17). Seventy-four of 105 (70%) beavers tested were successfully assigned to 1 of the 2 populations. Of these, 71 (98%) were assigned to the regional population in which they lived. It was interesting to note, however, that 1 beaver captured in central Illinois was genetically linked to the southern Illinois population and 2 individuals trapped in southern Illinois were genetically linked to the central Illinois population, consistent with our telemetry data that some long-distance dispersal occurs between the regions.

Harvested beaver.

Seventeen of 55 beavers (31%) from the central Illinois population and 14 of 50 beavers (28%) from southern Illinois were shown to be of mixed ancestry. Genetic analyses suggested that migration between the 2 regions is low to moderate (0.16 beavers/generation). This analysis suggests that the genetic ancestry of 83% of our beavers traces to the population from which the individual was trapped.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Sex Ratios and Age Structure

Beavers on our study areas exhibited sex ratios close to 1:1, which is typical of most beaver populations. Hill (1982) and Novak (1987) reviewed sex ratios in samples collected across the species' geographic range and concluded that ratios were approximately equal in most areas. However, sex ratios on both study areas tended to be skewed towards males in the youngest 2 age-classes. Other researchers have reported that males often outnumber females only in the kit and yearling classes, whereas older age-classes are skewed towards females (Osborn 1953, Woodward 1977). Higher proportions of males at birth may be an adaptive mechanism to offset higher mortality rates experienced by dispersing yearling and 2-year-old males (the predominant dispersers in Illinois), ensuring an operational sex ratio near unity.

Beaver scent mound.

The apparent age structure of beaver populations may be biased by the method, location, or intensity of trapping. Snares and leghold traps set on land near scent mounds or dams are more likely to capture adults (Hill 1982). Unbiased estimates of the age structure of beaver populations are more likely when the entrances to lodges or dens are trapped intensively using submerged conibear sets (Hill 1982) as we did in central Illinois during the first 2 years of this study. Consequently, we believe that the age structure of the beavers that we trapped during that period is representative of harvested beaver populations in Illinois.

Although 74% of the beavers that we trapped were <2 years old, a number of old beavers were present in the sample, including 7 individuals ≥10 years old. Beavers in the wild typically do not exceed 10 years of age; however, individuals as old as 21 and 24 years old have been harvested (Larson 1967, Brown 1979). The percentages of kits, yearlings, and adults in central Illinois colonies were similar to the composite percentages of these age classes from 10 previous studies (30%, 23%, 47%) reported by Hill (1982). In southern Illinois, the age-structure of our research colonies (38% adults, 47% juveniles, and 15% kits) was slightly older, with more juveniles and fewer kits. This may reflect delayed dispersal brought on by the high density of this population (McNew and Woolf 2005). Busher and Lyons (1999) reported a similar age-structure (48% adults, 38% juveniles, and 15% kits) for a beaver population thought to be near carrying capacity in Massachusetts.

A higher proportion of yearlings and 2-year-old beavers were harvested by commercial trappers than was present in our research colonies (Table 6). This may be because trappers tended to trap on dams and scent mounds which are frequented by yearlings and 2-year-olds during dispersal. Differences in the age-structure of trapped samples may also reflect the history of trapping these colonies. Few trappers attempted to remove all of the beavers from a colony, instead taking a few animals from the same colonies year after year. This may truncate the older classes, leaving predominantly younger animals. In contrast, several of our research colonies were located in areas that were rarely trapped, potentially leading to increased longevity of resident beavers. The literature corroborates this hypothesis. The mean age of beavers taken from heavily trapped nuisance colonies in Wisconsin was 1.6 years of age (Peterson and Payne 1986), whereas the mean age of beavers from untrapped or lightly trapped populations has ranged from 2.6 years old in Ohio to 3.8 years old in Newfoundland (Henry and Bookhout 1969, Payne 1982).

Population Density and Colony Size

Typically, beaver abundance is estimated from surveying an area for beaver activity (e.g., lodges, cache, cuttings), generally via aerial surveys (Baker and Hill 2003, Woolf et al. 2003). The effectiveness of aerial surveys in locating known colonies is variable, and range from 98% (Bergerud and Miller 1977) to only 28% (Robel and Fox 1993). Helicopter surveys followed by ground searches conducted in central and southern Illinois during the first 2 years of this study suggested that aerial results were correct 80% (range 75-90%) of the time (Woolf et al. 2003). The optimal times for conducting surveys occurred after leaf-off in the fall, but before December when snow, ice, and high water conditions made sighting food caches and fresh cuttings difficult.

Table 6. Number and percentage of beavers in each age-class from trapped-out research colonies versus those harvested by cooperating trappers in central Illinois, 2001–06.

	Research colonies		**Cooperating trappers**	
Age-class	***n***	**%**	***n***	**%**
Kits	55	32.5	22	31.4
Yearlings	37	21.9	20	28.6
2-y old	21	12.4	21	30.0
3-y old	17	10.1	2	2.9
≥ 4-y old	39	23.1	5	7.1
Total	**169**		**70**	

However, aerial surveys are of limited value unless biologists also have corresponding information on the size of colonies from local populations as determined from trapping or visual observations. Based on our estimates, the southern Illinois study area had one of the highest beaver densities (3.3 colonies/square kilometer) ever reported in the wildlife literature (Table 7). According to a review by Novak (1987), beaver densities may be as high as 4.6 colonies/square kilometer. However, prior to our study the highest published density was 1.3 colonies/square kilometer. It seems likely that beaver density on the southern Illinois site was higher than in other studies due to: (1) protection from harvest and high quality habitat suitability, (2) differences in the methods by which density can be estimated, or (3) a combination of these. Regardless, beavers were very abundant on this site and probably near the carrying capacity of these wetlands. This high beaver density represents a situation increasingly evident on many such areas throughout North America.

Similarly, the average size of colonies in southern Illinois (9.9 beavers/colony) is one of the highest reported in the wildlife literature (Table 8). Colonies here were larger than those in central Illinois and we found more adults residing in southern Illinois colonies (mean = 5; 2.5 times the typical number reported by Bradt 1938). When a high percentage of additional adults live in a colony, it usually indicates that the population is near carrying capacity (Muller-Schwarze and Schulte 1999). We found that 7 out of 8 colonies on this site had multiple adult females, and 5 of 7 colonies contained multiple adult males. Most surprising was the fact that 3 colonies had >1 pregnant female. Typically, only the dominant female in the colony produces young, but a few examples of 2 lactating females have been reported (Busher et al. 1983, Novak 1987).

Table 7. Comparison of beaver colony densities from the wildlife literature. Harvested populations are followed by an H.

State/province	Colonies/km^2	Study
Newfoundland	0.34	Payne (1982)
Northwest Territories	0.40 (H)	Aleksiuk (1968)
Newfoundland	0.51 (H)	Bergerud and Miller (1977)
Massachusetts	0.58	Howard and Larson (1985)
Central Illinois	0.80 (H)	this study
Minnesota	1.02	Broschart et al. (1989)
Alberta	1.06	Larson and Gunson (1983)
Manitoba	1.07	Larson and Gunson (1983)
Wisconsin	1.30	Zeckmeister and Payne (1998)
Southern Illinois	3.27	this study

In contrast, colonies in central Illinois were smaller (5.6 beavers/colony), in the midrange of reports from across North America (Table 8). However, 1 colony living in prime habitat that had not been trapped in recent years contained 11 individuals. Colonies tended to be larger along the main Embarras River channel than along tributaries or drainage ditches. Often, river colonies produced 3–5 kits, whereas those on tributaries produced only 1 or 2. Colonies on drainage ditches were usually occupied by unrelated males or a young adult pair without kits, apparently dispersers that were pushed into unoccupied or marginal habitats. Habitat quality is thought to influence colony size and composition (Huey 1956, Gunson 1970). Generally, optimal habitats provide an abundance of preferred woody foods during the winter, whereas marginal habitats lack these (Hill 1982). Small streams and ditches in Illinois appear to provide suboptimal habitat because they quickly flood during periods of heavy rain, yet are often dry during the summer. Consequently, they do not provide the stable water levels preferred by beavers. In addition, woody winter foods are generally sparse along ditches because landowners mow brush to maintain flow.

Table 8. Mean number of beavers on Illinois study areas relative to those recorded from other North American studies.

State/province	Colony size	Study
New Brunswick	3.2	Nordstrom (1972)
Alaska	4.1	Boyce (1974)
Michigan	5.1	Bradt (1938)
Central Illinois	5.6	this study
Ohio	5.9	Svendsen (1980)
Massachusetts	8.1	Brooks et al. (1980)
Nevada	8.2	Busher et al. (1983)
Southern Illinois	9.9	this study

A high percentage (43%) of central Illinois colonies also contained ≥1 additional non-breeding adult suggesting that this population also was near carrying capacity. Muller-Schwarze and Schulte (1999) reported that 22-88% of the colonies in high-density populations had additional adults present, whereas <13% of colonies in low-density populations had additional adults. This is probably because the lack of unoccupied habitat discourages dispersal (Hill 1982, Zeckmeister and Payne 1998). As in southern Illinois, the central population exhibited delayed dispersal apparently because the population is high relative to the availability of quality habitat.

Yearlings and nonbreeding adult offspring contribute to the maintenance of the lodge and dams, cooperate in collecting food for the cache, and help care for kits (Hodgdon and Lancia 1983, Novak 1987). Therefore, we hypothesized a positive correlation between the number of these older offspring and the number of surviving kits in colonies. Kin selection theory suggests that it may be adaptive for sexually mature offspring to forego breeding and help parents raise siblings if these individuals increase their indirect fitness by augmenting the reproductive success of their parents or their direct fitness by gaining familiarity with the skills of parenting (Hamilton 1963, Feldhamer et al. 2004). However, we found little evidence that colonies with resident older siblings produced more kits. This is consistent with Smith's (1997) conclusion that these auxiliary siblings were not associated with increased reproduction in colonies in Wisconsin and Minnesota. Perhaps these older siblings increase their fitness by gaining experience with parenting, maintaining lodges, and defending territories. They also may increase their chances of survival by staying with their parents when there is little chance of finding a suitable, unoccupied territory (Heske and Bondrup-Nielsen 1990).

Reproductive Rates

The breeding season for beavers typically runs from October through March (Hill 1982, Novak 1987). Beavers are polyestrous and will come into heat repeatedly every 14 days until bred. As in other regions, female beavers in Illinois are not sexually mature until they are ≥1 year old (Hill 1982, Novak 1987). Even yearlings typically do not breed and contribute little to a population's overall production of young. We found only 2 reproductively active yearlings and both were taken from areas that were heavily trapped. Mueller-Schwarze and Schulte (1999) noted that yearling beavers are more likely to reproduce in harvested populations. When populations are legally trapped, adult survivorship decreases which vacates territories and enhances survivorship and reproduction of dispersing yearlings (Boyce 1981). Dieter (1992) found no reproduction by yearlings in a lightly-trapped sample from South Dakota, however Peterson and Payne (1986) found 13% of yearlings bred in colonies that were trapped regularly. The highest percentage of breeding yearlings (44%) was reported by Lyons (1979) for beavers in Massachusetts.

Natality rates in Illinois were near the high end of those reported from other regions (Table 9). However, the percentage of females that bred in southern Illinois (36%) was considerably lower than the 77% breeding in central Illinois. This difference is likely due to differences in density since reproduction is density-dependant in beavers (Gunson 1970, Boyce 1974, Payne 1984). Furthermore, this lower percentage of breeding females (and not low natality) explains why we found fewer kits in southern Illinois relative to central Illinois.

Table 9. Comparison of beaver natality rates from the wildlife literature. Exploited populations are followed by an H (harvest).

State/province	Offspring/ bred female	Study
Mississippi	2.6 (H)	Wigley et al. (1983)
Ohio	2.7	Svendsen (1980)
Newfoundland	2.9 (H)	Payne (1984)
New Brunswick	3.0	Nordstrom (1972)
Wisconsin	3.1	Zeckmeister and Payne (1998)
Southern Illinois	3.6	this study
Maryland	3.8 (H)	Larson (1967)
South Dakota	4.0 (H)	Dieter (1992)
Central Illinois	4.0 (H)	this study

In our study populations, natality rates increased with age through the first 4 years of life, but ovulation rates were somewhat lower than those reported by others. Since fecundity in beavers is thought to be negatively correlated with population density (Boyce 1974, Payne 1984), this appears to be additional evidence that beavers on our sites were at high ecological densities. Schulte and Mueller-Schwarze (1999) noted that pheromones of dominant female beavers apparently suppress ovulation in subordinates. Though we did not test this phenomenon directly, we found some support for it in our central Illinois trapping records. We caught 8 adult females at colonies where an older pregnant female had already been removed. Five were trapped within a week after the dominant female and none of these subordinates had ovulated. However, in the 3 cases when the dominant female had been trapped >2 weeks earlier, the subordinate subsequently had ovulated. On the other hand, in southern Illinois, we found several colonies in which multiple females were lactating. Whether these females bred while occupying the same lodge or bred separately and subsequently occupied the same lodge could not be determined.

Mortality Rates

In female beavers, some ova are not fertilized, some fertilized ova do not implant in the uterus, and some embryos are resorbed during development (Provost 1958, Henry and Bookhout 1969). Collectively, these losses constitute prenatal mortality and they cause birth rates to be lower than ovulation rates. Novak (1987) reviewed previous studies and reported that prenatal mortality can be high in beavers with preimplantation losses ranging from 4% to 38% and postimplantation losses from 3% to 17%. In Ohio, Henry and Bookhout (1969) found that 16% of ova were lost before implanting and 7% of embryos were resorbed or lost. Our estimate of 13% prenatal mortality should be considered conservative in that it covers only losses through early gestation, the time that we stopped trapping females.

Few beaver studies report kit survival rates. Payne (1984) found kit survival to 6 months of age to be 48% in Newfoundland, similar to the 43% survival rate that we estimated in central Illinois. In southern Illinois, where kit survival was estimated to 11 months of age, the survival rate was lower (28%), not surprising since this estimate quantified survival over a longer time period. We observed no confirmed kit mortality during the period that we video-taped kits in their dens (Apr-Jul). Consequently, we believe the peak mortality of kits occurs between August of the birth year and March of the next year. High mortality during this period may occur because it coincides with the time that kits are becoming more independent, increasing the distance traveled away from the lodge and spending more time outside the lodge where they are more vulnerable to predators such as coyotes and bobcats (*Lynx rufus*). The lodge is a safe place from predators in Illinois because no large predators are capable of digging into the lodge. In addition, kits are protected from aggressive encounters from other beavers while in the lodge.

Longevity, Survival, and Population Growth Rate

Analytical tools used by wildlife biologists to summarize and explain the dynamics of animal populations include life tables, fecundity tables, and survivorship curves (Table 10, Figure 6). A static (or time-specific) life table can be constructed from the age distribution of a standing population if we assume that the differences in the numbers of animals in successive age classes are due to mortality (Molles 2009), and we used a static life table to assess growth rate of beavers in central Illinois. Other assumptions for deriving valid estimates of population parameters from a life table are that: (1) the population is closed to immigration and emigration, (2) the population is stable, (3) aging techniques are accurate, and (4) an unbiased sample of the standing population is aged (Caughley and Sinclair 1994). These assumptions are often violated in wildlife populations and may not apply to the beavers that we studied. However, the methods we used to sample and age beavers reduced the probability of violating the third and fourth assumptions. Complete removal trapping of colonies avoids the bias towards adults which is common in many trapping studies (Buckley and Libby 1954). Our colonies were not closed populations, but movements were somewhat restricted by ice, and genetic structure suggested relatively low levels of movement between populations (Larson 1967). Finally, these populations may not be stable, but the high proportion of adults found in our population is typical of stable beaver populations (Boyce 1974, Busher 1987). Therefore, the life table that we present may be a useful tool for assessing mortality patterns and estimating the potential for population growth.

A striking result from the life table analysis and our field work is that the mortality rate from the fetal stage through the first 6 months of life is relatively high (57%). This contrasts with previous studies that

Table 10. Life and fecundity table for beavers based on trapped-out colonies in central Illinois. The number of kits at birth was estimated from the age of breeding females in each colony and age-specific fetal rates.

			Age-specific			No. of
Age (years)	n_x	Survivorship l_x	Mortality d_x	Mortality q_x	Natality m_x	daughters $l_x m_x$
Birth	110	1.00	0.57	0.57	0.00	0.00
0.5	47	0.43	0.15	0.36	0.11	0.05
1.5	30	0.27	0.11	0.40	0.90	0.24
2.5	18	0.16	0.06	0.34	1.62	0.26
3.5	12	0.11	0.03	0.25	1.62	0.18
4.5	9	0.08	0.01	0.12	1.62	0.13
5.5	8	0.07	0.02	0.24	1.62	0.11
6.5	6	0.06	0.01	0.18	1.62	0.10
7.5	5	0.05	0.01	0.20	1.62	0.08
8.5	4	0.04	0.01	0.25	1.62	0.06
9.5	3	0.03	0.01	0.33	1.62	0.05
10.5	2	0.02	0.01	0.50	1.62	0.03
11.5	1	0.01	0.00	0.00	1.62	0.01
			Net reproductive rate (R) = 1.30			
			Per capita growth rate (r) = +0.23			

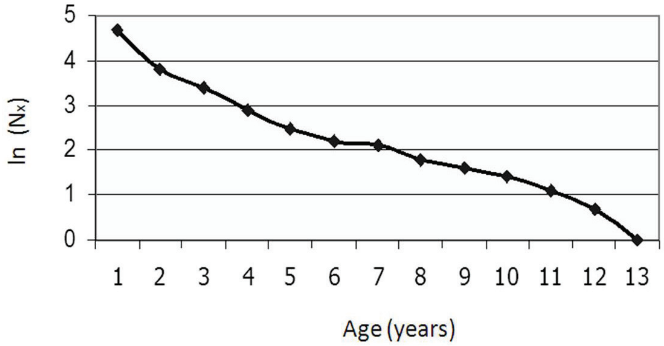


Figure 6. Survivorship curve for beavers in central Illinois based on the ages of 148 individuals removed from trapped-out colonies, 2001–06.

have concluded that kit mortality is low in beavers. Novak (1987) cited several studies that estimated juvenile mortality rates to be <10%, but also reported several studies that found first-year mortality rates ranging from 19% to 52%. Payne (1984) estimated 52% mortality among Newfoundland beavers from the embryo stage through the first 6 months of life, but noted that this rate may have been artificially high because trappers were restricted to 1 beaver/colony and may have discarded kits. Female beavers on our study areas were in good condition and winters were relatively mild, so it is unlikely that severe weather or starvation caused these losses. Rather, as noted earlier, most mortality appears to occur after kits leave the security of the den. Regardless of the cause of mortality, the number of surviving kits per colony was 1.7 and 1.1 in central and southern Illinois, respectively, which is similar to the rate of 1.3 kits/colony reported for beavers at or near carrying capacity (Taylor 1970).

Life table analysis also suggests that mortality rates are higher for yearling and 2-year-olds than for older adults. This is probably because beavers begin exploratory forays away from the den and some disperse at these ages. Others have suggested that mortality rates for emigrants are often high (Woodward 1977), but the mortality rates of dispersers and non-dispersers did not differ on our study areas. In Ohio, first year mortality was estimated to be 42% (Henry and Bookhout 1969). Bergerud and Miller (1977) reported that annual mortality averaged 46% in kits, yearlings and 2-year-olds, then dropped to 12% in older beavers in Newfoundland, estimates similar to ours. It should be noted however, that dispersing yearlings and subadults often live as singles and pairs in bank dens that are difficult to detect (Molini et al. 1981). Therefore, these classes may be underestimated in our sample and their mortality rates overestimated. Finally, with good estimates of age-specific survival and natality, the net reproductive (R) and *per capita* growth rate (r) of the population can be estimated. Based on our data, beaver populations in central Illinois have the capacity to increase by approximately 20% annually when suitable habitat is available.

Causes of Mortality

Causes of mortality for beavers in Illinois are similar to those reported by other researchers. Of our total sample of 154 "known-fate" radiomarked beavers, 54 (35%) died during the ~1 year period during which they were monitored. The majority of mortalities on both study areas occurred during the fall and winter. Eleven (20%) percent of mortalities were from unknown causes; 5 of these were located within active beaver lodges. We believe that these animals died from tularemia or from wounds sustained during aggressive encounters with other beavers. At least 7 more individuals died during the tularemia outbreak that hit both populations during the winter of 2004. A bacterial infection (yersiniosis) accounted for 3 more deaths. This disease has been reported sporadically in beavers in Ontario (Hacking and Sileo 1974), but has not been reported as an important mortality factor for beavers. Increased prevalence of yersiniosis is thought to be caused by stress and resource limitations (Gasper and Watson 2001). This is consistent with our observations that only juveniles were affected on our study areas, and no adults, presumably under less stress than juveniles, died from this disease (McNew 2003).

A major difference between the 2 study areas was that the central Illinois population was open to trapping, whereas the southern Illinois population was protected from harvest. Therefore, the role of trapping as a mortality factor differed between the sites. In southern Illinois, harvest accounted for few mortalities (7.4%); the 2 beavers harvested were taken on neighboring property after they moved off of the study site. In contrast, trapping accounted for 51.9% of the mortality in central Illinois. Of these 14 animals, 11 were harvested legally and 3 were poached. Predation rates were higher in southern than central Illinois (25.9% versus 7.4%, respectively) accounting for 9 of 54 recorded (17%) mortalities, similar to the 22% found by DeStefano et al. (2006). Coyotes, dogs, and bobcats were implicated in these kills. Higher predation rates in southern Illinois may occur because of higher predator densities in the region or may suggest compensatory mortality in the unharvested population, as other forms of mortality (disease, accidents, and poisoning) were generally comparable in the 2 populations.

Home Range and Spatial Distribution

Beavers often occupy linear habitats, which makes the computation of areal home ranges (e.g., minimum convex polygon or fixed kernel) generally inappropriate (Sauer et al. 1999, Blundell et al. 2001). Consequently, we calculated linear home ranges in central Illinois where beavers lived and moved almost exclusively along streams and areal home ranges for the southern Illinois population inhabiting a wetland complex. Typical linear home ranges for beavers calculated by other scientists have ranged from 0.6 to 5.2 kilometers (Bergerud and Miller 1977, Davis 1984). Of the few previous studies that have generated areal ranges, sizes have been highly variable ranging from 7.1 to 42.7 hectares (Boller 1991, Wheatley 1997). A series of studies conducted throughout North America have reported that average linear home ranges have varied from 0.5 to 5.2 kilometers (Nordstrom 1972, Bergerud and Miller 1977, Busher et al. 1983, Davis 1984).

Based on results from previous studies, southern Illinois beavers occupied areal home ranges and core areas (26 and 4 hectares, respectively) that were intermediate in size. Similarly, the linear home ranges and core areas (2.4 and 0.9 kilometers, respectively) observed among beavers in central Illinois were generally consistent with results from previous studies. The fact that beavers in central Illinois occupy core areas of about 1 kilometer is consistent with the facts that this species is highly territorial and the spacing of colonies along the Embarras River is usually about 1 kilometer apart. Home range size differed seasonally on both of our study areas, being largest in the winter when food resources were most limiting and smallest in the summer when food was most abundant and kits were in dens. In addition, water levels in Illinois are often highest during the winter and beavers expanded their home ranges to utilize newly flooded areas.

In southern Illinois, we estimated the amount of individual home range and core area overlap among seasons. Home range overlap was 58% among seasons, indicating a mild seasonal shift in home ranges. These shifts were most pronounced in the spring and fall coinciding with dietary shifts that occur from summer to fall and winter to spring. Another method that we used to assess habitat shifts was to compare the number of active lodges in core areas among seasons. Core areas contained more active lodges in the fall than in winter, suggesting seasonal shifts in core areas and use of lodges. During winter, beavers occupied the fewest lodges, provisioning these with food caches. However, during the fall, beavers traveled farther and foraged more on land, often using additional lodges for resting areas near foraging sites. In addition, water levels fluctuate considerably from fall (lowest water levels) to winter (highest water levels); therefore, beavers sometimes used multiple lodges to accommodate the fluctuating water levels. This was most evident along stream banks in central Illinois where the drainage of large, flat watersheds for agriculture leads to very flashy streams. Here it was common for colonies to have multiple dens situated at different bank heights or to have a single den with openings stacked at varying heights to accommodate fluctuating water levels.

Spatial Responses to Removal Trapping

To our knowledge, this is the first study to assess the impacts of localized removal trapping on the spatial organization of beavers using radiomarked animals and remote videography. On the southern Illinois site, we trapped beavers from 8 colonies reducing the population by ~50% to investigate how trapping affects the composition and distribution of colonies. Trapping occurred between the median dispersal date and the median settlement date during the period when 90% of the recolonization of open beaver habitat occurs (Houston et al. 1995). At each colony, we removed ≥1 adult female, including ≥1 bred females from 5 of the 8 colonies. Although we did not achieve complete removal of beavers from these colonies, our remote videography suggested that about 90% of the animals were removed.

None of our radiomarked beavers took residency in the removal area, however unmarked individuals did. At least 3 of the 12 beavers (not including kits) observed on camera were immigrants from other colonies.

Beavers of any age-class or family status are capable of recolonizing voids created by removals (Nordstrom 1972, Houston et al. 1995). On our study area, at least 2 of the 4 colonies that produced kits were joined by immigrants after trapping ended, another colony with kits built a lodge in a new location after trapping, and the fourth colony subsequently moved their kits to another lodge where the previous occupant had been removed. Trapping clearly vacated additional space as indicated by the fact that after trapping, a single individual occupied the habitat previously used by 3 colonies. We observed similar patterns of recolonization and den occupancy along central Illinois streams. Of the 28 colonies that were trapped out during the first 2 years of the study, 10 (35.7%) were occupied by the following fall and 20 (78%) were occupied within 2 years. New bank dens also were excavated and occupied during this period.

None of our radiomarked beavers shifted home ranges to encompass the removal area or shifted home ranges in the direction of the removal area. However, a few made exploratory forays into the removal area, including 1 transient. These findings indicate that when population densities are high, the spatial organization of beavers is fairly rigid (especially for adults). Neighbors did not move readily into territories occupied by residents. However, unmarked beavers did immigrate into the removal area and these individuals appeared to be transients that dispersed from outside the study area. In Tennessee, Houston et al. (1995) found that 89% of beavers immigrating into a removal area were <4 years old, suggesting that adults are unlikely to leave their home range and younger transients are more likely to disperse into vacated habitat. Furthermore, Houston et al. (1995) reported that <2-year-old beavers do the majority of recolonization of population voids during the normal dispersal period (Feb-May).

Kinship and Genetic Structure

The results of our genetic studies provide a unique and interesting perspective on the population dynamics and social structure of beavers. Few genetic surveys have been conducted to compare local differences within populations of socially monogamous mammals. We found that central and southern Illinois beaver populations represented very different demographic and social systems. The central Illinois population reflected the social structure typically associated with beavers, that of small colonies composed of single-family groups (Sun 2003), whereas the southern Illinois population was composed of large colonies with multiple breeding adults (Crawford et al. 2008). We believe that these differences in social structure are due largely to differences in environment. Specifically, colony size appears to be constrained and intercolony interactions restricted on streams and rivers in central Illinois (Havens 2006), whereas beavers inhabiting the wetland complexes of southern Illinois are free to interact with members of nearby colonies. Beavers in linear habitats, such as in central Illinois, defend a linear home range, whereas beavers inhabiting lakes are less able to mark and defend the nonlinear lacustrine environment. In addition, larger colony size in the unharvested southern Illinois population provided the opportunity for increased interactions at this study site.

These ecological differences between the central and southern Illinois populations clearly have genetic consequences. Contrary to our prediction that southern Illinois colonies would exhibit low F_{ST} values due to promiscuous intercolony mating, we documented a moderate level of subdivision, with an F_{ST} value of nearly 9%. Consistent with the results of our telemetry studies, the genetic evidence showed that females exhibit greater philopatry relative to males; females within colonies in southern Illinois were usually 1st-order relatives (Crawford et al. 2008).

Although it appeared that females remained in their natal colonies in southern Illinois, leading to moderate subdivision, parentage analysis also indicated recent intercolony mating and a promiscuous mating system (Crawford et al. 2008). Therefore, gene flow between colonies was maintained despite the fact that these colonies functioned primarily as distinct breeding units. Individual beaver colonies in central Illinois were too small to conduct tests of among-colony genetic subdivision, so the colonies were grouped into 3 local clusters that showed low levels of among-cluster genetic subdivision. This result is consistent with our radiotracking data that suggested beavers in this region disperse on average 12.2 km from their natal colony (Havens 2006).

Our study demonstrates significant population subdivision between central and southern Illinois beaver populations, and the techniques we used can be useful in wildlife management to designate biologically appropriate management units. Beavers are abundant within major river systems between the central and southern Illinois study sites (Woolf et al. 2003) and it is likely that these 2 populations were part of a metapopulation inhabiting the southern portion of the state. Despite relatively recent reintroductions of beavers to Illinois (Pietsch 1956), both populations showed moderate levels of genetic variation in microsatellite loci and our study suggests that limited dispersal occurs between these populations. This indicates that these aquatic furbearers are capable of long distance dispersal, a phenomenon that has been seldom observed in traditional radiotelemetry studies of dispersal. The combined results of our radiotracking and genetic analyses are remarkably consistent in showing that long-distance dispersal between central and southern Illinois occurs but is rare.

We designed this study to examine the degree to which beavers fit the model of monogamy, living in discrete, 1st-order family groups. Indeed, several empirical studies on behavior, dispersal, and pheromones support the view that this species is genetically monogamous (Sun 2003). However, our genetic analyses indicate that beavers are not always genetically monogamous and colonies are not necessarily discrete family groups.

Colonies in both populations showed a wide range of relatedness, including unrelated groups, as well as combinations of 1st- and 2nd-order relatives. Only 1 of 12 colonies in central Illinois contained a mated adult pair and their 2 offspring, although failure to detect other such single-family colonies may have been due in part to incomplete sampling. McTaggart and Nelson (2003) reported that colonies averaged 5.6 beavers in our central Illinois study area 4 years earlier. Because we averaged 3.8 beavers/colony in this area, we believe that some colonies were not trapped completely, explaining why some parents remained unidentified. As a result, our data may underestimate the number of single-family colonies.

The 4 large colonies were composed of extended relatives and 3 of these colonies contained >1 pregnant female. Although female beavers can become sexually mature by their second year, reproduction among subadults is thought to be suppressed by the presence of dominant adults in the den (Brooks et al. 1980, McTaggart and Nelson 2003). Sterilization of either adult in a colony has been shown to inhibit colony reproduction, suggesting that 1 or both dominant adults may prevent mating by subordinates, either through behavior or physiology (Brooks et al. 1980). McTaggart and Nelson (2003) reported 3 colonies in central Illinois in which ovulation had occurred in subordinate females when the pregnant adult female had been removed ≥2 weeks earlier. In contrast, subadult females that were trapped within a week of the removal of the pregnant female had yet to ovulate. Despite these findings, several studies have documented the presence of >1 pregnant or lactating female within a colony (Bergerud and Miller 1977, Busher et al. 1983, Wheatley 1993). It is possible that the ability of the dominant pair to restrict matings by other colony members may be limited in large colonies, which could explain our findings of multiple pregnant females within a colony.

Adult females within the same colony were always identified as 1st-order relatives, whereas adult males always were unrelated mates of females in the colony. Furthermore, the largest colonies sometimes contained several related adult females who had reproduced. Estimates of natal dispersal rates between sexes vary among studies. In southern Illinois, McNew and Woolf (2005) observed nearly equal dispersal rates between the sexes, but juvenile males were more likely to disperse than juvenile females in central Illinois (Cleere 2005, Havens 2006). Natal dispersal may be delayed in high density beaver populations (Brooks et al. 1980, Havens 2006, Mueller-Schwarze and Shulte 1999), and delayed dispersal has been documented repeatedly in telemetry studies in our study areas (Cleere 2005, McNew and Woolf 2005, Havens 2006, Bloomquist 2007). In addition, demographic studies showed that 43% of colonies in central Illinois contained ≥2 adults and all 8 colonies trapped out in southern Illinois contained ≥2 adults, further suggesting that delayed natal dispersal, particularly by females, may account for our genetic results (McTaggart and Nelson 2003, Bloomquist 2007).

We identified 3 (20%) of 15 colonies that contained ≥1 individual who was unrelated to others; 2 of these were young. Beavers use anal gland secretions to mark their territory and aggressively defend these against intruders (Rosell and Bjørkøyli 2002, Sun 2003). However, members of neighboring colonies may be tolerated. For example, Eurasian beavers *(C. fiber)* spend less time investigating and respond less aggressively to neighbors' scent-mounds than to strangers' scent-mounds (Rosell and Bjørkøyli 2002). At high densities, dispersing individuals from neighboring colonies may reside periodically in nonnatal colonies before establishing breeding territories (Svendsen 1980). Busher et al. (1983) observed frequent intercolony movement of subadults and adults of both sexes in a dense population in Nevada, whereas Sun et al. (2000) frequently observed natal or secondary adult dispersals to neighboring sites in an unharvested New York population.

We speculate that unrelated colony members in our study areas may be dispersers or, in the case of young, orphans. Extrapair matings occurred in >50% of litters and these were often the result of matings with neighbors. Although mated pairs usually share parental duties, cooperative activities may afford either parent opportunities to seek additional mates (Emlen and Oring 1977). Our results suggest that outbreeding is common in beavers; matings between neighbors are fairly common, but mated pairs within a colony are not close relatives. Although beaver colonies may inhabit several lodges, home range and movement data from both areas confirm that colonies in our study were discrete (Havens 2006, Bloomquist 2007), with mating between members of neighboring colonies reflecting intercolony mating rather than mating between members of the same colony occupying separate lodges. By accepting mates from outside of their colony, females may avoid inbreeding depression and secure additional resources for their offspring.

We observed that young born to parents from neighboring colonies resided periodically in either parent's colony and this may effectively double their territory and resources. This sharing may be facilitated by the fact that beavers recognize the secretions of close relatives and respond less aggressively to these than to those of unrelated strangers (Sun and Mueller-Schwarze 1997, Sun 1998). High population density, restricted habitat, and mild winters in central and southern Illinois may increase winter movements, female philopatry, and the duration of the dispersal season, increasing the likelihood of extrapair and intercolony matings (Sun 2003, McNew and Woolf 2005).

Geographic distance was not a significant predictor of average relatedness among individuals in either population. Previous studies reporting fewer aggressive interactions between neighboring colonies led us to hypothesize that adjacent colonies may be more closely related than distant ones (Svendsen 1980, Sun et al. 2000, Rosell and Bjørkøyli 2002). In central Illinois, the longest pairwise distance between colonies in our study area was nearly 70 km. Hence, our large-scale, coarse-grained sampling scheme did not provide data for a series of neighboring colonies, and we may have missed fine-scale patterns of intercolony relatedness. Nonetheless, in central Illinois, the median natal dispersal distance among juveniles was 12.2 km, indicating that offspring do not necessarily establish territories near their parents, but routinely disperse considerable distances before settling (Havens 2006). Other studies of natal dispersal have also reported that beavers typically disperse considerable distances from the natal colony (Van Deelen and Pletscher 1996, Sun et al. 2000), suggesting that beaver populations should be characterized by a high amount of gene flow rather than local genetic structuring. In southern Illinois, where dispersal distances are shorter (average = 5.9 km, McNew and Woolf 2005), we found a weak relationship (P = 0.06) between pairwise distances and relatedness for neighboring colonies. Although this association was not statistically significant, our mating studies suggest that neighboring colonies do contain related individuals. This sampling area was considerably smaller than that of central Illinois, with the longest pairwise distance between colonies at 4.3 km. McNew and Woolf (2005)

Data collection during beaver trapping.

reported a mean dispersal distance among juveniles of only 5.9 km in the population at the UCCA. Therefore, it is speculative but consistent with these data to suggest that the long, linear stream habitats of central Illinois may facilitate longer dispersal distances and more genetic mixing. In contrast, the interconnected wetland complexes of southern Illinois are associated with shorter dispersal distances and more genetic relatedness among adjacent colonies.

Beaver tracks in a muddy streambank.

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Photos courtesy of Clayton K. Nielsen, Southern Illinois University Carbondale; Thomas A. Nelson, North Georgia College & State University; and Robert Bluett, Illinois Department of Natural Resources

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