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Natal dispersal of beavers in the Embarras River watershed in central Illinois

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Natal Dispersal of Beavers in the Embarras River Watershed in Central Illinois

(TITLE)

BY

Erin A. Cleere

THESIS

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NATAL DISPERSAL OF BEAVERS

IN THE EMBARRAS RIVER WATERSHED IN CENTRAL ILLINOIS

A Thesis Presented

by

ERIN A. CLEERE

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ABSTRACT

Dispersal is an important mechanism influencing the dynamics, genetics, spatial distribution and size of wildlife populations (Gese and Mech 1991). Natal dispersal may afford individuals breeding opportunities and access to resources, while reducing inbreeding and competition with family members. However, dispersal also can be risky if mortality rates are high or if mates or suitable habitat are unavailable. When dispersal costs are high, subadults may be better off remaining in their natal territory.

Although a number of previous studies have investigated natal dispersal in beavers (*Castor canadensis*), conclusions regarding the percentage of subadults that disperse, timing of dispersal, evidence of sex-bias, and dispersal distances have differed depending upon the location of the study, characteristics of the research population, and the environments they inhabit. When I initiated this study, few ecological studies on beavers had been conducted in Illinois or the lower Midwest and the patterns and characteristics of beaver dispersal in this region were not well known. Therefore, the objectives of my study were to: (1) the percentage of subadult (yearling and two-year old) beavers that disperse, (2) the timing of dispersal and distances traveled, and (3) difference in dispersal rates or distances between males and females, and (4) mortality rates of dispersers and causes of death. During this 2-year study, I radio-tagged 18 subadult (yearling and 2-year-old) beavers, including 10 males and 8 females. Age was estimated by body weight. Tagged beavers were located at least 3 times each week during the dispersal

season from February through May. The overall rate of dispersal during this 2-year study was 33.3%; 42.8% during the first year and 27.3% during the second year.

The majority of dispersers (83.3%) were 2-year-old males; no yearlings dispersed. The median dispersal date was 22 February; the earliest dispersal was initiated on 23 January and the latest was 15 April. The shortest dispersal distance was 2.2 km, whereas the longest was 80 km. The median dispersal distance was 17 km. Mortality rates for both dispersing and non-dispersing beavers were low: 16.7% for dispersers and 8.3% for non-dispersers. All mortalities in both groups were attributed to trappers harvesting for fur or to remove nuisance animals.

My results suggest that a large proportion of subadults delay dispersal until they are at least 3-years-old, and that male subadults are more likely to disperse than females. This may be due to a high population density and saturated habitat on the study area, females delaying breeding until they are older and have higher fecundity, or a combination of these factors. With few natural predators or apparent diseases limiting this population, trapping is the primary mortality factor. In the absence of trapping, beaver populations would likely be limited by social constraints on breeding and the availability of habitat. Trapping probably is not necessary to keep beaver populations in check, but it is an important tool for removing nuisance animals. On my study area, there was a surplus of potential breeders capable of replacing individuals removed by trappers. Trapping creates vacant territories and removes some older breeders allowing younger animals the opportunity to breed. This in turn is likely to reduce the dispersal by subadults into marginal habitat and subsequent nuisance problems.

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BACKGROUND

Beavers (*Castor canadensis*) were trapped to near extinction in North America throughout much of the 1800's and early 1900's (Pietsch 1956, Jenkins and Busher 1979). Beaver trapping in Illinois was widespread and frequent until around 1850 when populations had been reduced to scattered, remnant colonies (Pietsch 1956). Subsequently, laws were enacted to restrict harvests and beavers were reintroduced into suitable habitat to restore the species. In 1929, the U.S. Fish and Wildlife Service (USFWS) assisted the Illinois Department of Conservation in releasing 2 pairs of adult beavers in Jo Davies Co. and Carroll Co., in northern Illinois (Pietsch 1956). Additional releases during 1935-36 were made by U.S. Forest Service personnel in Pope Co. and Union Co. in southern Illinois. Within 15 years of these reintroductions beaver populations had made notable recoveries in the state. Today, the species is found throughout Illinois and most of North America (Miller and Yarrow 1994). Beaver populations have grown substantially in most regions of Illinois and the species is common in suitable habitat in central and southern Illinois (McTaggart 2002).

Beavers are important not only because of their widespread distribution, but because of the impact they have on aquatic and riparian communities. They are recognized as ecosystem engineers because their dams create wetland habitats for a variety of wildlife, and their cutting of trees can retard forest succession and make canopy gaps (Jones et al. 1994, Naiman et al. 1986). In addition, they can have profound effects on water quality, species richness, and the species composition of streams, wetlands, and riparian habitats (Martinsen et al. 1998, Edwards and Otis 1999, Collen and Gibson 2000). Beavers also can cause problems for humans when they depredate crops or flood roads, properties, or timber. These conflicts have increased throughout the eastern U.S. as both human and beaver populations have increased (Woodward 1983).

Although much has been learned about the population ecology of beavers (Busher and Lyons 1999, Baker and Hill 2003), few studies have investigated the characteristics of dispersal or addressed this phenomenon in the Midwest (Smith 1997, McNew 2003). Consequently, the Illinois Department of Natural Resources, in cooperation with the Department of Biological Sciences at Eastern Illinois University, and the Cooperative Wildlife Research Laboratory at Southern Illinois University-Carbondale, initiated research to describe important aspects of beaver dispersal in Illinois. Specifically, the goals of my study were to investigate: (1) the percentage of subadult (yearling and two-year old) beavers that disperse, (2) the timing of dispersal and distances traveled, and (3) difference in dispersal rates or distances between males and females, and (4) mortality rates of dispersers and causes of death. Ultimately, my purpose was to describe the key characteristics of beaver dispersal in a riverine ecosystem in Illinois so as to contribute to our understanding and management of beavers.

LITERATURE REVIEW

Dispersal in mammals

Chepko-Sade and Halpin (1987) define dispersal as "the movement of an organism or propagule from its site or group of origin to its first or subsequent breeding site or group", and natal dispersal as "the movement of a propagule between birthplace or natal group and first breeding site or group". Researchers agree that dispersal is an important factor influencing genetic structure, the likelihood of inbreeding, spatial distribution, size and social organization of wildlife populations (Gese and Mech 1991). Dispersal can afford many benefits to an organism such as reproductive opportunities and higher quality forage, while reducing competition among siblings and between offspring and parents. However, if dispersal is risky juveniles may be better off remaining in their natal territory (Dobson 1982).

Motro (1991) noted that because of the personal cost imposed on a dispersing individual, it would benefit that individual if its siblings dispersed; thereby, allowing the sedentary individual to reap the benefits without incurring the costs. However, this would only benefit the sedentary individual, if the costs of dispersal outweigh the costs of intra-colony competition and inbreeding. Therefore, the detrimental effects of competition and inbreeding are recognized as ultimate factors influencing the probability of dispersal; whereas, a lack of breeding opportunities, ectoparasite loads, aggression from conspecifics, and physiological changes (e.g. changes in body mass) are cited as possible proximate causes (Gese and Mech 1991).

Dispersal in beavers

Beaver colonies are typically composed of a breeding pair of adults, their young of the year (kits), offspring from the previous year (yearlings) and sometimes two-year old offspring (Svendsen 1989). Beavers are monogamous, with few cases of multiple females giving birth in the same colony (Busher 1987, Svendsen 1989, Wheatley 1993). They are territorial and family members work cooperatively to maintain dams and dens, build food caches for winter, and defend their resources against intruders (Bradt 1938). Although it has been noted that yearlings can disperse and adults may even go through a secondary dispersal (Sun et al., 2000), beavers are generally 2-years-old at their first natal dispersal (Aleksiuk 1968, Hartman 1997). Because beavers are monogamous, they are not expected to exhibit differences in dispersal rates between the sexes (Dobson 1982). However, examples of sex-biased dispersal in beavers have been reported, often with males dispersing in higher numbers than females (Leege 1968, Smith 1997).

The costs of inbreeding have been found to have a significant effect on dispersal distances when one sex shows a higher proclivity for being sedentary (Motro 1991). To date, the findings have been inconclusive on whether dispersal distances differ between the sexes. Sun et al. (2000) showed that females dispersed significantly farther and more frequently than males. However, Leege (1968) and Smith (1997) found that males dispersed farther and more frequently. Therefore, beavers may be an exception to the hypothesis that monogamous species will not show a sex-bias in dispersal distances.

Dispersal distance also could be a function of local population density and/or habitat quality. Habitat suitability has been shown to affect dispersal, particularly dispersal distances (Sun et al. 2000). Presumably, beavers will colonize the most suitable habitat available to them. Smith (1997) suggested that the costs of reproduction may be high in habitats where preferred forage has been heavily exploited. This will impact the condition of other beavers in the colony and could affect future reproductive success. Smith (1997) found that dispersal occurred even in high density beaver populations, if suitable habitat was relatively close. However, dispersal would be delayed if the natal colony occupied better habitat than was available in surrounding areas. To date, the relationship between dispersal rates and habitat quality in natal territories is poorly understood.

Cooperative breeding occurs when some individuals, having reached sexual maturity, remain at their natal site and provide care for younger siblings (Stacey and Ligon 1991). Typically, only one female and one male reproduce in beaver colonies (Baker and Hill 2003, McTaggart and Nelson 2003). Other mature individuals in the colony are not afforded mating opportunities and, therefore, would be expected to disperse in order to procure a mate and further their genes in the population. Researchers have cited such things as kin selection and inclusive fitness as possible evolutionary reasons that cause sexually-mature individuals to forego dispersal and breeding (Hamilton 1964, Michod 1982).

In the only other study of beaver dispersal conducted in Illinois, McNew (2003) reported that 55% of yearlings and 73% of 2-year olds dispersed. The mean dispersal date was 16 February, although beavers occupying a managed wetland dispersed in December when water levels were drawn down artificially. Mortality rates were low among both dispersers and non-dispersers, suggesting that the decision to disperse is not influenced by a high mortality rate. Most dispersal movements were relatively short, averaging 1.7 km in land-locked areas and 5.9 km in areas where beavers had easy access to free-flowing water. McNew (2003) concluded that although beavers from areas of poor habitat quality showed greater dispersal rates, 2-year-olds did not show an increased tendency to delay dispersal.

STUDY AREA

This study was designed specifically to investigate natal dispersal by beavers occupying riverine habitats in Illinois. As such, it parallels a similar study conducted by McNew (2003) of dispersal by beavers in southern Illinois; however, McNew's study focused on beavers occupying ponds and wetland complexes. Specifically, I conducted research on beavers living in the Embarras River watershed in central Illinois, particularly on the river's main channel and 4 major tributaries: Kickapoo Creek, Polecat Creek, Hurricane Creek, and the Little Embarras River in Coles and Douglas counties (Figure 1).

The Embarras River is approximately 300 km in length, extending southeast from its origin in Champaign Co. to its confluence with the Wabash River in Lawrence Co. It is a moderate-sized, low-gradient river. I selected it as a study area because it is typical of many Illinois rivers occupied by beavers in that it drains a large, relatively flat watershed and its riparian zone has been impacted by agriculture and urban development. The study area is largely rural encompassing a mix of farmland and small towns typical of central Illinois. The composition of the watershed includes: 75% cropland, 11% grassland, 11% forests, and 2% urban or developed land. 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. Corn and soybeans are the predominant crops in this area (Wiggers 1998).

The watershed's topography is relatively flat and the river's gradient ranges from 2.1 to 3.4%. Annual precipitation averages 94 cm with approximately 28% of this water entering the river and its tributaries (Hamilton 1993). The large watershed and seasonal changes in precipitation cause water levels to fluctuate dramatically. Tilling of crop fields and extensive construction of drainage ditches have increased the volume and velocity of water entering the main channel, which increases bank erosion and sedimentation. Flooding along stretches of the river is common during the spring. In spite of siltation, 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 only 2% is severely degraded (Wiggers 1998).

Riparian zones and lowland forests adjacent to the river and its tributaries are dominated by sycamore (*Plantanus occidentalis*), cottonwood (*Populus deltoides*), sugar and silver maples (*Acer saccharum* and *A. saccharinum*), sweetgum (*Liquidambar styraciflua*), honey locust (*Gleditsia triacanthos*), white and swamp white oaks (*Quercus alba and Q. bicolor*), green and white ashes (*Fraxinus pennsylvanica var.subintegerrima* and *F. americana*), and basswood (*Tilia americana*). Upland forests frequently contain such characteristic tree species as black, red, and white oaks (*Q. velutina, Q. rubra,* and *Q. alba*), shagbark and mockernut hickories (*Carya ovata* and *C. tomentosa*), basswood, and sugar maple.

Beavers typically live in lodges or dig burrows into the river banks and occupy these "bank dens" along the river and its tributaries. A 2002 census conducted along the entire length of the main channel found a total of 125 beaver colonies, a density of 0.55 colonies/km (Cox 2005). The mean distance between adjacent colonies was 1.67 km (SD = 1.96) in the section of the river between Walnut Point State Park and Fox Ridge State Park where I conducted my study. A survey of beaver food caches on the study area showed that important winter foods included: silver maple (26%), green ash (18%), sycamore (13%), black willow (*Salix nigra*; 11%), corn (10%), box elder (*Acer negundo*; 6%); cottonwood (5.0%), and sandbar willow (*Salix exigua*; 5%; Thomas Nelson, EIU Department of Biological Sciences, unpublished data).

MATERIALS AND METHODS

Trapping and processing beavers

Beavers were trapped using 7x7 strand, 2.38-mm diameter stainless steel cable snares which were equipped with a swivel at the anchored end and a "deer stop" crimped approximately 30 cm from the other end of the snare (Figure 2). Swivels were necessary to allow snared beavers to roll without twisting and weakening the snare. Snares were anchored with 1.5-m lengths of 1-cm diameter rebar stakes which were driven ~1 m into the ground. Snare loops were opened to ~25 cm to target adult-sized beavers while reducing the capture of kits and non-target furbearers. Snares were set on haul-outs, trails, channels, and feeding areas. Best results were obtained when snares were set in shallow water in channels and haul-outs leading to feeding areas. Trapping was conducted from 15 October through 18 November 2002 and 18 August through 16 November 2003.

Captured beavers were restrained with a catch-pole and tranquilized to facilitate handling. They were immobilized with an intramuscular injection of ketamine HCl (6 mg/kg) and xylazine HCl (1 mg/kg) administered via syringe pole or hand injection. When a beaver was fully anesthetized (usually 5-15 minutes), the snare was removed and the animal was marked with a unique ear tag and PIT tag. PIT tags were injected under the loose skin between the scapulae. Body length, tail length, and tail width were recorded, as were any noticeable physical marks or injuries.

The sex of each beaver was determined by palpating the abdomen anterior to the pelvis for the presence or absence of a penis (Osborn 1955). Beavers were weighed to the nearest 0.5 kg using a spring scale. Age was estimated based on body weight (McTaggart 2002). Individuals weighing 7-11 kg were categorized as kits, yearlings were 11-16 kg, two-year-olds were 16-21 kg, and heavier beavers were categorized as adults. Beavers are born from April to June (Bradt 1939) and were trapped from September through November; therefore, kits were ~6 months old, yearlings were ~18 months, two-year-olds were ~30 months and adults were >42 months old.

Tail-mounted radio-transmitters (model ET-7, Telonics, Inc., Mesa AZ) were used to track beavers in this study. During the first trapping season, only two-year-olds were equipped with radio-transmitters. I put transmitters on yearlings and two-year- olds during the second trapping season. I attached transmitters by drilling a 4-

mm hole in the tail 6-8 cm from the base and 4 cm from the midline of the tail. Each tranquilized beaver was placed in a secure plastic bin until they had fully recovered from the effects of the drugs. Once beavers were able to sit up and move around normally, they were released at the trap site.

Radio-tracking

I tracked radio-tagged beavers from 3 December 2003 through 12 June 2004 during the day and evening using a Telonics telemetry receiver and hand-held, 2-element antenna. Each beaver was located at least twice weekly from the time of capture through January to establish the location of its den and winter home range. Just prior to and during dispersal season, from January through mid-June, I located beavers 3-5 times per week to track movements and dispersal. After the dispersal season, when dispersing individuals had settled into new territories and others had remained in or returned to their natal territories, I decreased tracking to twice weekly. Dispersal movements are defined as movements away from the natal lodge or den where the individual does not return to its natal area. Exploratory movements are defined as movements outside of the natal territory before it has been permanently left (Hartman 1997).

All locations were recorded as UTM (Universal Transverse Mercators) coordinates with a Garmin GPS receiver. Radio-transmitters had a battery life of approximately 12 months and were equipped with a mortality switch that doubled the pulse rate if the beaver remained inactive for 6 hours. Transmitters that had switched into mortality mode were recovered as soon as possible so that carcasses could be necropsied. In the field, I recorded any relevant data regarding the circumstances of death. A thorough necropsy was conducted on recovered carcasses and the probable cause of death determined based on gross examinations. I censored beavers from the study when transmitters failed, dropped off, or beavers were killed prior to the dispersal season.

Data analyses

Beavers that died in the snares prior to processing were not included in estimates of trapping success. Marked individuals that were killed or dropped their transmitters prior to the beginning of the normal dispersal season (February to May) were censored from all analyses except estimates of trapping success rates. All estimates of distances traveled by beavers, between natal dens and subsequent locations, were based on the assumption that individuals followed the shortest pathways between points while remaining in the river or tributaries. These distances were estimated by first transferring GPS-derived UTM coordinates from field notebooks to geo-referenced aerial photographs, then using the measuring tool in ArcView 3.2 to measure cumulative straight-line distances along each waterway. Dispersal date was recorded as the first date an individual was located away from its natal lodges. If the specific day was unknown, the date was recorded as the midpoint between the last location at the beaver's natal lodge and when it was next found. Dispersal duration was determined by the length of time between dispersal date and settlement date. Settlement was determined to be when a beaver had stopped exhibiting movements and was found consistently at the same lodge or den.

Fisher's exact test was used to test whether the frequency of dispersal differed between yearlings and 2-year-olds or between males and females.

Because neither the timing of dispersal, duration of dispersal, nor the distances traveled by dispersing beavers were normally distributed, I used non-parametric measurements (medians and ranges) to describe these data. The relationship between the number of dens available within a territory and the probability of dispersal by subadults was quantified using Spearman's rank correlation (rho, ρ).

RESULTS

Trapping success

A total of 38 beavers were captured in 937 trap-nights; a success rate of 4.1% (Table 1). Of these animals, 4 died (3 in 2002 and 1 in 2003) in the snare before they could be retrieved and 1 did not recover from anesthesia. Of the remaining 33 live-captured beavers, 9 were adults, 21 yearlings and 2-year olds, and 3 kits. Radio-transmitters were affixed to 24 of these beavers: 3 adults, 15 two-year-olds and 6 yearlings.

Prior to the beginning of dispersal season 1 transmitter was recovered that had fallen from the beaver when the locking nut failed, 1 transmitter failed, and 4 beavers were harvested by trappers. These beavers were censored from subsequent analyses. The remaining 18 individuals, including 10 males and 8 females, were tracked throughout the dispersal period (Table 1). The age distribution of these tagged beavers was 5 yearlings and 13 two-year-olds.

Characteristics of dispersal

I collected a total of 1,303 radio-locations on these 18 beavers from 8 January-12 December 2003 and 5 January- 12 June 2004. The mean number of locations recorded per beaver was 72 (range 26-131). Overall, 6 of 18 (33.3%) beavers dispersed from their natal colonies, including 3 of 7 animals (42.9%) in the first year of the study and 3 of 11 (27.3%) animals during the second year (Table 2). The majority of dispersers were 2-year-old males (83.3%; 5/6). The frequency of dispersal did not differ between yearlings and 2-year olds, but approached statistical significance (P = .245; Fisher's exact test), with 46% (6 of 13) of 2-year olds dispersing, whereas none of the 5 yearlings dispersed. Furthermore, although 50% (5/10) of males dispersed and only 12% (1/8) of females dispersed, this difference in the frequency of dispersal did not reach statistical significance (P = 0.152; Fisher's exact test).

Dispersal movements began as early as January for 2 individuals and as late as April for one beaver. The median dispersal date was 22 February. Settlement of dispersing beavers into new dens occurred from 15 February to 1 June, with 50% settling during May. The average duration of dispersal was 58 days (range = 19-95 days).

The distances covered by dispersing beavers were highly variable, but the median dispersal distance was 17 km (7 miles) with a range from 2 to 80 km. Dispersal distance is further defined by: 1) "dispersal distance": distance from the natal lodge to the new lodge, or the distance between the natal lodge and the last known location, and 2) "minimum distance moved": the minimum distance traveled while searching for a new territory. These distances are conservative estimates assuming that beavers traversed the shortest distances following the river channel or tributaries between their natal lodge, intermediate known locations, and eventual settling location. The longest observed movement over a 24-hour period was 5 km.

One individual settled in a colony adjacent to his natal territory. There were 2 individuals (a 2-year-old male and 2-year-old female) who made long dispersals requiring passage through the territories of numerous other beaver colonies. The male traveled from his natal lodge on the Embarras River near Lake Charleston upstream approximately 60 km past Walnut Point State Park; he then followed a tributary stream and agricultural drainage 20 km to his settling point on the ditch (Fig. 3). There he shared a bank den with 2 other subadult males of unknown origin. When these 3 built a dam on the ditch, they were considered to be nuisance animals by the landowner and were harvested by a local trapper. A female traveled to dens, both up and downstream from her natal lodge, above the Charleston spillway, before settling in a new territory on the northern boundary of Fox Ridge State Park. This animal traveled at least 60 km in the course of her dispersal movements.

Characteristics and movements of non-dispersing beavers

Twelve marked beavers did not disperse (7 females and 5 males), including all 5 yearlings. One 2-year-old female exhibited exploratory movements. Her movements extended downstream from her natal den in the main river channel. I detected no overland travel or movements into any tributaries (Fig. 4). The minimum total distance she moved was 47 km between 22 February and 14 May 2003; longest distance moved in a 24-hour period was 3 km. During these exploratory movements, she crossed the territories of at least 3 other colonies. The furthest distance that this beaver was located from her natal lodge was 15 km. She eventually settled back at her natal lodge and exhibited no further movements away from this colony during the subsequent 7 months she was tracked (at which point her battery was depleted). No other beavers exhibited exploratory movements.

Survival rates of dispersers and non-dispersers

Survival rates were generally high for all yearling and 2-year-old beavers marked during this study (Table 3). Of the 6 beavers that dispersed, 5 (83.3%) survived through the dispersal period and early summer. In turn, 11 of 12 (91.7%) non-dispersers survived through this period. Survivorship did not differ between dispersing and non-dispersing beavers ($P = 0.569$; Fisher's exact test).

The primary cause of death for both dispersing and non-dispersing beavers was trapping. Both beavers that died during the dispersal season were harvested by trappers. The one dispersing beaver was harvested by a trapper with a nuisance permit hired by the landowner to remove the beaver after it had dammed a drainage ditch on his property causing flooding of his corn fields. A non-dispersing beaver was found dead on the river bank near its natal den and adjacent to a dirt trail. Another marked beaver (harvested before dispersal season began) from the same colony was found on top of the ice above his natal den. Necropsies performed on these two individuals revealed cervical hemorrhages, broken ribs, and thoracic bruising consistent with injuries inflicted by conibear traps; both cases were classified as trapping-related deaths.

Natal colony characteristics

My radio-tagged beavers occupied 9 separate colonies. Three of these colonies each used one den site, but the other 6 colonies occupied multiple dens in their territories. The mean distance between familial den sites was 560 m (SE = 150 m; range = 90-1700 m). Of the 3 colonies that used only one den, all had at least 1 subadult that dispersed. In contrast, only 1 of the 3 colonies that occupied two dens contained a subadult that eventually dispersed and none of the 3 colonies that occupied 3 or more dens had dispersers. Therefore, there was a negative correlation between the number of familial den sites available within a territory and the frequency of dispersal by subadults from those colonies ($\rho = -0.822$; $N = 9$; $P = 0.007$).

DISCUSSION

Dispersal rates

Researchers have reported that natal dispersal typically occurs when beavers are 2-years old (Leege 1968, Van Deelen and Pletscher 1996, Sun et al. 2000). My results support this conclusion as all of the dispersing beavers in my marked sample were 2-year olds. Approximately 46% of marked 2-year-olds dispersed during my study, whereas no marked yearlings dispersed. Dispersal rates in the Embarras watershed were intermediate relative to those reported in other studies where rates ranged from 29% to 73% (Table 4). The relatively low dispersal rate of 2-year old beavers in the Embarras watershed suggests that at least half of this cohort delays dispersal until they are older. This situation is most likely to occur in crowded environments where suitable habitat is already occupied by other beavers (Stacey 1979).

Delayed dispersal can have a significant impact on the number of breeding individuals, population dynamics, and total size of a beaver population (Sun et al. 2000). To disperse successfully, individuals must survive the move to a new location, establish a territory, find a mate, and produce surviving offspring (Solomon 2003). These aspects of natal dispersal are difficult to study and little empirical information exists on this phenomenon in beavers. Several researchers have cited habitat saturation (the lack of suitable unoccupied breeding habitat) as the main cause of delayed dispersal (Stacey 1979, Emlen 1982). When I initiated my study, beaver habitat in the Embarras study area was thought to be saturated, with established colonies occupying most suitable habitat (McTaggart and Nelson 2003). My findings suggest that approximately 50% of subadult beavers in this area may delay dispersal due to a lack of suitable habitat.

However, some researchers (Stacey and Ligon 1991) have taken exception to habitat saturation as the only explanation for delayed dispersal, and cited numerous studies that questioned its validity due to a lack of empirical data and the logic of the model. As an alternative hypothesis, they proposed the "benefits of philopatry", stating that nonbreeding adult offspring should remain at home only when there is a net fitness benefit to doing so (Stacey and Ligon 1991). This is most likely to occur where territory quality varies greatly or when group cooperation leads to significant variance in the fitness of individuals within different sized groups.

Potential benefits for cooperative breeders include more family members to detect and warn of predators (Woolfenden and Fitzpatrick 1984). To date no empirical evidence exists to suggest that larger beaver colonies have lower predation rates than smaller colonies, but, if so, this might favor delayed dispersal. A lower predation rate of colonies with helpers has not been adequately explored, but this may be a contributing factor in deciding to delay dispersal. Also, although beavers that delay dispersal are foregoing breeding opportunities, they are increasing their inclusive fitness by helping to raise siblings. However, McTaggart and Nelson (2003) found no correlation between the number of subadult "helpers" in a colony and the number of kits surviving to 9-months of age. Perhaps long-term survival in larger colonies with extraparental helpers is increased through extra beavers to warn of threats and add to the food cache. Particularly in patchy habitats or crowded populations, the individual and inclusive fitness of beavers who delay dispersal may be increased through enhanced survival and the potential to inherit the natal territory.

A third hypothesis, the "delayed-dispersal threshold model", proposes that population density, territory quality, and spatiotemporal variability in resources are factors that determine whether individuals disperse or not (Koenig et al. 1992). The key distinction here is that neither habitat saturation nor the benefits of philopatry exclusively drive dispersal decisions, rather it is population density coupled with the amplified importance of territory quality as habitat saturation increases.

I found that dispersal was most common in the Lake Charleston area which appeared to have high quality habitat, but also had high beaver densities. In contrast, subadults in more isolated colonies (> 2-3 km from neighboring colonies) and with cornfields in close proximity tended to delay dispersal. These findings lend support to the delayed-dispersal threshold model and suggest that population density, natal territory quality, and habitat saturation are all important factors influencing natal dispersal (Koenig et al. 1992).

Timing of dispersal

Many studies have attributed the timing of dispersal to ice melt and/or high water levels associated with the spring thaw (Bradt 1947, Townsend 1953, Smith 1997, Sun et al. 2000). However, the results of my study do not support this. Some of my study animals initiated dispersal as early as January 2003, when much of the Embarras River was still frozen. The median dispersal date that year was 6 February. In contrast, December and January of the next year were unseasonably warm and the Embarras River did not freeze. In addition, heavy rains in January caused the river and its tributaries to flood. Previous dispersal studies suggest that flooding and ice-free conditions should have triggered early dispersal, yet the median dispersal date was later than it had been the previous year (9 March). These results indicate that while ice melt may play an important role in determining the timing of dispersal in colder regions, it did not appear to be the primary factor influencing dispersal in central Illinois.

Overall, dispersal occurred earlier in my study area than has been found in more northern climes. For example, Smith (1997) noted that some beavers initiated dispersal as late as August in Minnesota. Sun et al. (2000) reported two-year-olds in Massachusetts dispersed between early April and May, with no dispersal observed after mid-May. Van Deelen and Pletscher (1996) reported a mean dispersal date of 17 May in Montana, but noted that the timing of dispersal was highly variable. Beavers living at lower latitudes appear to disperse earlier. Dispersal dates in central

Illinois were found to be similar to those in southern Illinois (McNew 2005) and Mississippi (Weaver 1986).

Duration of dispersal

It has been suggested that beavers inhabiting areas with little suitable habitat may disperse over longer periods, whereas the duration of dispersal may be short when suitable habitat is readily available (McNew 2003). The broad variation in dispersal duration exhibited by beavers in my study area (19-95 days) is consistent with that reported by others. For example, Van Deelen and Pletscher (1996) reported dispersal durations from 16 to 181 days. McNew (2003) found dispersal took from 8 to 198 days in southern Illinois. It is important to note, however, that some of his study animals inhabited a site where water was artificially drained for waterfowl management in early winter. Therefore, it is difficult to determine whether these animals were exhibiting true dispersal behavior or whether they were forced to move as the site was drained. The latter would artificially extend the apparent duration of dispersal and bias his estimates.

Although Molini et al. (1981) and Hodgdon (1978) have suggested the existence of "floaters" who are unable to establish a territory and do not return to their natal site, this has not been adequately documented by other dispersal studies of beavers. Nolet and Rosell (1994) mentioned floaters in their research on settlement patterns within a beaver population, but did not discuss specifics of how long these floaters existed outside of an established territory or colony. There was some evidence of floater behavior in my study. One male was unable to establish a territory and then did not return to his natal site. However, his long-distance movements carried him beyond the boundaries of my study area and I was unable to verify whether or not he eventually settled into a territory.

Evolution would seem to select against floaters because: (1) beavers are monogamous and unpaired individuals apparently would have no opportunity to breed or enhance inclusive fitness by helping to rear siblings in an extended colony, (2) floaters may have prolonged exposure to aggressive encounters with territory holders, which may lead to severe, even fatal injuries for interlopers, and (3) water ways may freeze, reducing the survival of beavers who do not have access to a food cache (Slough 1978, Jenkins and Busher 1979). Without a food cache, floaters would have to rely on free-flowing water, accessible and nutritional winter browse, and a way to combat the energetically costly effects of cold temperatures while foraging. The widespread availability of corn in my study area, which can be stored easily and quickly in a bank den during the fall, may be critical to the survival of emigrants and floaters in the population. Although I saw little direct evidence of floaters in my population, beavers in the Midwest often have access to cornfields; this could potentially increase dispersal duration and the likelihood of floating behavior throughout the summer.

Dispersal distances

Early studies reported dispersal distances, but relied mainly on trapping data to determine these distances. This makes it difficult to distinguish between whole colony emigration, natal dispersal, and secondary dispersal (a.k.a. breeding dispersal) (Sun et al. 2000). More recent studies have distinguished between natal and secondary dispersal. For example, Hodgdon (1978) reported the mean dispersal distance of males to be 13.1 km and females to be 10.2 km. Van Deelen and Pletscher (1996) found a mean dispersal distance of 8 km for beavers of both sexes. Sun et al. (2000) found that males had a mean dispersal distance of 3.49 km, whereas females averaged 10.15 km. Hartman (1997) also reported that females moved further than males.

McNew (2003) reported much shorter dispersal distances in southern Illinois than what I found in central Illinois. Beavers on his 2 study sites moved an average of 5.9 km at one site and 1.7 km at another, which were considerably shorter than the median distance of 20 km that my beavers dispersed. A key difference between his study areas and mine, however, was that my beavers occupied linear riverine corridors, whereas his were on ponds and in managed green tree reservoirs. Consequently, McNew's study animals dispersed across land or followed small drainages from pond to pond, which may have limited their movements. In addition, as mentioned earlier, water levels were artificially manipulated in the green tree reservoirs. This may have forced beavers to disperse prematurely to the closest area with adequate water levels, thereby affecting both the timing of dispersal and distances moved.

Beavers mark their territories with scent-mounds, piles of mud and debris on which they deposit castor and anal gland secretions (Aleksiuk 1968). Schulte (1998) showed that individuals can distinguish between mounds marked by family members, neighbors and non-residents. These mounds allow dispersers and neighbors to determine whether an area is occupied. I noticed that some dispersers often moved during the day, a time when most other beavers are inactive. This behavior may reduce the number of aggressive encounters and lower the cost of dispersal. Although other studies have not reported dispersers exhibiting a pattern of daytime movements, this may be an important adaptation for reducing the costs of dispersal.

Exploratory movements

With the exception of one 2-year-old female, beavers in this study did not make exploratory movements. Another tagged 2-year-old female in this same colony did not engage in any exploratory movements. Other studies have reported exploratory movements and some researchers have observed forays that lasted several months before a return to the natal territory (Woodroffe 2003). Van Deelen and Pletscher (1996) reported that 3 of their non-dispersers and one disperser made movements of greater than 2.5 km from their natal colonies before returning. McNew (2003), however, did not find evidence of exploratory movements in the population he studied in southern Illinois.

If habitat saturation or the benefits of staying in a prime natal territory were factors contributing to the delayed dispersal that was apparent in my study animals, I would have expected to see more evidence of exploratory movements. How else would individuals know whether there is suitable habitat available unless they explore outside their natal territories? My findings show few instances of exploratory movements, which does not support the dispersal theory of habitat saturation or the benefits of philopatry with respect to natal territory quality. However, they are consistent with the notion that dispersal tendencies may be innate and stronger in some individuals than in others (Gaines and McClenaghan 1980).

Mortality rates & causes

Relative mortality rates are likely to be a critical factor influencing whether subadult beavers disperse from their natal areas or delay dispersal. Dispersal can be risky if mortality rates are high, available habitat is marginal, or mates are difficult to find. Smith (1997) found that mortality rates were low and similar for both dispersers and non-dispersers. Van Deelen and Pletscher (1996) also reported similar estimated survival rates for dispersers and non-dispersers, although their rate was slightly higher for dispersers. Mortality rates on my study area and in southern Illinois (McNew 2003) did not differ between dispersers and non-dispersers. Cumulatively, the results of these studies conducted in dissimilar habitats and across a broad expanse of this species' geographic range suggest that dispersers do not face higher risks of mortality than those that delay dispersal. It is interesting to note, however, that all of the mortalities that occurred during the dispersal season were due to trapping. In the absence of trapping, beavers on my study area appeared to have few deaths caused by predation or accidents.

Evidence of sex-biased dispersal

Sex-biased dispersal can have significant impacts on population dynamics, genetics, and the evolution of social and cooperative behavior (Radespiel et al. 2003). It is important to remember, though, that sex-biased dispersal may not only be expressed in the higher proportion of one sex emigrating but also in one sex dispersing further than the other (Radespiel et al. 2003). Previous research has suggested that dispersers will move only as far as necessary to establish a territory due to the cost of dispersing (Shields 1983). However, I found a wide range of dispersal distances, as well as instances of dispersers who traveled past areas (sometimes on several occasions) in which others later settled. To date, the mechanisms that beavers (and most other animals) use to evaluate habitat suitability are poorly understood.

Although some researchers have suggested that dispersal rates and distances should not differ markedly between sexes in a monogamous species such as beavers, no definitive patterns have been evident in studies conducted thus far. For example, Leege (1968) found that males disperse more often and tend to travel farther, a conclusion also supported by Smith's (1997) study. However, Sun et al. (2000) reported that females dispersed significantly farther, whereas Van Deelen and Pletscher (1996) found that dispersal rates and distances did not differ between the sexes. In southern Illinois, McNew (2003) found no sex-bias for either dispersal rate or distance. My results suggest that males tend to disperse more frequently; but, with small sample sizes and only 1 female dispersing during the 2-year study, establishing a relationship between sex and distance was not possible.

McNew (2003) reported that although he saw no sex-bias in propensity to disperse or dispersal distance, males moved more frequently when they were seeking out available territories. He suggested that males expend considerable energy to establish territories and then solicit females to join them. However, another study found that when the female was removed from a colony, her mate usually dispersed to find another female. When the male was removed, the female often remained in her territory until another mate came along (Svendsen 1989). The latter suggests that males are more likely to move in search of mates, which is consistent with the notion that males are more likely to be reproductively limited by the lack of a mate than by lack of habitat-related resources. Females may be more likely to delay dispersal, if in a prime natal habitat, until suitable resources open up elsewhere, allowing them the highest reproductive success possible.

Age of dispersers

Beavers reach sexual maturity between 1.5 and 2 years of age (Larson 1967). Demographic studies of beavers have reported a higher rate of reproductive success among females that are ≥3-years-old (Henry and Bookhout 1969, Payne 1984). There is some evidence that females may disperse as 3-year-olds. Smith (1997) found that only 9% of beavers who did not disperse as 2-year-olds dispersed as 3-year-olds; however, all of those who dispersed as 3-year-olds were females.

McTaggart and Nelson (2003), reported that the rates of ovulation on my study area were higher for females ≥3 years old than for 2-year-olds. Furthermore, they found a positive correlation between the weight of females and their ovulation rates. Therefore, selection may favor those females who delay dispersal in order to increase their weight before expending energy finding a suitable territory and mate. The transmitters that I used had an effective battery-life of approximately 13 months. This only allowed me to track individuals through one dispersal season. Future studies should strive to track individuals through a minimum of two dispersal seasons, so as to determine whether those individuals that do not disperse as 2-year-olds eventually disperse as 3-year-olds.

Natal Colony Characteristics

Beavers have been called "choosy generalists" in reference to their food habits (Jenkins and Busher 1979, Smith 1997). They feed heavily on willows and aspens, preferring sites where these species are abundant, but they also eat a variety of other foods including agricultural crops and ornamental plantings. On my study area, those colonies that had abundant willow patches also had higher population densities in the area. These colonies had a high prevalence of dispersers, thus supporting the premise that while natal habitat is important, population density also may drive subadults to disperse (Komdeur et al. 1995). Throughout much of the lower Midwest, corn provides beavers with an important, nutritious food source during the late-summer and fall. Although extensive research has documented preferred foods, their relative abundance and nutritional quality throughout much of the beaver's geographic range, the importance of corn in sustaining beaver populations has not been investigated.

Beavers in central Illinois use corn extensively as a summer and fall food. I observed individual beavers move several kilometers to feed in cornfields. This suggests that the availability and distribution of corn fields may influence the relative density of beavers in Illinois, their movements, and the number and distribution of den sites used by individual colonies. These factors may in turn influence the probability of natal dispersal by subadults. It appeared that colonies with abundant corn in their territories had fewer subadults disperse as 2-year-olds. In contrast, colonies that occupied territories lacking corn typically had higher rates of dispersal by 2-year-olds. The role that corn plays in influencing the population dynamics of Midwestern beavers should be addressed in future studies.

MANAGEMENT IMPLICATIONS

The majority of 2-year-old beavers (particularly females) in my sample delayed dispersal until at least their third year, an observation consistent with McTaggart and Nelson's (2003) report that beaver colonies in this area often contained 3-year-old (and older) offspring. These subadult animals may forego dispersal and breeding because population densities are high and suitable habitat is not available, or because they gain fitness advantages by delaying breeding until territory vacancies occur and/or their reproductive potential is higher. Regardless of the reason for delaying dispersal, the effect is likely to be that the average number of beavers in a colony increases and the effective size of the population is limited by the number of available territories. McTaggart and Nelson (2003) observed that 2- and 3- year old females did not ovulate when an older female was present in the colony. However, when the oldest female was removed these younger females ovulated soon thereafter.

In contrast to McNew's (2003) results in southern Illinois, beavers on my study area did not travel overland during dispersal; instead they followed the network of streams and ditches that comprised the watershed. Although some animals dispersed relatively short distances before settling, several individuals of both sexes made long-distance moves of over 50 km. These dispersal distances are among the longest reported in the literature and suggest that the species can rapidly fill vacant riparian habitat when it occurs. Although the results from previous studies are mixed, 2-year-old males appear to be the group most likely to disperse in the Embarras watershed.

Survival rates are high for dispersers and non-dispersers. Nuisance trapping was the primary source of mortality for both groups. When prime habitat is occupied or otherwise unavailable, subadults may settle in marginal habitats such as drainage ditches and small streams. Since water levels are low and fluctuating in these environments, beavers construct dams to hold and stabilize water levels and expand their wetland habitats. These wetlands alter existing landscape and are important for many plants and animals. However, in a region dominated by agriculture and urbanization, beaver dams also can flood crops, roads, and residential areas. Although my sample size was small, several dispersing subadults settled in marginal habitat. One of these was trapped in an agricultural drainage ditch after he and 2 yearling males dammed the ditch and flooded a cornfield. McTaggart (2002) found that beavers occupying ditches in central Illinois tended to be younger (1-4 years old) and colonies usually consisted of no more than 3 animals.

With few natural predators limiting this population, trapping is the primary mortality factor. In the absence of trapping, beaver populations appear to be limited primarily by social constraints on breeding and the availability of habitat. Trapping is probably not necessary to keep beaver populations in check; at high densities they are self-limiting. However, trapping is an important tool for removing nuisance animals whose activities cause economic damage. In addition, it appears that there is a surplus of potential breeders in this population, capable of replacing individuals removed by trappers. Moderate trapping levels are likely to create vacant territories and remove some older breeders allowing younger animals the opportunity to breed. This in turn is likely to reduce dispersal of subadults into marginal habitat and the nuisance problems that often follow.

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Table 1. Sex and age composition of beavers live-trapped in the Embarras River watershed during 2002 and 2003. Numbers in parentheses indicate the number of beavers tracked during the dispersal season.

Age-class	Male	Female	Total
< 1 year old (kits)	1	2	3
<2-years old (yearlings)	3 (2)	2 (2)	5
<3-years old (subadults)	8 (7)	10 (6)	18
> 3-years old (adults)	10 (1)	2	12
Totals	22	16	38

Table 2. Frequency of dispersal by beavers in each sex-age class on the Embarras River study area.

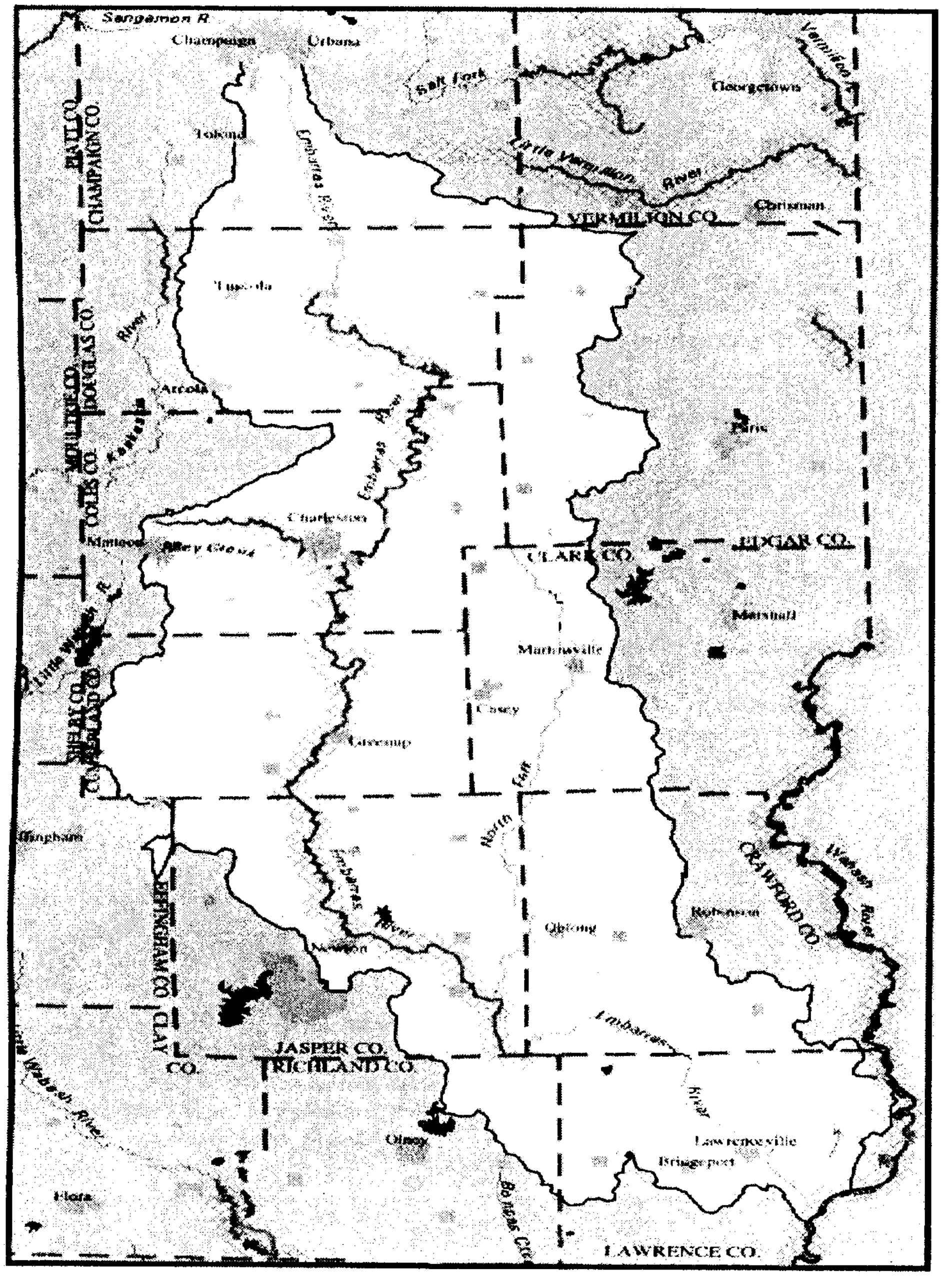
Sex-age class	N	% dispersing in central Illinois	
Male yearlings	2	0	(0.0%)
Female yearlings	2	0	(0.0%)
Male 2-year olds	7	5	(71.4%)
Female 2-year olds	6	1	(16.7%)
Male adult	1	0	(0.0%)
Total	18	6	(33%)

Table 3. Survival rates of dispersing and non-dispersing beavers during the dispersal period, February-May 2003 and 2004.

Sex-age class	N	No. surviving	Percent surviving
Dispersing beavers	6	5	83.3%
Non-dispersing beavers	12	11	91.7%
Total	18	16	88.9%

Table 4. Dispersal rates of 2-year old beavers reported in studies conducted in the United States.

Researchers	Location	Percentage of 2-year olds dispersing
McNew (2003)	southern Illinois	73%
Weaver (1986)	Mississippi	53-58%
Van Deelen and Pletscher (1996)	Montana	45%
Cleere (this study)	central Illinois	46%
Smith (1997)	Minnesota	33%
Davis (1984)	South Carolina	29%



Scale 1:760320

Fig. 1. The Embarras River watershed located in east-central Illinois. This study was conducted on the main channel of the river and its major tributaries in Douglas and Coles Counties.

Fig. 2. Typical cable snare set used to live-trap beavers. Snares usually were set in shallow water at haul-outs, dams, dens, and feeding stations.

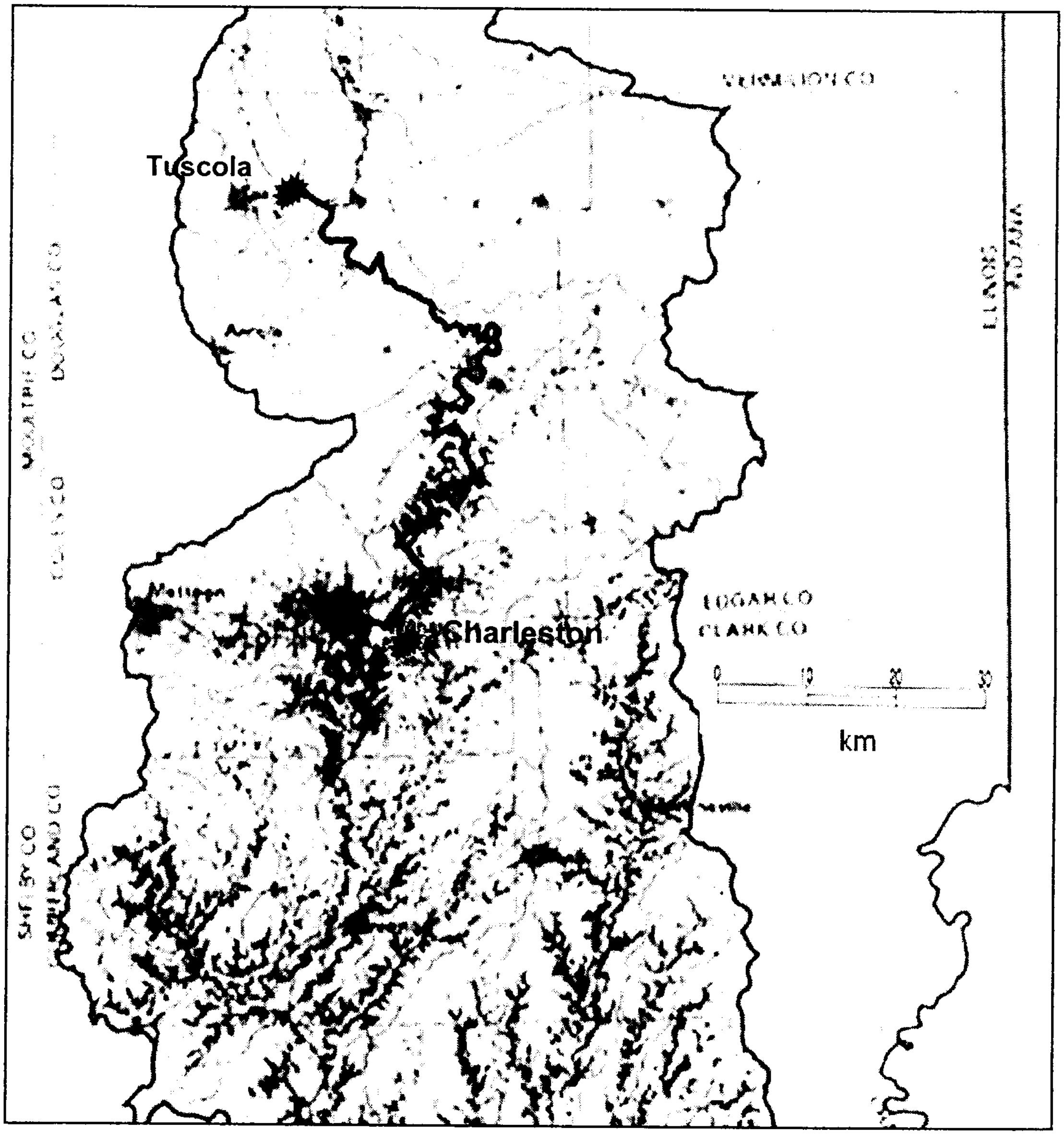


Fig. 3. Dispersal path of 2-year old male from Lake Charleston area to drainage ditch near Tuscola. This 80-km movement represented the longest natal dispersal by any beaver tracked during this study.

Fig. 4. 2-year-old female's dispersal movements along the Embarras River in east-central Illinois; Natal lodge to point A = 1.81 km, Jan 2004; Natal lodge to point B = 15.21 km, May 2004; Natal lodge to point C = 14.41 km, April 2004.

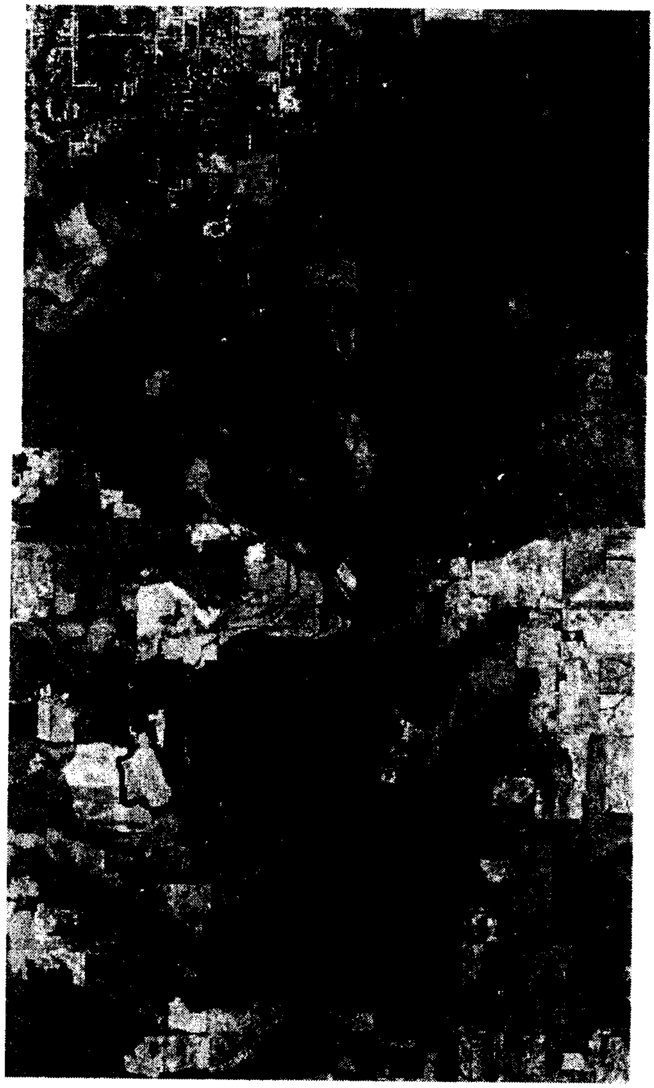


Fig. 5. 2-year-old female's exploratory movements along the Embarras River in east-central Illinois; Natal lodge to point A = 3.3 km, Mar 2003; Natal lodge to point B = 5.6 km, Mar 2003; Natal lodge to point C = 14.6 km, April 2003.