Am. Midl. Nat. 154:217–228

Dispersal and Survival of Juvenile Beavers (Castor canadensis) in Southern Illinois

LANCE B. McNEW, JR.[1] AND ALAN WOOLF
Cooperative Wildlife Research Laboratory, Southern Illinois University Carbondale, 251 Life Science II, Carbondale 62901

ABSTRACT.—We used radiotelemetry to estimate natal dispersal patterns and survival rates of 13 yearling and 19 subadult beavers (*Castor canadensis*) at two geomorphologically different sites in southern Illinois. Overall, we observed a 55% dispersal rate for yearlings and a 73% dispersal rate for subadults. Normally, juveniles (yearlings + subadults) initiated dispersal around 16 February (range = 28 Jan.–20 Mar.) and settled around 18 April, with juveniles remaining transient from late January through late June. Nine subadult beavers dispersed significantly earlier at one site ($\bar{x}$ = 25 Nov., range = 31 Oct.–16 Dec.), presumably due to intra-colony strife brought on by management-induced autumn flooding of wetlands for waterfowl. Dispersal occurred earlier than documented in northern regions. Beavers dispersed farther from natal colonies with free-flowing water access ($\bar{x}$ = 5.9 km) than those landlocked ($\bar{x}$ = 1.7 km). Males moved more frequently and traveled greater distances per individual move than did females, but overall dispersal distances were similar between sexes. Dispersal distances of beavers with access to free-flowing waterways generally were similar to other studies. Survival during dispersal was greater for beavers emigrating from lodges on the land-locked, less densely populated site (0.80), than for those dispersing in an area of higher population densities (0.43), but did not differ between dispersers and non-dispersers at either site.

INTRODUCTION

Dispersal and survival patterns have profound effects on population demography (Lidicker, 1975; Sun *et al.*, 2000). Dispersal affects composition, size and spacing of populations which, in turn, affects productivity of that species (Lidicker, 1975). Further, dispersal provides the primary means by which most mammals occupy new areas or areas where populations have been reduced. Beaver dispersal can potentially affect species management as well. Van Deelen (1991) noted colony-based indices were insufficient to estimate total beaver populations because they often ignored dispersing or transient individuals. These transients have the potential to significantly bias estimates garnered from methods historically used to survey beaver abundance.

Previous studies of juvenile beaver dispersal and survival have been conducted in the northern portions of the species range (Leege, 1968; Jackson, 1990; Van Deelen, 1991); few have been conducted in the Midwest (McTaggart and Nelson, 2003) and southern portion (Davis, 1984; Weaver, 1986) of their North American range. Information gathered regarding dispersal and survival in boreal systems probably is not applicable to the southern region because of differences in habitat and climate as well as differences in predatory species and harvest pressure. Further, few studies in the Midwest (none in Illinois) have used radiotelemetry to determine the fates of dispersing juvenile beavers. This study was designed to address dispersal patterns and survival rates of beavers in southern Illinois. The objectives of our study were to estimate distances and relative timing of juvenile beaver dispersal, test

[1] Corresponding author: Indiana Division of Fish and Wildlife, 553 E. Miller Dr., Bloomington 47401; Telephone: (812) 334-1137; FAX: (812) 339-4807; e-mail: lmcnew@dnr.IN.gov

whether dispersal patterns differed between sexes and landscapes and estimate survival and cause-specific mortality rates during the dispersal period.

MATERIALS AND METHODS

Study sites.—Research was conducted at 2 locations in southern Illinois, Amax Delta (AD) reclaimed surface mine and Union County Conservation Area (UCCA) between August 2001 and July 2003. The 543-ha AD site was located in the Southern Till Plain Division and UCCA in the Lower Mississippi River Bottomlands Division (Luman *et al.*, 1996). Intermittent surface mine reservoirs and farm ponds create a pot-hole landscape of suitable beaver habitat within a predominantly agricultural area surrounding the AD site. Dominant vegetation surrounding the waters of the mine was composed of reedgrass (*Phragmites australis*), buttonbush (*Cephalanthus occidentalis*) and maples (*Acer* sp.); oaks (*Quercus* sp.), hickories (*Carya* sp.) and elms (*Ulmus* sp.) were the dominant upland woody vegetation. Estimated beaver density at the AD site was 0.31 colonies/km^2 at the time of the study (McNew, 2003). At the 2512-ha UCCA site, stream tributaries and drainage ditches provide a network of connected wetlands and access to two free-flowing streams in the Mississippi River watershed. UCCA has been managed primarily as a wintering site for Canada geese (*Branta canadensis*) and flooded intentionally each year from October to February. Dominant species of the ca. 770-ha bottomland hardwood forest include sweetgum (*Liquidambar styraciflua*), pecan (*C. illinoensis*), pin oak (*Q. palustris*), black willow (*Salix nigra*) and cottonwood (*Populus deltoides*). Aquatic vegetation was dominated by buttonbush, elodea (*Elodea* sp.) and water lily (*Nymphaea* sp.). Permanently and seasonally inundated wetlands and lakes composed ca. 550 ha of UCCA. Estimated beaver density at UCCA was 0.45 colonies/km^2 (McNew, 2003). Data were collected at UCCA only during the second field season.

Capture, tagging and monitoring of beavers.—Beavers were captured during two sampling periods: 2 January–8 February 2002 and 28 August–28 November 2002 by use of snares (McKinstry and Anderson, 1998). Snares were set at lodges, dams, trail runs and channels. Sex was determined by palpation for bacula (Osborn, 1955). We assigned individual beavers to one of four age classes based on mass: 0–12 mo-old kits (<6.8 kg), 13–24 mo-old yearlings (6.8–10.8 kg), 25–36 mo-old subadults (10.9–16.0 kg) and ≥37 mo-old adults (>16 kg) (Patric and Webb, 1960). Telemetry data were obtained only for yearling and subadult beavers. These two age classes were categorized collectively as "juveniles" after Van Deelen (1991). Beavers were immobilized with an intramuscular injection of ketamine hydrochloride (6–12 mg/kg) and xylazine hydrochloride (0–1.25 mg/kg) to facilitate handling. Beavers were affixed with tail-mounted radiotransmitters (Telonics, Mesa, Arizona, USA) equipped with mortality sensors (Rothmeyer *et al.*, 2002; McNew, 2003). After handling, beavers were placed in a plastic crate near the capture site and allowed to recover before being released.

Beavers were monitored from 2 January 2002–20 June 2003 during daylight hours ≥3 times/wk from truck or on foot using a TR-2E/TS1 receiver/scanner (Telonics, Mesa, Arizona, USA) and handheld 2- or 4-element yagi antennas. A fixed-wing aircraft equipped with wing-mounted 2-element yagi antennas was used to locate animals that had dispersed and could not be located from the ground for two consecutive days. We located daytime resting locations via homing and recorded positions using a global positioning system (GPS) unit. If a mortality signal was heard, we homed in on the transmitter and retrieved the carcass. Cause of death was determined by field investigation and necropsies when possible and classified as: (1) predation, (2) disease, (3) other or (4) unknown. We right-censored data for beavers if transmitter signals were lost or failed.

Dispersal patterns.—We calculated linear distances from sites of capture (assumed natal) to resting locations as well as distances between sequential locations (*i.e.*, individual movements). Because juveniles were not located daily, the date when a beaver started to disperse was estimated as the midpoint between the last known date of occupancy at the natal site and the first time the animal was located away from its natal site and did not return. Settlement date was estimated in a similar manner; as the midpoint between the last known date of occupancy at a temporary site and the time of first location at the settlement site. Dispersers were defined as beavers that left their natal area and did not return. A temporary site was defined as a location that a beaver occupied for <30 d. A beaver was considered to have settled if it was located at the same site for ≥30 d.

For analyses, calendar days were sequentially numbered from 1 September to 20 June. We compared mean dispersal dates, duration of dispersal and settlement dates between sexes, age classes, sites and years using analysis of variance (ANOVA). Simple linear regression was used to assess whether dispersal distance was dependent on dispersal date and duration. Distance data were log-transformed for normality and ANOVA was used to test whether mean movement distances differed between sites and years. Data on distances traveled by beavers that had died while dispersing were not included in analyses. We used a *G*-test (Sokal and Rohlf, 2000) to test for sex-biased rate of dispersal (ratio of dispersers vs. non-dispersers) and 2-way ANOVA of log-transformed distance data (Sokal and Rohlf, 2000) to test for differences in mean dispersal distance between males and females and site by sex interaction.

Survival and cause-specific mortality.—Survival and cause-specific mortality rates were estimated using methods of Trent and Rongstad (1974) in the program MICROMORT (Heisey and Fuller, 1985). Because beavers were not monitored for an entire year, we estimated survival rates for a period of 230 d (1 September–20 June), during which all dispersal activities had occurred at both sites. Contingency tables and Chi-square tests in the program CONTRAST (Sauer and Williams, 1989) were used to test for differences in survival rates between sexes, and dispersers and non-dispersers. We also estimated cause-specific mortality rates for dispersing juveniles but sample sizes were too small in each category for statistical analyses. Statistical significance was assumed at $\alpha \leq 0.05$ for all tests.

Results

A total of 101 captures resulted in the handling of 75 individual beavers (32 M, 32 F, 11 unknown). Distribution by age class was 11 kits (14.7%), 13 yearlings (17.3%), 19 subadults (25.3%) and 32 adults (42.6%). Fourteen juveniles (7 yearlings, 7 subadults) were radiotagged at AD and 15 juveniles (5 yearlings, 10 subadults) were radiotagged at UCCA.

Dispersal.—Overall, 54.5% of yearlings and 72.7% of subadults dispersed from their natal areas. Seven of 9 (77.8%) juveniles (4 M, 3 F) dispersed from their natal areas in 2002 and 15 of 24 (62.5%) juveniles (8 M, 7 F; including two tagged the previous year) dispersed in 2003. Because there was no difference in dispersal rates of juveniles between years, data were pooled. The subadult dispersal rate at UCCA was 78.5% and did not differ statistically from that at AD (66.7%). The probability of a yearling dispersing differed between sites, but was not statistically significant (UCCA = 33.3%, AD = 62.5%). Dispersal rates were similar between sexes with 64.3% of females and 63.2% of males dispersing.

There was a bimodal distribution of dispersal dates at UCCA in 2003 (Fig. 1). The mean dispersal date of nine juveniles, which we labeled as "early" dispersers, was 25 November (range = 31 October–16 December). The mean dispersal date of the other four dispersers, which we referred to as "normal" dispersers was 22 February (range = 5 February–15 March) and did not differ statistically from that of the AD site ($\bar{x}$ = 13 February, range = 31 January–20 March); therefore, data from "normal" dispersers at both sites were pooled. Dispersal

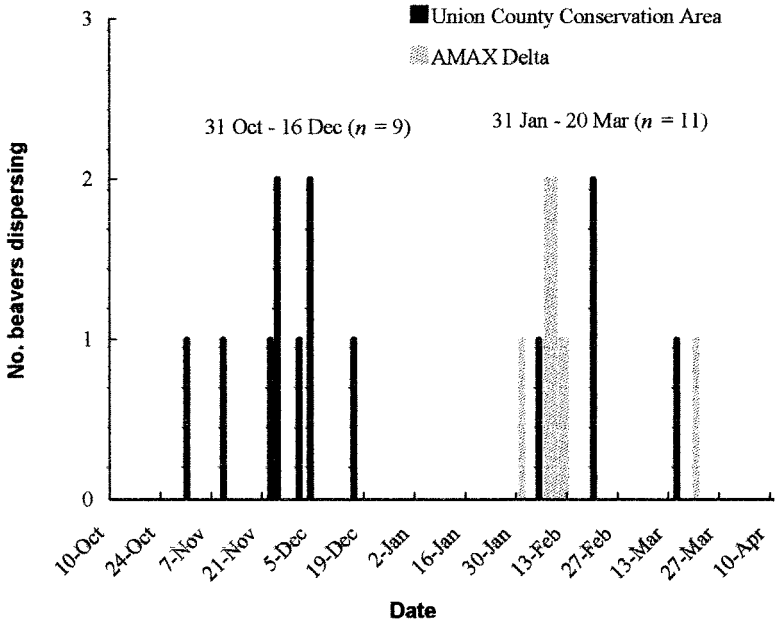

FIG. 1.—Distribution of estimated dispersal dates of 20 juvenile beavers (*Castor canadensis*) in southern Illinois, 2002–2003

dates of early and normal dispersers differed ($F_{1,19} = 168.5$, $P < 0.001$). Excluding early dispersers at the UCCA site, mean dispersal date (± SE days) of juvenile beavers from both field seasons was 16 February ± 4.3 (range = 31 January–20 March).

There was no difference in mean dispersal date between years at AD ($\bar{x}_{2002} = 8$ February; $\bar{x}_{2003} = 20$ March). Dispersal date (± SE days) did not differ between sexes either for normal dispersers ($\bar{x}_{male} = 16$ February ± 5.5; $\bar{x}_{female} = 17$ February ± 7.8) or early dispersers ($\bar{x}_{male} =$ 28 November ± 9.9; $\bar{x}_{female} = 15$ November ± 8.1). Dispersal date did not differ between age-classes of normal dispersers ($\bar{x}_{subadult} = 16$ February ± 5.4; $\bar{x}_{yearling} = 10$ February ± 5.9); no radio-tagged yearlings dispersed early.

Twelve of 20 (60%) known-fate dispersing juveniles successfully found settlement sites, the other 8 died during dispersal (Table 1). The overall mean settlement date for both sites was 22 April (range = 28 January–20 June; Table 1). Although dispersal dates differed statistically between early and normal dispersers at UCCA, settlement date did not ($\bar{x}_{early\ dispersers} = 26$ April, range = 28 January–17 June; $\bar{x}_{normal\ dispersers} = 9$ May, range = 6 April–10 June). Settlement dates were similar between sites ($\bar{x}_{AD} = 29$ April, range = 20 February–20 June; $\bar{x}_{UCCA} = 30$ April, range = 28 January–17 June) and sexes ($\bar{x}_{female} = 9$ April, range = 28 January–20 June; $\bar{x}_{male} = 8$ May, range = 4 April–17 June), and there was no evidence of a site-sex interaction. Mean settlement date of yearlings was 12 May (range = 25 April–28 May) and did not differ statistically from that of subadults ($\bar{x} = 25$ April, range = 28 January–20 June).

Mean dispersal distance (± SE) at AD pooled over years (1676 ± 511 m) was highly variable and was less than that at UCCA ($\bar{x} = 5911$ ± 2320 m; $F_{1,16} = 5.4$, $P = 0.04$; Table 1). We were not able to determine if the difference between sites was a result of a yearly variation because data were only collected for 1 y at UCCA. However, mean dispersal

Table 1.—Dispersal characteristics of known-fate juvenile beavers (*Castor canadensis*) in southern Illinois, 8 January 2002–20 June 2003. Distance represents linear distance from presumed natal site to settlement or mortality site. Fate was categorized as settled, died or unknown

Site	Beaver no.	Sex	Age[1]	Dispersal date	Dispersal duration (days)	Distance (m)	Fate	Settlement date
AD	030	M	Y	7 Feb.	96	1597	Settled	14 May
	240	M	Y	9 Feb.	75	415	Settled	25 Apr.
	260	M	Y	9 Feb.		512	Died	
	150	M	S	11 Feb.	52	1036	Settled	4 Apr.
	360	F	Y	7 Feb.	110	2033	Settled	28 May
	370	F	S	31 Jan.	140	4994	Settled	20 Jun.
	400	F	S	12 Feb.	8	813	Settled	20 Feb.
	570	F	S	20 Mar.		522	Died	
				$\bar{x}$ = 12 Feb.	80	1676		29 Apr.
UCCA								
early	9730	M	S	25 Nov.		1640	Died	
	9810	M	S	23 Nov.		2155	Died	
	9820	M	S	4 Dec.		5577	Died	
	9930	M	S	1 Dec.	198	4144	Settled	17 Jun.
	9630	F	S	25 Nov.	174	2282	Settled	15 May
	9640	F	S	4 Dec.		2018	Died	
	9710	F	S	16 Dec.		989	Died	
	9770	F	S	10 Nov.	79	20,931	Settled	28 Jan.
	9840	F	S	31 Oct.	191	1622	Settled	10 May
				$\bar{x}$ = 25 Nov.	160	7245		26 Apr.
normal	9700	M	S	20 Feb.	45	14,156	Settled	6 Apr.
	9720	M	S	15 Mar.	87	1028	Settled	10 Jun.
	9790	M	S	5 Feb.		1097	Died	
				$\bar{x}$ = 22 Feb.	66	5427		9 May

[1] Y = 13–24 mo-old yearling, S = 25–36 mo-old subadult

distances did not differ between sampling years at the AD site ($\bar{x}_{2002} = 1629 \pm 618$ m; $\bar{x}_{2003} = 1845 \pm 1157$ m).

Mean (± SE) dispersal distance for AD females was 2306 ± 640 m and 890 ± 715 m for AD males (Table 1). Mean dispersal distance for AD yearlings was 1545 m (729) and 1841 ± 815 m for subadults (Table 1). There was no statistical difference in mean dispersal distance between sexes or age-classes, and there was no first-order interaction.

Mean dispersal distance (±SE) for UCCA females was 6800 ± 3694 m and did not differ from males ($\bar{x} = 5200 \pm 3304$ m). All dispersing beavers at UCCA were subadults. Dispersal distance decreased as dispersal date increased ($r^2 = 0.25$, $F_{1,16} = 5.32$, $P = 0.03$), but was not related to dispersal duration ($r^2 = 0.02$, $F_{1,11} = 0.25$, $P = 0.62$).

A total of 138 individual movements was recorded based on 1120 radio-fixes of beavers from 2 January to 20 June 2002 and 2 September 2002 to 20 June 2003. Mean number of movements per dispersing beaver was 6.9. Normal-dispersing beavers (those which initiated dispersal in the spring) moved more frequently and traveled farther during individual movements in March with males and females averaging 4699 m and 2538 m per move, respectively (Fig. 2a). Movements by early-dispersers were bimodally distributed; individual movement distances and frequency generally increased through October and November, peaked in December and decreased through January and February. A second increase in

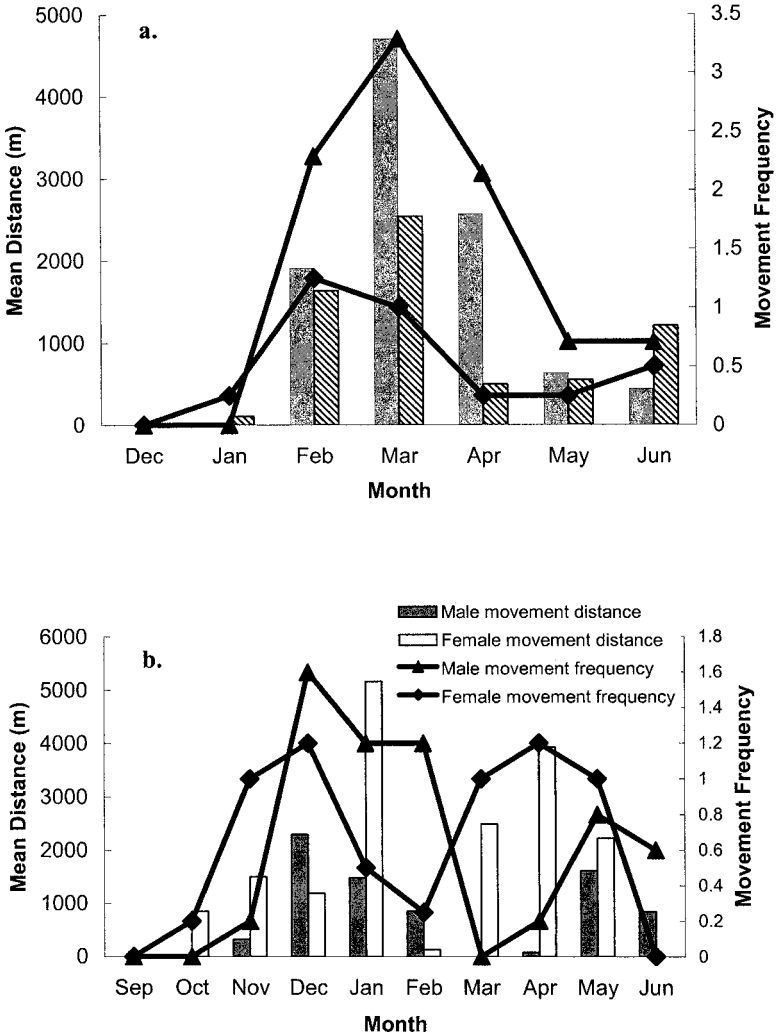

FIG. 2.—Average monthly movement frequencies and distances of normal (a) and early (b) dispersing male and female juvenile beavers (*Castor canadensis*) in southern Illinois, 1 September 2002–20 June 2003

mean distance and movement frequency was evident through late April (Fig. 2b). Although individual movement distances were similar between early- and normal-dispersing males and females, normal-dispersing males tended to make more movements than any other class.

Survival and cause-specific mortality.—The 32 juvenile beavers were monitored for 5606 radio-days ($\bar{x} = 175$ radio-days/beaver, range = 5–363) during 8 February 2002–20 June 2002 and 1 November 2002–20 June 2003. Twelve of 32 radio-tagged juveniles (37.5%) died during the study (7 M, 5 F). Estimated survival rate (S) of males did not differ statistically from that of females at either site so data for the sexes were pooled. Survival ($\pm$SE) of dispersers (0.794, SE = 0.10) was nearly identical to that of non-dispersers (0.793 $\pm$ 0.180) at

Table 2.—Estimated dispersal season (1 November–20 June) survival rates (*S*) for radio-tagged beavers (*Castor canadensis*) in southern Illinois, 2002–2003

Site	n	Radio-days ($\bar{x}$)	Mortalities	*S*	SE	95% CI
AD						
Kit	2	161 (80)	1	0.239	0.126	0.014–1.000
Juvenile	14	3140 (224)	3	0.802	0.100	0.626–1.000
Disperser	9	1998 (222)	2	0.794	0.100	0.577–1.000
Non-disperser	4	995 (249)	1	0.793	0.184	0.500–1.000
Adult	3	660 (220)	0	1.000	0.000	1.000–1.000
Pooled	19	3961 (208)	4	0.792	0.089	0.631–0.995
UCCA						
Kit	0					
Juvenile	18	2466 (137)	9	0.431	0.121	0.249–0.747
Disperser	13	2006 (154)	6	0.502	0.141	0.289–0.871
Non-disperser	5	460 (92)	3	0.222	0.192	0.040–1.000
Adult	9	1852 (205)	2	0.780	0.138	0.553–1.000
Pooled	27	4318 (160)	11	0.556	0.095	0.393–0.787

the AD site. Similarly, survival of dispersers at the UCCA site (0.502 ± 0.141) did not differ statistically from that of non-dispersers (0.222 ± 0.192). Hence, data from non-dispersers and dispersers were pooled to give juvenile survival rates at each site. Survival of juveniles at AD was greater than that of juveniles at UCCA ($\chi_1^2 = 6.23$, $P = 0.01$; Table 2).

Eight of 22 (36.4%) dispersers died while emigrating (Table 3); 3 of these (37.5%) died from pulmonary edema caused by a severe bacterial infection consistent with *Yersinia pseudotuberculosis*, and 3 died from predation during dispersal. Canids, presumably coyotes (*Canis latrans*), killed two juveniles; the other death appeared to have been caused by a bobcat (*Lynx rufus*). One dispersing juvenile drowned after its transmitter became entangled in a submerged fish seine. A subadult male, found in an advanced state of decomposition, died of unknown causes. Four of 10 nondispersing juveniles died: two (one yearling male, one subadult female) from canid predation and two (one subadult female, one subadult male) from unknown causes. Those having died from unknown causes were found floating in water with their internal organs having been eaten.

Table 3.—Cause-specific mortality rates (*M*) for beavers (*Castor canadensis*) at AMAX Delta (AD) reclaimed surface mine, and Union County Conservation Area (UCCA), in southern Illinois, 2002–2003

Site	Mortality cause	Adults			Juveniles			Kits		
		Mortalities	*M*	SE	Mortalities	*M*	SE	Mortalities	*M*	SE
AD	Predation	0	0.000	0.000	2	0.132	0.087	1	0.478	0.338
	Disease	0	0.000	0.000	1	0.067	0.063	1	0.478	0.338
	Unknown	0	0.000	0.000	0	0.000	0.000	0	0.000	0.000
	Other	1	0.294	0.245	0	0.000	0.000	0	0.000	0.000
UCCA	Predation	0	0.000	0.000	3	0.190	0.097			
	Disease	0	0.000	0.000	2	0.126	0.083			
	Unknown	1	0.110	0.103	3	0.190	0.097			
	Other	1	0.110	0.103	1	0.063	0.061			

DISCUSSION

Dispersal patterns.—Most authors have contended that beavers disperse at 2 y-of-age (Bradt, 1938; Townsend, 1953; Aleksiuk, 1968; Bergerud and Miller, 1977; Svendsen, 1980); it is probably for this reason that most recent research has been conducted primarily on this age-class (Weaver, 1986; Jackson, 1990; Van Deelen and Pletscher, 1996; Smith, 1997). Subadult dispersal rate (73%) in our study was considerably greater than that reported in the literature. Three of 11 (ca. 29%) subadults dispersed in South Carolina, with 43% not dispersing and almost 29% censored from the study (Davis, 1984). Dispersal rate of 2-y-olds was reported as 33% in Minnesota (Smith, 1997), 45% in Montana (Van Deelen and Pletscher, 1996) and 53–58% in Mississippi (Weaver, 1986).

Dispersal by yearlings was reported by Beer (1955) and Leege (1968), but neither reported the percentages of yearlings that had dispersed. At least 9 of 28 (ca. 32%) yearlings were recaptured away from their trap sites (assumed natal area) in Minnesota (Beer, 1955). In Idaho, 70% of retrapped yearlings had moved >1.6 km (Leege, 1968). In contrast, Sun *et al.* (2000) noted dispersal of yearlings was relatively rare (14%) during their mark-recapture study in New York. However, this percentage represents the proportion of dispersers that were yearlings, not the proportion of marked yearlings that dispersed. In addition, many beavers were thought to have dispersed and were not recovered, probably biasing the results. In an area of low beaver density in south-central Sweden (0.13 colonies/stream km), 5 of 9 (55.5%) yearling European beavers (*C. fiber*) dispersed from their natal areas (Hartman, 1997). Overall, we observed a 55% dispersal rate for yearlings, with a greater percentage of yearlings dispersing at the AD site (63%) than at UCCA (33%). This difference suggests that dispersal of juvenile beavers may have been delayed at the UCCA site.

Dispersal by juvenile beavers may be delayed in areas with high densities (Lyons, 1979; Brooks *et al.*, 1980; Hodgdon and Lancia, 1983; Hartman, 1997), and the presence of additional adults is more common in colonies occurring in high-density populations than those in low-density populations (Müller-Schwarze and Schulte, 1999). In our study, the greater density of colonies per wetland likely hindered yearling dispersal at the UCCA site. Smith (1997) hypothesized that delaying dispersal under such conditions allows young beavers to maximize their lifetime inclusive fitness by aiding in the raising of siblings and defending territories. In addition, another year of growth and experience probably increases their chances of successfully establishing independent territories. A second hypothesis suggests that poor quality habitat is the primary cause of dispersal (Gunson, 1970; Jackson, 1990). Colonies in better habitats are able to support additional beavers, thus there are no habitat-related reasons for emigrating, whereas beavers occupying less suitable habitats are more likely to disperse in an attempt to locate better habitats (Gunson, 1970). We did not quantify habitat-quality, but preferred woody species (*e.g.*, willows, birch, maples) and aquatic vegetation appeared to be more abundant at UCCA. Poor habitat quality at AD likely influenced a greater proportion of yearlings to search for better conditions. We agree with Smith (1997) that delayed dispersal likely is the result of a combination of factors, including population density and habitat quality.

Most reports of dispersal chronology have been anecdotal, simply stating that beaver dispersal coincides with the spring thaw, or that increasing water levels from spring run-off initiates dispersal (Bradt, 1947; Townsend, 1953; Hodgdon and Lancia, 1983). Few studies have been designed to specifically address when juveniles emigrate and settle into new areas. Average dispersal date of juveniles in Montana was 28 May and ranged from 7 April–20 August (Van Deelen, 1991). Subadults emigrated from their natal colonies between early April and May in New York (Sun *et al.*, 2000). Juveniles dispersed from ice breakup through

late August in Minnesota (Smith, 1997) and dispersal movements were greatest in April in Massachusetts (Molini *et al.*, 1981). We found that beavers in southern Illinois dispersed substantially earlier than documented in northern regions. Under normal environmental conditions, mean dispersal date in southern Illinois was similar to that in Mississippi (Weaver, 1986), with juveniles emigrating around 16 February and settling around 22 April. We believe geographical differences in dispersal dates likely are the result of regional climate differences, and our data do not disagree with either the spring thaw or run-off theories. Because ice-off (if any) occurs earlier in southern Illinois than in northern areas, it is reasonable that dispersal also would occur earlier.

We observed autumn dispersal for over half the radio-tagged beavers at UCCA and believe this resulted from flooding for waterfowl management at the site. Ten of 12 active colonies were flooded out of their primary lodges and beavers were forced to occupy smaller auxiliary bank dens within their territories. Our data support our conclusion that subadult beavers likely were forced away from the family unit because of resource limitations caused by this disturbance. Interestingly, autumn-dispersers showed a second increase in movements during the normal dispersal season.

Mean dispersal distance at UCCA (5.9 km) was similar to that reported in other studies (Leege, 1968; Sun *et al.*, 2000; Van Deelen and Pletscher, 1996; Weaver, 1986). Mean distance was much shorter at AD (1.7 km), probably because juveniles had to disperse overland to establish independent territories. Beavers may limit overland movements to reduce vulnerability to predation and inclement weather. In a study conducted in Wisconsin that compared movement distances of beavers released in streams and pot-holes, mean movement distance of beavers transplanted into streams was more than twice that of beavers transplanted into land-locked waters (7.4 vs. 3.2 km, respectively; Knudsen and Hale, 1965).

Exploratory movements of juveniles away from their natal colonies have been reported in previous studies (Aleksiuk, 1968; Hodgdon, 1978; Weaver, 1986; Van Deelen, 1991). These ventures away from and back to natal areas may provide dispersal-aged beavers with information about local population densities (Aleksiuk, 1968; Molini *et al.*, 1981). In areas of high densities, juvenile explorers return to their natal sites for another year or two (Molini *et al.*, 1981). None of the beavers in our study displayed exploratory behavior from the natal site, possibly indicating a less dense population in southern Illinois as compared to these other studies; however, beavers did show exploratory behavior from non-natal temporary sites. Juveniles often left occupied temporary bank dens, hollowed logs, or abandoned lodges for a few days, presumably to seek more suitable settlement sites. If none were found, they returned to the temporary location. Alternatively, juveniles might leave these temporary sites to locate potential mates, but we have no data to document or dispute this.

The only sex-biased dispersal pattern we observed was that of males having moved more frequently and traveled greater distances per move than did females. This pattern suggests that males spent more time seeking available territories, and may have initiated territory establishment. This pattern could have implications to managers because few data are available on how young beavers establish territories or how pair bonds are formed (Novak, 1987). To illustrate, we documented 1 instance in which a male settled in an abandoned bank den, followed in 2 weeks by a dispersing female.

Existing data exhibit no clear pattern regarding sex-biased dispersal in beavers. In Idaho, 45% of tagged adult males were recaptured >1.6 km from their previous capture site compared with 18% of adult females (Leege, 1968). Sun *et al.* (2000) however, reported that mean dispersal distance of males was significantly less than that of females. Jackson (1990) observed that male beavers in western Montana dispersed greater distances than females. However, another study in the same area using some of the same colonies reported that both

the probability of dispersal and dispersal distance were independent of sex (Van Deelen and Pletscher, 1996). Beer (1955) reported a mean linear dispersal distance of 15.7 km for males and 3.7 km for females in Minnesota, but did not separate natal dispersal by juveniles from secondary dispersal of adults. Sun *et al.* (2000) argued that inbreeding of monogamous species (*e.g.*, beaver) imposes stronger selection pressures on females, and females will attempt to avoid inbreeding by dispersing greater distances than their male siblings. They found that on average females dispersed significantly farther than males and proposed that greater female dispersal indicates a denser population of beavers (Sun *et al.*, 2000). In southern Illinois, we observed similar dispersal distances and dispersal probabilities between sexes and areas of different densities, which is typical of monogamous animals (Dobson, 1982). If juveniles do avoid excessive inbreeding, data from our study suggest that differential dispersal might not be the mechanism by which they do it. However, it could be argued that the New York researchers experienced greater beaver densities than we did, resulting in more selective pressure on females to disperse farther.

Survival and mortality factors.—Theoretically, dispersing beavers should be subject to higher mortality than nondispersers due to the hazards of dispersal, including increased exposure to predators, unfamiliarity of new areas and the general inexperience of juveniles (Bradt, 1938; Lidicker, 1975; Lyons, 1979). Gunson (1970) observed low mortality in beavers <1.5 y old, increased mortality in beavers 1.5–2.5 y old and decreased mortality in beavers >2.5 y old. He suggested that high mortality in the intermediate age-class resulted from dispersal-related deaths. Payne (1984) supported Gunson's suggestion, reporting similar age-class mortality rates of 4% for kits, 40% for juveniles, and 32% for adults in Newfoundland, and Van Deelen (1991) reported 70% survival for 2-y old beavers in Montana. McTaggart and Nelson (2003) reported age-specific mortality was highest for beavers in Illinois between 8 mo and 2 y of age.

Data from our study agree with previously noted trends: juvenile mortality rates were greater than those of adults at both sites (McNew, 2003). We did not observe a greater mortality rate for dispersing juveniles than nondispersers; however, juvenile survival did differ between sites. Survival at AD was similar to that documented in other studies (Bergerud and Miller, 1977; Van Deelen, 1991), whereas survival was much lower at UCCA. Many factors can affect survival rates of beavers (*i.e.*, climate, density, and habitat), but data were insufficient to differentiate between causes. However, resource limitations, lack of available settlement sites, and hostile encounters caused by higher densities (Nordstrom, 1972) may have subjected young beavers to lower survival at UCCA. In addition, an increased abundance of predators in areas of increased prey abundance, such as UCCA, likely subjected beavers to lower survival rates overall. Predation by canids and bobcats was more frequent at UCCA than AD (Table 3).

Causes of mortality for beavers range from severe winter weather to predation to human harvest (refer to Novak, 1987 for a complete list of beaver mortality causes). Predation was the main cause of juvenile mortality in our study. Predation rates were similar to those reported by Smith (1997) in Minnesota who noted that 14% of dispersers were killed by predators (*i.e.*, wolves and black bears). However, predation in his study may have been underestimated because the fates of ca. 43% of dispersers were unknown and these animals could have died as the result of predation (Smith, 1997).

Approximately 25% of juvenile deaths in our study were caused by a bacterial infection known as yersiniosis. The disease has been reported sporadically in beavers in Ontario (Hacking and Sileo, 1974), but has not been reported as a major mortality factor for beavers in other studies. Increased prevalence of yersiniosis in animal populations likely is caused by resource limitations. Also, animals under increased stress are more susceptible to disease

(Gasper and Watson, 2001). This is supported by the fact that none of the adults radio-tagged at these colonies, presumably under less stress than juveniles, died from yersiniosis (McNew, 2003; Table 3). In addition, mortality from yersiniosis was greater for UCCA juveniles than for AD juveniles, adding support to the argument that increased densities contribute to increased stress and overall lower survival of juvenile beavers.

Acknowledgments.—Capture and handling procedures were approved by Southern Illinois University Carbondale's (SIUC) Institutional Animal Care and Use Committee (Southern Illinois University Carbondale Animal Assurance # 01-020). This project was funded by the Federal Aid in Wildlife Restoration Project W-135-R-3/4, the Cooperative Wildlife Research Laboratory at SIUC and the Illinois Department of Natural Resources (IDNR). We thank B. Bluett and T. Nelson for support and advice. C. Bloomquist and G. Mohr provided field and computer assistance, respectively. C. Nielsen and S. Johnson reviewed the manuscript.

Literature Cited

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis*). *J. Mammal.,* **49**:759–761.

Beer, J. R. 1955. Movements of tagged beaver. *J. Wildl. Manage.,* **19**:492–493.

Bergerud, A. T. and D. R. Miller. 1977. Population dynamics of Newfoundland beaver. *Can. J. of Zool.,* **55**:1480–1492.

Bradt, G. W. 1938. A study of beaver colonies in Michigan. *J. Mammal.,* **19**:139–162.

———. 1947. Michigan beaver management. Michigan Department of Conservation, Game Division, Lansing, Michigan, USA. 56 pp.

Brooks, R. P., M. W. Fleming and J. J. Kennelly. 1980. Beaver colony response to fertility control: evaluating a concept. *J. Wildl. Manage.,* **44**:568–575.

Davis, J. R. 1984. Movement and behavior patterns of beaver in the Piedmont of South Carolina. M.S. Thesis, Clemson University, Clemson, South Carolina, USA.

Dobson, F. S. 1982. Competition of mates and predominant juvenile male dispersal in mammals. *Anim. Behav.,* **30**:1183–1192.

Gasper, P. W. and R. P. Watson. 2001. Plague and yersiniosis, p. 313–329. *In:* E. S. Williams and I. K. Barker (eds.). Infectious diseases of wild mammals. Iowa State University Press, Ames, Iowa, USA.

Gunson, J. R. 1970. Dynamics of the beaver of Saskatchewan's northern forest. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada.

Hacking, M. A. and L. Sileo. 1974. *Yersinia enterocolitica* and *Yersinia psuedotuberculosis* from wildlife in Ontario. *J. Wildl. Diseases,* **10**:452–457.

Hartman, G. 1997. Notes on age at dispersal of beaver (*Castor fiber*) in expanding population. *Can. J. Zool.,* **75**:959–962.

Heisey, D. M. and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.,* **49**:668–674.

Hodgdon, H. E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. Ph.D. Dissertation, University of Massachusetts, Amherst, Massachusetts, USA.

——— and R. A. Lancia. 1983. Behavior of the North American beaver, *Castor canadensis. Acta Zoologica Fennica,* **174**:99–103.

Jackson, M. D. 1990. Beaver dispersal in western Montana. M.S. Thesis, University of Montana, Missoula, Montana, USA.

Knudsen, G. J. and J. B. Hale. 1965. Movements of transplanted beavers in Wisconsin. *J. Wildl. Manage.,* **29**:685–688.

Leege, T. A. 1968. Natural movements of beaver in southeastern Idaho. *J. Wildl. Manage.,* **32**:973–976.

Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals, p. 103–128. *In:* F. B. Golley, K. Petrusewicz, and L. Ryszkowski (eds.). Mammals: their productivity and population dynamics. Cambridge University Press, London, England.

LUMAN, P., M. JOSELYN AND L. SALOWAY. 1996. Critical trends assessment project: landcover databases. Illinois Natural History Survey, Champaign, Illinois, USA.

LYONS, P. J. 1979. Effects of induced sterility on reproduction and dispersal patterns in beaver colonies. M.S. Thesis, University of Massachusetts, Amherst, Massachusetts.

MCKINSTRY, M. C. AND S. H. ANDERSON. 1998. Using snares to live–capture beaver. *Castor canadensis. Can. Field Nat.,* **112**:469–473.

MCNEW, L. B., JR. 2003. Dispersal characteristics of juvenile beavers in southern Illinois. M.S. Thesis, Southern Illinois University, Carbondale, Illinois, USA.

MCTAGGART, S. T. AND T. A. NELSON. 2003. Composition and demographics of beaver (*Castor canadensis*) colonies in central Illinois. *Am. Midl. Nat.,* **150**:139–150.

MOLINI, J. J., R. A. LANCIA, J. BISHIR AND H. E. HODGDON. 1981. A stochastic model of beaver population growth, p. 1215–1245. *In:* J. A. Chapman and D. Pursley (eds.). Worldwide Furbearer Conference Proceedings. Worldwide Furbearers Conference, Inc., Frostburg, Maryland, USA.

MÜLLER-SCHWARZE, D. AND B. A. SCHULTE. 1999. Behavioral and ecological characteristics of a "climax" population of beaver (*Castor canadensis*), p. 161–177. *In:* P. E. Busher and R. M. Dzieciolowski (eds.). Beaver protection, management, and utilization in Europe and North America. Kluwer Academic/Plenum Publishers, New York, New York, USA.

NORDSTROM, W. R. 1972. Comparison of trapped and untrapped beaver populations in New Brunswick. M.Sc. Thesis, University of New Brunswick, Fredricton, New Brunswick, Canada.

NOVAK, M. 1987. Beaver, p. 283–312. *In:* M. Novak, J. A. Baker, M. E. Obbard and B. Malloch (eds.). Wild furbearer management and conservation in North America. Ashton-Potter Limited, Concord, Ontario, Canada.

OSBORN, D. J. 1955. Techniques for sexing beaver. *J. Mammal.,* **36**:141–142.

PATRIC, E. F. AND W. L. WEBB. 1960. An evaluation of three age determination criteria in live beavers. *J. Wildl. Manage.,* **24**:37–44.

PAYNE, N. F. 1984. Mortality rates of beaver in Newfoundland. *J. Wildl. Manage.,* **48**:117–126.

ROTHMEYER, S. W., M. C. MCKINSTRY AND S. T. ANDERSON. 2002. Tail attachment of modified ear-tag radio transmitters on beavers. *Wildl. Soc. Bul.,* **30**:425–429.

SAUER, J. R. AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.,* **53**:137–142.

SMITH, D. W. 1997. Dispersal strategies and cooperative breeding in beavers. Dissertation, University of Nevada, Reno, Nevada, USA.

SOKAL, R. R. AND F. J. ROHLF. 2000. Biometry. 3rd ed. W. H. Freeman and Company, New York, New York, USA.

SUN, L., D. MULLER-SCHWARZE AND B. A. SCHULTE. 2000. Dispersal pattern and effective population size of the beaver. *Can. J. Zool.,* **78**:393–398.

SVENDSEN, G. E. 1980. Population parameters and colony composition of beaver (*Castor canadensis*) in southeast Ohio. *Am. Midl. Nat.,* **104**:47–56.

TOWNSEND, J. E. 1953. Beaver ecology in western Montana with special reference to movements. *J. Mammal.,* **34**:459–479.

TRENT, T. T. AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *J. Wildl. Manage.,* **38**:459–472.

VAN DEELEN, T. R. 1991. Dispersal patterns of juvenile beavers in western Montana. Thesis, University of Montana, Missoula, Montana.

——— AND D. H. PLETSCHER. 1996. Dispersal characteristics of two year old beavers, *Castor canadensis*, in western Montana. *Can. Field Nat.,* **110**:318–321.

WEAVER, K. M. 1986. Dispersal patterns of subadult beavers in Mississippi as determined by implant radiotelemetry. M.S. Thesis, Mississippi State University, Starkville, Mississippi, USA.

SUBMITTED 10 MAY 2004 ACCEPTED 15 DECEMBER 2004