Dispersal Characteristics of Two-year-old Beavers, *Castor canadensis*, in Western Montana

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The movements of 22 two-year-old Beavers (*Castor canadensis*) were monitored in montane habitat using radio-telemetry. Twelve did not disperse. Dispersal distance, dispersal dates, and settlement dates of 10 dispersers varied. Disperser survival rate was 0.70. Wide variation in dispersal dates, and settlement dates, suggests the existence of a summertime sub-population of transient Beavers, unattached to traditional colonies.

Key Words: Beavers, *Castor canadensis*, Montana, dispersal.

Two-year-old Beavers disperse from natal colonies to establish new colonies, and to replace breeders lost to trapping or natural mortality (Bradt 1938; Svendsen 1980). However, not all two-year-olds disperse from their natal colonies. Observations of colony composition indicate delayed dispersal (Brooks et al. 1980; Peterson and Payne 1986) that might be related to high population density (Bergerud and Miller 1977; Payne 1982; 1984; Busher et al. 1983).

Dispersers generally leave natal colonies in late winter or early spring and live as a "floating" population of transients before settlement (Townsend 1953; Aleksiuk 1968; Svendsen 1980; Allred 1981). They typically move along waterways through occupied territory but are prevented from staying by resident Beavers (Townsend 1953; Aleksiuk 1968; Allred 1981; Hodgdon and Lancia 1983).

Nearly all of what is known about Beaver dispersal comes from mark-recapture studies, a technique limited by recapture success. Mark-recapture studies also provide little information on the timing of dispersal and settlement, or movement during the dispersal-settlement interval. We used radio-telemetry to describe the timing and movement characteristics associated with the dispersal of two-year-old Beavers in western Montana.

Study Area

Study areas consisted of four secondary drainages of the Clark Fork River in west-central Montana (approximate latitude 47° 00' N, approximate longitude 114° 30' W); Upper Willow and Meadow Creeks in Granite County, Rattlesnake Creek in Missoula County, and Fish Creek in Mineral County. Dominant bank vegetation in all areas consisted of willows (*Salix* spp.), alders (*Alnus* spp.), and Red Osier Dogwood (*Cornus stolonifera*). Surrounding uplands were montane conifer forests (Jackson 1991).

Mean annual precipitation was 40–80 cm/year and mean annual snowfall was 80–160 cm/year. Mean January temperature was -1.1–-17.8°C with 150–210 days/year when temperatures were below freezing (0°C, United States Department of the Interior Geological Survey 1970). In spite of the cold temperatures, these streams were free-flowing and relatively ice-free during the winters of 1989/90 and 1990/91. Springtime high water periods occurred between mid-April and late June (Van Deelen 1991).

Methods

Beavers were captured in Hancock live-traps (Hancock Trap Co., Custer, South Dakota) baited with fresh Cottonwood (*Populus trichocarpa*), aspen (*Populus* spp.), or willow twigs and a castor-based lure. In 1989 and 1990, trapping began the third week of March and continued through the first week of June.

We immobilized live-trapped Beavers with 150–200 mg of ketamine hydrochloride and 2.5 mg of acepromazine maleate to facilitate morphological measurement and sex determination (Jackson 1991). We assigned age-classes based on morphological development (Patric and Webb 1960; Payne 1979; Jackson 1991). Two-year-old Beavers were intraperitoneally implanted with radio-transmitters (Model IMP400, Telonics Inc., Mesa, Arizona.) using methods described by Jackson (1991). The next day, Beavers were released at the capture site. Radio-transmitters were configured for a minimum battery life of 24 months.

We located transmitter-equipped Beavers weekly in 1989 and every other day in 1990. The increased effort in 1990 was an attempt to refine the move-

ment data. We recorded locations for each Beaver from the time of their release in the spring until construction of a food cache and continued use of the same daytime resting site suggested that the Beaver had selected a site to spend the winter. Dispersal date was defined as the date of the last location in the natal colony. Settlement date was defined as the date of the first location in the subsequent over-wintering site. Beavers alive at the end of the field season were located the following spring to determine over-winter mortality. We located Beavers during daylight hours using signal strength to "home in on" daytime resting sites (White and Garrott 1990), and used fixed-wing aircraft to find Beavers which had moved extensively. Nocturnal or daytime movements that did not require radio-equipped Beavers to establish new resting sites were not considered.

For each record of telemetry locations, we used a plan measure (Alvin and Co., Inc., Windsor, Connecticut) to measure the shortest stream distance from release site to Beaver location (= daytime resting site). We recorded distances to the nearest 0.1 km.

Dispersers were defined as those Beavers that left their capture site (assumed to be within the natal colony's home range) without returning. In all cases, dispersals involved capture site to settlement site distances >2.2 km, the stream distance home range of Beavers in Manitoba (Novakowski 1965). Interpretations of dispersal movements were necessarily subjective. Ours were based on a knowledge of colony locations in the study areas and the assumption that subadult Beavers trapped in a colony were pre-dispersal members of that colony.

A two-tailed Wilcoxon Rank Sum test (Johnson and Bhattacharyya 1987) was used to test for sex-biased dispersal distance, and to test if the distributions of median, maximum upstream, and maximum downstream movements differed between 1989 and 1990. Simple linear regression (Sokal and Rohlf 1995) was used to determine if dispersal dates and dispersal-settlement interval lengths were related to dispersal distances. A G-test (Sokal and Rohlf 1995) was used to test if dispersal proabability was independent of sex. We used the KAPLAN computer program (copyright 1988, Missouri Department of Conservation, Columbia, Missouri) for survival analysis. It is based on Pollock et al.'s (1989) modification of the Kaplan-Meier estimator for the staggered entry of radio-marked animals. Samples from 1989 and 1990 were pooled for survival analysis because of small sample size. Survival was estimated from the Beavers' release in the spring until 6 April of the following year. The survival estimate is roughly equivalent to the life table statistic p_x (Caughley 1977).

Results

We radio-equipped eight Beavers in 1989 and 14 in 1990. There was no mortality due to the surgical procedures. The Beavers from 1989 were located 279 times and 46 movements > 2.5 km from the release site were detected. We obtained 1299 locations for the Beavers from 1990 and detected 468 movements > 2.5 km from the release site. The mean maximum upstream movement was 3.0 km (SD = 3.5, n = 8, range = 0.2– 5.5 km) in 1989 and 4.7 km (SD = 4.7, n = 14, range = 0.1 - 15.1 km) in 1990. The mean maximum downstream movement was 7.0 km (SD = 13.7, n = 8, range = 0.5 - 40.6 km) in 1989, and 4.7 km (SD = 5.0, n = 14, range = 0.1 - 15.7 km) in 1990. Average median movements were 2.1 km (SD = 2.1, n = 8, range = 0.2 - 5.9 km) in 1989, and 1.2 km (SD = 1.0, n = 14, range = 0.1 - 3.7 km) in 1990. There were no differences in the distributions of median movement distances (Z = - 0.61, P = 0.54), maximum upstream distances (Z = 1.00, P = 0.32), or maximum downstream distances (Z = 0.55, P = 0.58) for Beavers between 1989 and 1990. We saw no evidence of over-land travel.

Three of the Beavers from 1990 were probably captured outside of their natal colonies since they were captured and released at sites that were not near known active colonies. Two of these three had fresh puncture wounds on the hip and tail areas which are indicative of intra-specific fighting (Novak 1987). By contrast, none of the juvenile Beavers caught in active colonies had similar wounds. Movements for the Beavers caught outside of their natal colony were analyzed as if the capture/release site were the natal colony. One of these Beavers settled and was classified as a non-disperser. The other two continued moving and were classified as dispersers.

Four of the dispersing Beavers settled within 16 days. The remaining six dispersers settled between 35 and 181 days. Twelve Beavers (five in 1989, seven in 1990) did not disperse. Three of the non-dispersers and one of the dispersers made exploratory movements to resting sites > 2.5 km from their natal colonies and then returned.

Mean dispersal date (17 May) was highly variable (n = 10, SD = 44 days, range: 7 April - 20 August), as was mean settlement date (24 July, n = 10, SD = 86 days, range: 9 April - 12 November), and the length of the dispersal-settlement interval ($\bar{x}$ = 68 days, n = 10, S.D. = 69, range: 2– 181 days). Dispersal distance was highly variable ($\bar{x}$ = 7.7, n = 10, SD = 5.9 km, range = 2.9– 22.2 km), and not correlated with dispersal date (r = 0.29, P = 0.38), or the length of the dispersal-settlement interval (r = 0.16, P = 0.76).

The sex ratio of the 10 dispersing Beavers was 6 males : 3 females : 1 unknown. The probability of dispersal was independent of sex (G = 0.52, P = 0.47) as was dispersal distance (Z = 0.36, P = 0.64).

Of the eight Beavers from 1989, two (one disperser, and one non-disperser) died during the summer of unknown causes and one (a disperser) died during the winter of unknown causes. One (a non-disperser) was censored (censorships indicate loss of radio sig-

nals despite extensive aerial searches). The sample from 1990 had four mortalities and one censorship. Two (non-dispersers) were removed by a commercial trapper during the trapping season in 1990–1991, one (a non-disperser) was probably killed by a Black Bear (*Ursus americanus*), and one died (a disperser) during the winter of unknown causes. The estimated annual survival rate for the pooled samples of two-year-old Beavers was 0.67 (n = 22, SE = 0.11). For dispersers it was 0.70 (n = 10, SE = 0.14) and for non-dispersers it was 0.64 (n = 12, SE = 0.16).

Discussion

Dispersal by two-year-old Beavers generally coincides with the birth of the colony's kits, spring runoff, and high water (Svendsen 1980; Hodgdon and Lancia 1983). Dispersal dates were variable in Montana Beavers, and generally coincided with the 10 April - 29 June high water period in 1990 (Van Deelen 1991).

Idaho Beavers in montane habitat dispersed in both upstream and downstream directions (Leege 1968) as did Beavers in this study. Michigan Beavers dispersed over land (Bradt 1938). In the rugged terrain of the western Montana, Beavers are more restricted to travel along the stream courses (Allred 1981), although Leege (1968) reported that one Idaho Beaver crossed the divide between two adjacent drainages.

Dispersal distances in this study varied, but were comparable to the mean airline distance of 5.6 km reported for Idaho Beavers (Leege 1968). At least three non-dispersers and one disperser exhibited large (>2.5 km) exploratory movements away from the natal colony. Nocturnal locations might have enabled us to identify more explorations. These might provide potential dispersers with a method of assessing local colony density by encountering scent mounds (Aleksiuk 1968) and other Beavers (Aleksiuk 1968; Bergerud and Miller 1977; Allred 1981). High density might cause potential dispersers to delay dispersal or return to the natal colony permanently (Molini et al. 1980; Payne 1982).

Twelve of the 22 radio-equipped two-year-olds in this study did not disperse. This is consistent with frequent reports of non-breeding adults in Beaver colonies, and might indicate a high population density relative to the habitat's carrying capacity (Novakowski 1965; Gunson 1970; Payne 1982; Busher et al. 1983; Hodgdon and Lancia 1983). Alternatively, Svendsen (1980) reported 100% dispersal for two-year-old Beavers in a high density population that had no predators and was protected from trapping by being in a state park. We believed that Beaver densities in the study areas were relatively high during the course of the study because fur prices were low and trapping was light.

Late summer settlement and variation in settlement times among dispersers (this study) results in a summer sub-population of transient juvenile Beavers (Townsend 1953; Aleksiuk 1968; Molini et al. 1980) and is probably linked to pair formation. Svendson (1988) found that pair formation among dispersing Ohio Beavers occurred throughout year but peaked during September, October, and November as transients either paired with other transients that recently settled at suitable sites, or were incorporated into existing family groups where the same-sex adult was missing.

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