Territorial Behavior of Beaver in the Piedmont of South Carolina.

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Abstract: Territorial behavior of beaver (*Castor canadensis*) has not been well documented in the Southeast. Study of this behavioral mechanism may lead to methods which may aid in the control of nuisance beavers in economic and environmentally sensitive areas. Territorial behavior was evaluated for beaver in 4 study areas in the Piedmont of South Carolina by monitoring scent marking and movements of adjacent colonies. Scent marking was observed during January 1982 to June 1985 on 1 area with high ($\geq$ 0.8 beavers/ha) and 3 areas with low densities ($\leq$0.3/ha), of beaver. Beaver (N = 9) from 2 adjacent colonies were implanted intraperitoneally with radio transmitters and monitored from February 1983 through March 1984. Beaver on the high-density area built and maintained scent mounds from mid-September through mid-June. Beavers built new mounds from mid-September to late December. Scent mound relative visitation frequencies peaked at 55% per week during October and November, declined to 35% in December and 25% in January and February. Scent mounds were observed on only 1 of 3 low-density areas. These mounds appeared during October or November and were usually visited only when constructed. Interactions between 2 adjacent colonies were highest in fall and winter and were close to a common boundary delineated by scent mounds, indicating a scent-fence function. Higher levels of intra-colony interaction caused by competition for woody forage during fall and winter may be responsible for increased scent marking activities during this period.

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The North American beaver has been the subject of several scent marking investigations (Aleksiuk 1968; Hodgdon 1978; Svendsen 1978, 1980; Butler and Butler 1979, Bollinger 1980; Muller-Schwarze and Heckman 1980). Scent mounds consisting of mud, leaves, twigs, and other debris are usually located

on the edge of a body of water. Beaver deposit secretions from paired castor and anal glands onto the mound (Svendsen 1978), and may periodically return to add more debris and deposit more scent.

There are contrasting hypotheses as to the function of beaver scent mounds. Aleksiuk (1968) suggested that scent mounds served to maintain a territory and signal occupancy of the lodge. In Maine, Muller-Schwarze and Heckman (1980) reported that scent mounds exhibited a "scent-fence" function and were effective in deterring transient beaver from utilizing existing but uninhabited lodges. However, Svendsen (1980) reported that in Ohio, scent mounds did not conform to a "scent-fence" model, and that the main function was the effect on the motivational state of resident and non-resident beavers.

Studies using telemetric monitoring of beaver to describe beaver behavior are limited. Lancia (1979) used radio collars to monitor seasonal activity of beaver in Massachusetts. Busher (1975) monitored beaver movements in California for 4 months using tail-mounted radio transmitters. In the Southeast, transmitters were implanted intraperitoneally to monitor beaver activity, dispersal, home ranges, and habitat use in South Carolina (Boller 1991, Davis and Guynn 1993) and in Mississippi (Reinke 1986, Weaver 1986). However, information describing movements of beaver and their relation to territorial behavior are lacking.

The purpose of our paper is to describe the territorial behavior of beaver in the Piedmont of South Carolina. We attempted to prove: expression of territorial behavior in the form of scent marking is density dependent; scent marking is seasonal; scent marking is related to woody forage availability; and scent mounds exhibit a "scent-fence" function.

Methods

We conducted the study on the Clemson Experimental Forest in the western Piedmont of South Carolina during January 1982–June 1985. The area is characterized by slightly to moderately rolling hills with elevations up to 305 m above sea level (Natl. Oceanic and Atmos. Admin. 1974). Access by the general public was limited, and hunting and trapping were not allowed. Four study sites were selected based on beaver population densities. The high density area was located at Lake Issaqueena. Beaver impoundments along feeder streams were estimated to be >10 years of age (Edwards 1983). Capture of 41 beavers by live-traps and kill-traps (36 and 5, respectively) during September 1982–December 1983 and abundance of bank burrows, dams, and beaver signs indicated that the beaver population on this area was dense ($\geq$0.8/ha). Eight distinct habitat types occurred on this area: pine, upland hardwoods, tag alder, bottomland hardwoods, privet, pond lily, marsh, and kudzu (Davis and Guynn 1993). For comparison, 3 study sites with young beaver impoundments (<5 years old) and low beaver densities were located on streams that drained directly into Lake Hartwell. Access to these areas by the general public was limited, and trapping

was not allowed. Habitat types included: pine, mixed pine hardwoods, upland hardwoods, and bottomland hardwoods. The smaller number of dams, impoundments, and sign as well as the low number of beaver that we were able to live-trap ($N = 11$) on these 3 impoundments during September 1982–May 1983 indicated density of beaver populations was much lower ($\leq$0.3/ha) than on the Lake Issaqueena area.

Lake and stream banks of each study area were walked 2–3 times/week to locate new mounds and determine visitation of old mounds. Scent mounds were monitored by tying black sewing thread approximately 10 cm high onto 4 sticks surrounding each mound. Mounds were checked 1–3 times per week to determine if the string had been disturbed. If the string was disturbed, the mound was examined for fresh mud and debris and the smell of fresh castor. Monthly mound visitation frequencies by beavers were calculated as total number of scent mound visits divided by total number of mound-days, where mound days equal the total number of days each mound was checked. Monthly estimates of visitation frequency were calculated from the combined data over the 3-year period. Visitation frequencies were compared by month using goodness of fit tests.

We sampled use of woody vegetation by beaver at 2 ponds on the Lake Issaqueena area and 2 ponds on the Lake Hartwell area. Around each pond, 5-m wide transects perpendicular to the water's edge were located at 40-m intervals. The first line was randomly selected within 40 m of the dam. Number of transect lines varied between study sites, but relative area sampled was constant. We calculated density of stumps, trees, and saplings which were grouped according to species, distance from water (m), and stem diameter (cm). Importance to beaver of each species, distance, and size class were determined by computing a value index (VI) for each pond (Chabreck 1958). VI data by species and size class were reported by Edwards and Guynn (1984).

Two adjacent colonies on the Lake Issaqueena study area were monitored to determine level, frequency, and location of intra-colony interactions and to determine if a territorial boundary or fence between the 2 colonies existed. Beavers were live-captured in Bailey traps or snares and surgically implanted with radio-transmitters (Davis et al. 1984). Sex was determined by external palpation for an os penis or testes (Osborn 1955) and age classes (adults, subadults, yearlings, or kits) were determined by weights and body measurements (Patric and Webb 1960, Shipes 1979). All beavers were ear tagged, but only adults and subadults were implanted with radio-transmitters. Beavers were released at their capture site. Animal monitoring began no sooner than 8 days after surgery to allow recovery from the surgery. Subsequent examination of re-trapped beaver revealed little or no effect on health of beaver (Guynn et al. 1987).

Beavers were monitored 3–4 times/month and were located once/hour from the time they left the lodge in the evening until movements ceased soon after sunrise. Telemetry techniques used in this study were described by Davis and Guynn (1993). Movements, activity periods, and primary use areas for each

colony were determined and comparisons were made between the 2 colonies (Davis and Guynn 1993). Dams, impoundments, lodges, and scent mounds were located and mapped using aerial photographs and ground reconnaissance. Beavers occupying the same lodges were assumed to belong to the same colony.

We examined the hypothesis that scent marking by beavers was associated with territorial behavior. We drew a line from the approximate center of the largest concentration of scent mounds on the west side of the study area through the largest concentration of scent mounds located just south of the stream colony's lodge on the east side of the lake. A chi-square statistic indicated no difference in probabilities of each colony being located within the 50-m zones to the north or south of the arbitrary territorial line. Frequencies of colony locations were tested in this fashion on a monthly, bimonthly, and seasonal basis.

Results and Discussion

Scent Marking

Beaver on the Lake Issaqueena area (high density) built and maintained scent mounds for most of the year (Table 1). Scent mounds were small, usually about 0.37 m^2 at the base and $\leq$ 0.30 m high, and consisted of a pile of mud, leaves, and twigs on the bank. Mounds were generally <1 m from the water. Scent marking was not detected from mid-June through mid-September (Table 1): no new or refreshed mounds were observed and most mounds from the previous spring were covered with vegetation. Building new mounds began in mid-September in the same area as the old mounds, but usually not in the same location. New mound construction continued in November and December, but

Table 1. Visitation frequencies of scent-mounds by beavers in the Piedmont, South Carolina, 1982–1985.

Month	Mean *N* mounds	*N* mound-days[a]	*N* visits	Relative visitation frequency[b]
Aug	—	—	—	—
Sep	7	131	53	0.40a
Oct	17	176	98	0.55b
Nov	34	281	156	0.56b
Dec	40	417	148	0.35c
Jan	36	500	115	0.23d
Feb	37	492	122	0.25d
Mar	37	475	83	0.17e
Apr	37	471	62	0.13ef
May	37	430	40	0.09fg
Jun	37	403	23	0.06g
Jul	37	—	—	—

[a]Total number of mounds multiplied by number of days mounds were surveyed.

[b]Values followed by the same letter are not significantly different ($P \leq 0.05$).

was negligible after January 1. Number of mounds decreased during January because rains and flooding washed some away.

Visitation frequency on the Lake Issaqueena area increased dramatically from September to November (Table 1). Highest visitation frequency occurred during October and November. Visitation frequency declined significantly during winter and spring, and visitation essentially stopped by the end of June. Scent mounds were observed on only 1 of the 3 low population density sites. On this area, an occasional barely perceptible "mud pie" of debris was located. These mounds generally appeared during October or November and were usually visited only at the time of construction.

Peak scent marking activity by beaver in this study differed from beaver farther north. In Ohio, peak scent marking occurred during April–June (Fabel 1977, Svendsen 1980), declined after June, and remained low through October. In Massachusetts, scent marking was reported from mid-March through May with a peak in late April to June and low levels of scent marking occurring in October and November (Hodgdon 1978, Bollinger 1980). In Maine, scent marking occurred from March to November with peaks in early April to mid-May (Butler and Butler 1979) and from May to June (Muller-Schwarze and Heckman 1980). Peak scent marking occurred during July in Montana (Townsend 1953).

Regressions of a value index (VI) on distance interval (D) were significant for high-density areas ($VI = 130.09 - 8.44D + 0.139D^2$, $r^2 = 0.79$, $P = 0.0001$) and low-density areas ($VI = 435.04 - 42.62D + 1.05D^2$, $r^2 = 0.90$, $P = 0.0001$). The zone of influence extended farther from water on the high-density Lake Issaqueena area (35 m) than at the low-density Lake Hartwell area (27 m). This larger zone of influence compared to other studies (Shipes 1979, Woodward 1977) was most prevalent at the high density ponds and may be due to a shortage of food near the water. This evidence supports Shipe's (1979) suggestion that as a beaver pond ages, feeding moves farther from water.

Breeding activity and use of woody vegetation followed trends similar to monthly visitation frequencies observed on the Lake Issaqueena area. Typically, breeding activity for beavers in the Piedmont of South Carolina began in November (males) and December (females) and continued through March, with a peak during late December and early January (Woodward 1977). However, appearance of sexually active males and collections of pregnant females in June and September indicated an extended breeding season for some individuals in South Carolina. Lack of scent marking during these warmer months and lack of scent marking behavior on the 3 low-density sites during peak breeding periods suggests that scent marking is not solely a function of breeding activity.

Beavers in the Southeast use relatively little woody food during May–July, begin to increase use during August, show a great dependence on woody vegetation during October–January, and decrease use during February–April (Shipes et al. 1979, Roberts and Arner 1984). If scent marking by beaver is a function of the availability and use of woody foods, our data are consistent with the

conclusion of Muller-Schwarze and Heckman (1980) that scent marking increased with higher beaver density (and competition for desirable woody vegetation) and hence more social contact between beavers.

Movements

Nine beaver were monitored on the Issaqueena study area from 3 February 1983 until 26 March 1984 (Davis 1984). Five radio-marked beavers (2 adult females, 1 adult male, 1 female sub-adult, and 1 male sub-adult) shared lodges that occurred on Lake Issaqueena and were designated as the lake colony. Four radio-marked beavers (1 female adult, 2 female sub-adults, and 1 male sub-adult) shared lodges located on the banks of Six Mile Creek (a stream feeding into Lake Issaqueena) and were identified as the stream colony. Complete sex and age compositions for colonies on the study area were not determined. Two to 4 beavers were monitored each month from the lake colony and 1 to 4 beavers were monitored each month from the stream colony. Total locations for the entire 14-month period were 1,659 and 1,245 for the lake and stream colonies, respectively. Monitoring periods averaged 200 days/beaver. Movement patterns, activity periods, primary use areas (PUA's), and habitat use were determined for each colony (Davis and Guynn 1993). Differences in activities between sex and adult and sub-adult age classes were not compared due to the small sample sizes. We compared colonies assuming that there were no differences in movements or behavior within or between sex and age classes.

Because of the quality and distribution of forage, it appeared that the stream colony possessed the superior primary use area (PUA) and the lake colony had a lesser quality PUA especially for fall and winter months (Davis and Guynn 1993). This was less evident for summer when kudzu (*Pueraria lobata*) provided an abundant food source for lake colony beaver. As kudzu, aquatic emergents, and other herbaceous plants diminished in late fall, the PUA of the lake colony was more used and use of the secondary use area, which included the area containing kudzu, correspondingly declined. Even though there was some overlap of PUA's in all seasons, frequency of the lake colony locations within the overlapped area of the PUA's increased substantially during fall and winter (Table 2), as did size of the overlap area. Percentage of overlap peaked during November–December. These findings indicate that level of intra-colony encounters was highest during the fall and winter.

Shipes (1979) reported that beavers in the Upper Coastal Plain of South Carolina showed a great dependence on woody vegetation during October–January. This is consistent with movements of the lake colony during fall and winter. Also, because scent mounds were clumped within or near overlapped areas and because of the lack of scent mounds in other portions of the lake colony PUA including around the lodges of the lake colony, it seems likely that the primary causation of scent-mound construction was increased encounters of intra-colony beavers caused by availability of woody forage.

Two instances of intra-colony interaction which initiated scent-marking re-

Table 2. Frequency of locations within overlapped primary use areas and percentage of overlap area included in the primary use area for 2 beaver colonies monitored in the Piedmont, South Carolina (Apr 1983–Mar 1984).

	Lake colony		Stream colony	
Month/ year	Location frequency%	Area %	Location frequency	Area %
Apr/83	10	8.6	46	11.6
May/83	2	.5	35	0.4
Jun/83	7	0	38	0.0
Jul/83	5	3.2	39	4.3
Aug/83	6	5.1	31	5.3
Sep/83	6	1.1	24	1.2
Oct/83	11	8.5	20	8.0
Nov/83	19	13.9	25	18.4
Dec/83	13	8.8	37	6.8
Jan/84	14	2.8	27	3.4
Feb/84	9	4.0	30	5.4
Mar/84	12	2.8	26	2.4

sponses were observed on the Lake Issaqueena area. A beaver from the lake colony was captured November 1983 in a snare located within the boundary of the stream colony's primary use area. This beaver sustained several bites on the tail and rump and 4 new scent mounds were constructed within 7 m of the beaver. During February and March, 1983, beavers from 1 of the low-density areas were placed in pens located within the primary use area of the lake colony. A beaver from the lake colony was radio-tracked to these pens on 2 different nights and fresh scent mounds were constructed within 1 m of the holding pens on both occasions. Both instances show that beaver scent-marking was initiated by actual contact with an intruder and occurred when woody vegetation was the primary forage type. During April 1985, a beaver captured outside the study area was placed in a holding pen at this location for 5 nights. No scent mound activity or indications of strife with other beavers were observed and is probably indicative of an abundance of herbaceous vegetation available at this time of year. These occurrences add support to the theory that competition for woody forage (resulting in more intra-colony contact) may initiate scent marking in beaver.

In California, Busher (1975) detected no interaction between members of 2 adjacent stream colonies and described a 100–150 m stretch of stream between the colonies which beavers from both colonies avoided. A similar behavior was noted in this study. Beavers from the lake colony were more likely to be located in the southern than the northern half of the 100-meter band, whereas, the stream colony was more likely to occur in the northern than the southern half. The chi-square goodness of fit test for nonrandomness of colony locations within these areas yielded significant values ($P < 0.05$, df = 1) for all seasons,

Table 3. Chi-square values derived from tests for territorial behavior of 2 beaver colonies monitored in the Piedmont, South Carolina (Feb 1983–Mar 1984).

Month/ year	X^2	Bimonthly period	X^2	Season	X^2
Mar/83	3.59	Mar–Apr	6.94[a]		
Apr/83	5.58[a]			Spring	29.56[a]
May/83	8.57[a]	May–Jun	24.84[a]		
Jun/83	16.29[a]				
Jul/83	11.41[a]	Jul–Aug	31.78[a]	Summer	50.24[a]
Aug/83	18.08[a]				
Sep/83	19.71[a]	Sep–Oct	34.72[a]		
Oct/83	16.45[a]			Fall	53.98[a]
Nov/83	32.97[a]	Nov–Dec	39.30[a]		
Dec/83	6.99[a]				
Jan/84	18.08[a]	Jan–Feb	31.60[a]	Winter	11.56[a]
Feb/84	12.99[a]				
Mar/84	2.71				

[a] X^2 values significant at alpha = 0.05, df = 1.

all bimonthly periods, and all months except March 1983 and March 1984 (Table 3). These results suggest that beaver recognized a boundary between the 2 colonies and add support to the conclusions of Muller-Scharze and Heckman (1980) that scent mounds constitute a territorial fence.

Conclusions

Comparisons of beaver scent-marking on low density and high density areas indicated that scent marking by beavers is positively correlated with colony density. Scent marking was seasonal with peaks during fall and winter and was almost non-existent in summer. From these results we concluded that scent-marking was initiated in response to increased intra-colony interaction caused by availability of the competition for woody plant forages. On the high density area, Davis and Guynn (1993) describe the primary use areas of both colonies and concluded that the stream colony PUA was superior in that woody plants preferred by beaver on this area were more abundant within the stream colony PUA. During warmer months when kudzu and herbaceous forages were abundant, there was a marked decline in scent marking, frequency of interactions, and PUA overlaps. During colder months as woody forage replaced herbaceous forages, interactions between the 2 colonies increased with a corresponding increase in scent marking along the boundary of the 2 colonies. The 2 colonies respected a common boundary defined by the placement of scent mounds indicating scent marking by beaver constitutes a territorial fence function (Muller-Schwarze and Heckman 1980). Artificially scented mounds deter transient beaver from occupying specific sites (Muller-Schwarze and Heckman 1980, Welsh

and Muller-Schwarze 1989). Using this technique during fall may prove effective in keeping beaver from occupying sites where they may be a nuisance.

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