Beavers (Castor canadensis) live in family units and construct mud mounds marked with urine-based castoreum, at least in part as territorial advertisement. Marking varies in degree by season and in a density-dependent fashion among sites (families). I examined predictions of a territorial hypothesis for scent marking based on the ability of beavers to detect and discriminate scents and whether signs of intrusion stimulated mound building. Intruders could be adjacent adult territory holders (neighbors), more distant adults (nonneighbors), or offspring of either (juveniles). I determined the extent of investigatory responses and number of additional mounds built by beavers in response to beaver scent mounds (BSM) and to castor fluid from adult and juvenile males placed on human-made experimental scent mounds (ESM) in the field. Beavers distinguished scented from unscented mounds and discriminated among at least castor-fluid scents from family, neighbor, and nonneighbor adult males. Adult beavers exhibited the least interest in castor fluid from their own offspring. Beavers did not build more mounds in response to any treatment, but scented ESMs were over marked more often than family BSMs or blanks. Unless intrusion rates are very high, intrusion alone cannot explain differential scent mounding among sites. However, anticipated intrusion and site quality may establish initial mounding behavior that is modified by intrusion and subsequent over marking.

Key words: Castor canadensis, beaver, scent mark, territory, behavior, New York
Beavers alter riparian habitats to create a home site that is typically shared by a monogamous breeding pair and their offspring (1-2-year-olds, called juveniles, and young-of-the-year, called kits). All beavers except kits may deposit scent, but the adult pair, especially the male, is the primary marker (R. R. Buech, in litt.; Hodgdon, 1978; Svendsen, 1980).

Scent marking by beavers may serve several functions, but previous research supports a territorial function. Scent marks may send a signal to another family member that serves to orient a beaver maneuvering around the site at night (Müller-Schwarze and Heckman, 1980), synchronize sexual activity between adults (Houlihan, 1989), or bond the family unit (either through individual recognition or a colony odor—Butler and Butler, 1979). Scent marking occurs primarily in spring and early summer during peak dispersal (Svendsen, 1980). Abundance of scent marks varies with density of beaver sites but not with size or complexity of sites or with family size (Houlihan, 1989; Rosell and Nolet, 1997). Variations in the number of scent marks are not explained well by hypotheses that propose them to be primarily for communication among family members. They may announce territory ownership or availability of a potential mate. A beaver site occupied by an adult pair with offspring often contains a large number of scent mounds (Hodgdon, 1978; Houlihan, 1989; Nolet and Rosell, 1994; B. A. Schulte, in litt.), arguing against a mating signal as a primary function.

A territorial role for scent marking by beavers is supported by several lines of evidence: 1) colonization is lower at unoccupied sites marked with beaver scent compared to unmarked sites (Müller-Schwarze and Heckman, 1980; Welsh and Müller-Schwarze, 1989), 2) the greatest degree of scent marking is coincident with dispersal of young and increased movement of some adults (Rosell and Nolet, 1997; Svendsen, 1980; Townsend, 1953), and 3) the number of scent mounds constructed by a family of beavers is correlated positively with the number of beaver sites within 5 km of their site (Houlihan, 1989), proximity of nearest neighbors (Butler and Butler, 1979; Müller-Schwarze and Heckman, 1980; Svendsen, 1980), or density of beaver sites (Rosell and Nolet, 1997).

A territorial function suggests that certain behavioral patterns should be evident by territory holder and intruder (Gosling, 1982; Gorman, 1984). A resident individual should distinguish between scented and unscented mounds, marks from family and nonfamily members, and current versus old scents from family members. Although these predictions are not unique to the territorial hypothesis, their negation would be evidence against a territorial function.

In addition, if scent marks communicate primarily among families (not within), then the origin of the odor may affect the evoked response. Animals that display territorial behavior often exhibit lower aggression toward neighboring individuals compared to less familiar conspecifics (termed a "dear-enemy" response by Fisher, 1954; Ydenberg et al., 1988). Yet, the dear-enemy phenomenon is not observed in all territorial species (Temeles, 1994). The relative threat of neighbors and nonneighbors to a territory holder may determine the response evoked by an intruder. For instance, a neighboring adult beaver may be an established territory holder and signs of its intrusion may be perceived as not a threat. However, an intruding juvenile neighbor or an unfamiliar beaver (adult or juvenile) may represent a potential competitor for space, eliciting more extensive responses by the territory holder. A dear-enemy response would not be expected for any functional hypothesis other than a territorial one, although the absence of dear-enemy behavior does not negate the territorial hypothesis. Only the territorial hypothesis would suggest that beavers might distinguish among neighbors and nonneighbors or among juveniles and adults (nonfamily)
of the same sex as the responding beaver (e.g., a male resident responding differentially to scent marks from nonfamily males).

Assuming a territorial function for marking, intrusion is considered the primary proximate stimulus for mound building and marking (called the "intruder hypothesis" by Houlihan, 1989) and the reason mound numbers vary in a density-dependent fashion (Hodgdon, 1978; Rosell and Nolet, 1997). As density increases, rates of intrusion increase. Thus, a beaver should not only maintain a current odor field but build additional mounds in response to intrusion. Beavers may sniff, scratch, and over mark the odor of foreign beavers and occasionally build new scent mounds (Bollinger, 1980; Hodgdon, 1978; Houlihan, 1989; Rosell and Nolet, 1997). However, these studies were not designed to test the intruder hypothesis and suffer from small sample sizes (e.g., \( n = 2 \) sites; Hodgdon, 1978) or only indirectly examine the relationship between signs of intrusion and scent marking.

In this study, I examined predictions of the territorial hypothesis as a function for scent marking by beavers, including the possibility that beavers exhibit dear-enemy behavior (never previously explored). In addition, a proximate stimulus for marking was investigated by testing predictions of the intruder hypothesis. Working with a relatively large population of beavers (18 colonies), I used a single source of odors (i.e., castoreum) from living beavers of known age, sex, territorial status (e.g., resident adult of an established site), and proximity to other beaver sites to examine these hypotheses. Only castoreum was used rather than castoreum and fluid from anal glands because castoreum was thought to be a more likely source of territorial-odor signal (Schulte et al., 1994, 1995b), whereas fluid from anal glands may send a sex-related message (Schulte et al., 1995a). I used castor fluid from adult and juvenile male beavers only, primarily because only male fluid was obtained in adequate volume but also males are thought to be the primary markers and responders to marks. I observed responses to these scents by both family and nonfamily members (subdivided into neighboring families and nonneighboring families). Specifically, I tested the predictions that in response to unscented mounds and castoreum scents from different male beavers, resident beavers distinguished among scents, exhibited a dear-enemy response, overmarked foreign scents, and built new scent mounds.

**MATERIALS AND METHODS**

*Study area.*—I conducted the study from April to July 1991–1992 at Allegany State Park, Cattaraugus Co., New York, on an unharvested beaver population that had been live-trapped, ear-tagged, and observed since 1985 (D. Müller-Schwarze, pers. comm.). Beaver sites consisted of one to several small ponds located on streams. Each year, I observed 16 different beaver sites (18 total). Average (±1 SD) family size was 5.5 animals ±2.9. The use of the word "family" refers to beavers that occupied a common site over the course of a spring and summer in 1 year of the study. I assumed that adults were parents of juveniles and kits at the same site, but I did not genetically verify these relationships.

*Beaver sites.*—For a particular assay, a beaver site was classified as "family" if the castor fluid was collected there and assayed there, or as "nonfamily" if the castor fluid was collected elsewhere but assayed there. Nonfamily sites were subcategorized as neighbor (next site up- or downstream from the site of castor fluid collection), and nonneighbor (site distant from the site of castor fluid collection). The distance (±1 SD) between neighboring sites averaged 0.95 km ± 0.47 (\( n = 12 \)), measured from the lowest dam of the upper site to inflow into the highest pond of the lower site. Sites on the same stream always had regions of unoccupied stream between them. Nineteen of the 34 nonneighbor trials used castor fluid acquired at sites on different watersheds. Remaining trials used castor fluids collected from beavers whose sites were on the same watershed at an average (±1 SD) distance of 4.1 km ± 2.1 apart and in all but one case (sites separated by >3 km) had at least one intervening neighbor site. To avoid problems with pseudoreplication (Kroodsma, 1990), I only
used unique combinations of assay sites and castor fluid donor (the specific individual from whom I collected) within a single year. A beaver site had no more than two neighbors (one upstream and one downstream), so no site or castor fluid was used in more than two neighbor or nonneighbor trials. I used most sites in both years of the study, but each year was assumed to be independent because family composition changed annually. I only used castor fluid in the year that it was collected. Castor fluid from adult males was used for 12 family, 19 neighbor, and 22 nonneighbor trials, and castor fluid from juvenile males was used for 8 family, 12 neighbor, and 12 nonneighbor trials.

Collection of castor fluid.—Beavers trapped with Hancock Live-Traps were immobilized with a 1:2 mixture by volume of Rompun (xyloazine) and Ketaset (ketamine) (0.67 and 6.7 mg/kg body weight, respectively). Each beaver was assigned to an age class based on weight and size, its sex was determined, and it was ear-tagged (Schulte, 1993). To collect castor fluid from sedated beavers, I first evacuated the rectum and rinsed the cloaca with water. Next, I massaged the abdominal region by hand with a gentle rolling motion oriented downwards from the urinary bladder toward the cloaca and over the castor sacs. This action usually caused a release of urine-based castoreum that I collected in a wide-mouthed cup. The yellowish castor fluid was transferred to 7-dram glass vials, sealed with lids lined with Teflon, and stored frozen (within 2 h of collection) until used in field bioassays. Mean (± 1 SE) storage time for castor fluids was 52.7 days ± 2.16 before being used in an assay. This was necessary to create an old but not completely unfamiliar scent for assays at the same site of collection (family).

Logistically, it was necessary to complete trapping (5 April–8 May) before beginning behavioral studies (15 May–31 July).

Behavioral bioassays.—Behavioral bioassays were conducted from May to July each year. Trials were conducted after the peak period of natural scent mounding (April and early May) to provide a lower background level of daily mound construction. This would permit easier detection of increased mound building in response to intruder odors. Beavers are capable of marking throughout the year (Svendsen, 1980). Three field assistants were trained each year in all aspects of setup and data collection. In training trials using videotapes and field observations, assistants had at least 90% concordance with the primary investigator for all behaviors before conducting solo trials.

The observer presented 0.25 ml of castor fluid on the surface of a size-18 cork that was centered in an experimental scent mound (ESM; 30-cm diameter by 10-cm height). The volume applied was within the range for similar scents used in previous studies (Bollinger, 1980; Hodgdon, 1978; Schulte et al., 1994, 1995b; Svendsen and Huntsman, 1988). The mud for the ESM was scooped from the pond with a small container and held by gloved hand to avoid transmittal of human odor. To detect subtle disturbances to the ESM overnight, one-half of a tongue depressor was placed vertically into the mound (Svendsen, 1980) adjacent to the cork. The presence of the tongue depressor did not interfere with beavers inspecting or re-marking the mound, but displacement of the tongue depressor and footprints near the ESM indicated that a beaver had inspected the mound during the night. The ESM was placed upwind of the beaver lodge and ca. 50 cm from the edge of a bank where beavers were able to exit from the water.

Two controls (blank and dried castoreum) were used as potential minimum and maximum response elicitors, respectively, based on previous studies (Müller-Schwarze and Houlihan, 1991; Schulte et al., 1994). Use of blank ESMs (no scent added) permitted me to examine if the human-made mound itself was eliciting responses. Castor-sac material acquired from many beavers outside of the study population (i.e., with no history of contact) was purchased from Butcher’s Trapping Supply (Shushan, NY). I assumed that any potential individual identifiers would be lost or confused in this mixture of dried ground castoreum. In 1992, I also used fresh beaver scent mounds (BSM) as a treatment by placing a cork and applicator into an unmoved BSM (n = 6) or after relocating the BSM to the other side of the pond (n = 8). I did not move BSMs to other sites for reasons similar to those stated by Hodgdon (1978); primarily, I did not know who in the family marked the mounds and I could not find enough fresh mounds from different sites to relocate.

The ESM was built and the scent applied at ca. 1700 h, which was 0.5–1 h before the first beaver emerged. Observations began after build-
ing the ESM and ended with fading daylight (2000–2130 h). A continuous recording method (Altmann, 1974) was used for all animals in view, using a computer program created by P. Houlihan and modified by C. Sack for the Tandy 102 portable computer. This program automatically registered the time of each behavior. When one or more beavers approached the ESM, observations were focused on these individuals, and other beavers in the pond were ignored.

**Beaver mound censuses.**—To determine the number of mounds built by beavers following a trial, I censused beaver mounds at each site on the morning of the scheduled bioassay and the following day. In both years, I performed similar censuses with no treatment (termed “non-ESM” trials) at sites to determine a baseline number of mounds constructed overnight. I sniffed beaver mounds for beaver odor and placed a flag ca. 0.5 m behind the mound to facilitate relocation. I marked the position of the mound on a scaled site map. On the day following the bioassay, I checked all flagged mounds for beaver odor and signs of fresh activity. I recorded the position of any mounds constructed overnight on the site map and sniffed them for beaver odor. At least to the human nose, beavers build both scented and unscented mounds (Bollinger, 1980; Rosell and Nolet, 1997; Schulte, 1993). It is likely that unscented mounds are marked, but the odor is not discernible by humans (Schulte, 1993). Because the proportion of freshly constructed scented-to-unscented mounds was consistent across all treatments (ca. 1:1) and followed identical trends, I present only data on total mounds constructed (scented + unscented).

**Experimental design and statistical analyses.**—I defined a behavioral trial as a test using one ESM (or BSM) on 1 evening. I recorded whenever a beaver in the water oriented toward the ESM (<5 m) and noticeably raised its head in a sniffing motion. I counted number of sniffs and their duration. However, I focused my analysis on behaviors related to exiting the water and visiting the ESM. Specifically, I recorded the duration of the first land visit, calculated average duration of all land visits, and determined number of land visits per trial. Land visits began when a beaver exited the water near the ESM and ended when a beaver re-entered the water or walked away from the ESM (≥3 m). For analysis, I included only trials with land visits to compare duration (all nonzero values), but I used all trials to compare number of land visits. The proportion of trials in which responses were elicited also was examined. The odor source (beaver scent mound, blank, dried castoreum, adult or juvenile male castor fluid) and site type (family or nonfamily, where nonfamily can be separated into neighbor and nonneighbor) combinations were termed treatments.

In addition to evening observations, all ESMs and BSMs were checked the next morning for signs of visitation during the night and separated into three categories: 1) intact, 2) beaver prints or scratch marks, and 3) flattening or marking (fresh castoreum odor) of the mound by beavers. Marking was detected by removing the cork with the original scent and sniffing the experimental mound area within a 50-cm radius of its center.

I assumed independence of trials for statistical analysis. I examined my planned comparisons using analysis of variance (and specific contrasts) with Type III sum of squares because of unequal sample sizes (Neter et al., 1985). In cases when data did not fit assumptions of distribution and homogeneity of variance for parametric analysis, I used a nonparametric Kruskal-Wallis (H) or Mann-Whitney U-test (z), maintaining a 0.05 alpha level. Using contingency tables, I compared proportions of total trials in which observed responses (sniffing-from-the-water and land visits) and overnight visits were recorded. I used the Fisher Exact Test or computed the G-statistic, using William or Yates' correction factors as a conservative measure for testing the null hypothesis that the groups within a set did not differ (Sokal and Rohlf, 1995).

**Results.**

**Discrimination of odors.**—Beavers clearly detected applied odors on the ESMs. The proportion of trials with observed and overnight responses was higher to all treatment ESMs than to blank ESMs or BSMs (G-tests, \( P < 0.001 \), Table 1). The proportion of trials with observed (G-Yates = 2.2, \( P > 0.10 \)) or overnight (G-Yates = 2.4, \( P > 0.10 \)) responses to blank ESMs or BSMs did not differ. I never witnessed land visits to treatment BSMs.

Durations of first land visits were similar to blank ESMs and those treated with castor fluid from the adult male in the family (F
TABLE I.—Percentage of total trials (N) with observed and overnight responses by beavers to beaver scent mounds (BSMs) or experimental scent mounds (ESMs) marked with male castor fluid, dried castoreum, or blank. Observed responses were defined as “none” when beavers were present but did not appear to notice the odor stimulus, as “sniff from water” when a beaver oriented toward the odor stimulus (<5 m) and sniffed by raising its head, or as “land visit” when a beaver exited the water near the odor stimulus and investigated it. Overnight changes in the mound were defined as “intact” when during next day inspection there was no indication that a beaver had visited the odor stimulus, as “beaver footprints” when the only evidence was footprints or scratches on or around the odor stimulus, or as “flat/marked” when the ESM had been walked over or over marked by a beaver.

<table>
<thead>
<tr>
<th>Odor stimulus</th>
<th>N</th>
<th>Observed responses</th>
<th>Overnight change in mound</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>None</td>
<td>Sniff from water</td>
</tr>
<tr>
<td>Ad M Fam</td>
<td>12</td>
<td>33.3</td>
<td>25.0</td>
</tr>
<tr>
<td>Ad M Ngh</td>
<td>19</td>
<td>36.8</td>
<td>15.8</td>
</tr>
<tr>
<td>Ad M NonN</td>
<td>22</td>
<td>9.1</td>
<td>13.6</td>
</tr>
<tr>
<td>Juv M Fam</td>
<td>8</td>
<td>12.5</td>
<td>25.0</td>
</tr>
<tr>
<td>Juv M Ngh</td>
<td>12</td>
<td>9.1</td>
<td>25.0</td>
</tr>
<tr>
<td>Juv M NonN</td>
<td>12</td>
<td>33.3</td>
<td>8.3</td>
</tr>
<tr>
<td>DC</td>
<td>25</td>
<td>20.0</td>
<td>16.0</td>
</tr>
<tr>
<td>BL</td>
<td>28</td>
<td>67.9</td>
<td>21.4</td>
</tr>
<tr>
<td>BSMb,c</td>
<td>14</td>
<td>92.9</td>
<td>7.1</td>
</tr>
</tbody>
</table>

* Odor stimulus placed on ESM except for last row; abbreviations: Ad = adult; Juv = juvenile (1 or 2 year old); M = male; Castor fluid from: Fam = family site, Ngh = neighboring site, NonN = distant, nonneighboring site; DC = dried castoreum; BL = blank, no scent added.

The number of trials with responses to blank mounds and BSMs were significantly less than to the other odors for both observed (G-Williams = 51.2, d.f. = 8, P < 0.001) and overnight (G-Williams = 66.9, d.f. = 8, P < 0.001) responses. Rows 1–7 above formed nonsignificant subsets.

BSM trials were performed in 1992 only by using a fresh beaver scent mound, adding a cork and applicator, and leaving the mound unmoved (N = 6, one trial with beaver footprints) or moving the mound across the pond (N = 8, two trials with beaver footprints).

= 0.15, d.f. = 1,63, P = 0.70, Fig. 1a); however, the average durations of first land visits were greater to the remaining treatments than to blank ESMs (F = 4.66, d.f. = 1,63, P = 0.03, Fig. 1a). Number of land visits (n = 138) to the mound types differed (H = 32.37, d.f. = 7, P < 0.001, Fig. 1b). Beavers made a greater number of land visits to the scented ESMs than to the blank ESMs (z = 4.55, P < 0.001).

I investigated if beavers discriminated between family and nonfamily scents and between neighbor and nonneighbor scents from adult and juvenile males. The first land visit (n = 31) was longer to castor fluid from nonfamily than family adult males (H = 5.22, d.f. = 1, P = 0.02, Fig. 1a). A similar difference for this same comparison was not evident for the average duration of all land visits although the pattern of response was comparable (H = 3.05, d.f. = 1, P = 0.08). When castor fluid from adult males was used as a treatment (n = 53), beavers made about twice as many land visits per trial to nonneighbors (2.36 ± 0.42 SE) compared to family (1.0 ± 0.51) or neighbors (1.05 ± 0.34) (H = 7.2, d.f. = 2, P = 0.027, Fig. 1b).

Responses to the family and nonfamily juvenile castor fluid (n = 21) did not differ for durations of first land visits (H = 0.3, d.f. = 1, P = 0.56, Fig. 1a), or for the average duration of all land visits (H = 0.90, d.f. = 1, P = 0.34). Neither did the number of land visits (n = 32) to juvenile scents differ among family, neighbors and nonneighbors (H = 0.32, d.f. = 2, P = 0.85, Fig. 1b).
Fig. 1.—a) Mean duration of first land visits, and b) mean number of land visits per trial by beavers to experimental scent mounds (ESMs) treated with castor fluid of adult and juvenile males at family (Fam) or nonfamily (i.e., neighbor = Ngh and nonneighbor = NonN) sites; controls were dried castoreum (DC) and blank mounds (BL).

Durations of first land visits to ESMs with dried castor sac material \((n = 16)\) were most similar to those with castor fluids of nonfamily adult males, and they were longer than the three observed land visits to the blank ESMs \((z = 2.35, P = 0.02)\). Durations of first land visits to blank mounds resembled responses to castor fluid of family adult males (Fig. 1a). Number of land visits also differed among the controls (dried castoreum \((n = 25)\) versus blank \((n = 28)\), \(z = 3.67, P = 0.0002\)) with blank mounds visited at most once per trial \((n = 3, \text{Table 1})\).

To examine for loss of potency while frozen, I checked for variation in the duration
TABLE 2.—Responses to castor fluids of adult and juvenile males expressed as percentage of trials with observed land visits in which adult or juvenile beavers responded; the responses in a trial were not mutually exclusive so the percentages for the sexes do not sum to the value for the age class with the sexes combined.

<table>
<thead>
<tr>
<th>Responding beaver*</th>
<th>Castor fluid of adult male</th>
<th>Castor fluid of juvenile male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Family Neighbor Nonneighbor</td>
<td>Family Neighbor Nonneighbor</td>
</tr>
<tr>
<td>Adult</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>100</td>
<td>77.8</td>
</tr>
<tr>
<td>Female</td>
<td>40</td>
<td>66.7</td>
</tr>
<tr>
<td>Juvenile</td>
<td>20.0</td>
<td>44.4</td>
</tr>
<tr>
<td>Male</td>
<td>20</td>
<td>33.3</td>
</tr>
<tr>
<td>Female</td>
<td>0</td>
<td>33.3</td>
</tr>
<tr>
<td>Unknown</td>
<td>20</td>
<td>0</td>
</tr>
</tbody>
</table>

* Sample size for total number of observed land visits was determined from Table 1 by multiplying N by percent of observed land visits (e.g., castor fluid from family adult male had five total observed land visits = 12 x 0.417).

that castor fluid had been stored and for differences in number or identity of beavers responding. The treatments did not differ by the duration of storage of the adult or juvenile castor fluid (F = 1.47, d.f. = 5, 79, P = 0.21) or the average (±1 SE) number of beavers observed per trial (4.4 ± 0.21, F = 0.56, d.f. = 8, 143, P = 0.81).

Identity of the beaver responding to castor fluids differed for trials with observed land visits (Table 2). Overall, adults responded in a significantly greater proportion of these trials than juveniles (sexes combined) (G-Yates = 11.98, P = 0.0005). Yet, this result varied depending on the source of the castor fluid. Adults visited castor fluid from family juvenile males less often than the other castor fluids (one-tailed Fisher Exact Test, P = 0.04). In contrast, the trend, although nonsignificant, was for juvenile beavers to respond more often to castor fluid from family juvenile males than to the other scents (one-tailed Fisher Exact Test, P = 0.13). Juveniles visited their own (two trials) or their siblings’ (two trials) castor fluid in four of the five trials (80%) with land visits, but castor fluid from the adult male (their presumed father) in only one of five trials (20%). Visits by juveniles to other scents were relatively low compared to adults (sexes combined). Juveniles visited castor fluid from nonfamily juvenile males in only five of 16 trials (31.25%), whereas adults visited in 14 of 16 trials (87.5%). Juveniles visited scents from nonfamily adult males in 14 of 26 trials (53.8%), yet adults made visits in 21 of 26 trials (80.8%).

If adult males are the primary markers of mounds, then they appear capable of distinguishing their old from their more recent scents. Beavers were never observed to make land visits to the BSMs in 1992 (n = 14, Table 1); however, adult males responded to their own castor fluid in all five trials with land visits (n = 12, Table 2).

Beaver scent mounds also might send a mating-related signal. If so, responses to the castor fluid of a nonfamily male might differ between sexes of a resident pair, but this was not evident (Table 2). For trials with land visits to castor fluid from nonfamily males, female beavers made equal proportions of visits to males (G-Yates = 0.02, P = 0.89). Adult females made land visits in 14 of 26 trials (53.8%) to castor fluid from nonfamily adult males and nine of 16 (56.25%) to nonfamily juvenile males. Adult males made land visits in 16 of 26 trials (61.5%) and 11 of 16 trials (68.75%), respectively. No differences were apparent between juvenile female and male responders either (G-Yates = 0.25, P = 0.61). Juvenile females made land visits to castor
FIG. 2.—Mean number of a) beaver mounds built or manipulated, and b) mounds including the experimental scent mounds (ESM) if remarked, following trials with castor fluid from adult or juvenile males at family and nonfamily (neighbor, nonneighbor) sites, or trials with controls (legend of Fig. 1 defines acronyms).

fluid from nonfamily adult males in nine of 26 trials (34.6%) and nonfamily juvenile males in three of 16 trials (18.75%). Juvenile males made land visits in eight of 26 trials (30.8%) and one of 16 trials (6.25%), respectively.

Mound building.—The total number of mounds built did not differ among treatments, including the additional control sites at which I counted the mounds built overnight following no treatment \((H = 6.92, d.f. = 9, P = 0.64, n = 214, \text{Fig. 2a})\). Beavers built fresh mounds and marked established (beaver-built) mounds in <50% of the trials for any source or age of castor fluid or even for blank and non-ESM trials. However, when a marked ESM was included as a new mound, a difference was evident among the treatments \((H = 30.9, d.f. = 9, P = 0.0003, n = 214, \text{Fig. 2b})\). Average number of
mounds built or marked was greater after nights with scented ESMs (castor fluid from adult and juvenile males plus dried castoreum, \( n = 110 \)) than with the blank, BSM, or no treatment controls (shown in positions 1-3 in Fig. 2b, \( n = 104 \)) (\( z = 4.28, P < 0.001 \)). However, there were no differences in the number of mounds built in response to different sources of castor scent (\( H = 5.62, d.f. = 6, P = 0.47, n = 110 \)). Furthermore, the average number of new mounds was only about one (Fig. 2b), regardless of the treatment.

Flattening or over marking of the scented ESMs happened more often (44.5%, \( n = 110 \), Table 1) than remarking of beaver-made family mounds. I counted 435 scented mounds and 3,290 total mounds at 45 sites in the 2 years of the study. Only 2.8% of the scented mounds were remarked overnight, and only 2.0% of the total mounds were modified by marking or the addition of fresh mud overnight. The 14 BSMs used as treatments in this study were never remarked overnight (Table 1).

**DISCUSSION**

A territorial function for scent marking was supported by my results, but castoreum odor of nonfamily males was not an adequate proximate stimulus for mound building. Beavers responded to the beaver scent on the mound and not to the unscented mound itself, and they distinguished their current scent from their own older scent. Beavers regularly remarked castor fluid from the family male, although this occurred after sunset in some trials. Chemical composition of castor fluid may change over time, as is known to occur for scent marks in other species (Johnston and Schmidt, 1979; Wellington et al., 1983). Updating their old scent creates a sign post with a current olfactory signature.

Beavers behaved differently to the three sources of castor fluid from adult males. Beavers spent less time investigating scent from the resident adult male than they did neighboring or nonneighboring adult males (Fig. 1a). This indicated that beavers could identify, either through specific individual cues or through a scent-matching memory (Gosling, 1982, 1985), the resident male more readily than nonfamily males. Scent of nonfamily males in resident territory would be of concern for territory holders. Beavers visited the castor fluid from nonneighbor adult males nearly twice as often as the scents from family and neighboring adult males (Table 1). Such behavior is suggestive of a dear-enemy effect in which completely unfamiliar individuals are the greatest threat. No other data supported a dear-enemy treatment of neighboring territory holders by resident beavers and further work is needed to clarify this issue.

I expected that responses to castor fluid from family and nonfamily juvenile males also would be distinct. The intruder hypothesis for scent mounding proposes that high scent-mound numbers in the spring months are related directly to dispersal of young beavers and relocation of some adults. Typically, beavers disperse as 2-year-olds in the spring (Svendsen, 1980). However, my results showed that duration and number of land visits did not differ among the juvenile scents (Fig. 1). Yet, identities of responding beavers changed in response to family or nonfamily juvenile scent (Table 2). Resident adults were twice as likely to visit castor fluid from nonfamily than family juvenile males. Juvenile beavers also may distinguish scents, perhaps being especially curious about their own scent or that from a sibling on a mound. In general, juveniles were not highly responsive to the castor scents. Adults are the territory holders and defenders and primary scent markers (Hodgdon and Lancia, 1983). It seems apparent that they can differentiate their own scent and those of their male offspring and respond accordingly.

Contrary to the prediction of the intruder hypothesis, a family-nonfamily effect was not evident for mound building. The dried castoreum on controls was used in part to eliminate individual identifier cues that
might affect responsiveness (e.g., if individuals were recognized and considered not a threat). However, even the generalized castoreum odor did not evoke significant levels of mound building.

Scented foreign mounds were regularly over marked. When these over marks were included in the analysis of new mounds, a significant increase in marking was evident compared to controls. Beavers are known to build >100 mounds in early spring (Hodgdon and Lancia, 1983; Houlihan, 1989; Rosell and Nolet, 1997; Schulte, 1993; Svendsen, 1980). Rosell and Nolet (1997) reported two instances in which a resident adult male over marked a scent mound made by an intruder. Still, the relationship (if any) between the extent of intrusion and the number of new mounds constructed is not understood. My results indicated that scent of male intruders did not initiate additional scent marking by resident beavers beyond over marking of the foreign scent.

Scent marking by beavers may be stimulated by direct interactions with other beavers in “neutral” areas or by indirect cues related to resource quality. These factors could be correlated positively to proximity or number of neighbors. For instance, extent of settlement by beavers (e.g., number of colonies) on a stream may be directly related to food availability and quality. Nolet and Rosell (1994) reported that the degree of scent mounding by the European beaver was related not only to population density but also quality of the territory. These two factors were correlated positively. They defined quality by age of the site (investment by beavers) and food resource (type, availability). C. fiber settled initially in the richest food areas, but site density increased steadily over time in these regions of the stream. Unfortunately, Nolet and Rosell (1994) did not have scent mound data over the period of colonization but only at the endpoint when density of sites was high (E. Rosell, pers. comm.).

Such data are critical to determine the mechanism that stimulates marking. For example, if intrusion stimulates marking, the number of scent marks per site should increase as a region becomes more colonized. However, if some assessment of site quality promotes marking, scent marking may decrease as food resources become depleted, increase as investment in the site increases, or change in either direction (or not at all) if these two factors interact in some manner. Even if intrusion does stimulate scent marking regularly, the amount is likely to be modulated by energetic considerations and possibly a past history of intrusions at the site. For instance, degree of scent marking by male coypus (Myocastor coypus) in autumn was correlated to the increase in competing males during the previous season and to frequency of fighting scars (Gosling and Wright, 1994). Beavers are known to take early spring forays (R. Lancia, pers. comm., and B. A. Schulte, in litt.) that may provide them with information on both resource richness and proximity of conspecifics. Beavers may over mark all signs of intruders but build mounds in proportion to the quality of their habitat and the anticipated extent of intrusion.

ACKNOWLEDGMENTS

Special thanks go to D. Müller-Schwarze for his support and guidance throughout this research and State University of New York—College of Environmental Science and Forestry for the field camp at Allegany State Park. Thanks to L. L. Wolf, J. A. Randall, L. E. L. Rasmussen, R. E. Johnston, F. X. Webster, S. V. Stehman, L. C. Drickamer, R. A. Lancia, and an anonymous reviewer for comments on earlier drafts, the management and staff of Allegany State Park, and the numerous field assistants. Animals were handled using procedures approved by the Humane Use of Animals Committee at the State University of New York. Support for this research was provided by National Science Foundation Grant No. BNS-8819981 to D. Müller-Schwarze and F. X. Webster, and a grant to the author from the Theodore Roosevelt Fund.

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Submitted 16 August 1996. Accepted 4 March 1997. Associate Editor was Robert K. Rose.