

SEXUAL DIMORPHISM IN THE DEVELOPMENT OF SCENT STRUCTURES FOR THE OBLIGATE MONOGAMOUS EURASIAN BEAVER (*CASTOR FIBER*)

FRANK ROSELL AND BRUCE A. SCHULTE*

Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, N-3800 Bø in Telemark, Norway (FR)

Department of Biology, Box 8042, Georgia Southern University, Statesboro, GA 30460, USA (BAS)

Scent marking is a common form of territorial demarcation in mammals and differential marking by the sexes may select for differences in scent gland developmental rates or size. Rates of marking reflect level of defense and so behavioral dimorphism in marking by the sexes may select for dimorphism in scent structures. Eurasian beavers (*Castor fiber*) are monogamous, territorial mammals that show some behavioral dimorphism in territoriality. Beavers have 2 primary scent structures, anal glands and castor sacs. Anal gland secretion appears to serve as a family or individual identifier. Castor fluid is the main source of chemical signals used for marking territories. We examined beavers collected from 3 different habitats, namely streams, creeks and tarns (small lakes), which varied in the density of beaver sites. The objectives of this study were to examine if morphological attributes of Eurasian beaver scent structures reflected differences in adult beaver territorial function or in the ontogeny of the sexes. We hypothesized that male beavers would have larger castor sacs and anal glands, and that beavers from sites of greater density, and thus greater rates of intrusion, would have larger castor sacs and anal glands. Our results showed that investment did not differ by habitat type. Although the combined weight of the scent structures did not differ between the sexes, males developed significantly larger anal glands but somewhat smaller castor sacs than females. Total investment to scent structures may be limited but allocation is flexible. Males patrol the territory more extensively and may benefit by releasing anal gland secretion to signal their identity to potential intruders. Higher rates of marking may decrease castor sac size by reducing the amount of stored scent material. Hence, even in monogamous mammals, sexual dimorphism can arise from behavioral dimorphism.

Key words: Castoridae, chemical ecology, ontogeny, scent marking, territory

Monogamous mammals show reduced or no apparent sexual dimorphism relative to polygamous species (Kleiman 1977; Ralls 1977). Both sexes of monogamous pairs provide parental investment (Trivers 1972), and contribute to territorial defense (Clutton-Brock 1989). However, males and females may demonstrate different activity patterns and play different roles. Minimally, female mammals nurture the young during lactation, whereas males purportedly perform other tasks more frequently, such as territory maintenance and defense. Scent marking is a common form of territory demarcation and announcement of status in mammals (Ralls 1971). Sexual selection may shape such olfactory communication (Blaustein 1981; Darwin 1871), resulting in differential investment in scent structures and their products between the sexes (Heymann 1998; Jannett 1986).

Genetic variation in the sexes could account for differences in developmental rates and size of scent structures. Environmental components also could be important. In general, habitat quality influences developmental rates, adult size, and susceptibility to disease of animals (Dixon and Kundu 1998; Judson and McFarlane 1998) in the classic sense of allocation and life history trade-offs (Cody 1966; Stearns 1976). Hence, it is plausible to hypothesize that variation in nutrition among the sexes could influence investment in secondary characteristics such as scent structures. In addition, behavioral factors could influence marking rates and resultant investment in scent structures and chemical signal production (Collins et al. 2001). For example, if one sex ranged further than the other, the former may encounter more intruders or unmarked regions and respond by marking at higher rates. Selection could then favor individuals of this sex with relatively larger or more active scent structures.

Eurasian (*Castor fiber*) and North American (*C. canadensis*) beavers are obligate monogamous mammals and are relatively long lived; they pair bond for multiple years to life and exhibit little external morphological sexual dimorphism (Novak 1987;

* Correspondent: bschulte@georgiasouthern.edu

Svendsen 1989; Wilsson 1971). Beavers use extensive scent marking to demarcate and maintain territories (Aleksiuk 1968; Rosell 2002a; Schulte 1993; Wilsson 1971). The number of scent marks is density dependent. Beavers with many close neighbors (highly challenged) scent mark more often to be unambiguously recognized as territory owners. Beavers living in higher densities may reside in higher-quality habitat and incur greater rates of intrusions, stimulating increased marking (Rosell and Nolet 1997). Some behavioral differences in adult males and females have been observed, especially during spring and summer when young are reared (Buech 1995; Hodgdon and Larson 1973; Schulte and Müller-Schwarze 1999; Wheatley 1997; Wilsson 1972). Two recent studies on mated male and female Eurasian beavers suggest that males have significantly larger kernel home ranges (Herr and Rosell 2004) and that males allocate significantly more time to travel (Sharpe and Rosell 2003). Male Eurasian beavers also perform more scent marking and hence territorial maintenance than do female beavers (Thomsen 2002). As yearlings, female North American beavers act more like adults, whereas males behave more like kits (Busher and Jenkins 1985), although this may not be the case for scent-marking behavior (Hodgdon 1978). Maturation rate may affect morphological characteristics related to behavioral activities such as marking.

Beavers have 2 primary scent structures, anal glands and castor sacs (Rosell et al. 1998; Svendsen 1978). These are located in 2 cavities between the pelvis and base of the tail (Valeur 1988; Walro and Svendsen 1982). The anal gland is a holocrine secretory gland, but the castor sac is only a pocket lined with a layer of nonsecretory epithelium. They both open into the urogenital pouch (cloaca—Svendsen 1978). The castor sac is used to store what is believed to be a mixture of secondary metabolites from urine, collectively called castoreum (Walro and Svendsen 1982). The generic name, *Castor*, refers to this pair of castor sacs, which are unique to members of this genus. Copious amounts of castoreum deposited on scent mounds result from a process not dissimilar to urination except that urine flushes through the contents of the castor sacs. This material can be deposited on the scent mound without the animal contacting the substrate with the cloacal region. Scent mounds are small piles of mud and debris placed by beavers near the water's edge. However, anal gland papillae must be rubbed on the substratum in order to deposit anal gland exudates (Svendsen 1978; Wilsson 1971). Composition of anal gland secretions is characteristic to each sex for beavers (Rosell and Sun 1999; Schulte et al. 1995), but no sexual dimorphism in appearance is known for castor sacs. The function of anal gland secretion is unclear. The secretion is not a prominent part of scent marks, at least not during winter (Rosell and Sundsdal 2001), although placement of anal gland secretion from strange beavers on experimental scent marks evokes significant investigation by resident beavers (Rosell and Bjørkøyli 2002). Although beavers groom extensively and appear to rub anal gland secretion into their coat, the chemicals are not found regularly in the pelage (Rosell 2002b). The secretion may serve as an individual or family identifier and may be released into the water (Grønneberg and Lie 1984; Rosell

2002b; Sun and Müller-Schwarze 1998). Castor sac fluid is deposited on the shoreline of a beaver site, especially at the territory boundaries (Rosell et al. 1998), and appears to be the main source of territorial chemical signals (Rosell and Sundsdal 2001; Rosell et al. 1998; Schulte 1998).

The objectives of this study were to examine if morphological attributes of Eurasian beaver scent structures reflected differences in adult beaver territorial function or in the ontogeny of the sexes. We hypothesized that investment in castor sacs would vary between the sexes throughout development and with the density of sites. Two opposing predictions could follow. First, castor sacs would be larger in animals likely to scent mark at higher rates such as males and individuals in high-density areas. Alternatively, castor sacs could show reduced weights because high flushing rates are likely to release and thus reduce material in the sacs, lowering the weight. Because the function of the anal gland and its secretion is not clear, a directional prediction on the relationship of gland size with age and sex is more difficult. If anal gland secretion serves as an identifier of the individual, then size may be correlated with degree of marking. Anal glands are true glands, so benefits of greater use could select for increased investment over evolutionary and possibly ecological and developmental time scales.

MATERIALS AND METHODS

Study site and animals.—Eurasian beavers from 59 sites were caught in lethal traps (Conibear no. 330, Woodstream Corp., Litzitz, Pennsylvania) or shot with a rifle in Bø and Nome municipalities (59°25'N, 9°3'E), Telemark County, southeastern Norway, during the normal hunting and trapping season of 1 October–30 April 1996–1997, 1997–1998, and 1999–2000 ($n = 119$). Additional beavers were collected during a 15-day extension from 1 to 15 May during 1997–1999 ($n = 32$). The Norwegian Directorate for Nature Management and the respective landowners granted permission to hunt beavers beyond the normal hunting season. The Norwegian Directorate for Nature Management approved the hunting process, and we adhered to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

We delineated 3 seasons as autumn (October), winter (December to March), and spring (April and May). A majority of the beavers (86%) from which a full data set was acquired were captured in the spring. Shortly after death, carcasses were brought to the laboratory where castor sacs and anal glands were dissected and excess tissue was removed. Both left and right sacs and glands were weighed (to the nearest 0.1 g) and measured by a slide caliper (length and width at the middle, to nearest 1.0 mm). Precautions were taken to minimize fluid loss from the sacs and glands. Age, sex, body weight (nearest 0.1 kg), habitat, and date of collection also were recorded for each beaver. Beavers were sexed by color of the anal gland secretion (Rosell and Sun 1999) and by absence or presence of the os penis (Osborn 1955).

Beavers are generally classified into 3 age classes (Hartman 1992; Rosell and Pedersen 1999): 1 year old (<12 months, 0–10 kg), 2 years old (12–24 months, 10–15 kg), and adult (≥ 24 months, ≥ 15 kg). Because weights only provide approximate age classes, we used a more specific method of aging to separate developmental periods. For most of the beaver specimens ($n = 124$), we examined tooth root closure and annual cementum and dentine layers of the 2nd molar (van Nostrand and Stephenson 1964). We used these 124 beavers for the statistical analyses involving different age classes. At age 3 years, beavers are 1st entering adulthood, so we considered this age as part of

the early developmental process. For comparisons to the traditional adult age class delineated by using weights only, we also considered 3-year-old animals as adults but only for separate analyses. Final sample sizes for each age group were as follows: 1 year old (11 females, 7 males), 2 years old (9 females, 18 males), 3 years old (9 females, 8 males), and >3 years old (28 females, 34 males). For analyses of adult age classes (>2 years old), we included 9 additional beavers (5 females, 4 males) not aged by their teeth but clearly adults.

Beavers were collected from 3 different habitats (tarns, rivers [>10 m wide], and creeks [<10 m wide]) that differed in the density of beaver sites. Territorial boundaries were determined based on location of scent mound concentrations (Rosell and Nolet 1997; Rosell et al. 1998), and/or from regular sight observations of animals moving up- and downstream of the lodge (Rosell et al. 1998). Number of neighbors (referred to as site density) was calculated as number of territories located together, that is, bordering on each other with no unoccupied stretch of stream area separating them.

Data compilation and analysis.—Weights of left and right anal glands or castor sacs were summed to give a total scent structure weight for each type gland. Length and width were multiplied to give area and then added (left and right anal gland or castor sac) to give a total area. The correlation between weight and area was determined. Because weight was a more reliable and meaningful measure than area, we limited most analyses to weight. All means are presented as mean \pm SE. Analysis of variance was performed by using Statistica software (StatSoft, Inc. 1999). Logarithm of weight was used in analyses to normalize the data. Log of body weight was used as a covariate so that differences in scent structure size could not be accounted for simply by differences in body weight. A test of parallelism was used to examine if the slopes of linear regression lines differed.

RESULTS

Seasonal differences.—No significant differences were found in scent structure weights by season ($P > 0.15$ for anal gland and castor sac). Because of insignificant results and small sample sizes in autumn ($n = 5$) and winter ($n = 12$) compared to spring ($n = 107$), the data sets were combined across season.

Habitat differences.—The number of beaver sites with neighbors differed among the 3 habitats (rivers, tarns, and creeks; $F = 13.97$, $d.f. = 2$, 46 , $P < 0.001$), with an average of 1.2 ± 0.16 neighbors per site in the river habitat, 0.4 ± 0.13 neighbors in the tarn, and 0.2 ± 0.11 neighbors in the creek habitat. However, size of scent-producing structures did not differ significantly by habitat for adult beavers of either sex ($n = 79$, age 3 years and greater). This was true for area of the anal gland ($F = 1.72$, $d.f. = 2$, 72 , $P = 0.19$), weight of the anal gland ($F = 1.34$, $d.f. = 2$, 72 , $P = 0.27$), area of the castor sac ($F = 1.02$, $d.f. = 2$, 74 , $P = 0.36$), and weight of the castor sac ($F = 1.88$, $d.f. = 2$, 74 , $P = 0.16$). We made planned comparisons by combining tarns and creeks, which iced over in winter, whereas rivers in our study did not. However, no significant differences were evident (all $P > 0.08$). The weight and area for each scent structure were highly and significantly correlated (anal gland: $r^2 = 0.54$, $n = 78$, $P < 0.001$; castor sac: $r^2 = 0.48$, $n = 81$, $P < 0.001$). To check that beavers from the same site were not overrepresented (and thus to avoid pseudoreplication), we repeated analyses with only 1 adult beaver from each site (5–12 of each sex per habitat type). For the 3 site types (river, creeks, and tarns), no difference in

weight of the anal gland ($F = 0.20$, $d.f. = 2$, 41 , $P = 0.82$) or castor sac ($F = 1.57$, $d.f. = 2$, 41 , $P = 0.22$) by site type was apparent. Age of adult beavers at the 3 sites ($n = 11$ – 17) also did not differ ($F = 1.54$, $d.f. = 2$, 37 , $P = 0.23$); age averaged 6.2 ± 0.79 years at river sites, 5.0 ± 0.54 years at tarns, and 7.3 ± 1.17 years at creeks.

Ontogeny of the scent structures.—Beavers showed a typical growth curve, with no statistical difference in mean weight between males and females across all ages ($F = 2.14$, $d.f. = 1$, 121 , $P = 0.15$), although rate of growth differed (test of parallelism: $F = 15.3$, $d.f. = 1$, 120 , $P < 0.001$; Fig. 1a). The weight of the scent-producing structures (anal gland plus castor sac) showed a similar pattern of no significant difference between sexes, but a difference in weight change with age ($F = 0.46$, $d.f. = 1$, 121 , $P = 0.5$; test of parallelism: $F = 5.1$, $d.f. = 1$, 120 , $P = 0.025$; Fig. 1b).

Male and female beavers showed differential investment in the 2 scent-producing structures. Males exhibited a significantly greater investment than females in anal gland weight relative to body weight ($F = 57.8$, $d.f. = 1$, 117 , $P < 0.0001$; test of parallelism: $F = 30.2$, $d.f. = 1$, 116 , $P < 0.0001$; Fig. 2a). Castor sacs of females were generally larger than those of males but differences were not significant (Fig. 2b). Early developmental differences were apparent in the growth of both anal glands and castor sacs. Considering only beavers younger than 4 years, a significant difference existed between males and females for weight of the anal gland ($F = 10.2$, $d.f. = 1$, 59 , $P = 0.002$) and the castor sacs ($F = 7.06$, $d.f. = 1$, 59 , $P = 0.01$; Fig. 3). These young females had average anal gland weights of 25.5 ± 2.24 g compared to 40.4 ± 3.72 g for young males. These same females had average castor sac weights of 95 ± 14.2 g compared to 78.5 ± 8.02 g for males. The slopes differed for the linear fits for anal glands (test of parallelism: $F = 17.5$, $d.f. = 1$, 58 , $P < 0.0001$) but not for castor sacs (test of parallelism: $F = 0.24$, $d.f. = 1$, 58 , $P = 0.63$). Hence, for anal glands, both the amount and rate of investment differed between the sexes during the 1st few years of life, whereas for castor sacs, the amount of investment but not the rate of investment differed between males and females.

DISCUSSION

The study revealed sexual dimorphism in the development of scent structures in Eurasian beavers. Males and females invested differently in the 2 types of scent structures (anal glands and castor sacs). This investment was most apparent in the first 3 years of life. Beavers from different habitats that also differed in the density of beaver sites had similarly sized scent structures.

Castor sac material serves as a territorial scent mark (Rosell and Sundsdal 2001; Rosell et al. 1998; Schulte 1998). Males spend more time devoted to marking and territory investigation than do females (Herr and Rosell 2004; Thomsen 2002). A study of North American beavers indicated that males and females had similarly sized castor sacs, but the samples came mainly from adult beavers (Bollinger et al. 1983). The current study found that young males had relatively smaller castor sacs than young females, but sizes were not significantly different in adults.

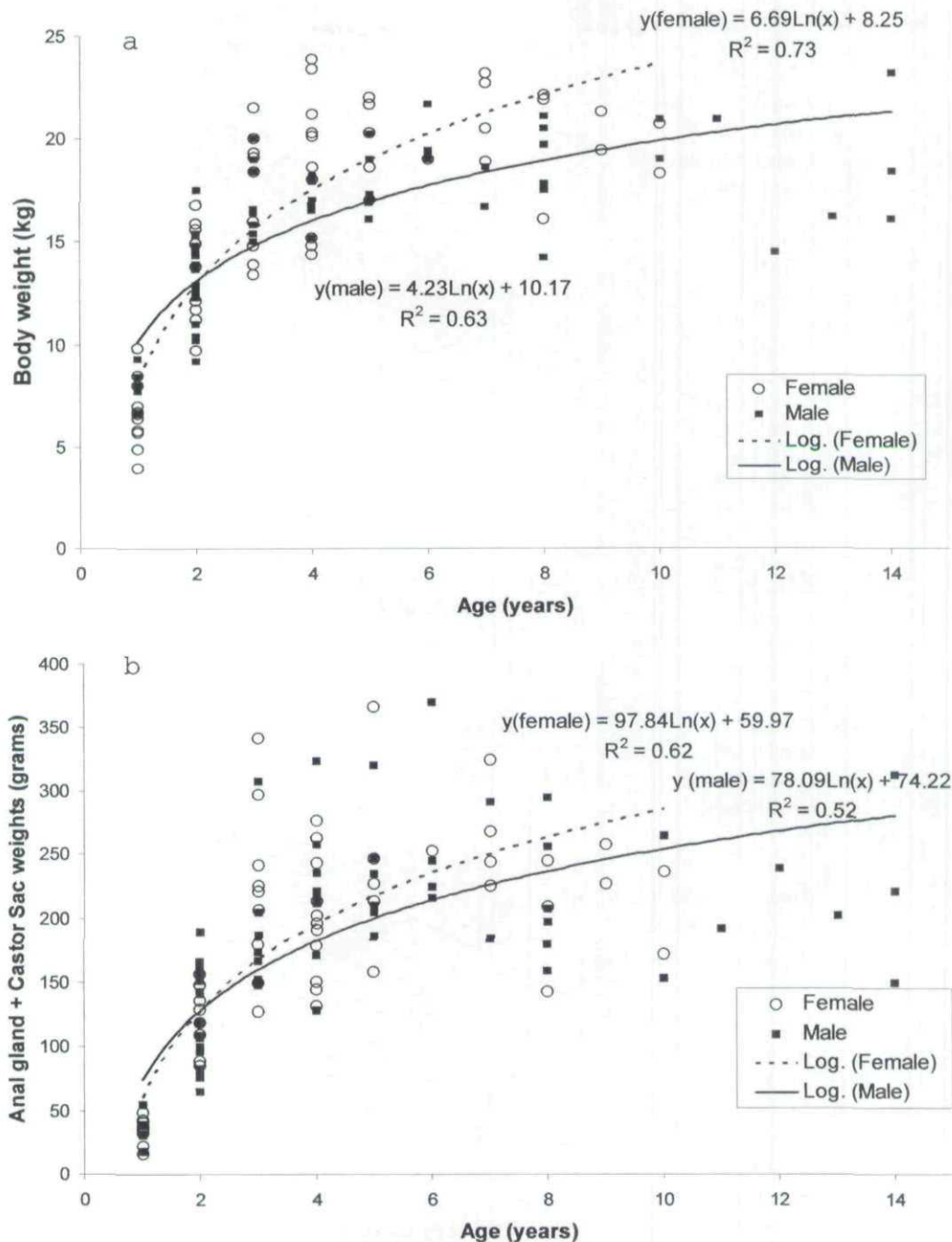


FIG. 1.—a) Body weight (kg) of male and female Eurasian beavers plotted against age in years as determined from tooth analysis. b) Scent structure weight (g) for anal glands plus castor sacs plotted against age. The best-fit log line is shown for each sex separately.

Because males clearly did not have larger castor sacs than females, use and investment in size are not directly related. This contradicts our 1st prediction on a direct relationship between marking rates and castor sac size. Our 2nd prediction stated that castor sacs of males could be smaller because of increased use. Higher flow rates of urine through the sacs could deplete scent material, resulting in lighter castor sacs. This does not explain why young males would have lighter castor sacs than young females, unless young, male Eurasian beavers mark more than do young females. This would be different from 1 population of North American beavers, where young of each sex marked

previously created mounds at similarly frequencies (Schulte 1998), possibly to create a family scent. In the current study, smaller observed sizes of castor sacs in young males might occur if castor sac size was influenced by investment in the anal gland.

Previous studies have suggested that anal gland secretion acts as an individual identifier by being released into the water (Grønneberg and Lie 1984; Rosell 2002b; Sun and Müller-Schwarze 1998). Individuals who are most likely to meet other beavers may use anal gland secretion more readily. This would permit intruders an opportunity to match the scent mark to its owner (the scent-matching hypothesis—Gosling 1982).

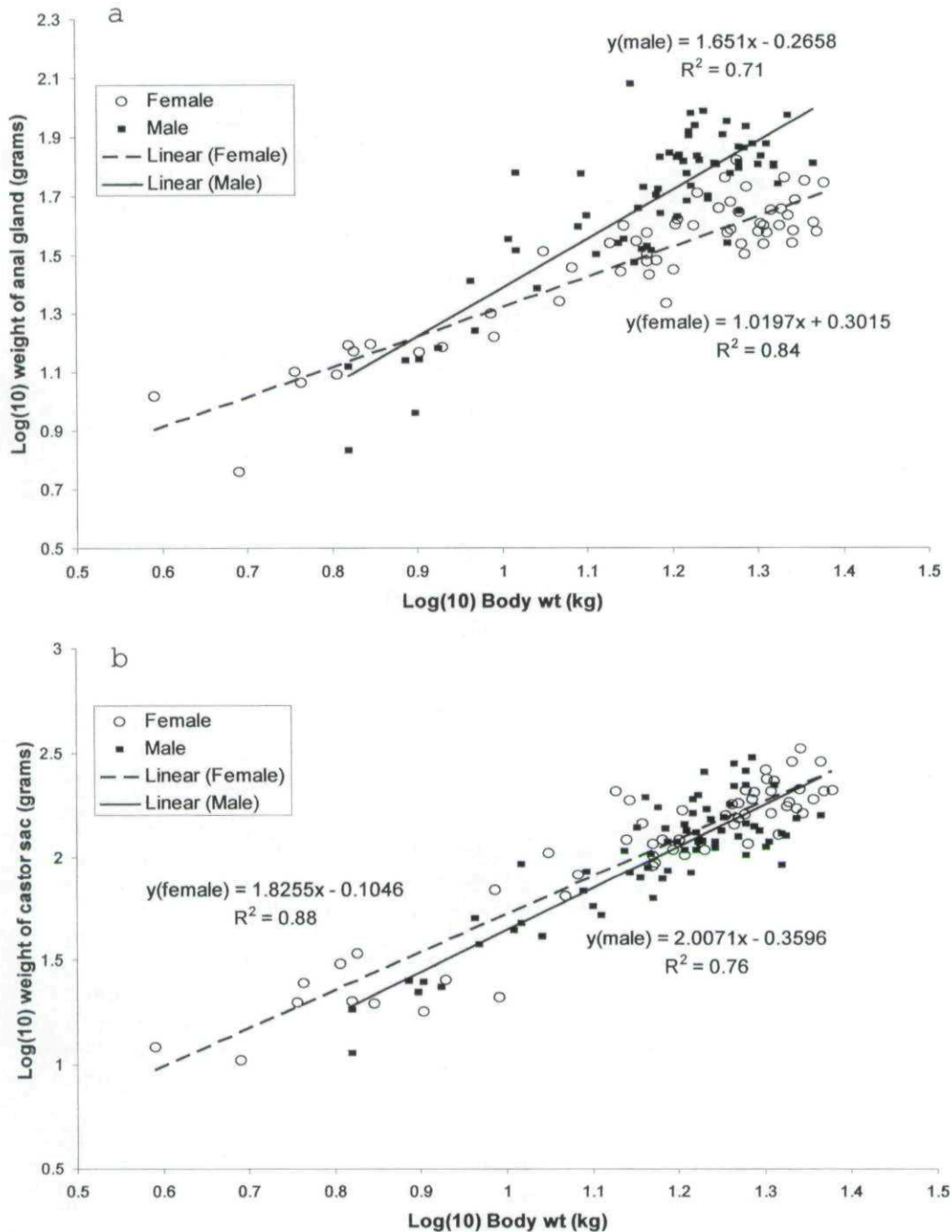


FIG. 2.—a) Anal gland weight and b) castor sac weight (\log_{10} g of weight) of male and female Eurasian beavers plotted against body weight (\log_{10} kg of weight).

Because males appear to spend more time patrolling the territory, they are most likely to interact with nonresident beavers. In a study by Bollinger et al. (1983), male North American beavers had slightly larger anal glands than females. In the current study, males had an increased level and rate of investment in anal gland weight compared to females throughout development and into adulthood. Thus, males had smaller castor sacs but larger anal glands than females, but overall investment in scent structures did not differ between the sexes. Size of the scent structures increased with age in an allometric fashion, showing the same relative growth as overall body weight.

Males may require more equitable investment in both the individual identifier scent structure (anal gland) and the territory demarcation scent structure (castor sac) than females. If higher flushing rates reduce castor sac size, then this size reduction may create more space for larger anal glands. Combined, these ideas suggest that castoreum and anal gland secretion are both important signalers from a territory holder. This hypothesis makes testable predictions for future studies. First, males should respond to experimental scent marks on the periphery of the territory sooner or more often than females. Second, males should make or update outlying scent marks (those on extremes

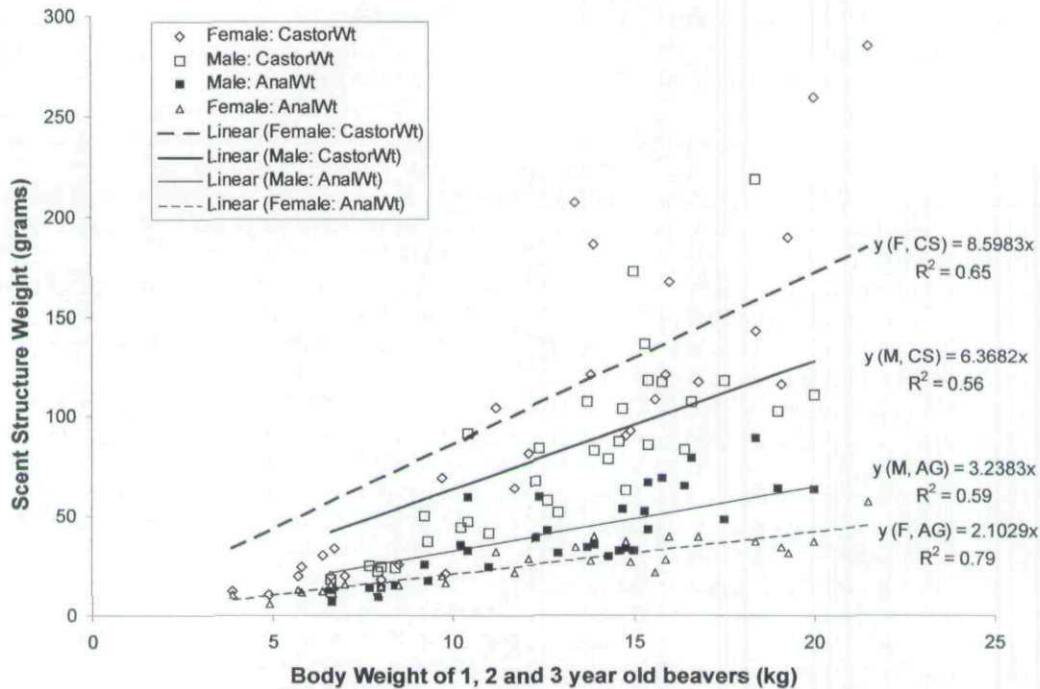


FIG. 3.—Anal gland and castor sac weights (g) plotted against body weight (kg) for Eurasian beavers in age class years 1, 2, and 3 as determined from tooth analysis. The best-fit line is shown for males ($n = 33$) and females ($n = 29$) for each scent-structure type. All fits were significant ($P < 0.001$). Intercepts were set to 0.

of territory) more than females. Third, males should encounter nonresident beavers more frequently. The 3rd prediction is partially supported by the observation that in a population of North American beavers, adult males had more tail scars and notches than adult females (Müller-Schwarze and Schulte 1999). Such injuries indicate a greater frequency of competitive interactions between beavers from different sites.

Beavers exhibit a monogamous mating system with high levels of parental investment by both sexes. Morphological sexual dimorphism is generally absent in such species (Kleiman 1977) and only slight behavioral dimorphism is apparent, as is typical in such obligate monogamous species (Clutton-Brock 1989; Svendsen 1989; Wilsson 1971). As with many mammals, beavers rely heavily on scent to communicate within the species, especially to communicate territoriality (Ralls 1971; Rosell 2002a; Schulte 1998). We suggest that a difference in territorial behavior between male and female beavers has led to differential investment in scent structures. Total allocation to scent structures is apparently constrained, because each sex exhibits a similar combined weight relative to total body weight. However, this similar total investment arises from very different functional ends. We propose that females have larger castor sacs (low flushing rates) and smaller anal glands (infrequent use) because of reduced employment of both glands for territorial purposes, whereas males have just the opposite configuration because of enhanced use of both glands in territorial demarcation. Hence, behavioral dimorphism selects for morphological dimorphism in signal-producing structures, even in an obligate monogamous species, but the extent of the divergence is limited by total developmental allocation to the structures.

ACKNOWLEDGMENTS

We thank Frode Bergan, Tore Bjørkøyli, Bjørnar Hovde, Howard Parker, Jørn Ingar Sanda, Øyvind Steifetten, and other hunters who helped supply us with beavers for this study. R. Chandler and A. Harvey provided helpful insights on analyses and valuable review comments. Georgia Southern University provided support for BAS. Our study was financially supported by The Norwegian Directorate for Nature Management; the Conservation Commissions in Akershus, Aust-Agder, Buskerud, Hedmark, Oppland, Oslo, Østfold, Sør-Trøndelag, Telemark, Vest-Agder, and Vestfold counties; and the Department of Environmental and Health Studies, Telemark University College.

LITERATURE CITED

- ALEKSIUK, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). *Journal of Mammalogy* 49:759–762.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BLAUSTEIN, A. R. 1981. Sexual selection and mammalian olfaction. *American Naturalist* 117:1006–1010.
- BOLLINGER, K. S., H. E. HODGDON, AND J. J. KENNELLY. 1983. Factors affecting weight and volume of castor and anal glands of beaver (*Castor canadensis*). *Acta Zoologica Fennica* 174:115–116.
- BUECH, R. R. 1995. Sex differences in behavior of beavers living in near-boreal lake habitat. *Canadian Journal of Zoology* 73:2133–2143.
- BUSHER, P. E., AND S. H. JENKINS. 1985. Behavioral patterns of a beaver family in California. *Biology of Behaviour* 10:41–54.
- CLUTTON-BROCK, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London, B. Biological Sciences* 236:339–372.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174–184.

- COLLINS, S. A., L. M. GOSLING, R. W. WATKINS, AND D. P. COWAN. 2001. Artificially increasing scent mark rate increases urogenital gland size in mice *Mus musculus*. *Physiology & Behavior* 74: 517–522.
- DARWIN, C. 1871. *The descent of man and selection in relation to sex*. Murray, London, United Kingdom.
- DIXON, A. F. G., AND R. KUNDU. 1998. Resource tracking in aphids: programmed reproductive strategies anticipate seasonal trends in habitat quality. *Oecologia* 114:73–78.
- GOSLING, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie* 60:89–118.
- GRØNNEBERG, T. Ø., AND T. LIE. 1984. Lipids of the anal gland secretion of beaver, *Castor fiber*. *Chemica Scripta* 24:100–103.
- HERR, J., AND F. ROSELL. 2004. Space use and movements patterns in monogamous adult Eurasian beavers (*Castor fiber*). *Journal of Zoology (London)* 262:257–264.
- HEYMANN, E. W. 1998. Sex differences in olfactory communication in a primate, the moustached tamarin, *Saguinus mystax* (Callitrichinae). *Behavioral Ecology and Sociobiology* 43:37–45.
- HODGDON, H. E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. Ph.D. dissertation, University of Massachusetts, Amherst.
- HODGDON, H. E., AND L. S. LARSON. 1973. Some sexual differences in behaviour within a colony of marked beavers (*Castor canadensis*). *Animal Behaviour* 21:147–152.
- JANNETT, F. J., JR. 1986. Morphometric patterns among microtine rodents. I. Sexual selection suggested by relative scent gland development in representative voles (*Microtus*). Pp. 541–550 in *Chemical signals in vertebrates 4* (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, eds.). Plenum Press, New York.
- JUDSON, G. J., AND J. D. MCFARLANE. 1998. Mineral disorders in grazing livestock and the usefulness of soil and plant analysis in the assessment of these disorders. *Australian Journal of Experimental Agriculture* 38:707–723.
- KLEIMAN, D. G. 1977. Monogamy in mammals. *Quarterly Review of Biology* 52:39–69.
- MÜLLER-SCHWARZE, D., AND B. A. SCHULTE. 1999. Behavioral and ecological characteristics of a "climax" population of beaver (*Castor canadensis*). Pp. 161–177 in *Beaver protection, management, and utilization in Europe and North America* (P. E. Busher and R. M. Dzieciowski, eds.). Plenum Press, New York.
- NOVAK, M. 1987. Beaver. Pp. 283–312 in *Wildlife furbearer management and conservation in North America* (M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds.). Ashton-Potter Limited, Ontario Ministry of Natural Resources, Concord, Ontario, Canada.
- RALLS, K. 1971. Mammalian scent marking. *Science* 171:443–449.
- RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist* 111:917–938.
- ROSELL, F. 2002a. The function of scent marking in beaver (*Castor fiber*) territorial defence. Ph.D. dissertation, Norwegian University of Science and Technology, Trondheim, Norway.
- ROSELL, F. 2002b. Do Eurasian beavers smear their pelage with castoreum and anal gland secretion? *Journal of Chemical Ecology* 28:1697–1701.
- ROSELL, F., F. BERGAN, AND H. PARKER. 1998. Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. *Journal of Chemical Ecology* 24:207–219.
- ROSELL, F., AND T. BJØRKYLI. 2002. A test of the dear enemy phenomenon in the Eurasian beaver. *Animal Behaviour* 63: 1073–1078.
- ROSELL, F., AND B. A. NOLET. 1997. Factors affecting scent-marking behavior in the Eurasian beaver (*Castor fiber*). *Journal of Chemical Ecology* 23:673–689.
- ROSELL, F., AND L. SUN. 1999. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *C. fiber*. *Wildlife Biology* 5:119–123.
- ROSELL, F., AND L. J. SUNDSDAL. 2001. Odorant source used in Eurasian beaver territory marking. *Journal of Chemical Ecology* 27:2471–2491.
- SCHULTE, B. A. 1993. Chemical communication and ecology of the North American beaver (*Castor canadensis*). Ph.D. dissertation, College of Environmental Science and Forestry, State University of New York, Syracuse.
- SCHULTE, B. A. 1998. Scent marking and responses to male castor fluid by beavers. *Journal of Mammalogy* 79:191–203.
- SCHULTE, B. A., AND D. MÜLLER-SCHWARZE. 1999. Understanding North American beaver behavior as an aid to management. Pp. 109–127 in *Beaver protection, management, and utilization in Europe and North America* (P. E. Busher and R. M. Dzieciowski, eds.). Plenum Press, New York.
- SCHULTE, B. A., D. MÜLLER-SCHWARZE, AND L. SUN. 1995. Using anal gland secretion to determine sex in beaver. *Journal of Wildlife Management* 59:614–618.
- SHARPE, F., AND F. ROSELL. 2003. Time budget and sex differences in the Eurasian beaver. *Animal Behaviour* 66:1059–1067.
- STATSOFT, INC. 1999. *Statistica* version 5.5. StatSoft Inc., Tulsa, Oklahoma.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3–47.
- SUN, L., AND D. MÜLLER-SCHWARZE. 1998. Anal gland secretion codes for relatedness in the beaver, *Castor canadensis*. *Ethology* 104:917–927.
- SVENDSEN, G. E. 1978. Castor and anal glands of the beaver (*Castor canadensis*). *Journal of Mammalogy* 59:618–620.
- SVENDSEN, G. E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). *Canadian Journal of Zoology* 67:336–340.
- THOMSEN, L. R. 2002. Sex difference in scent marking in a monogamous mammal, the Eurasian beaver (*Castor fiber*). M.S. thesis, University of Aarhus, Aarhus, Denmark.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 in *Sexual selection and the descent of man, 1871–1971* (B. Campbell, ed.). Aldine Press, Chicago, Illinois.
- VALEUR, P. 1988. Beverens territorial-atferd som populasjonregulerende faktor. *Fauna* 41:20–34.
- VAN NOSTRAND, F. C., AND A. B. STEPHENSON. 1964. Age determination for beavers by tooth development. *Journal of Wildlife Management* 28:430–434.
- WALRO, J. M., AND G. E. SVENDSEN. 1982. Castor sacs and anal glands of the North American beaver (*Castor canadensis*): Their histology, development, and relationship to scent communication. *Journal of Chemical Ecology* 8:809–819.
- WHEATLEY, M. 1997. Beaver, *Castor canadensis*, home range size and patterns of use in the taiga of southeastern Manitoba: II. Sex, age and family status. *Canadian Field-Naturalist* 111:211–216.
- WILSSON, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). *Viltrevy* 8:115–266.

Submitted 4 November 2003. Accepted 16 July 2004.

Associate Editor was Penny S. Reynolds.