

Predator cues reduce American beaver use of foraging trails

WILLIAM J. SEVERUD, Northern Michigan University, Department of Biology, 1401 Presque Isle Avenue, Marquette, MI 49855, USA wseverud@nmu.edu

JERROLD L. BELANT, Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA

JOHN G. BRUGGINK, Northern Michigan University, Department of Biology, 1401 Presque Isle Avenue, Marquette, MI 49855, USA

STEVE K. WINDELS, 360 Highway 11 East, International Falls, MN 56649, USA

Abstract: Herbivores must balance energy needs with avoiding risks, using various cues to assess predation risk. The American beaver (*Castor canadensis*) is a semi-aquatic herbivore vulnerable to predation on land by wolves (*Canis lupis*). We tested the use of wolf urine as a potential tool to reduce human–beaver conflicts. We used infrared cameras to monitor use of terrestrial foraging trails by beavers during food cache construction in Seney National Wildlife Refuge, Michigan, from September to November 2008. Two foraging trails at 15 colonies (30 total trails) were monitored for 1 week to establish baseline use. One trail from each colony was then treated with wolf urine, and all trails were monitored an additional week to estimate changes in trail use. Mean number of beavers detected decreased 95% on urine-treated trails and was unchanged on untreated trails. Beavers also spent 95% less time on urine-treated trails as estimated by photograph time stamps, but did not change time spent on untreated trails. Sixteen other taxa of wildlife were detected; however, avoidance of urine-treated trails was not observed in these taxa. Species richness increased with urine treatment, mostly due to increased visitation by carnivores. Beavers appear to use olfaction to assess predation risk on land. Wolf urine may be a suitable deterrent for beaver herbivory.

Key words: American beaver, *Castor canadensis*, foraging, human–wildlife conflicts, Michigan, olfaction, optimal foraging theory, predation risk, risk allocation hypothesis

OPTIMAL FORAGING THEORY predicts that animals will maximize food intake while minimizing time spent foraging (MacArthur and Pianka 1966, Pyke et al. 1977). Animals must also balance foraging with avoiding risks, such as predation (Sih 1980). The recognition of risk-sensitivity can help in understanding behavior of foragers, which sometimes avoid areas with seemingly plentiful food if the threat of predation exists (Ripple and Beschta 2004). The risk allocation hypothesis accounts for temporal variation in predation risk and how variation affects foraging (Lima and Bednekoff 1999). This hypothesis predicts that foragers exposed to chronic risk will show less pronounced antipredator behavior than foragers exposed to brief and infrequent pulses of risk. For example, a meta-analysis of terrestrial foraging and predation risk trade-offs revealed a large decrease in foraging effort with increased predation risk, and many rodents avoided areas treated with predator scent (Verdolin 2006).

Predation risk may be perceived by observing the predator, indirect cues (e.g., odors) or habitat cues (Verdolin 2006). The presence of a

predator may cause foragers to avoid foraging areas (Díaz et al. 2005) even after the predator has vacated the area (Sih 1992). Odor from predator urine or feces has been effective at inducing risk-sensitive behavior in mountain beavers (*Aplodontia rufa*), wood mice (*Apodemus sylvaticus*), and golden hamsters (*Mesocricetus auratus*; Epple et al. 1993, Herman and Valone 2000, McPhee et al. 2010). In a cafeteria-style feeding experiment, Engelhart and Müller-Schwarze (1995) found that American beavers (*Castor canadensis*) avoided feeding on quaking aspen (*Populus tremuloides*) treated with solvent extracts of predator feces. Eurasian beavers (*C. fiber*) suppressed territorial scent marking in response to scent of sympatric Eurasian lynxes (*Lynx lynx*) and historically sympatric but now allopatric wolves (*Canis lupus*; Rosell and Sanda 2006).

American beavers eat a variety of terrestrial and aquatic plant species (Baker and Hill 2003). Beavers are central place foragers that balance the costs of travel from water with the benefits of foraging in a particular area (Jenkins 1980, Belovsky 1984, McGinley and Whitham 1985, Baker and Hill 2003). For example, beavers

varied their selection of small and large aspen stems, depending on distance from water, which indicates that beavers trade off maximization of energy gain against minimization of predation risk (Basey and Jenkins 1995). Beavers felled more large trees and were more selective as distance from shore increased in high quality habitat (Gallant et al. 2004, Raffel et al. 2009). However, in habitats of lower terrestrial forage quality, beavers may select more hazardous foraging sites and engage in riskier behavior (Sih 1980).

Predators of beavers include gray wolves, coyotes (*Canis latrans*), cougars (*Puma concolor*), bears (*Ursus* spp.), wolverines (*Gulo gulo*), Canada lynxes (*Lynx canadensis*), and bobcats (*Lynx rufus*). The impact of wolf predation on beavers can be locally significant, varying with wolf density and available alternate prey (Baker and Hill 2003). In Ontario, when white-tailed deer (*Odocoileus virginianus*) populations declined over a 9-year period, beavers became the most important summer prey of wolves, with 55% of wolf scats containing beaver remains (Voigt et al. 1976). Smith and Peterson (1988) reported 47% of wolf scats in northern Minnesota during spring contained beaver remains. Black bears (*Ursus americanus*) suppressed beaver populations on Stockton Island in Lake Superior (Smith et al. 1994). Beavers may perceive direct or indirect cues from large terrestrial predators, such as wolves and bears, and, in response, decrease foraging on terrestrial vegetation.

Our objectives were to determine whether beavers use olfaction to assess predation risk, and whether wolf urine could be used as a potential tool to mitigate human-beaver conflicts. We hypothesized that beavers would alter their behavior in response to an indirect predator cue. Specifically, we predicted that foraging trails treated with predator urine would be used less than untreated control trails.

Study area

We conducted this study in Seney National Wildlife Refuge (SNWR), Schoolcraft County, Michigan (46° 14'N, 86° 00'W) from September 18 to November 13, 2008. The refuge is 38,678 ha, with 24,682 ha of marsh and 2,932 ha of open water (Herman et al. 1975). Most open water is

contained in 21 constructed pools. Emergent vegetation covers 43% of the wetlands and includes cattail (*Typha latifolia*), sedges (*Carex* spp.), and bulrushes (*Scirpus* spp.). Forests cover 84% of the uplands and contain pines (*Pinus* spp.), quaking aspens, and paper birch (*Betula papyrifera*; Baker et al. 1995). Beavers use wetlands throughout SNWR; potential predators include gray wolves, black bears (*U. americanus*), coyotes, northern river otters (*Lontra canadensis*), bobcats, and American minks (*Neovison vison*; D. Olson, U. S. Fish and Wildlife Service, personal communication). Monthly mean temperatures during the study ranged from 1.8° to 15.1° C, and monthly mean liquid precipitation ranged from 1.27 to 1.52 mm. In November, 47.5 cm of snow fell (NOAA Midwestern Regional Climate Center).

Methods

We conducted this study when beavers increased tree-cutting activities for constructing food caches (Busher 1996). We selected 16 beaver lodges based on recent tree-cutting activity, and we randomly assigned lodges equally to one of 4 groups based on accessibility. Each lodge was >200 m from its nearest neighbor (11 lodges were >750 m away). If lodges were in the same body of water, active food caches were used to estimate if >1 colony was present. We sampled each group of 4 lodges for 2 weeks. At each lodge, we selected the 2 most active foraging trails and randomly selected one of those trails for urine treatment, while the other trail was assigned as a sham or control. Responses to control trails were not different and were combined in all analyses as controls. One lodge was omitted due to lack of equipment, yielding 15 treatment trails and 15 control trails over the 8-week period. An infrared camera (Reconyx Silent Image Cameras RM30, Reconyx Inc., Holmen, Wis.) was placed on each trail 10 cm above ground, 2 m from shore. Cameras were aimed at shore and set to take a picture every 0.5 seconds, once activated by heat and motion.

We monitored trails for 1 week before we applied 90 ml of wolf urine (Deerbusters, Frederick, Md.) to treatment trails. Urine was placed 50 cm from shore on either side of the trail in a PredatorPee Dispenser (Lexington Outdoors, Robinston, Me.) about 10 cm above ground. We placed empty PredatorPee

Table 1. Results from generalized linear mixed model analyses ($df = 1, 57$) testing the effect of treatment (urine or control), and week (week 1 or week 2) with time used as a random factor, on (a) mean number of beavers detected and mean duration of detection of beavers, (b) mean species richness and mean carnivore species richness, and (c) mean number of muskrats detected and mean number of raccoons detected on beaver foraging trails, Seney National Wildlife Refuge, Michigan, September–November 2008.

a.

Source	Number of beavers		Duration of detection	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	15.67	<0.001	17.56	<0.001
Week	0.28	0.596	2.51	0.119
Treatment × week	9.49	0.003	34.43	<0.001

b.

Source	Species richness		Carnivore species richness	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	5.64	0.021	4.06	0.049
Week	5.08	0.028	0.79	0.378
Treatment × week	4.26	0.044	3.82	0.056

c.

Source	Number of muskrats		Number of raccoons	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	2.55	0.116	<0.01	0.999
Week	1.77	0.189	0.28	0.596
Treatment × week	0.98	0.326	0.03	0.864

Dispensers on sham trails and placed nothing on control trails. We continued monitoring trails 1 week post-treatment before moving cameras to another group of lodges. Methods followed procedures approved by Northern Michigan University's Institutional Animal Use and Care Committee.

We counted the number of beavers photographed and the mean amount of time beavers spent at the camera station per camera trap station. The amount of time spent was calculated using the time stamp difference between the first image and last image of the animal, recorded in seconds. We used a generalized linear mixed model to test the Poisson loglinear full factorial model of treatment (urine or control), and week (week

1 or week 2) with time (September 18, October 2, October 16, or October 30, 2008) used as a random effect (SAS Institute Inc., Cary, N.C.). We decided *a posteriori* to conduct the same analyses for northern raccoons (*Procyon lotor*) and muskrats (*Ondatra zibethicus*) based on descriptive summaries of detections.

Results

We obtained 60 beaver visits (Figure 1), with 14 visits on 15 control trails and 46 visits on 15 urine trails, representing 13% of all images ($n = 448$). Mean number of beavers detected on urine trails declined 95% from week 1 ($\bar{x} = 2.9$ images, $SE = 1.5$, $n = 15$) to week 2 ($\bar{x} = 0.1$, $SE = 0.1$, $n = 15$; Fig. 2, Table 1a). In contrast, mean number of beavers detected on control

Table 2. Total number of detections by cameras on beaver foraging trails pre- and post-treatment by taxon, Seney National Wildlife Refuge, Michigan, September–November 2008.

Taxon	Number of detections			
	Control trails (<i>n</i> = 15)		Urine trails (<i>n</i> = 15)	
	Week 1	Week 2	Week 1	Week 2
Small mammal	43	28	22	27
Muskrat (<i>Ondatra zibethicus</i>)	34	23	10	14
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	20	10	31	14
American mink (<i>Neovison vison</i>)	8	5	1	3
American beaver (<i>Castor canadensis</i>)	8	6	44	2
Raccoon (<i>Procyon lotor</i>)	6	9	6	6
White-tailed deer (<i>Odocoileus virginianus</i>)	5	0	1	0
Long-tailed weasel (<i>Mustela frenata</i>)	4	0	2	0
Eastern chipmunk (<i>Tamias striatus</i>)	3	0	0	0
Common snipe (<i>Gallinago gallinago</i>)	1	0	0	1
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	1	0	0	0
River otter (<i>Lontra canadensis</i>)	1	0	0	0
Black bear (<i>Ursus americanus</i>)	1	0	0	0
Unknown passerines	1	7	2	6
Fisher (<i>Martes pennanti</i>)	0	4	3	7
Wood duck (<i>Aix sponsa</i>)	0	0	1	1
Snowshoe hare (<i>Lepus canadensis</i>)	0	0	0	1



Figure 1. Photos taken of American beaver (top left), raccoon (top right), river otter (bottom left), and black bear (bottom right) on beaver foraging trails, Seney National Wildlife Refuge, Michigan, September–November 2008.

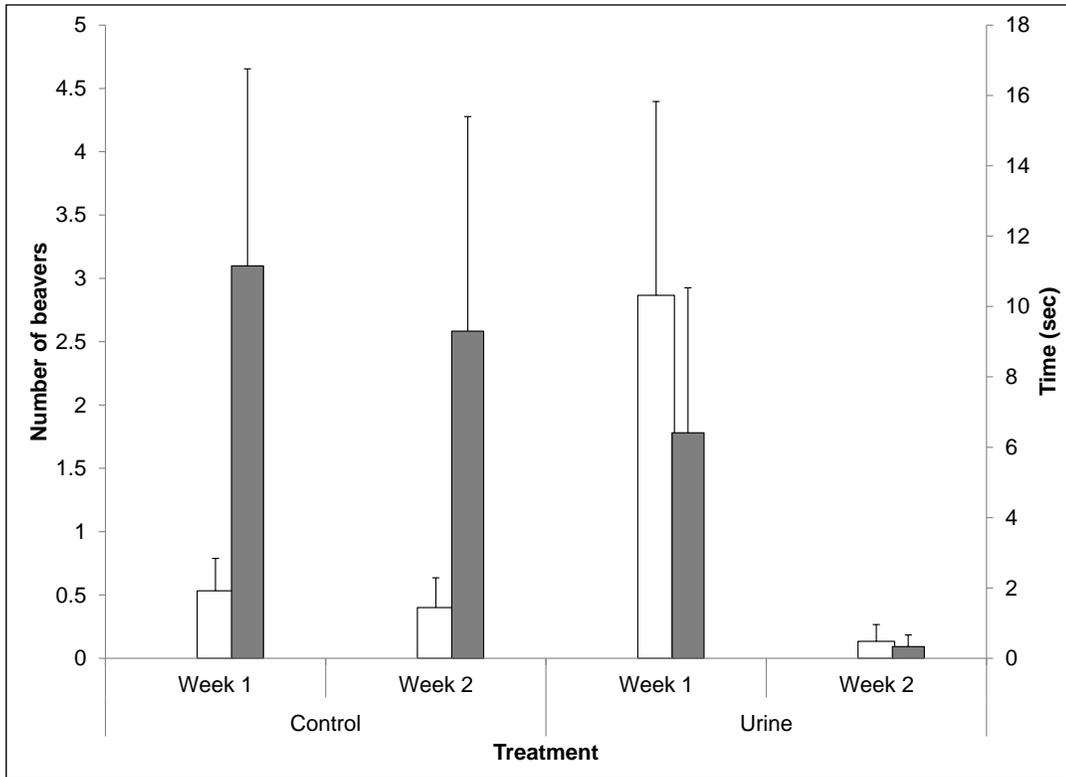


Figure 2. Mean (+ SE) number of American beavers photographed (open bars), and mean (+SE) duration of detection (sec = seconds; shaded bars) on urine-treated and control trails from week 1 to week 2 on 15 beaver foraging trails, Seney National Wildlife Refuge, Michigan, September–November 2008. Wolf urine was distributed along urine-treated trails only during week 2. During week 1, all trails were untreated.

trails during week 1 (\bar{x} = 0.5 images, SE = 0.3, n = 15) and week 2 (\bar{x} = 0.4, SE = 0.2, n = 15) was similar. Mean number of beavers detected on urine trails was greater than on control trails during week 1 but not week 2.

There was an interaction between week and treatment for mean duration of beaver detections (Table 1a). Mean duration of beaver detections on urine trails declined 95% from week 1 (\bar{x} = 6.4 sec, SE = 4.1, n = 15) to week 2 (\bar{x} = 0.3, SE = 0.3, n = 15; Figure 2), while mean duration of detections on control trails remained unchanged from week 1 (\bar{x} = 11.2 sec, SE = 5.6, n = 15) to week 2 (\bar{x} = 9.3, SE = 6.1, n = 15).

We obtained images from 16 taxa other than beaver (Figure 1, Table 2). Unidentified small mammals were most abundant (27% of total images), followed by muskrats (18%), red squirrels (*Tamiasciurus hudsonicus*; 17%), and northern raccoons (6%). Mean total species richness decreased 40% from week 1 (\bar{x} = 3.5 species, SE = 0.6, n = 15) to week 2 (\bar{x} = 2.1, SE

= 0.4, n = 15) on control trails, and increased 9% from week 1 (\bar{x} = 2.1, SE = 0.4, n = 15) to week 2 (\bar{x} = 2.3, SE = 0.5, n = 15) on urine trails (Figure 3, Table 1b). Mean carnivore species richness decreased 33% from week 1 (\bar{x} = 0.8, SE = 0.3, n = 15) to week 2 (\bar{x} = 0.53, SE = 0.2, n = 15) on control trails and increased 120% from week 1 (\bar{x} = 0.3, SE = 0.1, n = 15) to week 2 (\bar{x} = 0.7, SE = 0.2, n = 15) on urine trails.

Mean numbers of muskrats (*Ondatra zibethicus*) and raccoons detected were similar for treatment and control trails (Table 1c). There was no interaction between treatment and week for muskrats or raccoons. Mean number of muskrats detected on urine trails during week 1 (\bar{x} = 0.7, SE = 0.3, n = 15) was similar to the number during week 2 (\bar{x} = 0.9, SE = 0.7, n = 15), and similar to the number on control trails during week 1 (\bar{x} = 2.2, SE = 0.9, n = 15) and week 2 (\bar{x} = 1.5, SE = 0.7, n = 15). Mean number of raccoons detected on urine trails during week 1 (\bar{x} = 0.4, SE = 0.3, n = 15) was similar to the number during week 2 (\bar{x} = 0.4, SE = 0.2, n =

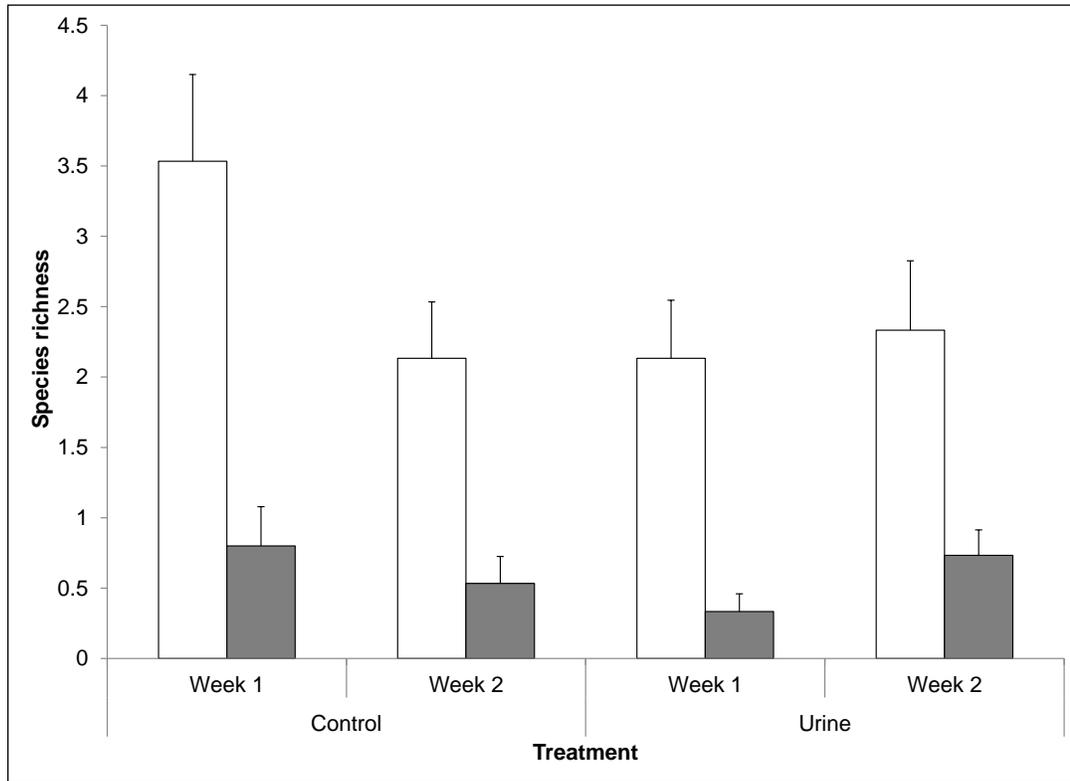


Figure 3. Mean (+SE) total species richness (open bars) and carnivore species richness (shaded bars) on urine-treated and control trails from week 1 to week 2 on 15 beaver foraging trails, Seney National Wildlife Refuge, Michigan, September–November 2008. Wolf urine was distributed along urine-treated trails only during week 2. During week 1, all trails were untreated.

15), and similar to the number on control trails during week 1 ($\bar{x} = 0.4$, SE = 0.2, $n = 15$) and week 2 ($\bar{x} = 0.5$, SE = 0.3, $n = 15$). We did not achieve model convergence for comparisons of mean durations of detections for muskrats or raccoons.

Discussion

We found a 95% reduction in beaver numbers at camera stations containing predator urine, indicating that beavers altered their space use in response to an indirect cue of predation risk. Beavers also spent 95% less time at urine-treated camera stations and exhibited no decrease in time spent at control camera stations. Decreased time spent at urine-treated camera stations suggests that antipredator behavior in beavers in our study area was strong, consistent with the risk allocation hypothesis (Lima and Bednekoff 1999). Decreased use and time spent at urine-treated camera stations suggests that wolf urine is an effective deterrent to beaver activity and that beavers use olfaction to assess predation

risk. In our study area, wolves have large territories and range extensively (Mech 1974); hence, beavers may experience only occasional temporal pulses of risk from wolves. These pulses of risk may be perceived by beavers regardless of actual predation events, which may be affected by available alternate wolf prey (Voigt et al. 1976). Although our study was short in duration, it represented a brief pulse of elevated predation risk. That beavers avoided camera stations containing wolf urine supports the tenet of the risk allocation hypothesis, which states that brief, infrequent pulses of high risk will elicit strong antipredator behaviors in prey species (Lima and Bednekoff 1999). Our data suggest that beavers either reduced total foraging activity or began using unmonitored or untreated trails. American and Eurasian beavers both have exhibited use of olfaction to assess risk by repressing scent-marking behavior (Rosell and Sanda 2006) and foraging (Engelhart and Müller-Schwarze 1995, Rosell and Czech 2000) in response to predator odors.

Beavers also foraged closer to shore on an island with bears than on an island without bears (Smith et al. 1994). Our study supports Laundré et al.'s (2010) conclusion that foragers can learn and respond to elevations in predation risk.

Richness of carnivore species increased 120% following the application of urine. Carnivores increase activity around urine of other carnivore species (Roughton and Sweeny 1982, Gerht and Prange 2007). Scent may provide information about conspecifics or other carnivore species, and this information may be used to avoid antagonistic encounters or to increase the likelihood of beneficial encounters (Howard et al. 2002). Semiochemicals in urine are produced during digestion, and digestion of high-protein foods leads to higher levels of sulfur in urine (Mason et al. 1994). These sulfuric compounds attract carnivores and omnivores, yet repel herbivores (Mason et al. 1994, Nolte et al. 1994). Thus, the urine effect on beavers may have been enhanced by scent-marking of other carnivores attracted to the wolf urine.

Beavers can comprise a large portion of wolf diets (Mech 1974, Voigt et al. 1976, Paquet and Carbyn 2003, Urton and Hobson 2005), with beaver remains found in 7 to 75% of scats (Mech 1970, Voigt et al. 1976). Consequently, wolves can be an important source of mortality for beavers where they are sympatric (Baker and Hill 2003). Raccoons (Chavez and Gese 2005) and muskrats are rarely killed or consumed by wolves (Voigt et al. 1976, Urton and Hobson 2005), although muskrats comprised 16% of wolf diets when ungulates were at low densities in northwestern Minnesota (Chavez and Gese 2005). Beavers demonstrated aversion to wolf urine, while raccoons and muskrats showed no avoidance, suggesting that prey species are more sensitive to predator scents than were non-prey species. Apfelbach et al. (2005) suggested that prey will not react to predator odors from predators with which they do not share evolutionary history. The risk allocation hypothesis states that prey animals subject to temporally uniform high or low risk should exhibit weak antipredator behaviors (Lima and Bednekoff 1999). Perhaps raccoons and muskrats are under a constant threat of predation from a variety of sources; thus, a perceived pulse of risk from wolf urine would not elicit an antipredator response.

Management implications

Beavers can be viewed as nuisance animals where their activities conflict with human interests (Baker and Hill 2003). Annual timber losses to beaver impoundments were estimated to be \$22 million in the southeastern United States, not including trees felled or damaged by gnawing (Conover et al. 1995). Nonlethal control measures for nuisance animals are more acceptable to the general public (Baker and Hill 2003). Bone tar oil, a deer repellent, has been equivocal in its effectiveness as a beaver deterrent (Owen et al. 1984, Hammerson 1994). Baisey (1999) used extracts from a non-preferred forage species (Jeffrey pine [*Pinus jeffreyi*]) to inhibit feeding on a preferred species (quaking aspen). Engelhart and Müller-Schwarze (1995) claimed that predator odors would be effective feeding repellents against beavers; our results demonstrate that wolf urine can be effective in deterring beavers from foraging areas in the short term, and may attract carnivores. Extant predators, habituation to scent, and availability of resources may affect urine efficacy. Rosell and Sanda (2006) suggested that Eurasian beaver responses to predator feces were innate, but response from sympatric predators was stronger and refined through learning. The risk allocation hypothesis states that if risk becomes chronic, antipredator behavior will be weak (Lima and Bednekoff 1999), and animals in low quality habitat may engage in riskier behavior (Sih 1980). Thus, application of wolf urine and odors from other predators may have only short-term efficacy in deterring beavers from selected foraging areas.

Acknowledgments

We thank Northern Michigan University (Biology Department, Bruggink Wildlife Research Lab, Excellence in Education Grant, and Charles C. Spooner Grant), Seney National Wildlife Refuge, Voyageurs National Park, and the Ohio Department of Natural Resources for financial, equipment, and logistical support. S. J. Schaar provided valuable field assistance. A. J. Rebertus provided helpful guidance. The Ruffed Grouse Society and Michigan Waterfowl Association provided additional financial support.

Literature cited

- Apfelbach, R., C. D. Blanchard, R. J. Blanchard, R. A. Hayes, and I. S. McGregor. 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience and Biobehavioral Reviews* 29:1123–1144.
- Baker, B. W., and E. P. Hill. 2003. Beaver (*Castor canadensis*). Pages 288–310 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Baker, B. W., B. S. Cade, W. L. Magnus, and J. L. McMillen. 1995. Spatial analysis of sandhill crane nesting habitat. *Journal of Wildlife Management* 59:752–758.
- Basey, J. M. 1999. Foraging behavior of beavers (*Castor canadensis*), plant secondary compounds, and management concerns. Pages 129–146 in P. E. Busher and R. M. Dzięciołowski, editors. *Beaver protection, management, and utilization in Europe and North America*. Kluwer Academic/Plenum, New York, New York, USA.
- Basey, J. M., and S. H. Jenkins. 1995. Influences of predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology* 73:2197–2208.
- Belovsky, G. E. 1984. Summer diet optimization by beaver. *American Midland Naturalist* 111:209–222.
- Busher, P. E. 1996. Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. *American Midland Naturalist* 135:343–348.
- Chavez, A. S., and E. M. Gese. 2005. Food habits of wolves in relation to livestock depredations in northwestern Minnesota. *American Midland Naturalist* 154:253–263.
- Conover, M. R., W. C. Pitt, K. K. Kessler, T. J. DuBow, and W. A. Sanborn. 1995. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin* 23:407–414.
- Díaz, M., I. Torre, A. Peris, and L. Tena. 2005. Foraging behavior of wood mice as related to presence and activity of genets. *Journal of Mammalogy* 86:1178–1185.
- Engelhart, A., and D. Müller-Schwarze. 1995. Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *Journal of Chemical Ecology* 21:1349–1364.
- Epple, G., J. R. Mason, D. L. Nolte, and D. L. Campbell. 1993. Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). *Journal of Mammalogy* 74:715–722.
- Gallant, D., C. H. Bérubé, E. Tremblay, and L. Vasseur. 2004. An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality. *Canadian Journal of Zoology* 82:922–933.
- Gehrt, S. D., and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behavioral Ecology* 18:204–214.
- Hammerson, G. A. 1994. Beaver (*Castor canadensis*): ecosystem alterations, management, and monitoring. *Natural Areas Journal* 14:44–57.
- Herman, C. M., J. H. Barrow, and I. B. Tarshis. 1975. Leucocytozoonosis in Canada geese at the Seney National Wildlife Refuge. *Journal of Wildlife Diseases* 11:404–411.
- Herman, C. S., and T. J. Valone. 2000. The effect of mammalian predator scent on the foraging behavior of *Dipodomys merriami*. *Oikos* 91:139–145.
- Howard, M. E., G. L. Zuercher, P. S. Gipson, and T. R. Livingston. 2002. Efficacy of feces as an attractant for mammalian carnivores. *Southwestern Naturalist* 47:348–352.
- Jenkins, S. H. 1980. A size-distance relation in food selection by beavers. *Ecology* 61:740–746.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- Mason, J. R., G. Epple, and D. L. Nolte. 1994. Semiochemicals and improvements in rodent control. Pages 327–345 in B. G. Galef, M. Mainardi, and P. Valsecchi, editors. *Behavioral aspects of feeding: basic and applied research in mammals*. Workshop of the International School of Ethology, Chur, Switzerland.
- McGinley, M. A., and T. G. Whitham. 1985. Central

- place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). *Oecologia* 66:558–562.
- McPhee, M. E., A. Segal, and R. E. Johnston. 2010. Hamsters use predator odors as indirect cues of predation risk. *Ethology* 116:517–523.
- Mech, L. D. 1970. *The Wolf*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Mech, L. D. 1974. *Canis lupus*. *Mammalian species* 37:1–6.
- Nolte, D. L., J. R. Mason, G. A. Epple, E. Aronov, and D. L. Campbell. 1994. Why are predator urines aversive to prey? *Journal of Chemical Ecology* 20:1505–1516.
- Owen, C. N., D. L. Adams, and T. B. Wigley. 1984. Inefficacy of a deer repellent on beavers. *Wildlife Society Bulletin* 12:405–408.
- Paquet, P. C., and L. N. Carbyn. 2003. Gray wolf (*Canis lupus*) and allies. Pages 482–510 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- Raffel, T. R., N. Smith, C. Cortright, and A. J. Gatz. 2009. Central place foraging by beavers (*Castor canadensis*) in a complex lake habitat. *American Midland Naturalist* 162:62–73.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54:755–766.
- Rosell, F., and A. Czech. 2000. Responses of foraging Eurasian beavers *Castor fiber* to predator odours. *Wildlife Biology* 6:13–21.
- Rosell, F., and J. I. Sanda. 2006. Potential risks of olfactory signaling: the effect of predators on scent marking by beavers. *Behavioral Ecology* 17:897–904.
- Roughton, R. D., and M. W. Sweeny. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. *Journal of Wildlife Management* 46:217–229.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist* 139:1052–1069.
- Smith, D. W., and R. O. Peterson. 1988. The effects of regulated lake levels on beaver in Voyageurs National Park, Minnesota. U.S. National Park Service, Research/Resources Management Report MWR-11. Midwest Regional Office, Omaha, Nebraska, USA.
- Smith, D. W., D. R. Trauba, R. K. Anderson, and R. O. Peterson. 1994. Black bear predation on beavers on an island in Lake Superior. *American Midland Naturalist* 132:248–255.
- Urton, E. J., and K. A. Hobson. 2005. Intrapopulation variation in gray wolf isotope (δ^{15N} and δ^{13C}) profiles: implications for the ecology of individuals. *Oecologia* 145:317–326.
- Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60:457–464.
- Voight, D. R., G. B. Kolenosky, and D. H. Pimlott. 1976. Changes in summer foods of wolves in central Ontario. *Journal of Wildlife Management* 40:663–668.
-



WILLIAM J. SEVERUD is a biological science technician at Voyageurs National Park in Minnesota. He received his B.A. degree in biology from Carleton College, and will receive his M.S. degree in biology from Northern Michigan University. His research interests include predator–prey interactions, risk-sensitive foraging, and wildlife management.



JOHN G. BRUGGINK received B.S. and M.A. degrees in biology from Northern Michigan University and a Ph.D. degree in zoology from Southern Illinois University. He served as the eastern shore and upland game bird specialist for the Office of Migratory Bird Management of the U.S. Fish and Wildlife Service from 1994 to 1998. He currently is a professor at Northern Michigan University where he teaches wildlife and ecology courses. He has been involved with a variety of wildlife research projects.



JERROLD L. BELANT is an associate professor in the Department of Wildlife, Fisheries, and Aquaculture and Director of the Carnivore Ecology Laboratory at Mississippi State University. He received his B.S. and M.S. degrees from the University of Wisconsin–Stevens Point and his Ph.D. degree from the University of Alaska–Fairbanks. His research interests include carnivore ecology, resource selection, and human–wildlife conflicts.



STEVE K. WINDELS is a wildlife biologist at Voyageurs National Park in Minnesota. He received a B.S. degree from the University of Minnesota–Twin Cities, an M.S. degree from Texas A&M University–Kingsville, and a Ph.D. degree from Michigan Tech University. His research interests include plant–herbivore interactions, mammalian ecology, and landscape ecology.