

SIGNIFICANCE OF *BLARINA BREVICAUDA* AS A PREDATOR AND SOURCE OF TRAP-CAPTURE BIAS ON SMALL MAMMALS

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Evidence on whether the northern short-tailed shrew (*Blarina brevicauda*) is a significant predator or a source of bias in trap-capture success of small mammals is contradictory. We compared subsequent captures of 2 murid rodent species (*Clethrionomys gapperi* and *Peromyscus maniculatus*) after capture of either murid species or *B. brevicauda* by using 4 years of capture–release data from New Brunswick, Canada. Capture success for *P. maniculatus* in a trap after occupancy by *B. brevicauda* was 65% lower than expected, and for *C. gapperi*, 67% lower than expected. The response by *C. gapperi* and *P. maniculatus* to odors of a different species was similar to their response to odor of *B. brevicauda*. Although we conclude that examination of odor-response data does not permit a conclusion as to whether *B. brevicauda* is a significant predator, the ubiquitous distribution of *B. brevicauda* implies that their influence on trap-capture success is significant, particularly in forests where small-rodent species are of similar weight to *B. brevicauda*.

Key words: *Blarina brevicauda*, predator avoidance, short-tailed shrew, trap bias, trap odor

Debate exists as to whether the northern short-tailed shrew (*Blarina brevicauda*) is a significant predator of rodents and consequently a source of bias in capture success in small-mammal research. Bias is a concern in mark–recapture studies because of the assumption of equal probability of capture between trapping periods (Seber 1986). Publications since the mid-1800s (reviewed by Eadie 1944) described *B. brevicauda* killing captive meadow vole (*Microtus pennsylvanicus*) so efficiently that *B. brevicauda* was promoted as being of significant economic help for farmers (Merriam 1886). The predatory status of these shrews was reinforced by the discovery that *B. brevicauda* possesses venom that kills rodents; observations of *B. brevicauda*–vole interactions under natural conditions (Maurer 1970); the high frequency of vole hair in *B. brevicauda* scats (i.e., 14–56% frequency—Eadie 1952); and meadow vole population declines on islands after *B. brevicauda* was introduced (Lomolino 1984).

However, studies mainly based on experiments with captives and trap-odor trials suggest that *B. brevicauda* has only a minor predatory role. In a collection of *B. brevicauda* stomachs from

New York, only 14 (3%) of 460 contained vole hair (Hamilton 1941). An experiment by Getz et al. (1992) determined that captive *B. brevicauda* could capture immobile nestlings, but not adult meadow voles. In another study, *B. brevicauda* only captured *Peromyscus* in cages with floor dimensions less than 50 × 30 cm (Rood 1958), suggesting that depredation in open terrain would be unlikely. Boonstra et al. (1982) found that meadow voles not only avoided traps containing *B. brevicauda*, but also those containing vole odor; the lack of a response only to shrew odor was considered evidence that *B. brevicauda* is not a threat.

However, Wolf and Batzli (2002) recently found that the white-footed mouse (*Peromyscus leucopus*) responded specifically to the presence of odor of *B. brevicauda* in traps. We suspect that the contradiction in response by the meadow vole and white-footed mouse to trap odor of *B. brevicauda* may be related to body size and a predator's ability to capture larger prey. *B. brevicauda* weighs 12–27 g, a weight similar to several small-mammal species such as the deer mouse (*Peromyscus maniculatus*; 12–30 g) and southern red-backed vole (*Clethrionomys gapperi*; 20–28 g), but lighter than adult *M. pennsylvanicus* (30–60 g—Banfield 1974). The debate on depredation by *B. brevicauda* has focused on *M. pennsylvanicus* but, in much of North America, *C. gapperi* is equally as abundant as *M. pennsylvanicus*. *C. gapperi* replaces *M. pennsylvanicus* in coniferous forests of eastern North America, the Appalachians and

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TABLE 1.—Capture success of *Blarina brevicauda*, *Peromyscus maniculatus*, and *Clethrionomys gapperi* in traps that had previously contained either a conspecific or an individual of a different species. Expected frequencies are based on proportion of total captures used in the analysis. Observed frequencies are significantly different than expected frequencies (see text).

	2nd Capture						Total
	<i>P. maniculatus</i>		<i>C. gapperi</i>		<i>B. brevicauda</i>		
	Observed	Expected	Observed	Expected	Observed	Expected	
1st Capture							
<i>P. maniculatus</i>	241	138.3	19	84.2	9	46.5	269
<i>C. gapperi</i>	32	96.1	148	58.5	7	32.3	187
<i>B. brevicauda</i>	21	59.6	12	36.3	83	20	116
Total	294		179		99		572

Rocky Mountains, and throughout coniferous forests of mainland Canada. Within the range of *B. brevicauda*, the 3 most common small-rodent species in these communities (*P. maniculatus*, *C. gapperi*, and *B. brevicauda*—Banfield 1974) are of similar weight.

If prey body size is an important factor in assessing the significance of *B. brevicauda* as a predator, we predict that small-rodent species similar in size to *B. brevicauda* will avoid their odor, whereas larger species will not. To test this prediction we used capture results from a research project conducted in northeastern North America. Consistent with Fulk (1972), Boonstra et al. (1982), and Wolf and Batzli (2002), we infer that a strong negative response to odor of *B. brevicauda* is indicative of prey response to a predator.

MATERIALS AND METHODS

Small-mammal livetrapping was conducted from 1996 to 1999 in the private industrial forest of Fraser Papers Inc., New Brunswick, Canada (47°N, 67°W). The site is located in the Appalachian Forest of the Acadian Forest Region (Rowe 1972), with upland areas dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), and lowland areas dominated by spruce–fir (*Picea–Abies balsamea*) forest.

Small-mammal capture data were collected from two 4,900-ha study sites. Data were gathered for 4 years in spring (May to early June) and autumn (September to early October) by using an array of 5 Victor Tin-Cat type traps (26 × 16 × 6 cm, 3 × 4-cm entrance, Woodstream Corp., Lititz, Pennsylvania) placed in a 50-m radius plot, with plots a minimum of 125 m apart. The trap array provides intensive sampling of animals in the plot; to assess avoidance of traps with different odor it is important that animals have a choice of traps and odors to enter. A single trap would limit opportunity for capturing numerous animals at each site. Tin-Cat traps are repeat-capture traps but our results are comparable to single-capture traps (i.e., Tomahawk traps, Tomahawk Live Trap Co., Tomahawk, Wisconsin), because multiple captures of different species per trap night were not included in the analysis. Traps were baited with oats for 3 days then set for 4 consecutive trapping nights. Trapped mammals were identified for species, sex, and reproductive condition; weighed; marked with a 1-g Monel ear tag (National Band and Tag Co., Newport, Kentucky); and released. The sex and age of live *B. brevicauda* were determined when possible. Capture and handling protocols follow guidelines of the

American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by the University of New Brunswick Animal Care Committee.

We followed the analytical methods that Wolf and Batzli (2002) used to test response by *P. leucopus* to odor of *B. brevicauda* in order to facilitate comparisons from our work on 2 related murid rodent species, *P. maniculatus* and *C. gapperi*. The methods are based on comparing the frequency of capture success for traps that captured mice or voles after capture of *B. brevicauda* to the frequency of capture for traps that captured mice or voles after capture of either murid rodent. We also tested the response by males and females and how long the effect of odor of *B. brevicauda* lasted over the 3-day trap period by comparing captures from traps that caught animals only on the 1st and 3rd days. We did not test for differences associated with reproductive condition.

We evaluated avoidance by *P. maniculatus* and *C. gapperi* of traps with odor of either species to determine whether the rodents specifically avoided shrews. Success in capturing mice or voles after capture of the other murid species was compared to trap success after a capture of a shrew. The relative frequency of capture data was used to determine expected number of captures.

Predictions were tested by using a chi-square test of independence. Contingency tables were used to test for dependence between the 2 variables, 1st capture and 2nd capture. Haber's correction for continuity was used for 2 × 2 tables (Wolf and Batzli 2002; Zar 1999). Significance level was set at alpha = 0.05.

RESULTS

Trap success.—A total of 20,808 trap nights resulted in 2,724 small-mammal captures. Eighty-eight percent of captures were of 3 species, deer mouse (38%), northern short-tailed shrew (25%), and red-backed vole (25%). There were 89 unsexed adults, 407 juvenile, 568 female, and 792 male captures of *P. maniculatus*, *C. gapperi*, and *B. brevicauda*. Shrews of the genus *Sorex*, woodland jumping mice (*Napaeozapus insignis*), rock voles (*Microtus chrotorrhinus*), southern bog lemmings (*Synaptomys cooperi*), short-tailed weasels (*Mustela erminea*), and *M. pennsylvanicus* also were captured, but were too uncommon to include in the analysis. Only data on traps with repeated captures of different individuals over the trap period were used, resulting in capture events for 294 *P. maniculatus* (51.4% of the analyzed sample), 179 *C. gapperi* (31.3%), and 99 *B. brevicauda* (17.3%).

Response to trap odor.—Examination of our data suggests a strong association of previous occupant and subsequent capture success, likely due to odor remaining between captures. Conspecifics were positively associated with previous trap occupancy; 82.5% of all subsequent captures were of the same species. A negative response to odor from a different murid species, or *B. brevicauda* was apparent for all 3 species (Table 1). Capture of *C. gapperi* was 77% lower than expected after capture of *P. maniculatus* ($\chi^2 = 250.30$, *d.f.* = 1, $P < 0.001$) and *P. maniculatus* was caught 67% less than expected after the capture of *C. gapperi* ($\chi^2 = 252.04$, *d.f.* = 1, $P < 0.001$).

Trap success after capture of B. brevicauda.—The null hypothesis of no effect of a 1st capture of *B. brevicauda* on a 2nd consecutive capture of *P. maniculatus* was rejected ($\chi^2 = 217.80$, *d.f.* = 1, $P < 0.001$). *P. maniculatus* was captured 65% less than expected after *B. brevicauda* had been in a trap.

TABLE 2.—Comparison of successful captures of *Peromyscus maniculatus* on 3rd trap night to occupancy of trap by *P. maniculatus* or *Blarina brevicauda* on 1st trap night. In order to determine length of effect on trap period, we only used traps that captured animals on 1st and 3rd trap nights (after no captures on the 2nd night). Observed frequencies differed significantly from expected frequencies (see text).

	2nd Capture (3rd day)				Total
	<i>P. maniculatus</i>		<i>B. brevicauda</i>		
	Observed	Expected	Observed	Expected	
1st Capture					
<i>P. maniculatus</i>	37	27.4	6	15.6	43
<i>B. brevicauda</i>	7	16.6	19	9.4	26
Total	44		25		69

C. gapperi also avoided traps with odor of *B. brevicauda* odor ($\chi^2 = 171.91, d.f. = 1, P < 0.001$), with 12 of an expected 36 voles (67% less) caught after the presence of shrew, compared to 148 of an expected 59 *C. gapperi* (153% more) captured after *C. gapperi* had been in the trap.

The response of *P. maniculatus* to odor of *C. gapperi* (67% less than expected) was similar to the response of *P. maniculatus* captured after *B. brevicauda* had been in the trap (65% less than expected). The response by *C. gapperi* to *P. maniculatus* (77% less than expected) was similar to their negative response to *B. brevicauda* (67% less than expected).

The effect of *B. brevicauda* on subsequent captures of *P. maniculatus* when there were no captures on day 2 was significant for 2 days after a capture of *B. brevicauda* ($\chi^2 = 22.02, d.f. = 1, P < 0.001$). Capture of *P. maniculatus* on the 1st day increased the number of captures of *P. maniculatus* on the 3rd day above expected, whereas capture of *B. brevicauda* on the 1st day reduced capture of *P. maniculatus* below expected on the 3rd day (Table 2). We could not measure effect on voles because of insufficient sample size. No difference due to sex was found for trap success of male compared to female *P. maniculatus* after a capture of *B. brevicauda* ($\chi^2 = 0.00, d.f. = 1, P = 0.999$), or for *C. gapperi* ($\chi^2 = 0.14, d.f. = 1, P < 0.75$; Table 3).

DISCUSSION

We found that the presence of odor of *B. brevicauda* influenced the subsequent capture of *P. maniculatus* and *C. gapperi* of both sexes. There was equal avoidance of strange odors by *P. maniculatus* and *C. gapperi*; mice and voles avoided traps having previously held a *B. brevicauda* to the same extent they avoided traps having held another murid species. Interpretation of such results is problematic because several factors can result in the same response. Does an avoidance of traps that smell of *B. brevicauda* imply that their smell represents a potential predator, or simply a strange odor? Similarly, equal avoidance of strange odors does not negate a predatory association; voles may avoid mouse odor to limit competition, but avoid odor of *B. brevicauda* to limit mortality risk. Therefore, we believe that the use of trap-odor response as a measure of predatory status requires caution. For example,

TABLE 3.—Comparison of captures of female and male *Peromyscus maniculatus* and *Clethrionomys gapperi* on the 2nd day after capture of the same species or of *Blarina brevicauda* on the 1st day. Observed frequencies do not differ significantly between sexes from expected frequencies.

	2nd Capture				Total
	Female		Male		
	Observed	Expected	Observed	Expected	
<i>Peromyscus maniculatus</i>					
1st Capture					
Same murid species	43	43.4	90	89.6	133
<i>B. brevicauda</i>	4	3.6	7	7.4	11
Total	47		97		144
<i>Clethrionomys gapperi</i>					
1st Capture					
Same murid species	42	42.8	65	64.2	107
<i>B. brevicauda</i>	4	3.2	4	4.8	8
Total	46		69		115

in a study by Wolf and Batzli (2002), the response to *B. brevicauda* by rodents was greater than to other rodents and, because small-rodent species typically avoid odors of known predators (Derting 1989; Jędrzejewski et al. 1992; Stoddart 1976), the implication is that *B. brevicauda* is a predator. However, it is possible the response is not due to *B. brevicauda* being a potential threat but because rodents generally avoid strange odors (Boonstra et al. 1982), and the odor of a shrew is more foreign than individuals of the same species or order. Results indicating that *B. brevicauda* is not a threat are similarly difficult to interpret; Boonstra et al. (1982) found that *M. pennsylvanicus* did not avoid traps with odor of *B. brevicauda*, but Lomolino (1984) determined that *B. brevicauda* caused the decline and extinction of *M. pennsylvanicus* on islands.

We also found that captures of all 3 species were positively associated with previous trap occupancy by conspecifics. This likely indicates some degree of conspecific odor attraction, similar to the finding of Wolf and Batzli (2002), but it may also reflect a habitat effect. If a local site is good habitat for *C. gapperi*, there should be a higher probability of consecutive captures of *C. gapperi* at that site. Similarly, this same habitat effect could produce the appearance of heterospecific odor avoidance. We suggest that the best way to test for odor effects on trap success is through experimentally controlled conditions. For example, Powell and Banks (2004) recently conducted an experiment that demonstrated no avoidance of odor of red fox (*Vulpes vulpes*) by house mice (*Mus musculus*).

Accounts of predation on captive voles by *B. brevicauda* suggest that it is an inconsistent predator. The influence of body size may partially explain contradictory results on the role of *B. brevicauda* as a significant predator of small mammals. Large prey items (species or individuals) defended themselves or were not attacked when encountering *B. brevicauda*, and did not avoid odor of *B. brevicauda*. For example, Getz et al. (1992) recorded that large individuals of *M. pennsylvanicus* and all prairie voles (*M. ochrogaster*; 25–55 g) aggressively defended

themselves when *B. brevicauda* approached. Predation by *B. brevicauda* on smaller individual *M. pennsylvanicus* was more certain; for example, shrews attacked and ate juvenile *M. pennsylvanicus* (Getz et al. 1992; Lomolino 1984). Similar relationships of size between rodent and predator have been recorded for weasels. In trials with captive animals, predation by the least weasel (*Mustela nivalis*) was unsuccessful on adults (50–54 g) but always lethal for the smaller or lighter-weight pine voles (*M. pinetorum* 25 g—Derting 1989). The influence of body size is supported by odor-response studies; residual odor of *B. brevicauda* appears to have an influence on smaller rodent species (Wolf and Batzli 2002), but less so on rodent species larger than *B. brevicauda* (Boonstra et al. 1982).

We suggest that the significance of *B. brevicauda* as a predator should be assessed by using body size of the prey. Based on conclusions from a variety of studies (on stomach content, trap response, captive trials, and population studies), it is likely that *B. brevicauda* is generally a minor predator on adult *Microtus* species, occasionally a significant predator on juvenile *Microtus*, and of unknown significance on *Peromyscus* species and small voles such as species of *Clethrionomys*. We predict that the influence of *B. brevicauda* on prey populations would be greater in forested than in grassland systems because *B. brevicauda* is of similar weight to the 2 common rodents in northeastern forests. In grassland systems, *M. pennsylvanicus* is abundant and likely less influenced by the presence of *B. brevicauda*.

Our results suggest that the presence of heterospecific odor does significantly reduce capture of small-rodent species. Numerous variables in species being trapped, such as breeding condition, sex, and dominance, are known to influence trap success (e.g., Daly et al. 1980; Tew 1987). In our study, avoidance of strange odors reduced the subsequent trap success of 3 common species, and this occurred for up to 2 days (for *P. maniculatus*). This could produce a biased detection probability for some small-mammal species, especially where the sampling scheme has an inadequate number of traps or occurs over an inadequate number of nights. The average trapping period for small-mammal research projects is 4 trapping nights per trapping session (Bowman et al. 2001), suggesting that the bias caused by strange odor could occur in any given trap for 50% of trap nights. Also, the bias may not be consistent between years; periodic variation in population density could mean that higher capture success of a given small-mammal species over time may partly be a result of low heterospecific density, rather than an increase in the sampled population. Maintaining an adequate sampling effort would seem to be the best strategy for avoiding this potential source of bias.

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