

Eavesdropping of woodchucks (*Marmota monax*) and eastern chipmunks (*Tamias striatus*) on heterospecific alarm calls

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Individuals of 1 species might obtain information by eavesdropping on calls produced by a syntopic species. Intercepting alarm calls allows the eavesdropper to respond with antipredator behavior without the need to produce its own call, which might attract the attention of a predator. We examined eavesdropping on heterospecific alarm calls by nonsocial eastern chipmunks (*Tamias striatus*) and woodchucks (*Marmota monax*), which live in the same community, share some predators, are solitary, and produce distinct alarm calls. If these 2 species recognize heterospecific alarm calls, we should see antipredator behaviors similar to those displayed upon hearing a conspecific's alarm call. We broadcast single alarm calls of woodchucks, eastern chipmunks, and American crows (*Corvus brachyrhynchos*) to individuals of the first 2 species, using the territorial song of the syntopic male black-capped chickadee (*Poecile atricapillus*) as a control. Woodchucks became more vigilant after hearing both conspecific and heterospecific alarm calls compared with controls; however, they spent more time vigilant in response to conspecific alarm calls compared to heterospecific alarm calls. Thus, woodchucks apparently can recognize heterospecific alarm calls, but they appear to process conspecific and heterospecific calls differently. Eastern chipmunks responded to heterospecific alarm calls, but sample sizes were small and the results not definitive. Our results suggest that nonsocial mammals might benefit from eavesdropping on heterospecifics.

Key words: American crows, communication, eastern chipmunks, heterospecific eavesdropping, *Marmota monax*, *Tamias striatus*, woodchucks

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Communication involves a sender providing information in the form of a signal to a receiver and subsequent use by the receiver of that information in deciding how to respond (Bradbury and Vehrencamp 1998). If a signal travels farther than the average spacing between individuals, several individuals have the opportunity to communicate with each other, forming a communication network. Evidence is mounting that communication networks can be complex, with many individuals of different species potentially participating as signalers and receivers (Peake et al. 2005).

Eavesdropping, which involves an individual intercepting a signal from another individual, becomes possible in communication networks, whereby the eavesdropper can benefit from the information in signals (Peake 2005). Because alarm calls are conspicuous and create public information regarding risk, eavesdropping individuals located nearby potentially can intercept the calls (Templeton and Greene 2007). If animals accrue some advantage by intercepting information encoded in alarm calls, eavesdropping behavior could be favored (Peake

2005). Animals that successfully eavesdrop can identify and interpret heterospecific alarm calls as information denoting the presence of a predator, and they can respond to such calls with increased antipredator behaviors. Eavesdropping on alarm calls of nearby individuals might allow eavesdroppers to manage time allocated to daily activities and avoid predators, which can be of significant survival value (Dolby and Grubb 1998; Sullivan 1984b). Also, because eavesdropping prevents the need to produce calls, eavesdroppers do not reveal their location to predators, which might reduce the chances of being killed. In a community where 2 or more species share a predator in common and at least 1 of these species produces alarm calls, the ability to recognize and interpret a signaler's warning can benefit an eavesdropper.



Several studies have demonstrated heterospecific recognition of alarm calls between species in the same class (Magrath et al. 2007; Templeton and Greene 2007), and other researchers have studied eavesdropping between species from different classes (Lea et al. 2008; Rainey et al. 2004; Seyfarth and Cheney 1990). Primates, with their high cognitive abilities, eavesdrop on alarm calls of heterospecifics of the same class and heterospecifics of different classes (Eckardt and Zuberbühler 2004; Seyfarth and Cheney 1990). Some studies, especially those that involve mixed groups, demonstrate that individuals in 1 species eavesdrop on alarm calls of 2 or more species (Ramakrishnan and Coss 2000; Sullivan 1984a). Most studies of eavesdropping show social species as both alarm callers and eavesdroppers. Evolution of social complexity is associated with large alarm call repertoire (Blumstein and Armitage 1997). Therefore, because social species possess large alarm call repertoires, social species are more likely than asocial species to respond to heterospecific alarm calls (Lea et al. 2008).

Although research on eavesdropping has focused on social species, nonsocial species can aggregate or share overlapping home ranges, and thus they could benefit from eavesdropping on alarm calls (Lea et al. 2008; Randler 2006). However, some studies of eavesdropping in nonsocial species reported on unmarked individuals such that the same animals could have received call stimuli on multiple occasions and become habituated (Schmidt et al. 2008). Other researchers used calls from a single individual as the stimulus such that eavesdroppers might have responded only to that individual and not to the species as a whole (Kroodsma 1989; Vitousek et al. 2007).

To determine if nonsocial species eavesdrop on heterospecifics from the same and different taxa we measured responses of woodchucks (*Marmota monax*) and eastern chipmunks (*Tamias striatus*) to alarm calls of each species and to alarm calls of the American crow (*Corvus brachyrhynchos*). Both woodchucks and chipmunks are considered solitary yet live in aggregations (Clarke et al. 1993; Meier 1992), and they produce alarm calls (Dunford 1970; Lloyd 1972). We observed individually marked animals and used multiple exemplars of calls. If woodchucks and eastern chipmunks recognize heterospecific alarm calls as information denoting the presence of a predator, both species should exhibit antipredator behaviors similar to those displayed upon hearing the alarm call of a conspecific.

MATERIALS AND METHODS

Study site and populations.—We conducted this study at Gilsland Farm (43°42'N, 70°14'W), a 26-ha wildlife preserve located in Falmouth, Maine. This site contains salt marsh, mixed coniferous–hardwood forest, and 3 meadows that measure 2.4, 3.5, and 6.0 ha. The sanctuary is bordered by the Presumpscot River estuary to the west, United States Route 1 to the east, salt marsh to the north, and housing developments to the north, south, and east. Woodchucks, eastern chipmunks, American crows, and black-capped

chickadees (*Poecile atricapillus*) commonly occur at this site. Predators of eastern chipmunks, woodchucks, and crows that occasionally reside at Gilsland Farm include red-tailed hawks (*Buteo jamaicensis*), bald eagles (*Haliaeetus leucocephalus*), and red foxes (*Vulpes vulpes*).

Trapping and handling.—We used live traps (Tomahawk Live Trap; Tomahawk Live Trap Co., Tomahawk, Wisconsin; woodchucks: 20 × 30 × 81 cm, and eastern chipmunks: 5 × 5 × 16 cm) baited with apples and peanut butter to capture juvenile and adult woodchucks and eastern chipmunks. We trapped only during daylight hours and monitored traps hourly. Upon capture, the individual was transferred to a cone-shaped handling bag. We determined sex using anogenital distance. To each individual we applied a unique dye mark using black hair dye (Clairol Balsam Color; Clairol Inc., Stamford, Connecticut), which allowed us to identify and observe animals from a distance. We also placed a numbered metal ear tag (National Band and Tag Company, Newport, Kentucky; size 1005-1 for eastern chipmunks, 1005-3 for woodchucks) in each ear to provide a permanent identification mark. We then released the animal at the location where it was caught. We periodically retrapped animals to reapply dye marks lost due to molt. All procedures followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Southern Maine Institutional Animal Care and Use Committee (121807-01).

Playback recordings.—One of us (LMA) made all recordings using a Sennheiser ME-88 microphone (Sennheiser Electronic Co., Old Lyme, Connecticut) and a digital audio tape deck (Sony PCM-M1; Sony Electronics Inc., San Diego, California). We recorded alarm calls from woodchucks ($n = 8$ animals; mean call length $\pm SE = 0.66 \pm 0.05$ ms), eastern chipmunks ($n = 9$ animals, call length = 0.27 ± 0.05 ms), and crows ($n = 4$ animals, call length = 0.30 ± 0.03 ms) during March–May 2008 from free-living animals of each species calling in response to a natural stimulus or to an approaching human. We obtained territorial songs of male, free-living black-capped chickadees ($n = 4$ birds, song length = 0.97 ± 0.13 ms) resident at Gilsland Farm, which served as controls. We used multiple recordings of each species' call because the recorded song or call of 1 individual is not representative of the entire population and because recordings vary in quality (Kroodsma 1989). Using Cool Edit Pro 2.1 (Syntrillium Software, Phoenix, Arizona), we digitized all recordings onto a laptop computer (Gateway, Irvine, California) and transferred them to an iPod (Apple Inc., Cupertino, California) for use in the playback experiments.

Playback experiments.—In separate, counterbalanced trials we presented 13 woodchucks (2 yearlings and 11 adults) and 5 eastern chipmunks (unknown ages) with a total of 4 playback conditions: a woodchuck alarm call, an eastern chipmunk alarm call, an American crow alarm call, and a territorial song of a male black-capped chickadee. Each playback was presented alone and chosen in random order from May through August 2008. Each playback consisted of a single alarm call or song. Weather conditions varied from sunny to

overcast; however, if high winds or rain were forecast, we did not run trials on that day. Four chipmunks, which were exposed to playbacks of some but not all species, also were included in an analysis with the 5 chipmunks that received all playbacks. We selected individuals engaged in foraging activity. If the individual had already heard the playback, we looked for another individual that was foraging and set up the video camera and iPAL speaker system (Tivoli Audio, LLC., Boston, Massachusetts) 15–20 m from the individual's location. We then began to video record its activity as our means of data collection. We broadcast playbacks using an iPod and an iPAL speaker system. For woodchucks, after 2 min during which we heard no alarm calls (the preplayback interval), we broadcasted 1 playback. If the focal individual did not flee after we played the call, we continued to record it on video for an additional 2 min (the postplayback interval). Because chipmunks only spend, on average, 1 min at a feeding location (Weary and Kramer 1995), to insure the recording of both pre- and postplayback conditions we reduced preplayback and postplayback periods from 2 min to 1 min for chipmunks. Because chipmunks collect food and store it in their burrows, if the chipmunk retreated to its burrow during the preplayback interval, we assumed it made a caching trip. We suspended the trial and then continued recording when it resumed foraging. Woodchucks do not cache food, so we did not suspend trials in this way. If the focal individual (woodchuck or chipmunk) fled after playback but resumed foraging during the postplayback interval, we continued to collect data for the remainder of the trial. To minimize risk of habituation to experimental calls we conducted only 1 trial of each call type of each species per day. Once an individual was exposed to a call it did not receive another call for at least 24 h. If >1 individual was present during the playback, we noted all individuals present; however, we recorded the response of only 1 individual to the playback.

Data collection.—We analyzed responses to playbacks using video recordings, with frame-by-frame analysis (25 frames/s) of the 1- to 2-min preplayback interval, the playback, and the 1- to 2-min postplayback interval. For each trial we recorded the type of response to the call (flee, look up, or no response). Using JWatcher 1.0 (Blumstein and Daniel 2007), one of us (LMA) quantified the amount of time each individual allocated to vigilance, which we considered to represent a form of antipredator behavior whereby an animal can examine the area for potential threats. For both woodchucks and chipmunks we defined any movement toward a refuge and any upright posture accompanied by scanning or staring as vigilance. Also, if animals ran to cover after a playback, we considered the time that the individual spent in cover as time spent vigilant.

To compare responses to different alarm calls, we measured time to initial response, that is, time from the start of the playback to the initial antipredator behavior, and duration of that initial response, that is, time from the start of the initial antipredator behavior to the time at which the focal animal resumed foraging. We also recorded time spent vigilant in the preplayback and postplayback intervals and calculated the

TABLE 1.—Types of antipredator responses to playbacks (alarm calls and control call) for woodchucks (*Marmota monax*; $n = 13$) and eastern chipmunks (*Tamias striatus*; $n = 5$). Numbers correspond to number of animals making that response. Control = black-capped chickadee territorial call.

Call type	Woodchucks			Chipmunks		
	Flee	Look	No response	Flee	Look	No response
Woodchuck	7	6	0	1	4	0
Chipmunk	0	13	0	1	4	0
Crow	0	12	1	0	5	0
Control	0	11	2	0	5	0

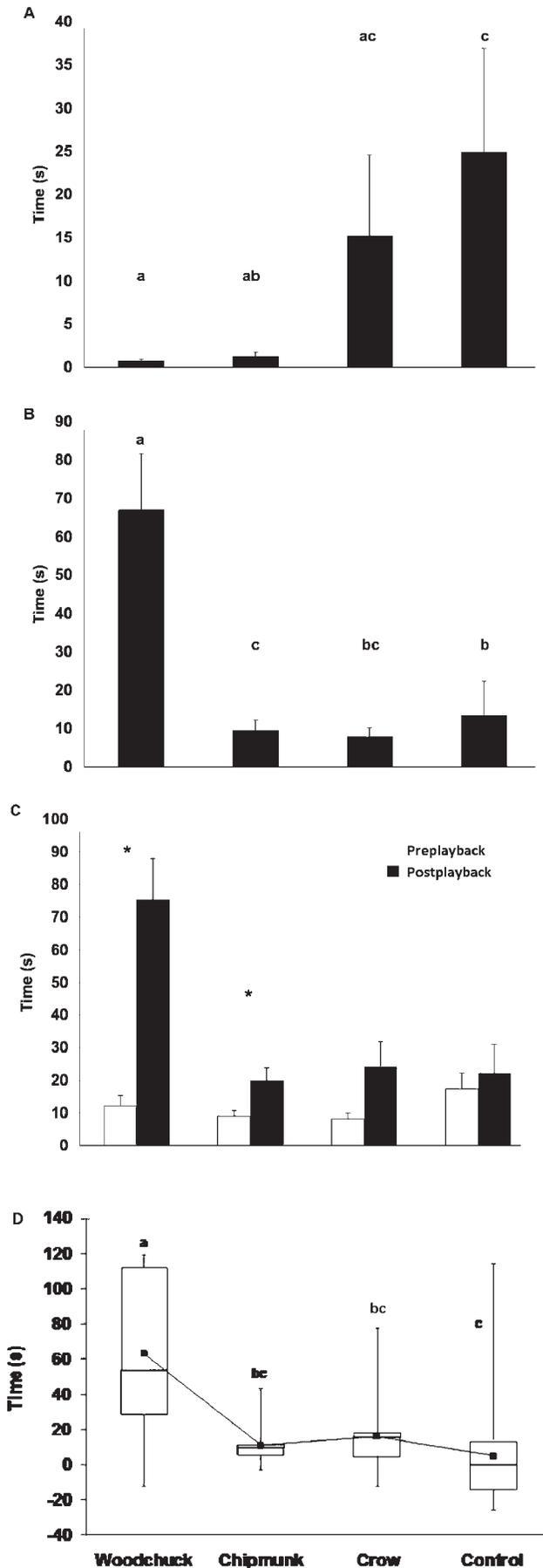
difference in vigilance by subtracting time spent vigilant before from time spent vigilant after the playback.

Data analyses.—To test for differences in types of responses depending on call type we conducted chi-square tests for woodchucks and for chipmunks. Data from woodchucks and chipmunks that received all 4 playbacks were analyzed using nonparametric Friedman tests (χ^2) to test for differences in time to initial response, duration of initial response, time spent vigilant before playback, time spent vigilant after playback, and difference in vigilance among call types. Data from chipmunks that received at least 1 playback were analyzed using nonparametric Kruskal–Wallis tests (H) to test for differences in time to initial response, duration of initial response, time spent vigilant before playback, time spent vigilant after playback, and difference in vigilance among call types. Wilcoxon signed-rank tests (Z) were carried out when Friedman tests indicated significant differences. We also conducted sequential Bonferroni corrections for multiple comparisons. Data were analyzed using SPSS 17.0 (SPSS, Inc., Chicago, Illinois) or JMP 7 (SAS Institute, Inc., Cary, North Carolina). All tests were 2-tailed. The criterion for statistical significance was $P < 0.05$ for all tests.

Using Microsoft Excel (Microsoft Corp., Redmond, Washington) we calculated effect sizes, which measure the strength of the relationship between 2 variables, and 95% confidence intervals (95% CIs) for time to initial response, duration of initial response, time spent vigilant before playback, time spent vigilant after playback, and total change in vigilant behavior among call types. If the 95% CI includes 0, no significant difference between the 2 means exists. Using R 2.9.1 (The R Foundation for Statistical Computing; <http://cran.case.edu/>), we ran a Monte Carlo analysis with 1,000 iterations to test whether vigilance of woodchucks and chipmunks before playbacks differed from vigilance after playbacks. For Monte Carlo analysis, the criterion for statistical significance was $P < 0.05$.

RESULTS

Woodchucks.—Woodchucks showed different antipredator responses depending on call type ($\chi^2_6 = 27.43$, $P = 0.001$; Table 1). Although they looked up in response to most playbacks, they fled only upon hearing woodchuck alarm calls.



Time to initial response differed among treatments ($\chi^2_3 = 19.00, P < 0.001$). Woodchucks responded faster to their own alarm calls and to eastern chipmunk alarm calls than to crow alarm calls and control calls, although the difference between responses to woodchuck and crow alarm calls was not significant after correction for multiple comparisons (woodchuck alarm call versus control call: $Z = -3.18, P = 0.001$; chipmunk alarm call versus control call: $Z = -2.76, P = 0.006$; woodchuck alarm call versus crow alarm call: $Z = -2.28, P = 0.023$; Fig. 1A).

Woodchucks differed in duration of initial response to playbacks ($\chi^2_3 = 18.14, P < 0.001$; Fig. 1B). Woodchucks remained vigilant longer after woodchuck alarm calls than after eastern chipmunk alarm calls, crow alarm calls, or control calls (woodchuck versus chipmunk: $Z = -2.69, P = 0.007$; woodchuck versus crow: $Z = -2.97, P = 0.003$; woodchuck versus control: $Z = -2.83, P = 0.005$; Fig. 1B).

The amount of time that woodchucks spent vigilant before playbacks did not vary among call types ($\chi^2_3 = 1.15, P = 0.76$; Fig. 1C). However, the amount of time that woodchucks spent vigilant after playbacks differed among call types, such that woodchucks spent more time vigilant following the playback of conspecific alarm calls than heterospecific or control calls ($\chi^2_3 = 16.11, P = 0.001$; Fig. 1C).

Woodchucks significantly increased postplayback vigilance following playbacks of conspecific and chipmunk alarm calls, whereas vigilance did not differ before and after hearing the control call (woodchuck alarm calls: $Z = -2.97, P = 0.003$; chipmunk alarm calls: $Z = -2.90, P = 0.004$; control calls: $Z = -0.38, P = 0.70$; Monte Carlo analysis: woodchuck alarm calls: mean difference = $-63.14, 95\% CI = -88.49$ to $-38.68, P = 0.001$; chipmunk alarm calls: mean difference = $-11.05, 95\% CI = -17.71$ to $-5.26, P = 0.001$; control calls: mean difference = $-4.91, 95\% CI = -24.93$ to $9.77, P = 0.69$; Fig. 1C). Responses to crow alarm calls did not differ after correction for multiple comparisons (crow alarm calls: $Z = -2.20, P = 0.028$; Monte Carlo analysis: crow alarm calls: mean difference = $-15.96, 95\% CI = -28.95$ to $-4.35, P = 0.028$).

Difference in vigilance also differed among call types ($\chi^2_3 = 23.77, P < 0.001$; Fig. 1D). Difference in vigilance in response to conspecific alarm calls changed significantly compared to difference in vigilance after playbacks of heterospecific alarm calls and control calls (woodchuck alarm call versus chipmunk alarm call: $Z = -2.62, P = 0.009$;

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FIG. 1.—Mean \pm SE responses to playbacks of alarm calls or control calls by woodchucks (*Marmota monax*; $n = 13$). A) time to initial antipredator response, B) duration of initial response, C) time spent vigilant preplayback (white bars) and postplayback (black bars), and D) difference in vigilance among call types, by woodchucks. Box plots show median and interquartile range from 25th to 75th percentiles. Whiskers above and below the box indicate minimum and maximum values. ■ indicates mean difference in vigilance for each call type. Different letters indicate significant differences among call types based on Wilcoxon signed-rank tests.

TABLE 2.—Mean ± SE responses (in s) exhibited by eastern chipmunks (*Tamias striatus*) to playback calls. Top rows of data for each response type indicate responses from chipmunks that received all 4 playback types. Bottom rows indicate responses from chipmunks that received at least 1 playback type. Control = black-capped chickadee territorial call.

Response	<i>n</i>	Woodchuck alarm	Chipmunk alarm	Crow alarm	Control
Time to initial response	5	0.60 ± 0.16	2.05 ± 1.11	1.80 ± 0.88	1.17 ± 0.37
	9	1.11 ± 0.51	1.38 ± 0.64	10.78 ± 5.37	6.75 ± 3.98
Duration of initial Response	5	9.78 ± 5.94	5.34 ± 2.28	5.13 ± 2.57	5.06 ± 1.37
	9	19.69 ± 7.78	11.35 ± 6.17	4.49 ± 1.50	5.63 ± 1.99
Vigilance before playback	5	11.58 ± 2.93	8.54 ± 3.09	12.43 ± 4.93	17.00 ± 9.95
	9	7.35 ± 2.34	5.83 ± 2.06	9.49 ± 3.71	10.11 ± 5.23
Vigilance after playback	5	29.05 ± 15.21	25.82 ± 11.30	17.70 ± 8.95	8.99 ± 3.10
	9	35.61 ± 8.99	23.60 ± 8.08	11.69 ± 5.31	14.48 ± 6.03
Difference in vigilance	5	17.47 ± 16.42	17.28 ± 11.28	5.26 ± 11.14	-8.01 ± 10.51
	9	28.25 ± 10.31	17.77 ± 8.22	2.19 ± 6.59	4.37 ± 8.91

woodchuck alarm call versus crow alarm call: $Z = -2.83$, $P = 0.005$; woodchuck alarm call versus control call: $Z = -3.18$, $P = 0.001$; Fig. 1D). Difference in vigilance in response to crow alarm calls did not change significantly compared to control calls after correction for multiple comparisons ($Z = -2.27$, $P = 0.023$; Fig. 1D).

Chipmunks.—Eastern chipmunks usually looked up in response to a playback; however, they did not differ significantly in their types of antipredator responses to different call types ($\chi^2_6 = 1.13$, $P = 0.77$; Table 1).

Eastern chipmunks did not differ in time to initial response among treatments ($\chi^2_3 = 0.36$, $P = 0.95$; Table 2). Furthermore, when we included in the analysis all eastern chipmunks that had received at least 1 playback, time to initial response still did not differ ($H_3 = 4.04$, $P = 0.26$; Table 2). However, effect sizes indicated that the larger sample of eastern chipmunks (includes all chipmunks that received at least 1 playback) responded faster to conspecific and woodchuck alarm calls than to crow alarm calls and control calls (Table 3).

Eastern chipmunks did not differ in duration of initial response following any of the 4 playbacks ($\chi^2_3 = 0.36$, $P = 0.95$; Table 2). With a larger sample that included all eastern chipmunks that had received at least 1 playback, duration still did not differ among treatments ($H_3 = 2.04$, $P = 0.57$;

Table 2). However, effect sizes indicated that chipmunks remained vigilant for a longer duration following conspecific and woodchuck alarm calls than after crow alarm calls and control calls, and they also remained vigilant longer following woodchuck alarm calls than after conspecific alarm calls (Table 3).

Eastern chipmunks did not differ in time spent vigilant before playbacks among call types ($\chi^2_3 = 0.60$, $P = 0.90$; Table 2). When we included in the analysis all chipmunks that had received at least 1 playback ($n = 9$), chipmunks did not differ in total vigilance before playbacks among call types ($H_3 = 0.23$, $P = 0.97$; Table 2). Effect sizes indicated that chipmunks in the larger sample were more vigilant before playbacks of conspecific alarm calls than before control calls and crow alarm calls (Table 3).

Eastern chipmunks did not differ in time spent vigilant following any of the 4 playbacks ($\chi^2_3 = 1.08$, $P = 0.78$; Table 2). When we included all chipmunks, they still did not differ in total time spent vigilant following all playback types ($H_3 = 0.23$, $P = 0.97$; Table 2). However, effect sizes indicated that with the larger sample of chipmunks vigilance was greater after playbacks of woodchuck alarm calls than after conspecific alarm calls, crow alarm calls, and control calls and after playbacks of conspecific alarm calls than after crow alarm calls (Table 3).

TABLE 3.—Effect sizes (lower 95% confidence limit, upper 95% confidence limit) for different pairwise comparisons of responses of eastern chipmunks (*Tamias striatus*) to playbacks of alarm and control calls. Boldface values represent significant differences ($P < 0.05$) between mean values. Control = black-capped chickadee territorial call.

Response	<i>n</i>	Pairwise comparison					
		Woodchuck–chipmunk	Woodchuck–crow	Woodchuck–control	Chipmunk–crow	Chipmunk–control	Crow–control
Time to initial response	5	0.81 (−0.55, 0.85)	0.85 (−0.51, 2.06)	0.87 (−0.50, 2.07)	0.11 (−1.14, 1.36)	0.48 (−0.82, 1.68)	0.43 (−0.87, 1.63)
	9	0.47 (−0.49, 1.38)	2.54 (1.20, 3.63)	1.99 (0.78, 3.00)	2.46 (1.14, 3.54)	1.88 (0.70, 2.89)	0.85 (−0.15, 1.77)
Duration of initial response	5	0.44 (−0.85, 1.65)	0.45 (−0.84, 1.66)	0.49 (−0.81, 1.70)	0.04 (−1.21, 1.27)	0.07 (−1.18, 1.30)	0.02 (−1.22, 1.25)
	9	1.19 (0.14, 2.13)	2.71 (1.33, 3.83)	2.48 (1.16, 3.56)	1.53 (0.42, 2.49)	1.25 (0.19, 2.19)	0.65 (−0.33, 1.56)
Duration of preplayback vigilance	5	0.45 (−0.84, 1.66)	0.42 (−0.87, 1.63)	0.33 (−0.95, 1.54)	0.09 (−1.16, 1.32)	0.42 (−0.87, 1.63)	0.26 (−1.01, 1.48)
	9	0.69 (−0.29, 1.61)	0.69 (−0.29, 1.61)	0.68 (−0.30, 1.60)	1.22 (0.16, 2.16)	1.08 (0.04, 2.01)	0.137 (−0.80, 1.06)
Duration of postplayback vigilance	5	0.11 (−1.14, 1.34)	0.41 (−0.88, 1.62)	0.82 (−0.54, 2.02)	0.36 (−0.93, 1.57)	0.91 (−0.47, 2.12)	0.59 (−0.73, 1.79)
	9	1.41 (0.32, 2.36)	1.28 (0.21, 2.22)	2.76 (1.37, 3.89)	1.76 (0.60, 2.74)	0.91 (−0.47, 2.12)	0.51 (−0.45, 1.42)
Difference in vigilance	5	0.01 (−1.23, 1.24)	0.38 (−0.90, 1.60)	0.83 (−0.54, 2.03)	0.47 (−0.83, 1.68)	1.04 (−0.37, 2.24)	0.36 (−0.93, 1.57)
	9	1.12 (0.08, 2.06)	3.01 (1.55, 4.18)	2.48 (1.16, 3.56)	2.09 (0.86, 3.12)	1.56 (0.44, 2.53)	0.28 (−0.66, 1.19)

After playbacks of conspecific and heterospecific alarm calls eastern chipmunks displayed no difference in time spent vigilant compared to time spent vigilant before each playback (woodchuck alarm calls: mean difference = -17.47 , 95% *CI* = -49.57 to 7.43 , $P = 0.38$; chipmunk alarm calls: mean difference = -17.28 , 95% *CI* = -37.48 to 0.98 , $P = 0.27$; crow alarm calls: mean difference = -5.26 , 95% *CI* = -27.30 to 11.18 , $P = 0.63$; control calls: mean difference = 8.01 , 95% *CI* = -4.59 to 29.23 , $P = 0.63$; Table 2). We also found no differences when analyzing the larger sample (woodchuck alarm calls: mean difference = -4.33 , 95% *CI* = -11.60 to 0.76 , $P = 0.54$; chipmunk alarm calls: mean difference = -8.65 , 95% *CI* = -20.97 to -0.23 , $P = 0.17$; crow alarm calls: mean difference = -14.11 , 95% *CI* = -29.23 to -1.31 , $P = 0.16$; control calls: mean difference = 2.75 , 95% *CI* = -4.68 to 14.69 , $P = 0.80$; Table 2).

Eastern chipmunks showed no significant differences in vigilance among call types ($\chi^2_3 = 0.36$, $n = 5$, $P = 0.98$; $H_3 = 3.47$, $n = 9$, $P = 0.33$; Table 2). However, effect sizes indicated that chipmunks had a greater overall change in vigilance with woodchuck alarm calls than with conspecific alarm calls, crow alarm calls, and control calls, and they were more vigilant after playbacks of conspecific alarm calls than after control calls and crow alarm calls (Table 3).

DISCUSSION

Woodchucks and eastern chipmunks did not respond to heterospecific alarm calls with antipredator behaviors similar to those exhibited after playbacks of conspecific alarm calls. Woodchucks became more vigilant following playbacks of alarm calls compared to preplayback vigilance, but they spent more time vigilant following playbacks of conspecific alarm calls compared to heterospecific alarm calls. Furthermore, the difference in vigilance did not change between heterospecific alarm calls and control calls. Thus, individuals might respond to heterospecific alarm calls, but responses are not similar to those exhibited after conspecific alarm calls.

Although time to initial response of a woodchuck following a woodchuck alarm call was similar to that following a chipmunk alarm call, woodchucks did not show similarities in duration of initial response and difference in vigilance. Thus, woodchucks might recognize chipmunk alarm calls but do not interpret them as immediate danger. Humans frequently visit Gilsland Farm, a wildlife sanctuary, and most woodchucks are habituated to humans (L. M. Aschemeier, pers. obs.), which can lead to decreased antipredator behavior (Griffin et al. 2007; McCleery 2009). Anecdotally, we noted that chipmunks produce alarm calls more frequently than woodchucks (L. M. Aschemeier, pers. obs.), possibly because the smaller size of chipmunks increases their vulnerability to predators. All woodchucks in this study responded to chipmunk alarm calls by ceasing foraging and looking up. Perhaps, following the broadcast of a chipmunk alarm call, woodchucks looked up and assessed the situation, and upon seeing a human, recognized no immediate danger and returned to foraging.

Alternatively, woodchucks might have habituated to eastern chipmunk alarm calls and reduced their antipredator responses (Seyfarth and Cheney 1990).

Eastern chipmunks did not show significant differences in time to initial response, duration of initial response, time spent vigilant after playback, and difference in vigilance among call types. Samples sizes for the full sequences of calls suffered because of disappearance of many individuals before the full series could be completed. However, when we examined effect sizes using all chipmunks, we found that chipmunks responded faster to conspecific and woodchuck alarm calls, remained vigilant longer following conspecific and woodchuck alarm calls, and increased postplayback vigilance following woodchuck and conspecific alarm calls compared to preplayback vigilance.

Different call lengths could explain different responses to call stimuli in woodchucks and chipmunks. Single alarm calls from eastern chipmunks and crows are shorter in length than single alarm calls from woodchucks and control calls. Attempts to equalize call lengths would distort species' alarm calls; therefore, use of another control call similar in length to chipmunk and crow alarm calls could benefit future studies. However, recent studies suggest that heterospecific recognition of alarm calls is not due to acoustic similarities but to understanding of call structure, which suggests that animals must learn to recognize heterospecific calls as alarms (Magrath et al. 2009). For woodchucks and eastern chipmunks to associate both conspecific and heterospecific alarm calls with danger, they must associate the alarm call with a predator.

To conclude, our study adds to the growing body of literature documenting that nonsocial species, and not just social species, eavesdrop on alarm calls of heterospecifics. Nonetheless, woodchucks did not respond to heterospecific alarm calls to the same magnitude that they responded to conspecific alarm calls, suggesting that woodchucks process alarm calls differently, depending on the source. Data on responses of chipmunks were less clear, although effect sizes suggest that chipmunks also respond to heterospecific alarm calls. Individuals might need to learn the meaning of heterospecific alarm calls to respond to them, but the frequency of heterospecific alarm calls at Gilsland Farm could result quickly in habituation and affect the ability to learn such meaning and the appropriate responses. Additional studies of communication networks involving less social species can further our understanding of cognitive ability in these species and antipredator benefits gained from eavesdropping.

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