

Use of predator hair to enhance perceived risk to white-tailed deer in a foraging context

THOMAS W. SEAMANS, USDA, APHIS, Wildlife Services' National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870, USA thomas.w.seamans@APHIS.USDA.gov

BRADLEY F. BLACKWELL, USDA, APHIS, Wildlife Services' National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870, USA

KIMBERLY E. LINNELL¹, USDA, APHIS, Wildlife Services' National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870, USA

Abstract: Deer react to predator scent in varying degrees even when exposed to unknown predators. This response could be genetically based and maintained as long as the population is exposed to predation. We tested whether predator scent in the form of hair would enhance perceived risk and serve as a foraging repellent to free-ranging white-tailed deer (*Odocoileus virginianus*). During the winters of 2013 and 2014, we quantified alert behaviors and consumption of whole-kernel corn in response to current (coyote [*Canis latrans*]) and extirpated (bobcat [*Lynx rufus*]; black bear [*Ursus americanus*]) predator species alone and in combination with a partial visual barrier. Due to changes in herd dynamics and weather conditions, we did not compare results between years. We found enhanced alert behavior in all experiments except the 2014 exposure to coyote hair. Alert behaviors were heightened for about 4 days after hair placement. However, corn consumption was reduced only in the 2013 coyote-hair experiment. Our results suggest predator hair, when used alone and in conjunction with a form of visual barrier, can provide an element of protection from deer damage, but energetic needs will override the enhanced perceived risk caused by predator hair. Further work integrating complete visual barriers with predator hair is warranted.

Key words: black bear, bobcat, *Canis latrans*, coyote, landscape of fear, *Lynx rufus*, *Odocoileus virginianus*, predation, *Ursus americanus*, white-tailed deer

WHITE-TAILED DEER (*Odocoileus virginianus*) populations in North America have grown from a low of <2 million to about 30 million (McCabe and McCabe 1997, VerCauteren et al. 2011). Current deer population levels in the United States contribute to human–wildlife conflicts via habitat degradation (Waller and Alverson 1997), agricultural damage (Humberg et al. 2007), heightened levels of zoonosis (VerCauteren et al. 2007, Conover and Vail 2015), property damage (Conover et al. 1995, Conover 1997), and an increasing frequency of deer–vehicle collisions (Conover et al. 1995, D'Angelo et al. 2004, Blackwell and Seamans 2009, Biondi et al. 2011). Although a wide variety of efficacious control methods are available (Conover 2002), no single method is sufficient to reduce all conflicts.

In urban areas experiencing deer problems, the use of predator hair or scent has been suggested as a nonlethal tool for use in and around residences (Conover 2002, Seamans et al. 2002). The threat of being killed by a predator

and the subsequent influence of predators on prey has been described as the ecology of fear (Brown et al. 1999) and the landscape of fear (Laundré et al. 2010), whereby prey respond to levels of predation by becoming more vigilant or by moving away from differing levels of predation risk. However, response to predation may vary based on the hunting style of the predator. Thaker et al. (2011) found responses by African ungulates to multiple predators varied based on predation style. Areas used by ambush predators were generally avoided while areas used by cursorial predators were not. Likewise, Wikenros et al. (2015) showed that roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) altered visitation rates but not vigilance when exposed to the odor of an ambush predator (Eurasian lynx [*Lynx lynx*]). Kuijper et al. (2014), working in the same area, found increased levels of vigilance and decreased foraging rates of red deer when exposed to the odor of a cursorial predator (wolf [*Canis lupus*]).

¹Present address: Montana Fish, Wildlife and Parks, 4600 Giant Springs Road, Great Falls, MT 59405, USA.

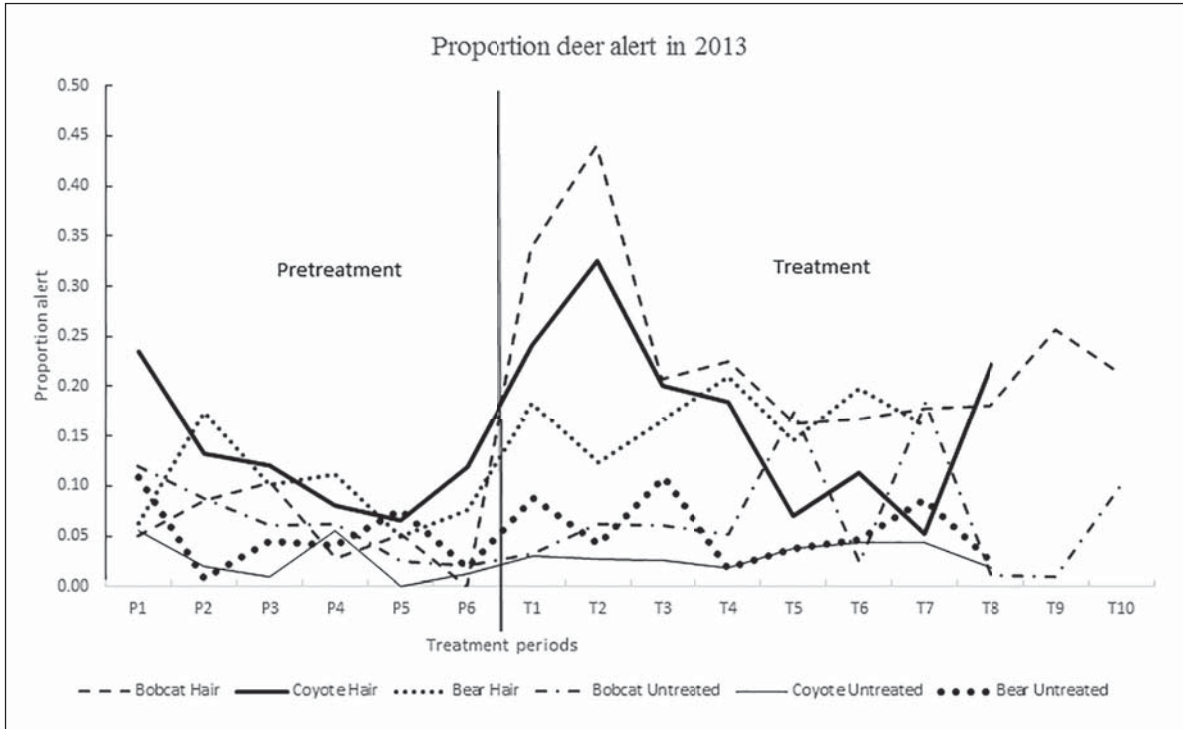


Figure 1. Proportion of deer approaching feeding troughs during pretreatment (P1–P7) and treatment (T1–T10) days fitted with bobcat, bear, coyote hair, or empty bags (untreated) that showed heightened alert toward the predator hair when within 1 body length of the trough during the winter of 2013 in Erie County, Ohio. Pretreatment periods connote only designation of a feeding station as untreated or treatment.

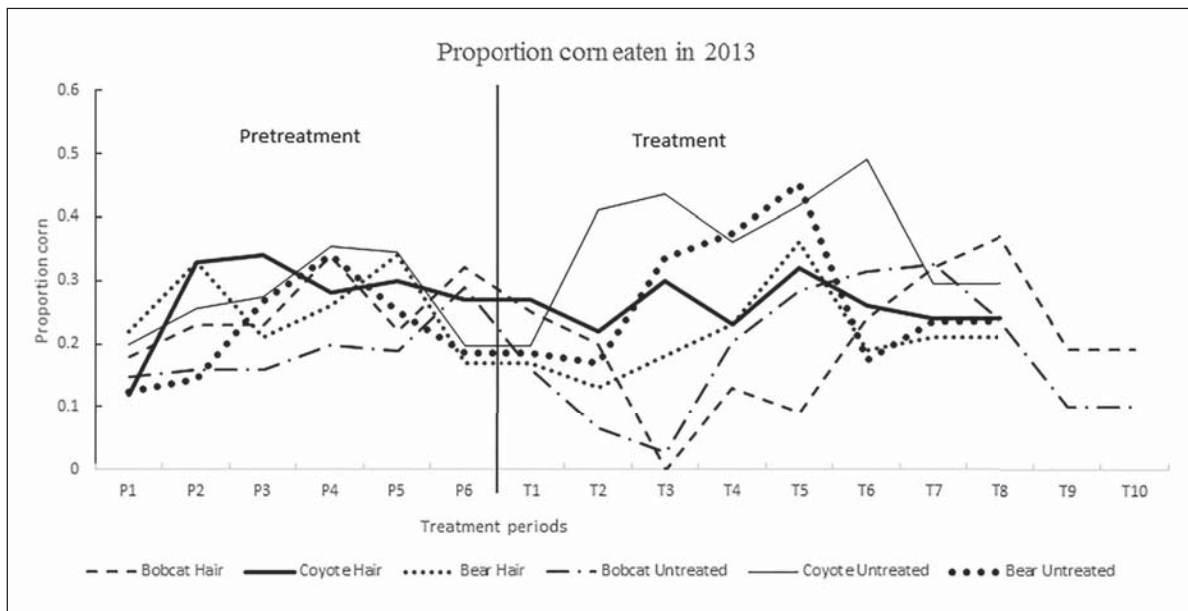


Figure 2. Proportion of available corn during pretreatment (P1–P7) and treatment (T1–T10) days that was eaten by deer while feeding at troughs treated with empty bags (untreated), bobcat, bear, or coyote hair during the winter of 2013 in Erie County, Ohio. Pretreatment periods connote only designation of a feeding station as untreated or treatment.

In each of the aforementioned studies, the predators were present within the study area, but what if the predator has been removed from the study area for over a century? White-tailed deer respond in varying degrees to predator odors, composed of sulfur and volatile fatty acids serve as the active ingredients (Bullard et al. 1978, Sullivan et al.

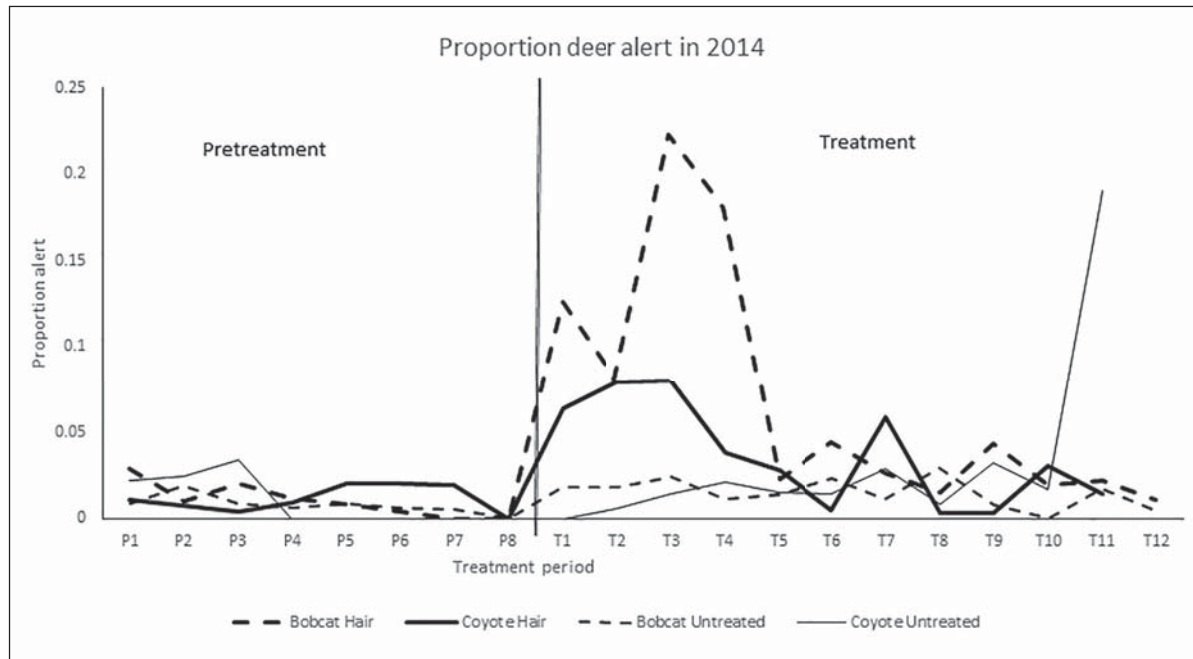


Figure 3. Proportion of deer approaching feeding troughs during pretreatment (P1–P8) and treatment (T1–T12 for bobcat, T1–T10 for coyote) days fitted with empty bags (untreated), bobcat, or coyote hair that showed heightened alert toward the predator hair when within 1 body length of the trough during the winter of 2014 in Erie County, Ohio. Pretreatment periods connote only designation of a feeding station as untreated or treatment.

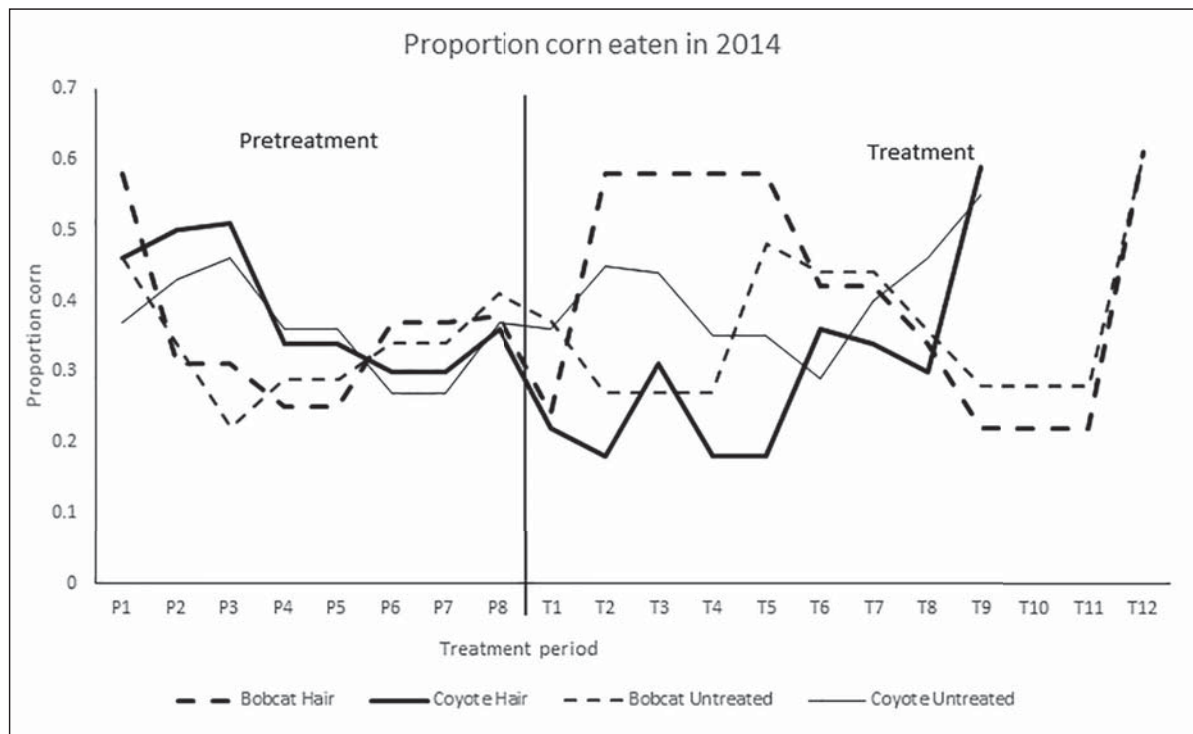


Figure 4. Proportion of available corn during pretreatment (P1–P7) and treatment (T1–T12 for bobcat, T1–T10 for coyote) days that was eaten by deer while feeding at troughs treated with empty bags (untreated), bobcat, or coyote hair during the winter of 2014 in Erie County, Ohio. Pretreatment periods connote only designation of a feeding station as untreated or treatment.

1985, Apfelbach et al. 2005). Swihart et al. (1991) reported deer responded to odors from predators and not to novel or nonpredator odors that did not represent a threat. Ferrero et al. (2011) isolated

2-phenylethylamine in the urine of 18 predator species and reported this as the chemical that triggers avoidance responses in rodents and presumably in prey animals in general.

One theory explaining deer responses to predator odors purports that the olfactory sensitivity is genetically based, as deer will respond to predatory species to which individuals have never been exposed (Müller-Schwarze 1972). Blumstein's (2006) multi-predator hypothesis suggests the presence of any predator interacting with a prey may be sufficient to maintain antipredator behavior for any other predator that the prey may encounter. Both theories may be partially explained by the presence of 2-phenylethylamine in the predator urine (Ferrero et al. 2011). Thus, a combination of chemical sensory cues and experience with any predator might explain predator avoidance by deer. However, neither theory addresses potential behavioral responses to odor from an ambush or cursorial predator.

In northern Ohio, the coyote (*Canis latrans*) is the only natural predator of white-tailed deer (Mech 1984) currently present. Bobcat (*Lynx rufus*), a known ambush predator of both adult and fawn white-tailed deer (Mech 1984, Labisky and Boulay 1998), and black bear (*Ursus americanus*), a predator particularly on white-tailed deer fawns (Mathews and Porter 1988, Kunkel and Mech 1994, Ballard et al. 1999), were extirpated from north-central Ohio around 1850 (Platt 1998). If the Müller-Schwarze (1972) genetic theory, the presence of 2-phenylethylamine (Ferrero et al. 2011), or Blumstein's (2006) multi-predator hypothesis are correct, we would expect white-tailed deer to show heightened alert behavior (e.g., head above the horizontal, ears erect, neck extended forward) and avoid foraging areas in which coyote, bobcat, or bear hair is concentrated. Further, as the bobcat is an ambush predator, we anticipate that deer would avoid areas with bobcat scent (Thaker et al. 2011, Wikenros et al. 2015). We recognize, however, that perception of risk posed by predator hair can be over ridden by the deer's energy demands driving risk-taking during foraging (Lima and Dill 1990, Illius and Fitzgibbon 1994, Brown 1999, Lima and Bednekoff 1999).

In addition, risk perception in white-tailed deer has also been shown to be influenced by visual obstruction because predators might use cover to launch an attack (LaGory 1987, Lingle and Wilson 2001, DePerno et al. 2003, Blackwell et al. 2012). It is unknown to what degree visual

obstruction might work synergistically with predator hair to enhance vigilance or avoidance behaviors. Cherry et al. (2015), however, contend that white-tailed deer can alter feeding levels in response to predator distributions and not habitat cues.

Our purpose in this study was 2 fold: (1) to discern the efficacy of predator hair alone and in combination with a partial visual barrier in effecting foraging reduction at feed stations in free-ranging white-tailed deer during a potentially energetically stressful period; and (2) to examine deer responses to scent from locally extirpated predators. Our specific objectives were to quantify alert behaviors in deer and consumption of whole-kernel corn supplied at feeding stations in response to hair/barrier treatment or corn only.

Methods

Study area

We conducted our study at the 2,200-ha National Aeronautics and Space Administration (NASA) Plum Brook Station (PBS; Erie County, Ohio, USA.; 41° 22' N, 82° 41' W) during January and February of 2013 and 2014. Habitat within PBS differs from surrounding agricultural crops or exurban development, comprising canopy-dogwood (*Cornus* spp.), old field and grasslands, open woodlands, and mixed-hardwood forests interspersed by abandoned and actively used structures relating to NASA and other operations, and paved roads that circle and bisect the station. The deer density on the facility, estimated from both nighttime and aerial surveys during the winters of 2013 and 2014, ranged from 15–27 deer per square kilometer, respectively (J. Linnell, U.S. Department of Agriculture, Wildlife Services, personal communication). Coyote presence was noted throughout the study area. Temperature range and snow depth were recorded from the National Oceanic and Atmospheric Administration Online Weather Data system location in Norwalk, Ohio, approximately 13 km south of PBS. We estimated daily percent snow cover for the study area based on coverage observations per feeding station.

Experimental protocol

We established 15 feeding stations ≥ 1 km apart on January 7, 2013 in locations that were

Table 1. Summary of mean (SD) temperature, monthly total snowfall (cm), and the maximum snow depth during January and February 2013 and 2014 13 km south of the NASA Plum Brook facility as recorded by the National Oceanic and Atmospheric Administration Online Weather Data system in Norwalk, Ohio.

	2013		2014	
	January	February	January	February
Mean temperature (°C)	-1.6 (7.2)	-2.9 (4.2)	-8.3 (6.9)	-7.3 (6.4)
Total snowfall (cm)	8	17	45	46
Maximum snow depth (cm)	10	8	20	33

similar in habitat and equal distance from edge vegetation. Based on DNA sampling from the PBS deer population and suspected movements by individuals (Belant et al. 2007), these stations can be considered independent as deer restricted themselves to individual stations. At each station, a 1.2-m-long feed trough was placed ≥ 10 m from the road and approximately 15 m from woody vegetation to reduce edge effect (LaGory 1986, 1987; Blackwell et al. 2012). We mowed all vegetation within the 15-m radius to a height of about 15 cm. A post was placed adjacent to the center of each trough to hold bags containing predator hair. Whole-kernel corn was supplied to each trough, and we monitored corn consumption at all sites 6 days every week by fitting the end of each trough with a metal indicator plate calibrated in 4.5-kg intervals for corn weight (see Belant et al. 1997). We added corn as necessary to maintain a constant food supply of about 23 kg.

To record indices of the number of individuals at stations and associated alert behaviors, a passive, infrared motion-detector activated, digital camera with infrared flash (RapidFire™, Reconyx, Inc., Holmen, Wisconsin, USA) was placed 5 m from the trough such that it focused on the trough and ≥ 3 -m radius area immediately surrounding the trough. We set all cameras such that when an animal triggered the camera, 10 date- and time-stamped photographs were recorded over 10 seconds. We used sets of 10 photographs taken ≥ 15 minutes apart to reduce the frequency of observations on the same animals within a 24-hour period. Only deer within 1 body length of the trough were counted to provide an index of use and not an actual total count. Each animal was assigned as either alert (head above the horizontal, neck extended forward, both ears

angled upward, tail flag or alert posture, and facing the feeding station; Lingle and Wilson 2001) or not alert.

On January 27, 2013, 20 days after initially placing corn, 10 stations had received consistent feeding activity over 7 consecutive days. Therefore, we randomly

selected 5 stations to receive 15 g of bobcat hair and 5 others to receive empty bags so that they could serve as untreated. The bobcat hair came from road-killed animals recovered in Michigan and was provided by the Michigan Department of Natural Resources. We placed 15 g of hair into a plastic mesh bag and attached the bag to the post so that the bottom of the bag was within 2 cm of the top of the trough. The 5 remaining stations from our initial sample had not received consistent use by deer at this point, but we continued to monitor the stations to determine when use was consistent.

After 7 days of treatment, we removed all bags (treatment and untreated stations) and continued to monitor corn consumption and collect digital photographs at the stations for another 7 days. On February 17, 2013 (after an 8-day interval without treatment), we placed 15 g of black bear hair at the same stations that had previously been treated with bobcat hair, plus 3 additional stations that had not been used but maintained during the bobcat test. The samples of bear hair also came from road-killed animals recovered in Michigan and were provided by the Michigan Department of Natural Resources. Empty bags were again placed at the untreated stations plus 2 additional stations not used previously. We recognize that following a predator-hair treatment with another treatment representing a different predator species posed a potential confounding effect between treatments because of possible residues. However, we were limited on availability of candidate stations for which we had genetic information on deer use (and therefore some idea of spatial independence between stations). Further, had we opted to designate those stations formerly

serving as untreated stations (in our previous bobcat hair experiment) as new treatment stations treated with bear hair; any confounding effect of residues of bobcat hair at stations now designated as untreated stations (i.e., formerly serving as bobcat hair treatment stations) could have influenced deer behaviors to the extent that our findings would be equivocal. We again monitored all stations for 7 days, then removed all bags and continued to monitor the stations for 7 additional days.

On February 26, 2013 (after an 8-day interval), we placed 15 g of coyote hair at the same previously treated stations and empty bags at the same untreated stations. Coyote hair was collected from animals lethally removed from airports in northern Ohio by the U.S. Department of Agriculture, Wildlife Services (WS) program in 2013. We followed the same sampling protocol as described above.

In January 2014, we re-established the original 15 stations and set up 3 individual 7.6-m-long, 1.5-m-high orange snow fence panels 7.6 m from the feed trough and along 3 sides of the area with a 3.8-m opening between corners (see Blackwell et al. 2012). The fourth side, facing the road, was left open. The snow fencing provided a partial physical barrier (deer could easily leap the fence) and partial visual barrier due to the ~2.5-cm mesh size. We did not mow herbaceous vegetation at the stations as in 2013, but snow cover flattened all the vegetation during the initial pretreatment period. In 2014, we tested bobcat hair (provided by the Ohio Department of Natural Resources from road-killed animals collected in southern Ohio) and coyote hair collected from animals lethally removed from airports in northern Ohio by WS in 2014. We did not use bear hair in 2014 due to a lack of availability. Due to the removal of black bear hair, we were able to increase the time bobcat hair samples were in place to 12 days.

Beginning January 10, 2014, we provided corn and began monitoring each station for deer use. Twenty days after providing corn, 12 stations had been consistently used over a 7-day period. We randomly selected 6 stations for provision of 15 g of bobcat hair and 6 stations as untreated (empty bags). The remaining 3 stations were not used consistently and were not included in the test.

After 12 days of hair treatment, the mesh bags

were removed and we continued to supply corn and monitor the stations for another 7 days. On February 19, 2014, we began coyote hair treatment, supplying the 6 stations that had been treated with bobcat hair with 15 g of coyote hair and the remaining 6 untreated stations with empty bags. We monitored stations until February 28, 2014.

Analyses

We used PROC GLIMMIX (SAS 9.2, Cary, N.C., USA) to model 2 response variables in each of our experiments: the proportion of available corn consumed standardized by mean group size per day and station, and the mean proportion of individuals alert (as defined above) per day for each station. Our data for the 2 response variables were not distributed normally in any of the 5 experiments, but right skewed. Our fixed effect, treatment (predator hair present or untreated) was categorical. We therefore modeled each response relative to a Weibull distribution using the Identity link. Given the repeated measures from each station (i.e., our response variables represent a respective station during each experiment), we included an R-side, or residual random effect with station as the subject and an autoregressive correlation structure. Because group size can have an inverse effect on individual vigilance levels (LaGory 1986, 1987; see Elgar 1989), we also included mean group size by station and day as a G-side, or conditional (i.e., the response|random effect) random effect. We used residual pseudo-likelihood as the parameter estimation technique and assessed fit using -2 residual log pseudo-likelihood. We examined each model for overdispersion via generalized chi-square/degrees of freedom. We calculated least squares means and examined differences by treatment at $\alpha = 0.05$.

Results

January and February of 2014 were colder and snowier than the same period in 2013 (Table 1). We had $\geq 50\%$ snow cover in 2013 and 2014 on 28% and 93% of the test days, respectively.

With the exception of our experiment with bear hair, the differences in alert responses across observations at individual stations over time represented $\geq 86\%$ of overall model variance; group size yielded negligible effects on

Table 2. Results of generalized linear mixed model analysis of 2 response variables, the proportion of available corn consumed by free-ranging white-tailed deer standardized by mean group size per day and feeding station, and the mean proportion of individuals alert (see text) per day for each station, during experiments conducted in Erie County, Ohio (41° 22' N, 82° 41' W) in January and February 2013 and 2014. We modeled each response relative to a Weibull distribution using the Identity link. Our response variables reflect observations per station, thus we included an R-side, or marginal random effect with station as the subject and an autoregressive correlation structure (AR1). Mean group size by station and day was included as a G-side, or conditional random effect. We used residual pseudo-likelihood (RPL) as the parameter estimation technique and assessed model fit using generalized chi-square/degrees of freedom.

Year/ treat.	Resp	Cov parm	Est.	SE	Fixed effect	Est.	SE	LS means			-2 log RPL	Gen. χ^2/df
								Est.	SE	est. (treat.)		
2013/ coyote hair	Corn	AR(1)	0.28	0.13	Intercept	0.04	0.06				-51.80	0.03
		Mn grp size	0.02	0.02	Untreated	0.12	0.05	0.17	0.07			
		Residual	0.03	0.01	coyote hair	0.00	-	0.04	0.06	88	2.6	0.01
2013/ coyote hair	Alert	AR(1)	0.26	0.12	Intercept	0.32	0.06				-62.56	0.03
		Mn grp size	0.01	0.01	Untreated	-0.13	0.04	0.18	0.06			
		Residual	0.03	0.00	coyote hair	0.00	-	0.32	0.06	88	-3.0	0.00
2013/ bobcat hair	Corn	AR(1)	0.64	0.08	Intercept	0.21	0.05				-108.00	0.03
		Mn grp size	0.00	-	Untreated	-0.02	0.06	0.19	0.05			
		Residual	0.03	0.01	bobcat hair	0.00	-	0.21	0.05	97	-0.3	0.77
2013/ bobcat hair	Alert	AR(1)	0.15	0.11	Intercept	0.23	0.02				-94.73	0.02
		Mn grp Size	0.00	-	Untreated	-0.16	0.03	0.07	0.02			
		Residual	0.02	0.00	bobcat hair	0.00	-	0.23	0.02	97	-4.8	<0.001
2013/ bear hair	Corn	AR(1)	0.48	0.10	Intercept	0.21	0.21				-79.33	0.03

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	Mn grp size															
2013/ bear hair	Residual	0.03	0.01	Untreated bear hair	0.00	-	0.06	0.06	0.27	0.04	0.03	88	1.1	0.28		
	AR(1)	0.00	0.11	Intercept	0.22	0.04									-70.76	0.02
	Mn grp size															
	Residual	0.02	0.00	Untreated bear hair	-0.09	0.03	-	0.03	0.13	0.04	0.04	88	-2.7	0.01		
2014/ bobcat hair	AR(1)	0.71	0.06	Intercept	0.34	0.07									-84.89	0.06
	Mn grp size															
	Residual	0.06	0.01	Untreated bobcat hair	-0.03	0.08	-	0.08	0.31	0.07	0.07	141	-0.4	0.70		
2014/ bobcat hair	AR(1)	0.14	0.08	Intercept	0.09	0.02									-267.23	0.01
	Mn grp size															
	Residual	0.01	0.00	Untreated bobcat hair	-0.05	0.02	-	0.02	0.04	0.03	0.02	153	-2.6	0.01		
2014/ coyote hair	AR(1)	0.60	0.08	Intercept	0.34	0.05									-71.67	0.05
	Mn grp size															
	Residual	<0.00	0.01	Untreated coyote hair	0.07	0.07	-	0.07	0.41	0.05	0.05	117	1.0	0.29		
2014/ coyote hair	AR(1)	0.32	0.16	Intercept	0.07	0.03									-230.73	0.01
	Mn grp size															
	Residual	0.01	0.00	Untreated coyote hair	0.00	0.02	-	0.02	0.04	0.07	0.07	129	0.2	0.87		

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model variance (Table 2). In addition, for each of our models, overdispersion was markedly <1 , indicating that model variance did not exceed the mean response (Table 2). We specified in our model that we anticipated random inter-station differences in measures over time, but also a correlation structure within stations that would decrease (e.g., after the first 4 days) with the lag between repeated measures. This trend is generally evident in both response variables (Figures 1–4). All treatments, with the exception of coyote hair in our 2014 experiment, yielded enhanced alert behavior in animals using the stations (Table 2). As for treatment effects on corn consumption, only coyote hair in our 2013 experiment contributed to a reduction (Table 2).

Discussion

Deer exhibited heightened alert behaviors when presented with bear, bobcat or coyote hair at feeding stations. This supported Blumstein's (2006) multi-predator hypothesis. In 2014, however, we noted that not only did deer fail to show a heightened alert toward coyote hair, but that a lower proportion of deer were alert toward all predator hair treatments in contrast to 2013 observations. This variation in responses might reflect multiple factors. The deer population had increased and was estimated to be 1.8 times more dense than in 2013 (J. Linnell, U.S. Department of Agriculture, Wildlife Services, personal communication), and the snowier winter of 2014 likely caused more pressure to feed at the trough due to the effort required to move through and find food in deeper snow (Moen 1976). Also, we could not measure herd composition due to the placement of the camera precluding a view of the entire area around each trough, and as antler drop begins in December in northern Ohio, we could not definitively determine the sex of deer at the trough area. However, herd dynamics (i.e., sex ratio, age structure) may have changed, resulting in different group dynamics (Cherry et al. 2015). Specifically, increased competition among females at foraging sites would limit the frequency of heightened alerts.

In addition, we provided a chronic risk by presenting predator hair for an extended period during 2014, and we may have observed an example of risk allocation whereby foragers exposed to a chronic risk show reduced vigilance

in comparison to those exposed to brief or infrequent pulses of risk (Lima and Bednekoff 1999). It is possible that greater numbers of deer congregated around the troughs because we had an increased deer population in 2014. If so, we would expect deer within the central area of the herd to be less vigilant than those outside the view of the camera (Blanchard et al. 2008).

Still, it is notable that, despite environmental and population factors, deer in our January 2014 experiments showed heightened alert behavior toward the extirpated bobcat (when compared to behavior at untreated stations), but not coyote hair. Such a reaction to an ambush predator could be expected (Thaker et al. 2011, Wikenros et al. 2015), but in this case the predator has been locally extirpated for >160 years. The Müller-Schwarze (1972) genetic theory might provide a partial explanation for this reaction. However, deer avoided stations treated with coyote hair when Seamans et al. (2002) fenced in smaller areas that provided only 1 access point and at least a partial visual barrier. Additionally, Blackwell et al. (2012) reported heightened alert behavior in deer when only visual barriers were in place. Therefore, we suggest that responses by deer to bobcat hair might reflect a degree of novelty relative to that of coyote hair. For example, we routinely found coyote tracks and scat near all of our stations and viewed coyotes on cameras on several occasions. Further, in our 2014 experiments that involved use of snow fencing, the fencing did not provide the same degree of visual barrier as the material used by Blackwell et al. (2012). Snow and wind made maintenance of a solid barrier logistically infeasible, hence our use of snow fencing alone. However, as snow and cold conditions continued into February 2014 when coyote hair was tested, the combination of a lack of significant visual barrier (Blackwell et al. 2012), pressure to feed (Moen 1976, Verme and Ullrey 1984), and the omnipresence of coyotes within the area likely contributed to an overall reduction in heightened alert behaviors (Lima and Bednekoff 1999; see Laundré et al. 2001).

Management implications

Our findings do not warrant dismissal of predator hair as nonlethal foraging repellent against white-tailed deer. As noted,

our experiments were conducted during energetically extreme conditions. When natural foods are more readily available, the integration of predator hair with other repellents (e.g., visual barriers) might well work toward effectively protecting crops or homeowner flowers, shrubs, and trees. However, we suggest future experiments combine both predator hair and a more extensive visual barrier during extreme cold and snowy conditions. To combat the effects of snow and wind, researchers might consider dual layers of snow fencing to enhance visual obstruction but allow snow and wind to pass through the fence.

Acknowledgments

We thank J. Jones and L. Tyson for field assistance. We thank E. Largent and D. Beyer of the Michigan Department of Natural Resources for providing bobcat and bear hair. We thank S. Prange of the Ohio Department of Natural Resources, Ohio Division of Wildlife for providing bobcat hair and C. Kauffman of the USDA/Wildlife Services for providing coyote hair. We thank 1 anonymous reviewer and M. Conover for suggestions that improved the paper. Mention of companies or commercial products does not imply recommendation or endorsement by the United States Department of Agriculture (USDA) over others not mentioned. The USDA neither guarantees nor warrants the standard of any product mentioned. Product names are mentioned solely to report factually on available data and to provide specific information. All procedures were approved by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Institutional Animal Care and Use Committee (QA-2073).

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THOMAS W. SEAMANS is a supervisory wildlife biologist for the USDA Wildlife Services' National Wildlife Research Center, Ohio Field Station. He has spent the last 29 years conducting research focused on finding biologically-sound solutions to conflicts between people and wildlife. He received a B.S. degree in wildlife science from Cornell University and an M.S. degree in wildlife management from the Ohio State University.



BRADLEY F. BLACKWELL works as a research wildlife biologist for the USDA Wildlife Services' National Wildlife Research Center, Ohio Field Station. His research interests include animal sensory ecology and antipredator behavior, particularly in application to understanding and reducing human-wildlife conflicts. He received his B.S. and M.S. degrees from North Carolina State University and his Ph.D. degree from the University of Maine.



KIMBERLY E. LINNELL is currently a conservation technician for Montana Fish, Wildlife, and Parks where she studies impacts of wind energy on wildlife, particularly birds and bats. As a former technician for the USDA Wildlife Services' National Wildlife Research Center, Ohio field station, she assisted in research on mitigating wildlife strikes with aircraft. She earned her B.S. degree in wildlife science from Utah State University and is interested in continuing working with and studying human-wildlife conflicts, especially in the context of sensitive species conservation.

