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RESPONSE OF SKUNKS TO A SIMULATED INCREASE IN COYOTE ACTIVITY

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An implicit assumption of the mesopredator release hypothesis (MRH) is that competition is occurring between the larger and smaller predator. When significant competition exists, the MRH predicts that larger species should affect population size, through direct predation or the elicitation of avoidance behavior, of smaller predators. However, there have been few manipulations designed to test these predictions, particularly regarding avoidance. To test whether striped skunks (*Mephitis mephitis*) avoid coyotes (*Canis latrans*), we intensively monitored 21 radiocollared skunks in a natural area in northeastern Illinois. We identified 2 spatially distinct groups and recorded 1,943 locations from September to November 2003. For each group, testing periods consisted of 4 weeks (2 weeks pretreatment, 1 week treatment, and 1 week posttreatment). We simulated coyote activity during the treatment week by playing taped recordings of coyote howls at 1-h intervals at 5 locations. Additionally, we liberally applied coyote urine to several areas within 20 randomly selected 100 × 100-m grid cells, and used the grid to classify cells as urine-treated, howling-treated, or control. We determined changes in home-range size and location, and intensity of cell use in response to treatment. We found no differences in home-range size related to treatment ($P \geq 0.248$). Although weekly differences in home-range drift approached significance when individuals from both tests were pooled ($P = 0.071$), drift was highly correlated with mean weekly low temperatures ($P = 0.004$). Use of howling- and urine-treated cells did not vary among weeks ($P \geq 0.307$), nor did proportions of locations within howling circles with assumed effective broadcast radii of 50–200 m ($P \geq 0.851$). Examination of our data did not support the prediction that skunks avoid areas of coyote activity on our study site.

Key words: avoidance, *Canis latrans*, competition, coyotes, *Mephitis mephitis*, mortality, skunks, top-down regulation

Coyotes (*Canis latrans*) have increased both in number and range over the last few decades, and currently play the role of ''top predator'' in many parts of North America, particularly in eastern portions of the United States (Gompper 2002; Hill et al. 1987; Laliberte and Ripple 2004; Lovell et al. 1998). Within these systems, however, the impacts of coyotes on populations of smaller predators are unclear. The mesopredator release hypothesis (MRH) predicts an increase in mesopredator numbers upon elimination or reduction in number of larger predators (Estes 1996; Terborgh et al. 1999, 2001). Conversely, increases in numbers of larger predators, such as coyotes, should result in declines in population sizes of mesopredators under this hypothesis. This type of ''top-down'' regulation on the basis of body size appears to exist among canids. Wolves (*Canis lupus*) often kill coyotes (Carbyn 1982; Switalski 2003). Similarly, coyotes represent a significant mortality source for kit foxes (*Vulpes macrotis*) and swift foxes (*Vulpes velox*—Cypher et al. 2000; Kitchen et al. 1999; Ralls and White 1995; Sovada et al. 1998; White et al. 2000), and are also known predators of red foxes (*Vulpes vulpes*—Gese et al. 1996; Harrison et al. 1989) and gray foxes (*Urocyon cinereoargenteus*—Fedriani et al. 2000).

The MRH also has been broadly applied to the regulation of noncanid mesopredators, such as raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), by coyotes (Crooks and Soulé 1999; Henke and Bryant 1999; Kamler and Gipson 2004; Rogers and Caro 1998). However, evidence supporting the MRH in terms of these species is largely correlative. The implicit assumption of the MRH is that competition is occurring between the larger and smaller predator (Gehrt and Clark 2003). Mesopredator species differ in diet and habitat preferences, as well as in size

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and defensive capabilities. The degree of dietary and habitat overlap between a mesopredator species and coyotes affects the level of competition they experience. Intensity of competition, coupled with the defensive capabilities of the mesopredator, should then largely determine the coyote's potential impact on the mesopredator population. Thus, the impact of coyotes on all mesopredator species is not likely equal and species-level, experimental studies are needed to clarify the relationships between coyotes and noncanid mesopredators. In this paper, we examine the relationship between coyotes and striped skunks.

Two nonexclusive predictions arise regarding the mechanism behind the MRH (Gehrt and Clark 2003). First, predation by the larger species should be significant enough to affect the population size of the smaller predator. Numerous studies involving coyote dietary analyses conducted throughout North America have failed to report the occurrence of skunks in coyote diets (Andelt 1985; Arjo et al. 2002; Bond 1939; Bowyer et al. 1983; Cypher 1993; Cypher et al. 1993; Dibello et al. 1990; Gipson 1974; Johnson and Hansen 1979; Kitchen et al. 1999; Litvaitis and Shaw 1980; Neale and Sacks 2001; Nellis and Keith 1976; Ortega 1987; Ozoga and Harger 1966; Rose and Polis 1998). Skunks occurred in diets of coyotes in Nebraska, Missouri, and Oregon, but constituted minor proportions (Nebraska: remains of 1 skunk found in 2,500 scats and 747 stomachs [Fichter et al. 1955]; Missouri: 0.5% of diet [Korschgen 1957]; Oregon: remains of 1 skunk found in 848 scats [Toweill and Anthony 1988]). Additionally, Sperry (1941) examined >14,000 coyote stomachs from 17 states, and mesopredators (including skunks) constituted <0.05% of total contents.

However, dietary evidence alone is not sufficient to determine whether coyotes affect skunk population size through direct mortality because victims of intraguild predation may not be consumed (Palomares and Caro 1999). It is more significant that predation, from any source, is not among the major mortality sources reported for striped skunks, which typically include disease, poor physical condition, and human-related causes (Gehrt 2005; Hansen et al. 2004; Sargeant et al. 1982; Verts 1967). Less than 5% of radiocollared skunks died because of predation in North Dakota (Sargeant et al. 1982), Saskatchewan, Canada (Lariviere and Messier 1998), Texas (Hansen et al. 2004), and at our study area in northeastern Illinois (Gehrt 2005). Greenwood et al. (1997) reported higher levels of predation, although 7 of 9 depredated skunks were rabid and may have been predisposed to predation or may have been scavenged after succumbing to the disease. It is notable that predation was not observed during the year before the rabies outbreak.

The 2nd prediction is that the larger predator should elicit avoidance behavior in the mesopredator. Although population size of skunks does not appear to be affected by coyote predation, the MRH may still apply to the skunk–coyote relationship if skunks avoid areas of coyote activity. However, evidence regarding the avoidance prediction is both sparse and contradictory. Examination of anecdotal and correlative data suggests that skunks do not avoid coyotes (Crooks and Soulé 1999; Sovada et al. 2000; Walton and Lariviere 1994). However, a study in Texas revealed increases in density of skunks after removal of coyotes (Henke and Bryant 1999), which the authors attributed to the previous avoidance of the areas by skunks. In order to better understand the relationship between these species, more information is needed in regard to the behavioral response of skunks to changes in coyote density.

We tested the avoidance prediction in a natural area in northeastern Illinois. To investigate the effect of a larger predator on a smaller one, or on the community as a whole, a typical study design is the removal of the larger predator from experimental areas (Bartmann et al. 1992; Henke and Bryant 1999; Kamler et al. 2003a). Because removal of coyotes was not possible at our study site, we conversely simulated an increase in coyote activity. We 1st documented the extent of spatial overlap between resident skunks and coyotes through radiotelemetry, and then simulated an increase in coyote activity through playbacks of taped coyote howls and the creation of scent marks with coyote urine. Spatial overlap provided a coarse-grained picture of skunk–coyote interactions, whereas simulated coyote activity allowed us to monitor the response of skunks to increased coyote activity at a higher resolution.

Materials and Methods

Our study area was the Ned Brown Forest Preserve in Cook County, Illinois. The Preserve consisted of approximately 51% woodland and 19% wetlands (including open water), with the remainder of the area (30%) composed primarily of grasslands. A heavily used, 4-lane highway bisected the study area (see Prange et al. [2003, 2004] for a more detailed description). The site was located in an urban landscape and received intensive human use. Although movements and spatial distribution of raccoons were significantly affected by the presence of anthropogenic resources at this site (i.e., refuse—Prange et al. 2004), both skunks and coyotes exhibited little response to these resources (Gehrt 2004, 2005; Prange and Gehrt 2004). Therefore, we do not believe anthropogenic resources affected the level of competition between skunks and coyotes at our site, and consequently did not alter the impact of coyote activity on skunk behavior. Urbanization has effects beyond the presence of anthropogenic resources, however, and we cannot state with certainty that our results were not affected by the nature of the surrounding matrix or human presence. For this reason and because our study was not replicated we have confined our inferences to our study area.

Capture, handling, and marking of skunks and coyotes followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). We captured and radiocollared skunks as part of a larger study on winter denning ecology and survival beginning in 1999 (Gehrt 2005). We captured skunks via livetrapping or spotlighting sessions conducted during spring and autumn, as described by Gehrt (2005). We immobilized captured skunks with an injection of Telazol (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa—Lariviere and Messier 1996a); measured, weighed, and determined the sex of individuals; and determined age by tooth wear and reproductive condition (Verts 1967). We fitted

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all adults and juveniles $\geq$ 2.0 kg with radiocollars (Advanced Telemetry Systems, Inc., Isanti, Minnesota), and released all individuals at the capture site immediately after handling. Because spring and autumn trapping sessions continued until unmarked skunks were no longer captured, we believe we radiocollared most skunks on the study area. Beginning in March 2000, we captured coyotes with padded foothold traps or cable restraint devices periodically throughout the year (Morey 2004). Similar to our handling protocol for skunks, we immobilized captured coyotes with an injection of Telazol; measured, weighed, and determined the sex of individuals; determined age class by tooth wear; and noted reproductive status (Morey 2004). We fitted all captured coyotes with radiocollars and released them at capture locations within a few hours of handling. Herein we present analyses of spatial overlap of skunks and coyotes during summers (June–August) 2001–2003. The experimental portion of this study, which included simulating an increase in coyote activity, was conducted from 15 September through 15 November 2003.

Spatial overlap.—We located all radiocollared skunks diurnally $\geq$2 times per week by homing in with a portable receiver and handheld antenna. We obtained nocturnal locations for all skunks at approximately 1-h intervals 1 or 2 nights/week through either visual observations or estimation of locations based on $\geq$2 bearings (usually 3) obtained via a truck-mounted 4-element antenna. Because skunks primarily occupied areas of short or mowed grass, most locations were based on visual observations. During nocturnal tracking sessions, we began locating skunks approximately 1 h after sunset and continued until we obtained at least 5 locations per skunk. However, if a skunk became inactive (e.g., returned to its den) during the night, locations were no longer recorded for that individual. We similarly located coyotes throughout the year, although we determined both diurnal and nocturnal locations through triangulation and occasional visual observations (Morey 2004). We located all coyotes diurnally $\geq$3 times per week, and obtained hourly nocturnal locations during at least 1 night/week for a minimum of 5 h, beginning 1 h after sunset. Although intensive telemetry locations (i.e., every 10 min) also were collected for coyotes during 2002, we only used locations separated by at least 1 h in home-range estimations (Morey 2004). One hour was sufficient time for skunks and coyotes to traverse their home ranges and therefore locations were considered biologically independent (Lair 1987; McNay et al. 1994). We estimated Universal Transverse Mercator (UTM) coordinates from bearings using LOCATE II (Pacer, Truro, Nova Scotia, Canada—Nams 1990). More information concerning coyote telemetry protocol can be found in Morey (2004).

To estimate telemetry error, we placed 10 skunk collars on the ground in areas typically occupied by active skunks and obtained 368 test bearings. Mean distance from estimated to actual location of collars was 36 m $\pm$ 24 *SD*. Similar tests were conducted with coyote collars hung from trees throughout the Preserve, and mean ground error was 108 m $\pm$ 87 *SD* (Morey 2004). However, this error measure was considered conservative because the observer was often $<$100 m from radiocollared coyotes (Morey 2004). For both species, we discarded any location with an error ellipse $\geq$5 ha, although error ellipses were typically much smaller. Mean size of error ellipses for skunks was 0.7 ha $\pm$ 1.0 *SD*. Time between bearings also can affect location accuracy when animals are active. Because the Preserve had numerous interior roads and paved bike trails, we were able to obtain successive bearings quickly. Bearings for both skunk and coyote locations were separated by $\leq$3 min.

We estimated seasonal home ranges using the fixed-kernel model (Worton 1989) in the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California). We used only summers (2001–2003) in analyses of spatial overlap because it is the period of greatest activity for skunks and when we radiotracked skunks most intensively at night. Furthermore, females are traveling with young and therefore may be most vulnerable to coyotes and other predators during this period. Because of the dependence of juveniles on their mother we used only adult skunks in these analyses. A minimum of 30 locations/individual was used as a criterion for home-range estimation (Seaman et al. 1999). Because we were interested in the response of skunks to coyotes, we determined the percent overlap of skunk home ranges (95% contours) with collective areas of coyote home ranges and core areas (50% contours), and percent overlap of skunk core areas with collective coyote core areas. We used a simple overlap index, in which values were based on the overall home-range area (or core area) of only 1 member of the pair (in this case, the skunk—Kernohan et al. 2001). Specifically, skunk home-range–coyote home-range overlap = (area of overlap between home range of skunk *i* and collective home ranges of all monitored coyotes/total home-range area of skunk *i*) $\times$ 100. Similarly, skunk home-range–coyote core-area overlap = (area of overlap between home range of skunk *i* and collective core areas of all monitored coyotes/total home-range area of skunk *i*) $\times$ 100, and skunk core-area–coyote core-area overlap = (area of overlap between core area of skunk *i* and collective core areas of all monitored coyotes/total core area of skunk *i*) $\times$ 100. Overlap values provided a rough indication of whether skunks were avoiding areas of coyote activity. Although choice of an overlap value to define avoidance would have been arbitrary, at a minimum we expected overlap of skunk and coyote core-use areas to be consistently low if avoidance was occurring.

Simulated coyote activity.—Spatial overlap analyses provided a coarse-grained assessment of avoidance of coyotes by skunks, but provided little detailed information regarding skunk response to coyote activity. Therefore, we simulated coyote activity and monitored responses of skunks during autumn (September–November) 2003. Although summer may be the period when female skunks are most vulnerable to coyotes, we could not conduct these manipulations until autumn because of the potentially biasing effects on our simultaneous study of skunk movements, which was conducted through summer 2003. However, autumn may represent a time of increasing competition among species for dwindling resources, and hence is also an interesting period during which to address the effects of increased coyote activity on skunk

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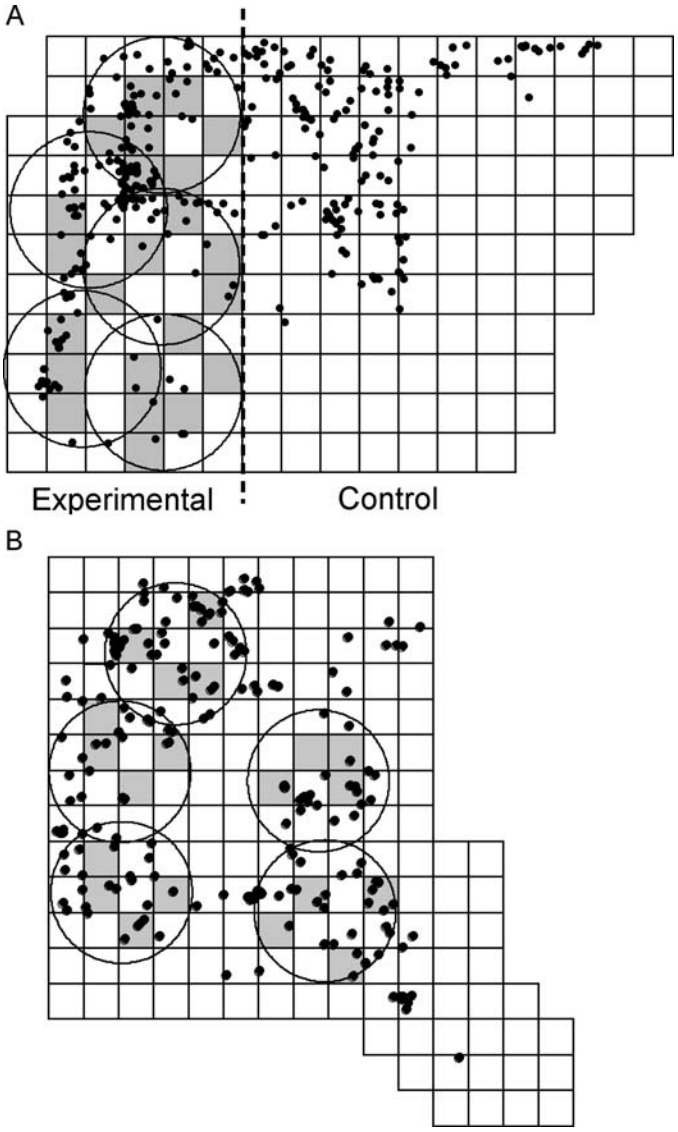


Fig. 1.—Grids (with 100 × 100-m cells) for A) test 1 and B) test 2 conducted during autumn 2003 in Ned Brown Forest Preserve, Cook County, Illinois. Circles represent howling-treatment areas (200-m radius from broadcast), and shaded areas represent urine-treatment cells. Dots are pretreatment skunk locations. Dashed line in A) separates the experimental and control sections for test 1.

behavior. Additionally, young are moving independent of their mother and may be particularly vulnerable.

From 1 to 14 September, we spotlighted and hand captured skunks to both check the fit of their collars and to radiocollar unmarked individuals. We believe we collared most skunks on the study area, but observed an uncollared skunk on 3 separate occasions during the experimental portion of this study (15 September–15 November 2003). During the experimental period, we monitored 21 radiocollared skunks distributed in 2 spatially distinct groups. We conducted 2 separate tests: Test 1 was conducted with skunks residing north of the highway, and test 2 with those occupying an area south of the highway. For both tests, we monitored skunks intensively over a 4-week period (2 weeks pretreatment, 1 week treatment, and 1 week posttreatment). We obtained diurnal locations for all skunks $\geq$2 times per week by homing in with a portable receiver and handheld antenna. We did not begin to intensively monitor the skunks residing south of the highway until we began test 2; however, we continued to intensively monitor the north-side skunks throughout the experimental period (i.e., during both tests 1 and 2). Intensive monitoring consisted of obtaining nocturnal locations at 1-h intervals 4 nights/week. We began acquiring locations approximately 1 h after sunset and obtained a minimum of 5 locations per skunk, unless a skunk became inactive during the night (in which case locations were no longer recorded for that individual). We determined locations through triangulation or by visual sightings. Because we needed precise locations for the experimental portion of this study, we attempted to obtain visual sightings whenever possible. However, we were careful not to approach the animal close enough to cause a change in behavior or location. Most locations were therefore based on visual sightings. When skunks were not observable, we estimated locations based on $\geq$2 bearings obtained via a truck-mounted 4-element antenna. Because grid cells were 1 ha in size (see below), we planned to discard any location with an error ellipse $>$ 1 ha; however, the largest error ellipse was 0.6 ha ($\bar{X}$ = 0.2 ha $\pm$ 0.2 *SD*).

For test 1, we constructed a grid (with 100 × 100-m cells) that encompassed all pretreatment locations of skunks and divided the grid into randomly selected experimental and control areas (Fig. 1A). Within the experimental area, we selected 5 stations in a uniform pattern at which to play the howling tapes. Howling stations were placed in a uniform pattern because our goal was to saturate the experimental area in terms of exposure to howling. We arbitrarily assumed the effective radius of the broadcast was 200 m (Fig. 1A). During the treatment week we played the recordings using a tape player and loudspeaker (Johnny Stewart, Waco, Texas) for 1 min at 1-h intervals. We played the tape at all howling stations each night with station order randomly selected. At the beginning of the treatment week we also liberally applied coyote urine to 3 or 4 locations within 20 randomly selected grid cells (Fig. 1A). To ensure that at least a portion of heavily used cells received urine treatment, we stratified our random sample of urine-treated cells by intensity of skunk use. We reapplied urine midweek.

We conducted test 2 after completion of test 1, and it differed only in the distribution of treatment areas. In this case, we did not randomly divide the grid into experimental and control areas. Rather, for maximum exposure to treatment, we placed howling stations in areas of heavy skunk use (Fig. 1B). Urine was applied in 4 randomly selected cells within each howling radius for a total of 20 urine-treated cells (Fig. 1B). We also continued to monitor the skunks north of the highway and these animals served as controls during test 2.

Analyses were similar for both tests. With the exception of control animals during test 2, all skunk home ranges contained treatment and control cells. Skunks may have either increased or contracted their home ranges in order to avoid treated areas. Therefore, we calculated fixed-kernel home ranges for each skunk during the pretreatment weeks (weeks 1 and 2), and

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TABLE 1.—Mean percentage of overlap of adult skunk home ranges (95% contours; HR) and core areas (50% contours; CA) with collective areas of coyote home ranges and core areas during summers 2001–2003 in a natural area (Ned Brown Forest Preserve, Cook County) in northeastern Illinois.

	Skunk HR−coyote HR		Skunk HR−coyote CA		Skunk CA−coyote CA		No. individuals monitored[a]	
Year	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	Skunks	Coyotes
2001	98.6	1.8	33.2	14.1	51.9	31.7	7 (2 M, 5 F)	5 (3 M, 2 F)
2002	79.7	24.4	15.0	15.5	4.7	9.6	10 (2 M, 8 F)	3 (2 M, 1 F)
2003	85.7	30.6	43.9	26.3	38.0	41.7	8 (2 M, 6 F)	4 (2 M, 2 F)

[a] M = male; F = female.

during the treatment and posttreatment weeks combined (weeks 3 and 4). We combined treatment and posttreatment weeks for home-range analyses because of the potential influence of the number of locations on home-range size. Although combining weeks 3 and 4 in home-range analyses may have potentially masked any weak or short-term response to treatments, we also conducted finer-scale analyses of weekly changes in individual cell use (see below). We compared home-range sizes between periods for test 1 with a 1-way analysis of variance (ANOVA), and conducted a 2-way ANOVA with period and group (experimental versus control) as main effects for test 2. Analyses differed for tests 1 and 2 because during test 1 original home ranges of all skunks contained sections of both experimental and control areas. Therefore, we could not divide our test 1 subjects into ''experimental'' and ''control'' groups, and could only test for effect of period (i.e., pretreatment versus posttreatment). For test 2, we likewise had the effect of period, but also had the effect of group. During test 2, all south-side skunks were exposed to treatment (i.e., belonged to an ''experimental'' group), whereas no treatment occurred for the north-side skunks (''control'' group).

In addition to changes in home-range size, skunks also may have responded to coyote activity by shifting home-range location, or patterns of activity within home ranges. To test for these potential reactions, we modified the approach of Doncaster and Macdonald (1991), who used cell survival to address drift in home ranges. For each animal, we calculated the proportion of cells used during week 1 also used during week 2 (pretreatment cell survival rate), the proportion of cells used during week 2 also used during week 3 (treatment cell survival rate), and the proportion of cells used during week 3 that were used during week 4 (posttreatment cell survival rate). We transformed proportions using an arcsine square-root transformation and tested for differences among weeks during test 1 with a 1-way ANOVA and during test 2 with a 2-way ANOVA with main effects of week and group (experimental versus control).

Finally, we examined reactions to treatment at a finer scale. Home-range size and location may have appeared unaffected, whereas intensity of cell use varied due to treatment. Thus, we compared the proportion of locations for each individual that occurred within treatment cells during pretreatment, treatment, and posttreatment weeks. We defined a howling cell as one with >50% of its area encompassed by a howling circle (200-m radius from source) and that did not receive urine treatment. Urine-treated cells occurred within howling circles and therefore received both treatments. For these analyses, we pooled experimental animals monitored throughout the 4-week study periods and compared use of treatment cells among weeks with repeated-measures ANOVAs. Additionally, because our choice of 200 m as the effective radius of howling broadcasts was arbitrary, we conducted additional tests to determine if effect varied with distance from loudspeaker. We used repeated-measures ANOVAs to compare the proportion of skunk locations within 200, 150, 100, and 50 m of howling stations among pretreatment, treatment, and posttreatment weeks.

RESULTS

Spatial overlap.—We obtained enough locations to determine spatial overlap for a total of 13 adult skunks (4 males and 9 females) and 6 coyotes (3 males and 3 females) during summers 2001–2003 (Table 1). A skewed adult sex ratio is not uncommon in striped skunks (Verts 1967), and adult males suffered significantly higher mortality rates at our study site (Gehrt 2005). Coyote home ranges were large (2.2–12.3 km^2) and therefore completely encompassed most skunk ranges. Both species exhibited substantial spatial overlap of core areas, although overlap values varied widely among individuals and years (Table 1). Home ranges of 4 skunks (31%) and core areas of almost half ($n = 6$; 47%) exhibited >50% overlap with coyote core areas during at least 1 summer. Lower overlap values for summer 2002 may have occurred, at least in part, because only 3 coyotes were radiocollared during this period.

Simulated coyote activity.—We monitored 21 skunks (11 males and 10 females) and collected a total of 1,943 locations. As in the analyses of spatial overlap, the adult sex ratio was skewed toward females (4 males and 8 females). Twelve skunks (6 males [2 adults and 4 juveniles] and 6 females [5 adults and 1 juvenile]) resided north of the highway and served as experimental animals during test 1, and the remaining 9 (5 males [2 adults and 3 juveniles] and 4 females [3 adults and 1 juvenile]) south of the highway served as experimental animals during test 2. Ten of the 12 north-side skunks also functioned as control animals during test 2.

We tested for differences in home-range size between the 2-week pretreatment and treatment + posttreatment periods. We found no differences in home-range size between periods for skunks in test 1 ($F = 0.26$, $d.f. = 1, 16$, $P = 0.615$; Fig. 2).

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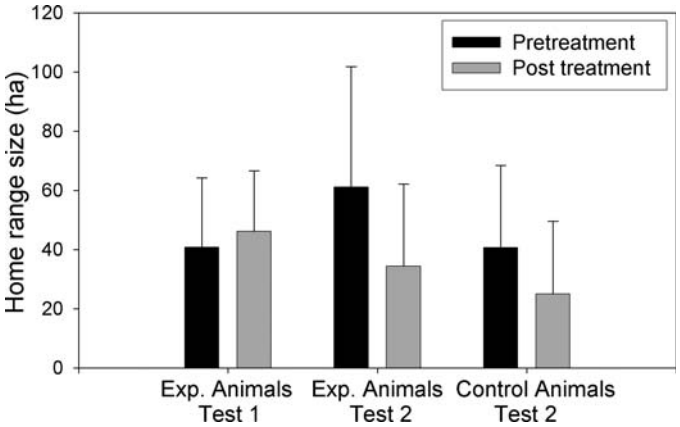


FIG. 2.—Mean pretreatment and posttreatment (treatment + post-treatment weeks combined) home-range sizes (± *SD*) for experimental skunks from tests 1 and 2, and control skunks from test 2 during autumn 2003 in Ned Brown Forest Preserve, Cook County, Illinois.

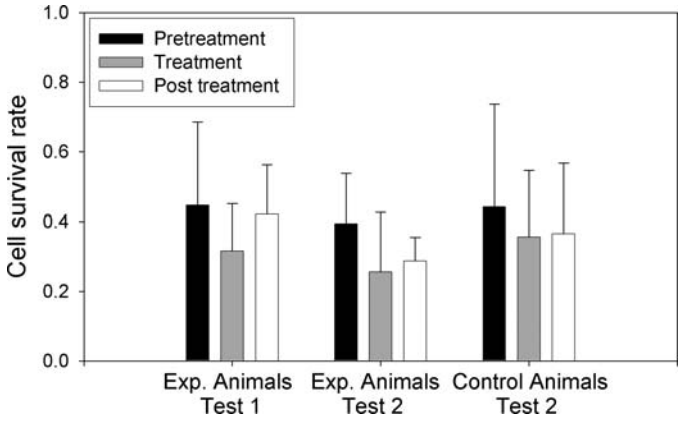


FIG. 3.—Mean weekly cell survival rates (± *SD*) for experimental skunks from tests 1 and 2, and control skunks from test 2 during autumn 2003 in Ned Brown Forest Preserve, Cook County, Illinois.

For test 2, the effect of period on home-range size approached significance for all animals combined ($F = 3.57$, $d.f. = 1, 27$, $P = 0.069$; Fig. 2). However, we observed no effect of group ($F = 1.75$, $d.f. = 1, 21$, $P = 0.248$) or interaction of group and period ($F = 0.24$, $d.f. = 1, 21$, $P = 0.625$; Fig. 2). Pooling experimental animals from tests 1 and 2 did not result in differences in home-range sizes between periods ($F = 0.85$, $d.f. = 1, 31$, $P = 0.362$).

In addition to changes in home-range size, we also examined the possibility that home ranges, or activity within home ranges, shifted because of treatment. Home-range drift, assessed by weekly cell survival rates, did not vary among weeks for experimental animals in test 1 ($F = 1.21$, $d.f. = 2, 22$, $P = 0.316$; Fig. 3). For test 2, cell survival rates did not vary by week ($F = 1.36$, $d.f. = 2, 34$, $P = 0.269$), group ($F = 1.39$, $d.f. = 1, 34$, $P = 0.247$), or the interaction of these factors ($F = 0.17$, $d.f. = 2, 34$, $P = 0.848$; Fig. 3). However, upon pooling experimental animals from tests 1 and 2 differences among weeks approached significance ($F = 2.82$, $d.f. = 2, 42$, $P = 0.071$), with lower mean cell survival rates occurring during treatment (pretreatment: $\bar{X} = 40.5\% \pm 2.9\%$ *SE*; treatment: $\bar{X} = 31.0\% \pm 2.8\%$; posttreatment: $\bar{X} = 36.8\% \pm 2.7\%$).

Although all experimental individuals were exposed to treatment, the level of exposure varied widely. For individual skunks, the percentage of occupied cells that received treatment ranged from 17% to 100%, and percentage of locations within treatment cells ranged from 13% to 100%. If treatment elicited cell abandonment, we would expect lower cell survival rates for those individuals exposed to higher levels of treatment. Therefore, we examined correlations between cell survival during the treatment week and the proportion of treatment cells occupied (urine, howling, and both treatments combined) immediately preceding treatment (i.e., during pretreatment week 2). Only the correlation between the proportion of howling cells occupied and cell survival rate approached significance ($r^2 = 0.24$, $P = 0.075$); however, this correlation was positive, indicating greater relative survival of cells during the treatment week with greater exposure to howling. We repeated this analysis at a finer scale by using the proportion of radiotelemetry locations within treatment cells during pre-treatment week 2 instead of simply the proportion of cells occupied, and a similar, positive relationship was obtained between exposure to howling and cell survival during treatment ($r^2 = 0.22$, $P = 0.089$). For both analyses, no correlations were observed between cell survival during the treatment week and exposure to urine-treated cells or all treatment cells combined ($r^2 < 0.08$, $P > 0.313$).

However, factors extraneous to treatment may have also resulted in changes in movement patterns and hence cell survival rates. Temperatures began to decline during the later half of test 2. Additionally, mean overnight temperature during the treatment week of test 1 fell by >7°C relative to the week before, with mean overnight temperatures rebounding by approximately 5°C during the following week. Furthermore, during test 1 temperatures fell below freezing only during the treatment week. Therefore, changes in weekly cell survival rates may have been due to changes in temperature, and weekly mean overnight low temperatures and mean cell survival rates were highly correlated ($r^2 = 0.90$, $P = 0.004$).

Finally, we pooled all experimental animals and determined changes in cell use by type with repeated-measures ANOVAs. Use of howling- and urine-treatment cells did not vary among weeks ($F \leq 1.25$, $P \geq 0.307$ for both tests; Fig. 4). Also, we found no differences in the proportions of locations within howling circles among weeks for assumed effective broadcast radii of 50, 100, 150, and 200 m ($F \leq 0.16$, $P \geq 0.851$ for all tests; Fig. 5).

DISCUSSION

If the MRH applies to the relationship between skunks and coyotes at our study area then we would expect coyotes to exhibit a measurable effect on populations of skunks through predation, an avoidance response by skunks, or both. Mortality due to predation was rare for skunks at our study area (Gehrt 2005). Similar results have been reported from other areas,

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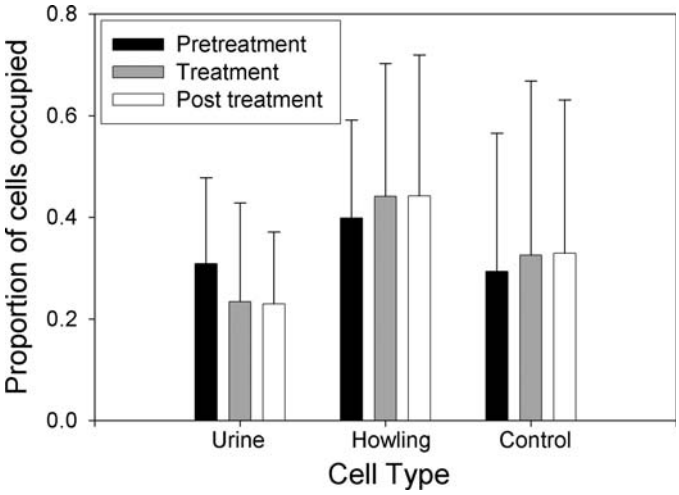


FIG. 4.—Mean proportion of cells used by type (± *SD*) and period in Ned Brown Forest Preserve, Cook County, Illinois, for all experimental skunks pooled during autumn 2003.

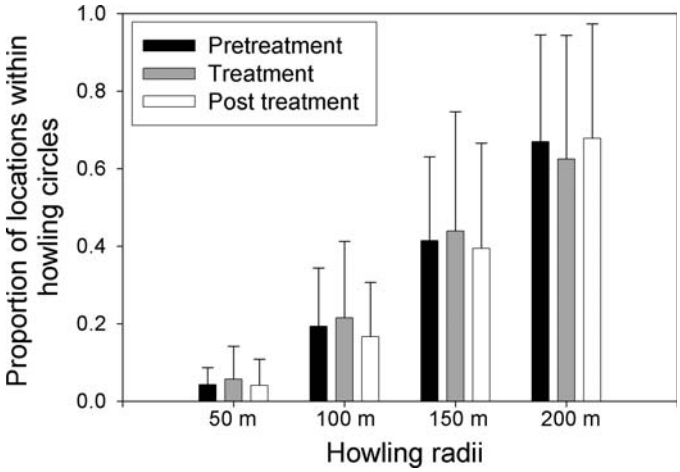


FIG. 5.—Mean proportion of locations (± *SD*) within howling circles with differing effective radii by period in Ned Brown Forest Preserve, Cook County, Illinois, for all experimental skunks pooled during autumn 2003.

which suggest predation, coyote or otherwise, is not a major mortality factor for skunks (Hansen et al. 2004; Lariviere and Messier 1998; Sargeant et al. 1982). Additionally, based on core-area overlap, skunks at our study site did not appear to avoid areas of coyote activity, with nearly half of our radiocollared skunks exhibiting >50% overlap of their core-use areas with core-use areas of coyotes during at least 1 summer.

Even given this level of spatial overlap, skunks may still avoid areas of intense coyote activity. However, we found no evidence of avoidance of either olfactory or auditory coyote signals, which would be expected to elicit a greater response than visual cues in skunks (Langley 1979; Nams 1991). Although declines in home ranges were observed during test 2, they occurred for both experimental and control animals, apparently in response to falling temperatures during the latter part of the study. At the extreme, 3 control animals with pretreatment home ranges of 9–43 ha restricted their posttreatment home ranges to <1 ha, remaining within winter dens at night or emerging for only short periods.

Similarly, although declines in cell survival during the treatment weeks were suggestive of a treatment effect, we found no negative correlation between exposure to treatment and cell survival rate, whereas mean weekly low temperatures were highly correlated with cell survival rates. We also observed a positive, albeit nonsignificant, correlation between treatment-week cell survival and exposure to coyote howls. During test 1 a portion of howling stations was placed in areas of high skunk use, as were all howling stations during test 2. Skunks likely exhibited greater fidelity for these high-use areas, and howling cells encompassed most winter dens. This may have accounted for the positive relationship between cell survival and exposure to howling.

In support of our results, Walton and Lariviere (1994) observed a skunk repelling 2 coyotes without spraying and continuing to forage, and we observed similar scenarios. On 1 occasion we observed a coyote approach a radiocollared skunk, which stood its ground and sprayed the coyote; the coyote retreated, whereas the skunk resumed foraging and did not seek cover or leave the area. We also observed a skunk repel a red fox without spraying. However, this type of antagonistic interaction was not commonly observed. More common (5 occasions) was the observation of coyotes and skunks in close proximity to one another (often <20 m apart) with no apparent interaction. Similarly, in at least 2 instances while playing howling tapes we observed skunks foraging 20–50 m from the loudspeaker, and these individuals failed to respond to the auditory stimuli in any discernable manner.

Other studies also have failed to document avoidance of coyotes. Sovada et al. (2000) reported that skunk activity was positively correlated with coyote activity in the Prairie Pothole region. Crooks and Soulé (1999) found a consistently negative correlation between total mesopredator (including domestic cats) and coyote abundance. However, specific to striped skunks, they found nonsignificant ($P > 0.10$) relationships between skunk abundance and either coyote abundance or coyote presence or absence. Crooks and Soulé (1999) presented mixed results in terms of temporal avoidance of coyotes by skunks. Limiting analyses to fragments in which coyote visitation was sporadic, skunk visitation rates to scent stations were somewhat higher during periods when coyotes were absent. However, of 5 fragments where mesopredator visitation rate increased as coyote visits decreased, the relationship between skunk and coyote visitation rates approached significance ($0.05 < P < 0.10$) at only 1, and the overall relationship was largely driven by interactions between cats and coyotes.

On the other hand, population sizes of skunks increased on treatment areas in Texas where density of coyotes was experimentally reduced, but remained low on control areas where coyotes were not removed (Henke and Bryant 1999). The authors concluded the increase was the result of previous avoidance of the treatment areas by skunks. However, the exact mechanism resulting in skunk increases was not specifically

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identified, and population size of skunks has been shown to fluctuate widely between years (Allen and Sharpton 1943; Brown and Yeager 1943; Verts 1967). Consequently, observed increases may have occurred in the absence of treatment.

An inherent assumption of the MRH, interference competition, may vary among mesopredators with degree of niche overlap. Habitat overlap of striped skunks and coyotes is likely high in most areas, and it occurred on our study site (S. D. Gehrt, in litt.). Skunks typically prefer grasslands and forest–field edge (Bixler and Gittleman 2000; Rosatte et al. 1991) and coyotes often prefer open areas as well (Andelt and Andelt 1981; Person and Hirth 1991; Roy and Dorrance 1985), although coyotes used all habitat types at our study site (S. D. Gehrt, in litt.). Dietary overlap also occurs; however, it is likely lower than overlap values among canids. Although both species are opportunistic omnivores, coyotes often rely heavily on mammals (Bekoff 1977; Fichter et al. 1955), whereas skunks are primarily insectivorous (Llewellyn and Uhler 1952; Wade-Smith and Verts 1982). Although we did not specifically assess diet of skunks at our study site, the diet of coyotes consisted largely of small mammals (Morey 2004), whereas skunks were often observed ''grubbing'' in short-grass areas (Gehrt 2004).

In addition to differences in levels of competition between mesopredator species and coyotes, mesopredators differ in size and defensive capabilities and these factors also contribute to the effect of the larger predator. Although small in size, skunks are equipped with a chemical defense system and their defensive capabilities are conspicuously advertised by black and white aposematic coloration (Caro 2005; Lariviere and Messier 1996b). Such coloration provides an interspecific warning signal and is common in poisonous, distasteful, or otherwise noxious species (Caro 2005). The effectiveness of their defense system also is mirrored in their behavior when threatened, during which they often exhibit warning signs (raise their tail, stomp, hiss, or charge) before spraying (Lariviere and Messier 1996b).

A final and often overlooked aspect of the MRH is that the relationship between predators can be expected to vary spatially and temporally. Intraguild competition is a prerequisite for the MRH, and the level of competition experienced between any 2 species will likely vary with differences in resource availability and distribution. Hence, the relationship between a larger and smaller predator may not be consistent across all areas of sympatry or at all times within any given area. For example, in some areas coyote home ranges occur near the periphery or outside of those of wolves (Fuller and Keith 1981), whereas coyotes and wolves overlap widely in other areas apparently because of the abundance of food resources (Paquet 1992; Thurber et al. 1992). Similarly, Kamler et al. (2003b) speculated that differences in resource availability may have been responsible for the discrepancy between the level of coyote predation of swift foxes observed during their study and a previous one (Kitchen et al. 1999).

Our study was conducted in an urban forest preserve, and although neither species appeared to be directly affected by the presence of anthropogenic food resources (Gehrt 2004, S. D. Gehrt, in litt.), we cannot dismiss the possibility that urbanization was a factor in our results. For example, although we never observed free-roaming dogs on our study area, people were commonly observed walking dogs along trails and roads and exposure to domestic dog urine might have contributed to the desensitization of skunks to canid urine. However, we would not expect skunks to become desensitized to canid urine if coyotes were truly a threat. Regardless of the potential effect of urbanization, differences in natural resource availability in northern Illinois and western Texas may have contributed to the disparate conclusions of the present study and those of Henke and Bryant (1999). Our study also was conducted during only 1 season. Although competition may be increasing during autumn, the effect of coyotes on female skunks may be greater during summer when they are traveling with young. Indeed, only long-term studies may be able to discern temporal variation in the level of competition between coyotes and skunks (or other mesopredators) in any given area, because of seasonal factors (i.e., reproductive status) and annual variation in resource availability.

Because coyotes already occupied our study area, there was the possibility that the skunks in the study area were already exhibiting their maximum response to coyote sign, hence explaining their lack of response to a simulated increase in coyote activity. However, skunk density was high, suggesting no negative effect of preexisting coyote activity. The majority of previously reported skunk densities have ranged from 1.8 to 4.8 skunks/km^2 (Wade-Smith and Verts 1982). Seasonal capture–mark–recapture estimates during 1999–2003 ranged from 2.1 to 5.9 skunks/km^2 (Gehrt 2005). During our study, 21 radiocollared skunks traversed a total area of 4.1 km^2 based on a 100% minimum-convex polygon for all telemetry locations, giving a minimum density of 5.1 skunks/km^2.

The MRH is often widely applied to the relationship between coyotes and other species of the mesopredator guild, irrespective of species-level differences. However, to our knowledge there is no evidence that suggests coyotes adversely affect skunk populations directly through predation. Additionally, we observed relatively high levels of spatial overlap between these species, and no avoidance of simulated coyote activity. Consequently, examination of our data failed to support the MRH in terms of these species, at least at our study site. Additional empirical studies are needed to determine the applicability of the MRH to the relationships between coyotes and other mesopredators, such as raccoons and Virginia opossums. Furthermore, additional studies throughout areas of sympatry and long-term studies are vital to understanding the potential effects of spatial and temporal variation in resources on the skunk–coyote and other intraguild relationships.

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