# Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis

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Some predator species appear to conform to the mesopredator release hypothesis (MRH), in which larger predators help limit populations of smaller predators. This hypothesis has been used to explain the possible relationship between coyotes, mesopredators, and resultant cascades involving nonpredators. However, relationships between coyotes and noncanid mesopredators are poorly understood, and predictions from the MRH have rarely been rigorously tested. We monitored sympatric raccoon and coyote populations to assess 2 predictions derived from the MRH: coyote predation is an important cause of mortality in raccoon populations or raccoons avoid areas used by coyotes. Between March 2000 and September 2001, we recorded 3553 locations for 27 radio-collared raccoons and 1393 locations for 13 coyotes captured on the Max McGraw Wildlife Foundation in Illinois, USA. No raccoon mortality from coyote predation was observed during the study, and raccoon survival was >0.7 each season. All raccoon 95% home ranges exhibited overlap with 95% coyote home ranges in each season. The mean proportion of raccoon locations within 95% coyote home ranges did not vary by sex but did vary by season. Raccoon overlap of coyote core areas varied considerably among individuals within seasons, ranging from 0% to 83%. However, 45% of raccoons had <10% overlap with coyote core areas, whereas only 14% of raccoons exhibited >50% overlap. Mean overlap with core areas did not vary by season or sex. For those raccoons with home ranges overlapping coyote core areas, mean proportion of observed raccoon locations within coyote core areas was generally greater than the mean proportion of random locations. Scent-station experiments failed to document raccoon avoidance of specific sites that had been marked with coyote urine. We did not find support for a mortality prediction or avoidance prediction to support MRH with regard to raccoons and coyotes. These results suggest that relationships among mammalian predators may not be simply dictated by body size, particularly for species outside the Canidae. *Key words: Canis latrans*, coyote, habitat use, mesopredator release, predation risk, *Procyon lotor*, raccoon, survival. *[Behav Ecol 18:204–214 (2007)]*

There is increasing interest in intraguild competition and mechanisms structuring carnivore communities, including intraguild predation (Polis et al. 1989; Polis and Holt 1992; Palomares and Caro 1999). How carnivore species interact can have important implications for other species in addition to carnivores (Terborgh et al. 1999), and there is evidence that shifts in the carnivore community can result in trophic cascades or possibly ecological meltdowns (Terborgh et al. 2001). Understanding the processes underlying community structure of carnivores has become increasingly important for ecologists concerned about carnivores and their prey.

The mesopredator release hypothesis (MRH) states that the elimination or reduction of large carnivores has resulted in increases of mesopredators with concomitant declines in prey species (Estes 1996; Terborgh et al. 1999, 2001). An implicit assumption is that interference competition (sensu Schoener 1983), often in the form of intraguild predation or killing, is the mechanism that drives MRH. This hypothesis has been used to explain the decline in nest success of many neotropical migrants (Soulé et al. 1988; Sieving 1992; Robinson et al. 1995), of which mesopredators (i.e., mammalian predators between 1 and 15 kg in body weight, sensu Buskirk 1999) have been implicated as a contributing factor (Whelan et al. 1994; Donovan et al. 1997; Chalfoun et al. 2002; Schmidt 2003). Despite its intuitive appeal, however, the evidence supporting

the MRH remains largely correlative (Wright et al. 1994; Litvaitis and Villafuerte 1996).

Another mechanism by which the MRH may operate, besides overt conflict via predation and a reduction in population size, is avoidance by smaller carnivores of space or habitat used by larger carnivores. If a change in space use by mesocarnivores results in an alteration in predation pressure, this would represent a behaviorally mediated trophic cascade (Lima 1998). Such avoidance among carnivores would be a variation of the "predation risk effect" often described for predator–prey systems, in which herbivores change their use of space (or habitat preferences, activity patterns, etc.) as a result of predation pressure (Lima and Dill 1990; Brown et al. 1999). Although predation risk effects have only recently received attention from ecologists, some investigations have suggested that they may be of the same magnitude as effects from actual changes in population size (Schmitz et al. 1997; Werner and Peacor 2003).

In North America, recent studies have suggested that coyotes (*Canis latrans*) may play a role as a top predator (Gompper 2002) by controlling smaller medium-sized mammals such as raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and opossums (*Didelphis virginiana*) (Rogers and Caro 1998; Crooks and Soulé 1999; Henke and Bryant 1999; Kamler and Gipson 2004). Some evidence indicates that interspecific competition may be an important factor in structuring predator communities within the Canidae (Johnson et al. 1996). Interference competition within this family appears to be manifested as a linear hierarchy based on body size. Coyotes have been identified as the primary source of mortality for kit foxes (*Vulpes macrotis*, Ralls and White 1995; Cypher et al. 2000; White et al. 2000), swift foxes (*Vulpes velox*, Sovada et al. 1998; Kitchen et al.

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1999), and potentially so for red foxes (*Vulpes vulpes*, Harrison et al. 1989; Gese et al. 1996) and gray foxes (*Urocyon cinereoargenteus*, Fedriani et al. 2000; Farias et al. 2005). For example, coyote-related mortality has been attributed to 40–80% of known-cause deaths of kit and swift foxes in a variety of systems (Ralls and White 1995; Sovada et al. 1998; Kitchen et al. 1999; White et al. 2000; Olson and Lindzey 2002).

Although there appears to be supportive evidence among interspecific relationships within the Canidae for the MRH, relationships between mesopredators outside the Canidae have received relatively little attention (Gehrt and Clark 2003). Moreover, predictions derived from the MRH concerning the potential effects of large predators on mesopredators have rarely been rigorously tested. If large predators limit the populations of mesopredators, effects of this pressure should be observable at the population or individual level.

The relationship between coyotes and raccoons is poorly understood but may have important conservation implications. Raccoons have often been identified as important predators of bird nests (Robinson et al. 1995; Chalfoun et al. 2002; Schmidt 2003), and recent studies have suggested that raccoons and other mesopredators have increased as a result of a lack of a dominant carnivore, the coyote (Rogers and Caro 1998; Crooks and Soulé 1999). In particular, Rogers and Caro (1998) and Crooks and Soulé (1999) proposed a relationship within the carnivore guild in which coyotes represent a large carnivore that limits the number of raccoons and other medium-sized omnivores (e.g., skunks and opossums) and thereby increases nesting success of avian species, such as song sparrows (*Melospiza melodia*) and other ground-nesting species (Schmidt 2003).

However, studies of raccoon survival have consistently reported low mortality rates from predators, including populations exposed to coyotes (see Gehrt 2003). Evidence supporting a negative relationship between coyotes and raccoons has generally been correlative (Rogers and Caro 1998; Crooks and Soulé 1999), with little direct evidence that coyotes limit raccoon populations. Thus, there appear to be inconsistencies between studies of nest predation and species-specific population studies of mammalian predators. In particular, predictions generated from MRH should be tested to elucidate intraguild relationships outside the canid community.

This paper addresses 2 nonexclusive predictions from MRH. One, predation is a significant mortality factor for a raccoon population cooccurring with a high-density coyote population. In particular, we expected to find predator-related mortality rates similar to those reported for fox species, which are known to experience interference competition with coyotes.

Two, through the predation risk effect raccoons avoid areas or habitats used heavily by coyotes so that interspecific home range overlap is low, or if raccoons and coyotes share space, raccoons avoid coyote activity at the microscale. Further, it is possible that relationships between raccoons and coyotes may vary by season and sex class. For example, female raccoons with dependent young during summer may be more likely to avoid high-use areas for coyotes than male raccoons. Therefore, we used a multiscale approach to compare spatial overlap and habitat use between raccoons and coyotes across seasons and between male and female raccoons. There is evidence that some carnivore species, for example red foxes, orientate their territories between coyote territories (Sargeant et al. 1987) or areas where coyotes do not occur (Gosselink et al. 2003).

At the microscale, we experimentally test for a predation risk effect by assessing raccoon response to simulated coyote activity. To date, this represents the first description of the relationship between raccoons and coyotes at the individual level with a combination of observational and experimental data.

## STUDY AREA

We conducted raccoon and coyote livetrapping and radiotelemetry on the Max McGraw Wildlife Foundation (MMWF) located in Kane County in northeastern Illinois, USA. The MMWF is a 546-ha private reserve comprised of heterogeneous patches of habitat, with major types represented by woodland (44%), agriculture (28%), grassland (15%), and wetlands or lakes (13%). The area is bisected into east and west halves by a 4-lane highway. Scent-station experiments were conducted on the MMWF and on a second area, the 1816-ha Poplar Creek Forest Preserve, which is located in Cook County, also in northeastern Illinois. Major habitat types were woodland (13%), agriculture (52%), grassland (29%), and wetlands (2%). Both areas were located within a larger urban landscape, the Chicago metropolitan region that includes more than 9 million people (Gehrt and Chelsvig 2003). The landscape immediately adjacent to the study areas, as well as the metropolitan area in general, is described in detail in previous publications (Gehrt and Chelsvig 2003; Prange et al. 2003). The coyotes on Poplar Creek Forest Preserve were livetrapped and radiotracked as part of a comprehensive coyote study (Gehrt SD, unpublished data) but raccoons were not. However, indications (livetrapping for unrelated research, tracks, and roadkill) were that raccoons were abundant on the area (Anchor C, Forest Preserve District of Cook County, personal communication). Because raccoons were not studied on this area, we do not present radiotelemetry data for coyotes from this site, and analyses were limited to scent stations. Raccoons and coyotes were protected from harvest on both areas during the study, with the exception of 1999 when raccoons on MMWF were subjected to an experimental fur harvest.

## METHODS

### Livetrapping and radiotracking

We captured raccoons during livetrapping sessions conducted during spring and autumn 1995–2002 as part of a long-term study of raccoon population dynamics (Gehrt 2002; Prange et al. 2003). During each trapping session, 30 box live traps were arranged in a permanent $3 \times 5$ grid encompassing 2.4 km$^2$ and maintained for 10–13 nights. The orientation of the trapping grid was such that 24 of 30 traps were located on the west side of MMWF. Therefore, most raccoons we radiocollared were captured on the west side of MMWF. Captured raccoons were immobilized with an injection of Telazol (Gehrt et al. 2001), marked with ear tags (monel #3 or #4, National Band and Tag Company, Newport, Kentucky), and classified by age and gender. All captured raccoons were released at the capture site. A subsample of adult ($\geq 1$ year) raccoons was radio-collared so that we maintained an approximate sample of 20 individuals per season. This study was limited, with the exception of some scent-station surveys, to the period of overlap between the larger raccoon and coyote studies (2000–2002).

Coyotes were captured during livetrapping sessions conducted periodically during the year, beginning in March 2000. The time and place of trapping were opportunistic with trapping conducted as necessary to maintain a sample of radio-collared coyotes throughout the year. Initially, trapping was confined to the west side of MMWF, but trapping was extended to the east side later in 2000. Coyotes were captured with padded foothold traps or with cable restraint devices. We followed a handling protocol similar to that of raccoons. All captured coyotes were fitted with radio collars and released at capture locations within a few hours of handling once they had fully recovered from immobilization.

Population sizes of raccoons were estimated with the $M_h$ closed-population model using the program CAPTURE (Otis

et al. 1978), which was determined by Gehrt (2002) as most realistic for raccoons. Density estimates were calculated by determining an effective trapping area with radiotelemetry data, which is reported in Prange et al. (2003) and was nearly identical to the trapping grid. For practical reasons, coyote trapping was not systematic and trapping data could not be used for density estimation. Therefore, we conducted 2 helicopter surveys during January–February 2002 to visually record numbers of coyotes, and we used opportunistic sightings from residents to obtain a minimum number of coyotes on the area. Radiotelemetry data indicated that coyotes occurred in 2 spatially distinct groups that rarely crossed the highway bisecting MMWF; therefore, we considered visual sightings of coyotes from each area as distinct groups. Density estimates were determined by scaling the population estimate by the area encompassed by the coyote territories, which corresponded closely with the boundaries of the study area.

We determined seasonal survival and cause-specific mortality for raccoons, with a focus on predation as a primary mortality agent. Raccoons were monitored each week, and dead raccoons were collected on receiving a mortality signal. Raccoons found dead in their dens or on the ground without injury were classified as poor physical condition or disease. Because this paper focuses on interference competition, causes of raccoon mortality were classified only as predation or nonpredation for mortality rates. Radiotelemetry data were partitioned into summer (April–September) and winter (October–March) because this coincided with trapping periods and radio collar disbursement, and causes of raccoon mortality may change with seasons. Seasonal survival and mortality rates were pooled between years (summer 2000–winter 2001/2002) and estimated with MICROMORT (Heisey and Fuller 1985). Study-related mortality ($n = 1$) was censored from mortality rate estimates. We considered raccoons monitored in both years as independent observations to maximize sample size.

### Spatial organization

Radio-collared raccoons were located primarily by triangulation from designated stations, and Universal Transverse Mercator coordinates were estimated from bearings with LOCATE II (Nams 1990). Raccoons were located once during diurnal hours, and twice during nocturnal hours, in a diel period. This protocol was followed twice each week throughout the year except during trapping sessions and during winter denning when raccoons were inactive, and we limited monitoring to 1–2 locations per week. Coyotes were located similarly throughout the year. Mean (standard deviation [SD]) error for test transmitters was 108 (87) m for coyotes (Morey 2004) and 20 (13) m for raccoons (Prange et al. 2004; telemetry error was determined separately for each species).

Interactions between raccoons and coyotes and relative habitat use may differ seasonally, therefore radiolocations were partitioned by the following seasons to estimate home ranges: spring (March–May), summer (June–August), and autumn (September–November). Although raccoons and coyotes were radiotracked during winter, raccoon activity was minimal during this period and we focused on other seasons (although we continued to monitor for survival patterns). Radiolocations were entered into ArcView (version 3.2), and seasonal home ranges were estimated using a fixed kernel model in the animal movement extension (Hooge and Eichenlaub 1997). Observation-area curves indicated a critical threshold of >20 locations in a season was necessary for home range estimation, so individuals with fewer than 20 locations were not included in subsequent analyses.

Coyote home ranges were considerably larger than raccoon home ranges, which confounded typical spatial overlap indi-

ces (sensu Walls and Kenward 2001). Because we were interested in how raccoons may respond to coyotes, we delineated the study area in terms of coyote home ranges. We plotted all coyote home ranges within a season and determined the proportion of locations for each raccoon that was recorded within the cumulative 95% and 50% contours. Throughout this paper, we use the term "home range" as analogous to a 95% contour and "core area" for a 50% contour for both species. We compared mean proportion of raccoon locations within coyote contours among seasons and between sexes with a 2-factor fixed analysis of variance during 2000 and 2001.

We were particularly interested in raccoon use of core areas in coyote home ranges. To determine if raccoons avoided areas used intensively by coyotes, we compared the number of observed raccoon locations within a coyote core area to a uniform random distribution of locations within the 95% contour of the raccoon home range. The difference between observed and random locations for each raccoon located within a coyote core area was compared with a paired $t$-test. This analysis was conducted for each season. We also conducted the analysis separately by gender and for the pooled sample. If raccoons avoid core areas within coyote home ranges, we predicted the mean proportion of random locations within core areas would be higher than the observed proportion of raccoon locations.

### Habitat selection

To assess the possibility that raccoons and coyotes selectively use different habitats and thereby partition overlap areas, we delineated habitats in ArcView using an aerial photo of the study area and ground truthing. We established 4 habitat categories: woods, grassland, agricultural areas, and water. The water category included all wetlands as well as lake edge. Lake edge was defined as water's edge plus a 10-m buffer.

We analyzed habitat use relative to availability at 2 spatial scales: composition of home ranges relative to study area (second-order selection) and habitats containing locations relative to home range composition (third-order selection; Johnson 1980). Because we were interested in comparing habitat selection between raccoons and coyotes within MMWF, the "study area" was defined by its boundaries. Furthermore, home ranges that extended somewhat beyond MMWF's boundaries were truncated to include only those areas within the Foundation. We restricted habitat analysis to animals with ≥30 locations per season to reduce the possibility of 0 count in a habitat class. Seasons corresponded to those used in spatial organization analyses. We determined habitat selection at both spatial scales from spring 2000 through autumn 2001 using compositional analysis (Aebischer et al. 1993). We did not use compositional analysis to address raccoon or coyote habitat selection per se; rather we used it to generate independent measures of habitat selection for use in models. Compositional analysis generates log-ratio values for utilized and available habitats relative to a reference habitat ($D$). We used log ratios ($d_i$) produced by compositional analysis as the dependent variable in general linear models to evaluate interspecific differences in habitat selection (Gosselink et al. 2003). We also used compositional analysis to construct a matrix of $t$ values (based on log ratios) for each species, to test whether selection differed between pairs of habitats (Aebischer et al. 1993). In the case of available but unused habitats, we replaced missing utilized values with 0.007 as suggested by Bingham and Brennan (2004). At the finer scale (locations vs. home range), missing values for available habitat also occurred for some individuals. In this case, we replaced residual log-ratio values derived from missing available habitats with the mean of all log ratios derived from nonmissing values for a given habitat type (Aebischer et al. 1993).

**Table 1**
**Habitat use models and explanation of effects**

| Model | Explanation |
|---|---|
| **Raccoon models** | |
| Hab | Habitat type alone determines habitat use, genders use habitats similarly across seasons. |
| Hab, Hab × Gen | Genders use habitats differently, within genders habitats are used similarly across seasons. |
| Hab, Hab × Gen, Hab × Gen × Sn | Habitat use varies by gender and genders use habitats differently within seasons. |
| Hab, Hab × Ovlp | Habitat use varies due to overlap, within overlap categories genders use habitats similarly and use does not vary across seasons. |
| Hab, Hab × Ovlp, Hab × Ovlp × Gen | Habitat use varies due to overlap, within overlap categories genders use habitats differently. |
| Hab, Hab × Ovlp, Hab × Ovlp × Sn | Habitat use varies due to overlap, seasonal habitat differs between overlap categories. |
| **Coyote–raccoon models** | |
| Hab | Habitat type alone determines habitat use, species use habitats similarly across seasons. |
| Hab, Hab × Sp | Species use habitats differently, within species habitats are used similarly across seasons. |
| Hab, Hab × Sn | Habitat use varies by season, within seasons species use habitats similarly. |
| Hab, Hab × Sp, Hab × Sp × Sn | Habitat use varies by species and species use habitats differently within seasons. |

Hab = habitat; Gen = gender; Sn = season; Sp = species; Ovlp = overlap.

General linear models assume that values for the dependent variable are continuous, independent, and normally distributed. D'Agostino tests failed to reject normality for our log ratios. Therefore, to the best of our knowledge the assumption of normality was met. We considered individual raccoons to be independent because of their solitary social structure. Although coyotes on the study area were members of 2 territorial groups, members were largely solitary and exhibited substantial variation in the use of their territories.

To determine if coyote and raccoon locations were independent, we used the program Biotas (Ecological Software Solutions, Schwägalpstrasse 2, 9107 Urnäsch, Switzerland) to examine the spatial association of coyote and raccoon locations by season. Biotas uses a grid-based test to compare point patterns. The test produces a $\chi^2$ value, and a Yates correction factor is calculated to account for bias when cell frequencies are low. Coyote and raccoon locations were not significantly associated in any season ($\chi^2 \leq 0.933$, $P \geq 0.334$).

Small sample sizes for coyotes precluded partitioning samples by gender for this species; however, we were interested in raccoon response to coyotes, and we have no reason to suspect raccoons might alter habitat use relative to coyote gender. On the other hand, raccoon habitat selection may vary by gender, possibly due to gender-related differences in response to coyote activity. Therefore, we first constructed models to determine the effect of gender, as well as the interaction of gender and season, on raccoon habitat selection (Table 1). Additionally, we were concerned raccoons whose home ranges overlapped areas of intense coyote activity might utilize habitats differently than those whose home ranges did not. If so, coyote–raccoon models might fail to recognize species-specific differ-

ences due to variability in habitat selection among raccoons. To address this problem, we constructed additional raccoon models including the effect of overlap and interactions of overlap with gender and season (Table 1). Raccoons were classified as having substantial overlap with coyotes if coyote core areas overlapped ≥20% of their home ranges.

We then constructed coyote–raccoon models to evaluate interspecific differences in habitat selection; these models included species, season, and their interaction (Table 1). If raccoon models indicated an effect of gender or overlap, we partitioned coyote–raccoon models accordingly. All models were performed at both spatial scales. Both the raccoon and coyote–raccoon model sets also contained a "null model," which included only the effect of habitat type on the dependent variable (log-ratio values). All covariate effects (e.g., gender, species) were modeled as interactions with habitat type (e.g., gender × habitat, species × habitat), and the main effect of habitat type was retained in all models.

Model selection was based on Akaike's information criteria corrected for small sample bias (AICc; Burnham and Anderson 2002). We used $\Delta_i$ to rescale the AICc values, which results in the model with the minimum AICc having a value of 0 ($\Delta_i = \text{AICc}_i - \text{AICc}_{min}$). The larger the $\Delta_i$ value, the less likely that model $i$ represents the best model (Burnham and Anderson 2002). Additionally, we calculated AICc weights ($w_i$) for each model. The $w_i$ values range from 0 to 1, such that the sum of weights for all models in the candidate set equal 1.0. The larger the $w_i$ value, the more likely that model $i$ represents the best model.

**Scent-marking experiment**

*Test 1*

We conducted a scent-marking experiment to determine if raccoons avoid coyotes at the microspatial scale. During November 2001 and August 2003, we established scent stations throughout MMWF. We assumed no differences in response between years and pooled data to maximize sample size. Because of the heterogeneous habitat matrix at MMWF, we stratified pairs of stations (1 treatment and 1 control determined randomly) by 3 habitat types: woodland, agriculture, and lake edge. Each station was 1 m² of raked dirt, and on the first night one stick dipped in fish oil was placed near the center of the station for treatment stations, and nothing was placed in control stations. Stations were checked early the next morning for 3 days and the tracks of mammalian species recorded. For the second phase of the test, we placed a stick dipped in coyote urine (Minnesota Trapline Products, Pennock, MN) on each treatment station (in lieu of fish oil), and nothing was placed in control stations. These stations were again checked for 3 days and tracks identified to mammalian species. Distances between stations within pairs ranged 160–614 m, and distances between pairs ranged 421–1829 m. Visitation rates between treatment and control stations, and between preurination and urination stages of the test, were conducted with chi-square tests.

*Test 2*

The size of MMWF limited the number of stations that could be established on the area without the risk of resampling the same individuals. Therefore, we conducted a second scent-marking test on the larger Poplar Creek Forest Preserve during April 2002. For this test, we again distributed scent stations across the Preserve in pairs of treatment and control stations (each treatment and control pair was separated by >50 m). In this case, we focused stations along edges of agricultural fields because this type of habitat was most common on the Preserve, and both species are frequently captured along this type of edge. To increase our ability to detect tracks, we placed scent

**Table 2**

**Survival and mortality rates for radio-collared raccoons on the MMWF, Illinois, USA**

|  | $N/d$ | Radiodays | Survival | Variance | Mortality rates Unknown (95%) | Other (95%) |
|---|---|---|---|---|---|---|
| Summer | 39/4 | 6188 | 0.79 | 0.0087 | 0.052 (0.00–0.15) | 0.158 (0.00–0.32) |
| Winter | 39/6 | 6343 | 0.71 | 0.0099 | 0.049 (0.00–0.14) | 0.243 (0.06–0.43) |

Raccoons were monitored from March 2000 to February 2002. $N/d$ = number of individuals/number of mortalities. Other includes roadkill, disease/physical condition and nuisance.

on the stations immediately after precipitation while the stations were muddy. For the first night, we placed sticks with fish oil on treatment and control stations. On the following day, we wiped out tracks if necessary and reapplied the fish oil treatment on both stations but liberally poured coyote urine (approximately 0.25 l) on a rock immediately adjacent to each treatment station. We believed that these alterations to the treatments and controls might elicit stronger reactions in raccoons. Subsequent tracks observed the following morning were again identified to species. Distances between treatment and control stations ranged 56–192 m, and distances between pairs ranged 315–1040 m. Because this protocol relied on a muddy substrate to identify tracks, we could only monitor stations for one night immediately after a rain, but we believed this technique improved our ability to detect visits to stations. Visitation rates between station classes were compared with Fisher's Exact tests.

We report on patterns of coyote activity in addition to raccoon activity for both tests. However, low visitation rates for coyotes precluded statistical analysis.

## RESULTS

We captured 54 raccoons in autumn 2000, 29 raccoons during spring trapping in 2001, 66 raccoons during autumn 2001, and 46 in spring 2002. Corresponding spring density estimates (standard error) increased from 13.3 (2.6) per km$^2$ in 2001 to 30.9 (5.6) per km$^2$ in 2002, and autumn density estimates were 36.4 (5.8) per km$^2$ in 2000 and 66.2 (9.0) per km$^2$ in 2001. In February 2002, the largest number of coyotes seen on MMWF was 10, which yielded a minimum density of 1.9 coyotes per km$^2$. This number did not include transients, or individuals separated from groups, which were known to use the area.

Between March 2000 and September 2001, 3553 locations were recorded for 27 radio-collared raccoons (16 males, 11 females) and 1393 locations for 13 (7 males, 6 females) coyotes. The number of raccoons radiotracked each season ranged from 15 to 22, and most of the raccoons were monitored in both years. The number of coyotes monitored each season ranged from 1 (the first season) to 7, including 7 subadult/adult and 6 pups from 2 distinct packs. Five coyotes eventually dispersed and were not used in spatial analyses.

### Raccoon mortality

Survival and mortality rates were determined from 12 531 raccoon radiodays for the period April 2000 through March 2002. We recorded 12 mortalities of which 5 were roadkill, 1 was nuisance-related, 1 was study-related, 3 were physical conditions and/or diseases, and 2 were unknown. None were identified as a result of predation, although the unknown mortalities were too decomposed to determine if cause of death was related to a predator. However, it was evident that they had not been consumed. Therefore, these mortalities were partitioned to estimate an unknown mortality rate, which could represent a maximum estimate of predation rate. Seven

raccoons were lost during the study; however, it is unlikely they were related to mortality as each radio collar had reached, or passed, their projected expiration date. Summer and winter survival rates were similar (both >0.70). The 95% confidence interval for unknown mortality was 0.00–0.15 during summer and 0.00–0.14 during winter (Table 2).

### Spatial overlap

Number of raccoon home ranges estimated per season ranged from 9 (autumn 2001) to 21 (autumn 2000). Pooling between years, 28 raccoon home ranges were estimated during spring, 31 in summer, and 30 in autumn. The number of coyote home ranges estimated each season ranged from 1 in spring 2000 (the first season of trapping) to 8 in summer 2001.

Size of raccoon 95% home ranges ranged from 16 to 238 ha across seasons (Table 3). Coyote home ranges were usually larger than raccoon home ranges, ranging from 84 to 625 ha (excluding dispersers). All raccoon 95% home ranges exhibited overlap with 95% coyote home ranges in each season (e.g., Figure 1). The mean proportion of raccoon locations within 95% coyote home ranges did not vary by sex ($F_{1,71}$ = 2.27, $P$ = 0.136) but did vary by season ($F_{2,71}$ = 6.09, $P$ = 0.004). There was no significant interaction between season and sex (interaction term: $F_{2,71}$ = 0.03, $P$ = 0.97). Mean (±SD) overlap was lower ($P$ < 0.05, least-squared test) during spring (67 ± 6%) than other seasons (summer 91 ± 6%, autumn 80 ± 6%). However, only one coyote was radio-collared during spring 2000 with a concomitant large range (3–98%) in overlap, whereas raccoon overlap was relatively higher (62–100%) during spring 2001 when more coyotes were radio-collared.

Raccoon core area overlap of coyote core areas varied considerably among individuals within seasons, ranging from 0% to 83%. Mean overlap with core areas did not vary by season ($F_{2,71}$ = 1.55, $P$ = 0.22) or sex ($F_{1,71}$ = 0.07, $P$ = 0.80), and the interaction term was also nonsignificant ($F_{2,71}$ = 0.12, $P$ = 0.88). Mean (±SD) overlap between core areas were spring 21 ± 23%, summer 23 ± 21%, and autumn 15 ± 23%. The large degree of variation in core overlap was the result of 45% of raccoons with <10% overlap with coyote core areas, whereas 14% of raccoons exhibited a high (>50%) degree of core overlap.

**Table 3**

**Mean (SD) size of 95% and 50% contours of fixed kernel home ranges (ha) for raccoons and coyotes on the MMWF, Illinois, USA**

|  | Raccoon | | | Coyote | | |
|---|---|---|---|---|---|---|
|  | $n$ | 95% | 50% | $n$ | 95% | 50% |
| Spring | 28 | 51 (40) | 7 (7) | 4 | 238 (120) | 18 (13) |
| Summer | 32 | 69 (35) | 10 (8) | 9 | 363 (185) | 22 (20) |
| Autumn | 29 | 50 (45) | 8 (11) | 8 | 332 (144) | 32 (18) |

Home range estimates were pooled between years 2000 and 2001.

**Figure 1**
Spatial distribution of 95% fixed kernel home ranges of raccoons (bold lines) ($n = 17$) and coyotes (gray shade) ($n = 4$) on MMWF during summer 2001, illustrating extensive spatial overlap. Dark-shaded areas are 50% contours for coyote home ranges. The heavy bold line was a highway separating east and west sides of the study area.

For those raccoons with home ranges overlapping coyote core areas, mean proportion of observed raccoon locations within coyote core areas was always greater than the mean proportion of random locations, and this pattern was consistent across seasons (Figure 2). For males, mean ($\pm$SD) proportion of observed locations ($0.33 \pm 0.25$) within core areas was greater ($t_{23} = -4.093$, $P < 0.001$) than the mean proportion of random locations ($0.23 \pm 0.18$). A similar pattern occurred for females (observed $0.21 \pm 0.21$, random $0.19 \pm 0.17$), although it was not significant ($t_{25} = -1.033$, $P = 0.312$).

**Habitat selection**

Overall, 21 raccoons (12 M, 9 F) and 7 coyotes (3 M, 4 F) had sufficient locations for comparisons of habitat selection and were included in our habitat selection models. Eleven raccoons exhibited ≥20% home range overlap with coyote core areas.

Type I error rates for the multivariate analysis of variance (MANOVA), which is typically conducted during compositional analysis, may be high due to the replacement of zero values for habitat use with a trivial value (Bingham and Brennan 2004). No zeros occurred for coyote habitat use at either spatial scale. For raccoons, approximately 4% of the log ratios were based on replacement values for zero habitat use. However, at both spatial scales the MANOVA for raccoon habitat selection was significant at $P < 0.0001$. Type I error rate for MANOVAs significant at $P < 0.001$ and having a replacement value of 0.007 was only 2.5% (Bingham and Brennan 2004; based on 5 habitat types, 30 animals with 30 observations). Therefore, based on the level of significance of our raccoon habitat analyses, we do not believe the replacement of a small percentage of zero habitat use values resulted in biases in our data.

*Second-order selection*

Of the raccoon models, the Habitat, Habitat × Gender model was most parsimonious ($w_i = 0.995$; Appendix A). All other
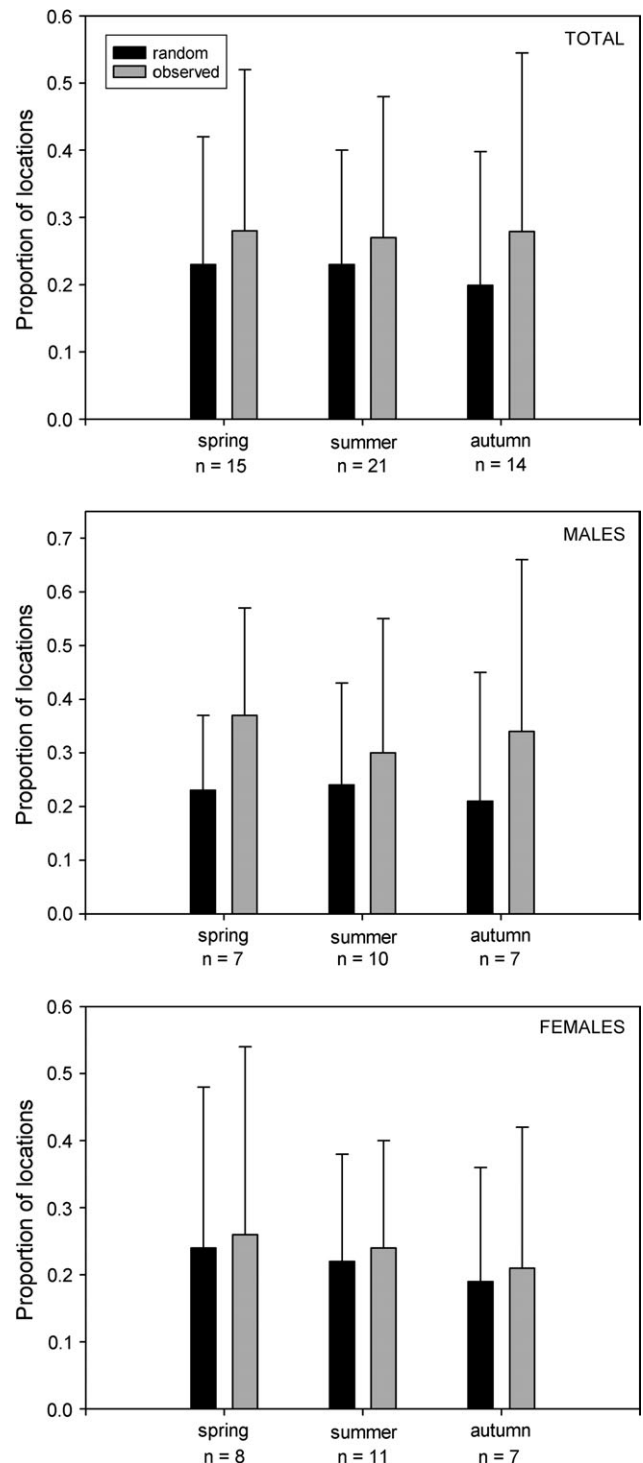


**Figure 2**
Mean (SD) proportion of observed and random raccoon locations located within core areas of coyote home ranges. Data are pooled between 2000 and 2001 for animals monitored on MMWF.

models, including those incorporating the effects of overlap with coyote core areas, received essentially no support ($\Delta_i \geq 10.78$, $w_i \leq 0.005$). Female raccoons exhibited greater selection of habitats than male raccoons. For females, all possible pairwise habitat comparisons (i.e., *t*-tests based on log ratios obtained during compositional analysis) detected significant differences. The range in percentages of habitat use was also
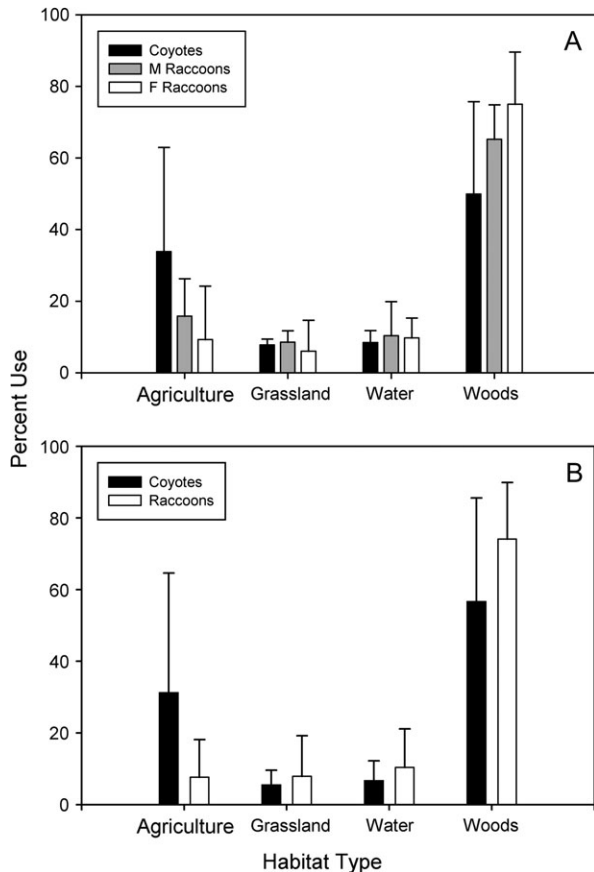
**Figure 3**
(A) Percentage of habitat use based on home range composition of coyotes and male and female raccoons at MMWF in northeastern Illinois. (B) Percentage of habitat use based on telemetry locations for coyotes and raccoons at MMWF in northeastern Illinois. For both graphs error bars represent 1 SD.

greater for female raccoons than males or coyotes (Figure 3A). Females exhibited greater selection of wooded areas relative to all other habitat types ($t \geq 3.31$, $P < 0.001$), greater selection of water relative to agricultural areas and grasslands ($t \geq 2.30$, $P \leq 0.030$), and greater selection of grasslands relative to agricultural areas ($t = 2.70$, $P = 0.012$). Four pairwise comparisons between habitats for males were significant. Males also selected wooded areas more than the 3 other habitats ($t \geq 3.11$, $P \leq 0.004$), and grasslands were selected more often than agricultural areas ($t = 5.44$, $P < 0.001$). No other significant differences in selection among habitat pairs were observed ($|t| \leq 1.80$, $P \geq 0.081$).

Due to gender-specific differences in habitat selection by raccoons, we constructed coyote–raccoon models separately for male and female raccoons. Of the coyote–female raccoon habitat models, the Habitat, Habitat × Species model was most parsimonious ($w_i = 0.875$; Appendix A). The Habitat model was second best, but little evidence of support existed for this model ($\Delta_i = 3.90$, $w_i = 0.125$). The remaining 2 models received essentially no support ($\Delta_i \geq 19.12$, $w_i = 0.000$).

Coyotes exhibited no evidence of habitat selection, and pairwise habitat comparisons revealed no significant differences between habitats (all comparisons $t \leq 1.81$, $P \geq 0.086$). Of the coyote–male raccoon models, the Habitat model was by far the best model in the candidate set ($w_i = 0.942$; Appendix A), and we found little evidence in support of other models ($\Delta_i \geq 5.61$, $w_i = 0.057$).

*Third-order selection*
Of the raccoon models, the Habitat model was most parsimonious ($w_i = 0.997$; Appendix B). All other models, including overlap models, received essentially no support ($\Delta_i \geq 12.75$, $w_i \leq 0.002$). Because gender was not included in the best model, coyote–raccoon models were performed with male and female raccoons combined. Of the coyote–raccoon models, the Habitat model was also the best model ($w_i = 0.997$; Appendix B), and other models received little support ($\Delta_i \geq 12.05$ and $w_i \leq 0.002$). Woods were selected more than all other habitats by both raccoons ($t \geq 3.51$, $P < 0.001$) and coyotes ($t \geq 2.49$, $P \leq 0.022$). No other pairwise differences occurred for raccoons ($|t| \leq 0.99$, $P \geq 0.326$) or coyotes ($|t| \leq 1.68$, $P \geq 0.109$). Percentages of habitat use were similar for raccoons and coyotes and differed primarily in regard to the use of agricultural areas (Figure 3B).

For both spatial scales, the smaller number of coyotes relative to raccoons may have affected our results; however, our sample size was apparently large enough to detect a difference between female raccoons and coyotes in terms of second-order habitat selection. More complex interactions, such as third-order interactions (e.g., habitat × species × season), might not have been detectable given our sample sizes, especially if the effect was not strong. From a biological standpoint, however, a smaller sample size for coyotes cannot be avoided given differences in densities. In most areas, including our study area, coyotes occur at substantially lower densities than raccoons.

**Scent-station experiment**

*Test 1, MMWF*
During the preurine phase, raccoons visited 44% ($n = 39$) of the treatment stations with fish oil, compared with 28% ($n = 39$) of control stations ($\chi_1^2 = 1.37$, $P = 0.249$). During the second phase when treatment stations received coyote urine, raccoon visitation rate was 54% compared with 33% for control stations ($\chi_1^2 = 3.34$, $P = 0.068$). There was no difference ($P > 0.3$) between visitation rates of the first and second phases for treatment or control stations (Figure 4).

Coyote visitation was low for either type of station during both phases of the experiment. During the first phase, no coyote visitation was observed for treatment stations and 2 visits to control stations. During the second phase, 1 visit was recorded for treatment stations and no visits to control stations. One treatment station with coyote urine received cooccurring tracks for both species.

*Test 2, poplar creek forest preserve*
Seven pairs of stations were established and checked on April 14 and 15 and 7 additional pairs during April 27 and 28. Raccoon visitation to treatment stations (29%) during the preurine stage was similar (Fisher's Exact test $P = 1.00$) to visitation at control stations (36%). Raccoon visitation was highest (64%) at treatment stations during the urine stage, which was marginally significantly (Fisher's Exact test $P = 0.054$) different from the visitation rate (21%) for control stations (Figure 4). The increase in visitation rate for treatment stations between treatments was not significant (Fisher's Exact test $P = 0.128$).

Coyote visitation rates were generally lower than raccoon visitation rates to stations, however there was a trend toward an increase in coyote visits in response to coyote urine, which was a similar pattern to raccoons. Visitation rates for coyotes were 21% for treatment stations and 36% for control stations during the preurine phase and 36% for treatment stations and 21% for control stations during the urine phase.

Raccoons and coyotes cooccurred at treatment stations 4 times, but no times at control stations, during the urine phase.
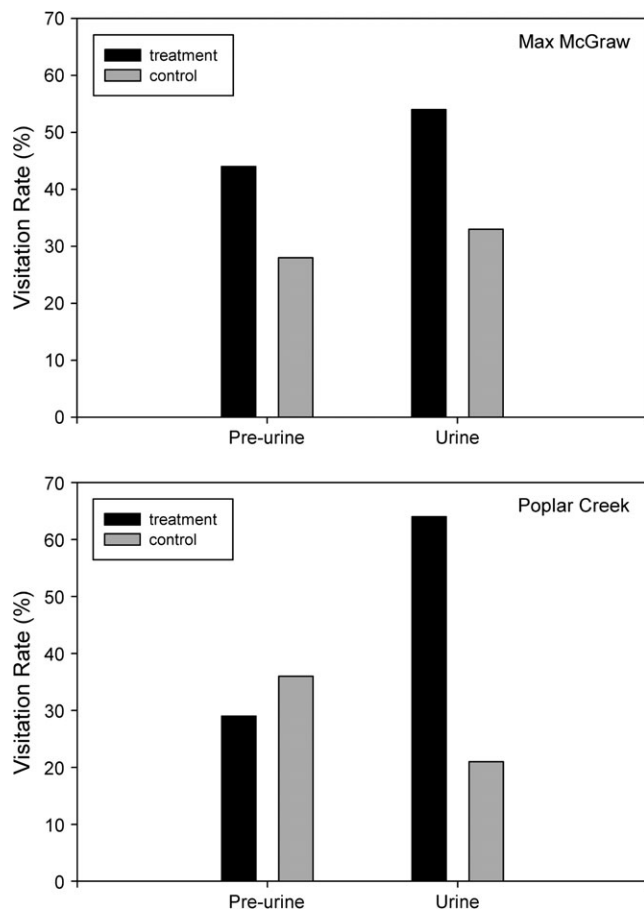
**Figure 4**
Visitation rates to scent stations for raccoons on the MMWF and Poplar Creek Forest Preserve, Illinois. At Max McGraw, treatment ($n = 39$) stations received a fish oil application during the preurine stage, which was replaced with coyote urine for the urine stage, and control stations ($n = 39$) had an untreated stick during both stages. At Poplar Creek, control ($n = 14$) and treatment ($n = 14$) stations received a fish oil application during preurine and urine stages, and treatment stations also had coyote urine applied during the urine phase.

The pattern was reversed during the preurine phase, where the species only cooccurred at control stations (3 times).

## DISCUSSION

### Prediction 1: predation

Coyotes and raccoons on MMWF presumably had frequent opportunities for interactions as both species were abundant in the area. Published raccoon densities derived from mark recapture have typically been less than 20 km$^{-2}$, with high densities more than 30 km$^{-2}$ (for reviews, see Riley et al. 1998 and Gehrt 2003). Prewhelping coyote densities are typically less than 1 km$^{-2}$ (Andelt 1985; Bekoff and Gese 2003), with high densities near 2 km$^{-2}$ (Windberg 1995). Despite a relatively high-density coyote population on MMWF during this study, we failed to document any confirmed raccoon mortalities as a result of predation, and possible predation was still minor even when we conservatively included unknown mortalities. Although the raccoon population during this study was rebounding from an experimental reduction in 1999 (Gehrt 2002), survival rates were similar to those observed for the population prior to the manipulation. Spring raccoon densi-

ties on MMWF ranged 41–49 raccoons per km$^2$ prior to the reduction during 1995–1997 (Gehrt 2002). During that period, 38 female raccoons were monitored, and of 18 mortalities none were related to predation (Prange et al. 2003) despite the presence of coyotes on the area. Thus, predation rates were nonexistent or low across a range of raccoon densities and for multiple years. We did not have population data for coyotes prior to this study, but frequency of observations and group sizes observed by residents and technicians working on the raccoon project suggested the coyote population has remained at a relatively high level since 1995.

The predation rates observed for raccoons on MMWF appear to be typical of other raccoon populations, including additional populations in northeastern Illinois (Prange et al. 2003). Coyote predation has typically made up <3% of known-cause mortalities during radiotelemetry studies of raccoons in various systems with coyotes, including exploited populations in Iowa (Clark et al. 1989; Hasbrouck et al. 1992) and Mississippi (Chamberlain et al. 1999) and in an unexploited raccoon population in South Texas with numerous potential predators, including an abundant coyote population (Gehrt and Fritzell 1999).

Although the Iowa studies of Clark et al. (1989) and Hasbrouck et al. (1992) are frequently cited as evidence for MRH, predation was a rare mortality event in those studies. Only 12% (90/744) of the raccoons in the Iowa study died from causes other than anthropogenic causes, and of that fraction 2% were caused by coyotes (Clark et al. 1989; Gehrt and Clark 2003). Therefore of all mortality, predation by coyotes accounted for <1%.

The consistently low frequency (<3%) of coyote predation of raccoons is in stark contrast to the 40–80% predation rates attributed to coyotes reported for kit and swift foxes in a variety of systems (Ralls and White 1995; Sovada et al. 1998; Kitchen et al. 1999; White et al. 2000; Olson and Lindzey 2002). Thus, if interference competition occurs between coyotes and raccoons, it does not appear to be maintained through predation (Gehrt and Clark 2003).

### Prediction 2: avoidance

In a review of interspecific killing among mammalian carnivores, Palomares and Caro (1999) reported that the incidence of intraguild predation was relatively low for procyonids, but they suggested avoidance by raccoons of larger carnivores may be important. However, as with prediction 1, we found little evidence that raccoons avoid areas or habitats used by coyotes at a variety of spatial scales. Patterns of interspecific overlap among core areas were similar among seasons and sex classes, and nearly similar results for overlap of 95% contours, indicating that raccoon–coyote relationships did not vary through the year or among classes of raccoons (especially for core areas). Most raccoons residing on MMWF had home ranges encompassed by the larger home ranges of coyotes and had potential interactions with coyotes.

However, there was considerable variation among individual raccoons in the degree of spatial overlap with coyote core areas. Raccoons were well distributed throughout the west side of the study area, as were coyote movements, but coyote core areas did not encompass the entire west side. Therefore, it was not surprising that some (or most) raccoons were rarely located in coyote core areas. For those raccoons that had home ranges that did overlap with coyote core areas, there was no indication raccoons avoided those areas within their home ranges and we actually observed a trend in the opposite direction. The shared use of space between the 2 species may reflect the ability of each species to take advantage of seasonally or otherwise temporarily available resources.

We found coyotes and raccoons on MMWF using habitat similarly with only minor differences at different spatial scales. Although female raccoons and coyotes differed in terms of second-order habitat selection, coyotes exhibited no selection of habitat types at this spatial scale. Consequently, habitat selection of female raccoons was apparently not due to avoidance of areas selected by coyotes, and overall patterns of habitat use were similar for female raccoons and coyotes (Figure 3A). Furthermore, both species exhibited a similar pattern of habitat selection at the third-order scale, with wooded areas selected over all other habitat types. This apparent lack of avoidance between species was further substantiated at the microscale with our scent-station trials, in which there actually was a trend for raccoons to increase their activity around coyote sign rather than to decrease it.

The lack of avoidance exhibited by raccoons toward coyotes is consistent with a low probability of predation that has consistently been reported from radiotelemetry studies. If predation rate is truly low for raccoons, there is little reason for them to avoid coyotes and consequently no predation risk effect in habitat use. Indeed, evidence for avoidance of coyotes has been mixed even among foxes (Sargeant et al. 1987; Harrison et al. 1989; White et al. 1994; Gese et al. 1996), where predation pressure is apparently much higher than for raccoons.

## Validity of MRH?

We failed to find support for a mortality prediction or avoidance prediction to support MRH with regard to raccoons and coyotes. This suggests that relationships among mammalian predators may not be simply dictated by body size, particularly for species outside the Canidae (Gehrt and Clark 2003). Among mesopredators occurring on MMWF, raccoons are the closest in body size to coyotes, although coyotes typically weighed twice as much as raccoons (Gehrt SD, unpublished data). Both coyotes and raccoons are opportunistic omnivores, although coyotes are more carnivorous than raccoons, which may reduce interspecific competition. The combination of a lack of competition and relatively large size of raccoons (compared with other potential prey) may explain the lack of interference competition between coyotes and raccoons. Coyotes may rarely depredate raccoons because raccoons effectively defend themselves or they may elude coyotes with their climbing ability. Other mesopredators on MMWF include striped skunks and Virginia opossums, which are smaller than raccoons and may have a different relationship with coyotes (Kamler and Gipson 2004), however their omnivory may also reduce their competition with coyotes.

Although the MRH appears to explain relationships among species within the canid community, the results of our study suggest that relationships among other carnivores are complex and not necessarily dictated by body size. Elsewhere Gehrt and Clark (2003) have argued that intensity of interference competition, and the validity of MRH, may be related to degree of niche overlap among carnivore species. That is, body size may be important between species occupying similar niches (e.g., high dietary overlap) where competition may be more substantial than for species occupying more disparate niches where competition is presumably mitigated. This may explain the mixed results of Crooks and Soulé (1999), in which some relationships among predators were significant but many were not.

Negative correlations between raccoon and coyote distributions over large spatial scales (e.g., Sargeant et al. 1993; Rogers and Caro 1998; Crooks and Soulé 1999) are probably the result of species differences in habitat preference rather than direct interference competition. Although we observed similar habitat selection between species in our study, the MMWF is a patch of undeveloped habitat surrounded by a metropolitan landscape, and its relatively small size may have caused one or both species to alter their typical habitat use. Within the urban landscape where human presence is high, coyotes may use woodlands as cover to a greater degree than in rural landscapes. However, it is important to point out that previous studies reporting support for MRH were also conducted in urban islands (Crooks and Soulé 1999) or habitat fragments (Terborgh et al. 2001).

The results from this study have conservation and educational implications. As coyotes have expanded their range and increased locally, some have suggested that coyotes may act as a biocontrol for overpopulated mesopredators such as raccoons, thus leading to the encouragement to manage for coyotes where possible (Rogers and Caro 1998). Although coyotes may perform important ecological services where they occur, our results and those of other studies question whether coyotes effectively limit raccoons. In addition, although our study has focused on the relationship between raccoons and coyotes, the implications extend beyond these species. The MRH has been used to predict relationships between carnivore species for which little is known concerning intraguild competition. However, our results contradict previous literature (Rogers and Caro 1998; Crooks and Soulé 1999) and suggest that relationships between mesopredators, particularly omnivores, may be more complex than a simple linear hierarchy based on body size. Our results illustrate the need for further research on intraguild competition among mesocarnivores as a mechanism for structuring their communities.

## APPENDIX A

$K$ (number of of parameters), AICc (Akaike's Information Criterion corrected for small sample bias), $\Delta_i$ ($\Delta$AICc), and $w_i$ (Akaike weights) for general linear models of second-order habitat selection (composition of home ranges relative to study area) by raccoons and coyotes at MMWF in northeastern Illinois, USA

| Model | $K$ | AICc | $\Delta_i$ | $w_i$ |
| --- | --- | --- | --- | --- |
| Raccoon models | | | | |
| Hab, Hab × Gen | 11 | 202.19 | 0.00 | 0.995 |
| Hab | 5 | 212.97 | 10.78 | 0.005 |
| Hab, Hab × Ovlp | 11 | 226.09 | 23.90 | 0.000 |
| Hab, Hab × Gen, Hab × Gen × Sn | 29 | 243.37 | 41.18 | 0.000 |
| Hab, Hab × Ovlp, Hab × Ovlp × Gen | 23 | 251.40 | 49.21 | 0.000 |
| Hab, Hab × Ovlp, Hab × Ovlp × Sn | 29 | 271.58 | 69.39 | 0.00 |
| Coyote–female raccoon models | | | | |
| Hab, Hab × Sp | 11 | 235.99 | 0.00 | 0.875 |
| Hab | 5 | 239.89 | 3.90 | 0.125 |
| Hab, Hab × Sn | 14 | 255.11 | 19.12 | 0.000 |
| Hab, Hab × Sp, Hab × Sp × Sn | 29 | 285.78 | 49.79 | 0.000 |
| Coyote–male raccoon models | | | | |
| Hab | 5 | −70.38 | 0.00 | 0.943 |
| Hab, Hab × Sp | 11 | −64.78 | 5.60 | 0.057 |
| Hab, Hab × Sn | 14 | −50.80 | 19.58 | 0.000 |
| Hab, Hab × Sp, Hab × Sp × Sn | 29 | −25.55 | 44.83 | 0.000 |

Hab = habitat; Gen = gender; Sn = season; Sp = species; Ovlp = overlap.

## APPENDIX B

$K$ (number of parameters), AICc (Akaike's Information Criterion corrected for small sample bias), $\Delta_i$ ($\Delta$AICc), and

$w_i$ (Akaike weights) for general linear models of third-order habitat selection (habitats containing telemetry locations relative to home range composition) by raccoons and coyotes at MMWF in northeastern Illinois, USA

| Model | $K$ | AICc | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|
| Raccoon models | | | | |
| Hab | 5 | 353.42 | 0.00 | 0.997 |
| Hab, Hab × Gen | 11 | 366.18 | 12.76 | 0.002 |
| Hab, Hab × Ovlp | 11 | 366.43 | 13.01 | 0.001 |
| Hab, Hab × Ovlp, Hab × Ovlp × Gen | 23 | 396.64 | 43.22 | 0.000 |
| Hab, Hab × Gen, Hab × Gen × Sn | 29 | 411.87 | 58.45 | 0.000 |
| Hab, Hab × Ovlp, Hab × Ovlp × Sn | 29 | 413.68 | 60.26 | 0.000 |
| Coyote–raccoon models | | | | |
| Hab | 5 | 432.12 | 0.00 | 0.997 |
| Hab, Hab × Sp | 11 | 444.17 | 12.05 | 0.002 |
| Hab, Hab × Sn | 14 | 447.06 | 14.94 | 0.001 |
| Hab, Hab × Sp, Hab × Sp × Sn | 29 | 484.56 | 52.44 | 0.000 |

Hab = habitat; Gen = gender; Sn = season; Sp = species; Ovlp = overlap.

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