EFFECTS OF URBANIZATION ON SURVIVAL RATES, ANTI-PREDATOR
BEHAVIOR, AND MOVEMENTS OF WOODCHUCKS (*MARMOTA MONAX*)

BY

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THESIS

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ABSTRACT

Urbanization is increasing at a rapid rate and creating novel environmental

conditions for wildlife species, even in already human-altered landscapes. We need a

better understanding of demographic and behavioral responses by mammals to

urbanization including those species that could be urban adapters. Furthermore, past

research has focused on carnivores, but herbivores could respond to additional factors

across urbanization gradients such as variation in real and perceived risk from

predators. I examined survival, cause-specific mortality, anti-predator behavior, and

movements of adult woodchucks (*Marmota monax*) across an urbanization gradient

within an agricultural landscape in central Illinois from 2007 to 2009. As predicted,

survival rates were related positively to urbanization. Survival rates of woodchucks

were higher, and effects of urbanization were stronger during the inactive season

relative to the active season for this hibernating species. Woodchucks in rural areas

mainly died from predation and probable starvation during hibernation, whereas

major causes of mortality for urban woodchucks were vehicle collisions or unknown

reasons. Three measures of anti-predator behavior—levels of vigilance, foraging

distance from burrows, and flight initiation distance—did not vary with urbanization.

Julian date was related to all components of anti-predator behavior in a consistent

manner, which indicates woodchucks take on more risk later in the active season as

hibernation approaches. Home-range size of woodchucks in urban areas was ~10% of

those in rural areas and urbanization had stronger effects on home-range sizes of

males compared to females. Woodchucks are multiple central-place foragers and their

use of burrows within home ranges also was influenced by urbanization. Number of burrows per individual decreased with urbanization, but the number of burrows was not scaled proportionally to home-range size. Distances between burrows increased in rural areas, and thus risk during inter-burrow movements could be greater for rural woodchucks. Aggregation of use among burrows increased with urbanization and was related positively to spatial connectivity of burrows. Urbanization created spatial variation in real risk for woodchucks and woodchucks responded by demonstrating substantial plasticity in movement behavior. However, although natural predators are reduced in urban areas, perceived risk affecting anti-predator behavior remained high overall for woodchucks in urban areas due to increased levels of human disturbance and lack of strong habituation to humans. My research demonstrates how combining demographic and behavioral studies can provide insights into responses to urbanization, and constraints to those responses, by an urban-adapter species.

ACKNOWLEDGMENTS

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CHAPTER 1:

EFFECTS OF URBANIZATION ON SURVIVAL AND ANTI-PREDATOR

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LANDSCAPE

1. Introduction

Urbanization is rapidly increasing and dramatically altering landscapes.

Between 1990 and 2000, urban sprawl, the expansion of urban boundaries into the

rural countryside, grew by as much as 50% in the United States (DeStefano and

DeGraaf, 2003; Heimlich and Anderson, 2001). By 2000, cities and suburbs

contained almost 80% of the human population and represented >5% of the surface

area of the United States (U.S. Census Bureau, 2001). In urban environments, natural

habitat is reduced and fragmented by human-made barriers such as buildings, parking

lots and high-traffic roads; food sources are artificial and concentrated; and

disturbance from humans is high (Ditchkoff et al., 2006; McKinney, 2002). As a

result, urbanization decreases biodiversity, and community structure shifts toward

"urban adapters" that can tolerate and adjust to such dramatic changes (McKinney,

2002). Urban adapters persist in metropolitan areas despite significant human

disturbance, partly due to increased availability of anthropogenic food sources and

reduced number of natural predators (McKinney, 2002; DeStefano and DeGraaf,

2003; Ditchkoff et al., 2006). Urban adapters may modify life-history traits and

behaviors to survive in urban areas; however, the details of these adjustments are

unknown for most species (Dickman and Doncaster, 1987, Ditchkoff et al., 2006). To

understand and predict effects of urbanization on wildlife species, we need more knowledge about mechanistic responses by species to spatial variation in real and perceived mortality risk created by urbanization gradients.

Studies examining mammalian responses to urbanization primarily have focused on movements or relative densities of carnivores (e.g., Rosatte, 1991; Riley et al., 2003; Atwood et al., 2004; Prange and Gehrt, 2004; Riley, 2006), whereas a focus on survival rates is less common (Prange et al., 2003; Gehrt, 2005; Gosselink et al., 2007). Estimates of survival rates allow us to evaluate how fitness varies across urbanizing landscapes and can inform us about potential source-sink dynamics (Kanda et al., 2009). Existing data indicate survival rates may be similar or higher in urban areas relative to rural areas, and that disease or vehicle collisions are primary sources of mortality in urban areas (Prange et al., 2003; Gehrt, 2005; Gosselink et al., 2007). Prey species may respond to risks similar to those affecting carnivores, but overall mortality risk of prey also may be affected by variation in predation risk across urban-rural gradients. However, few studies have quantified variation in survival rates of a mammalian prey species in relation to urbanization (but see Etter, 2002; McCleery, 2008).

Besides real mortality risk, perceived risk also could vary for prey species across an urbanization gradient. Natural predators generally are less abundant in urban areas (Gering and Blair, 1999; McKinney, 2002; Shochat et al., 2006), which should reduce perceived risk. However, disturbance from humans may replace the threat of natural predators (Frid and Dill, 2002). Thus, perceived risk in urban areas partly depends on the degree to which individuals are habituated to humans. In

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addition, local environmental factors affect the ability of prey to detect and escape from predators and contribute to perceived risk, such as distance from a refuge while foraging (Lima, 1987; Dill, 1990; Bonenfant and Kramer, 1996) and presence of conspecifics ("many eyes hypothesis"; Carey and Moore, 1986; Elgar, 1989; Lima, 1995). Adjustments to anti-predator behavior resulting from changes in perceived risk across urbanization gradients may translate into variation in survival rates as a result of trade-offs within activity budgets. Based on foraging theory, if perceived predation risk is reduced, individuals should spend less time engaged in anti-predator behavior and more time engaged in other fitness-dependent activities, such as foraging (Lima and Dill, 1990). Only one study has directly examined vigilance behavior of a mammalian urban adapter (McCleery, 2009), and investigations that simultaneously compare demography and behavior of any species in relation to urbanization are rare.

Woodchucks (*Marmota monax*) are an excellent study species for examining effects of urbanization on true and perceived risk because they occur in both urban and rural landscapes and are presumed "urban adapters" (McKinney, 2002). The species is medium-sized and diurnal, which allows for direct observation to assess perceived risk, Woodchucks are herbivores and because they hibernate, time dedicated to foraging is especially consequential for obtaining adequate body condition for over-winter survival (Davis, 1981). Predators of woodchucks include coyotes (*Canis latrans*; Hofmann, 2008) which generally decrease in abundance with urbanization (Gosselink et al. 2003; Randa and Yunger, 2006), and domestic dogs (Kwiecinski, 1998; Hofmann, 2008) which are typically leashed by owners in cities. Therefore, predation risk for woodchucks should be reduced in urban areas.

I examined variation in real and perceived risk by comparing survival rates and anti-predator behavior of woodchucks across an urbanization gradient within a human-dominated agricultural landscape in central Illinois. I predicted survival rates would be related positively to urbanization due to reduction of natural predators and abundant anthropogenic food resources (i.e., managed lawns and gardens) in urban areas. I also expected causes of mortality to vary across the gradient. To examine anti-predator behavior, I determined whether woodchucks adjust to changes in perceived risk by modifying levels of vigilance behavior and the distance at which they forage from burrows. To understand how woodchucks perceive humans, which would affect perceived risk, I examined habituation of woodchucks to humans by comparing flight initiation distance (FID) across the gradient. FID is the distance at which an animal begins to flee from an approaching predator (Bonenfant and Kramer, 1996) and is often used to examine the effect of human disturbance on wildlife (Cooke, 1980; Lord et al., 2001; Ikuta and Blumstein, 2003; Griffin, 2007). I expected woodchucks would habituate to humans in urban areas, and thus have shorter FIDs than do rural woodchucks. Assuming woodchucks habituate to humans and natural predators are reduced in urban areas, I expected perceived predation risk would decrease with urbanization and that urban woodchucks would adjust their behavior by spending less time vigilant and foraging farther from burrows. I also predicted perceived predation risk would contribute to overall mortality risk, specifically over-winter mortality. That is, if woodchucks in rural areas spend more time engaged in vigilance behavior and less time foraging, their body condition may be inadequate to survive the winter.

2. Methods

2.1. Study species

Woodchucks are herbivores that prefer vegetation common in urban areas such as grass, clover, and garden crops (Hoffmeister, 2002; Kwiecinski, 1998), and they are multiple central-place foragers that feed almost exclusively near burrows in which they escape from predators, rear young, and hibernate. Hibernacula generally are located in wooded edges, fencerows, steep inclines, or human-made structures, but woodchucks forage in open fields during the active season (Kwiecinski 1998). Woodchucks are polygynous, territorial (Maher, 2004), and breed only once per year, immediately upon emergence from hibernation in the early spring (Hoffmeister, 2002). Litters are born in April - May and juveniles emerge from the burrow once fully weaned (~44 days; Kwiecinksi, 1998). Timing and degree of philopatry can vary among populations, but most juveniles disperse within their first year (Kwiecinksi, 1998). Predators of woodchucks include dogs, coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), mink (*Neovison vison*), weasels (*Mustela sp.*), hawks, and owls (Kwiecinski, 1999; Hofmann, 2008). Badgers and bobcats are uncommon in central Illinois, and weights of adult woodchucks range from 3.4 – 6.7 kg (E. L. Watson, unpublished data), thus, it is unlikely that adult woodchucks are vulnerable to smaller predators like foxes, mink, weasels, hawks, and owls. Hence, we assumed the main predators of adult woodchucks in our study area were coyotes and domestic dogs. Woodchucks exhibit behavioral plasticity in relation to environmental heterogeneity (Swihart, 1992; Bonenfant and Kramer, 1996; Maher, 2004; Chapter 2).

2.2. Study area and urbanization gradient

I conducted my research in a 700-km^2 study area located around the twin cities of Champaign and Urbana in east-central Illinois. The Champaign-Urbana metropolitan area is a medium-sized community (2007 population estimate = 220,923), which grew 5% from 2000 to 2007 (U.S. Census Bureau, 2009). High densities of older buildings (~492 buildings/km^2); impervious surfaces in the form of roads (~12.8 km of roads/km^2), sidewalks, and parking lots; and established trees characterize the urban core. Extending out from the urban center, building density decreases, newer and sprawling residential subdivisions and office parks dominate, and tree density is reduced. The landscape eventually grades into one of the most intensive regions of row crop agriculture in the United States (Mankin and Warner, 1997) where corn and soybeans become the dominant land cover resulting in a landscape nearly devoid of cover between the fall harvest and spring planting (Warner, 1994). The rural landscape also is characterized by a low diversity of habitats including sparse forest fragments and fencerows, few homesteads (~9 buildings/km^2), minimal traffic, and ~1.1 km of roads/km^2.

I sampled woodchucks across an urbanization gradient defined by the percentage of urban land cover within a specific buffer size. For survival analysis, I used a 500-m buffer around each individual's favored burrow as determined from radiolocations (details to follow). This standard distance was chosen to encompass variation in home-range size of woodchucks related to sex and gradient position (see Chapter 2), and to represent potential risk encountered by woodchucks from the broader landscape. For the behavioral analysis, I used a 300-m buffer around the

burrow at which the observation took place. Here, I wanted to examine a spatial extent that would index potential disturbances at a more local scale. Key results regarding urbanization and behavior were insensitive to buffer size (from 100 to 500 m). I chose the burrow of observation to center buffers because many observed woodchucks were not radio-marked, and thus I had no information about their favored burrow or home-range size.

I classified land cover within buffers using digital orthophotographs (minimum resolution of 0.5 m) from 2008 (for 84 woodchucks) and from 2005 (3 woodchucks outside of Champaign County). Land cover was classified into 5 categories: "developed" included paved surfaces, buildings, and associated lawns and gardens; "urban open space" included maintained open areas such as cemeteries, parks, and golf courses; "urban forest" included forest surrounded by developed land cover; "urban grassland" included all unmaintained grass surrounded by developed land cover; and "rural" included all remaining land cover. To differentiate urban animals with home ranges without any natural habitat from those with home ranges that included natural habitat surrounded by developed land cover (urban grassland, urban forest), I considered urban land cover to include the categories of "developed" and "urban open space". I ground-truthed photographs during field visits and updated my classifications when necessary.

2.3. Capture and radiotracking

Woodchucks were captured from May to November 2007 using single-door collapsible Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin;

Model 207). Trapping techniques were approved by the University of Illinois'
Institutional Animal Care and Use Committee and met guidelines of the American
Society of Mammalogists (Gannon et al., 2007). I placed traps baited with apples and
peanut butter near active burrows (Swihart, 1992; Maher, 2004). Traps were set in the
early morning, checked every 2 hours, and closed by mid afternoon.

I transported adult woodchucks (≥1 year old; age determined by weight and
pelage; Kwiecinski, 1998) to the College of Veterinary Medicine at the University of
Illinois where a 32-g radio transmitter (Model #M1240, Advanced Telemetry
Systems, Isanti, Minnesota) was surgically implanted in the peritoneal cavity,
generally within 3 hrs of capture. Standard surgical procedures (Van Vuren, 1989;
Maher, 2009) were followed except medetomidine was used as the anesthetic rather
than a xylazine-ketamine mixture. While woodchucks were anesthetized, I
determined their sex and implanted passive-integrated transponders (PIT; Schooley et
al., 1993) in the interscapular region for long-term identification. Woodchucks were
released at their burrows of capture after full recovery. To monitor survival, I located
woodchucks 2-4 times per week during 2 active seasons (2007 and 2008) and 3 times
per month during 2 hibernation seasons (2007-2008, 2008-2009). Radio-monitoring
was less frequent during the 2009 active season (once every two weeks until July,
once every 3-4 weeks in August and September). Transmitters were equipped with a
mortality sensor that changed pulse rate when an animal had not moved in >8 hrs.
Carcasses were recovered and a cause of death was determined in the field or by
necropsy by the College of Veterinary Medicine at the University of Illinois if the
carcass was not too decomposed. Mortalities were attributed to predation when the

transmitter was discovered outside of the woodchuck, either alone or with evidence of a carcass nearby. Vehicle collision was determined as the cause of death when a carcass was found in or near a road, or if the necropsy results indicated massive trauma. If the woodchuck never left the den after the inactive season, the cause of death was attributed to hibernation.

2.4. Survival estimation

I used known-fate models in program MARK (White and Burnham, 1999) to estimate survival rates of radio-marked woodchucks across the urbanization gradient. Known-fate models allow for staggered entry of individuals and evaluation of survival covariates. Survival rates were estimated for 63 two-week intervals (45 active-season intervals, 18 inactive-season intervals). Because I did not know when woodchucks were physiologically hibernating, I defined active and inactive seasons based on denning dates using radiolocations. The inactive season began with the median date of settlement at the hibernaculum in autumn (den entry) and ended with the median date of the first location outside of the hibernaculum in spring (den exit). The median den entry date was 15 November in 2007 ($SE = 12.8$, $n = 35$) and 30 October in 2008 ($SE = 4.0$, $n = 20$). The median den exit date was 10 March in 2008 ($SE = 4.0$, $n = 33$) and 3 March in 2009 ($SE = 3.9$, $n = 19$). Because of considerable variation among individuals in den entry and exit dates, I applied a censoring procedure to woodchucks whose denning pattern did not coincide with median dates. If a woodchuck denned prior to the beginning of the inactive season, it was censored from the active season until the inactive season began. If a woodchuck denned later than

the median entry date, it was censored from the inactive season until the date when it denned. The same procedure was applied for den exit dates. Individuals also were censored for any interval for which their fate was unknown due to movement or transmitter failure.

To test for effects of urbanization and other covariates on survival rates, I evaluated 8 candidate models using Akaike's Information Criterion (AIC$_c$: corrected for small sample size; Burnham and Anderson, 2002). AIC allows for simultaneous comparison of multiple models by ranking them based on goodness of fit and complexity. Models with a ΔAIC value <2 are considered competitive (Burnham and Anderson, 2002). The candidate models included combinations of urban land cover (urban), sex, and season (active = 0, inactive = 1) as predictors plus an interaction term for urban x season. I also examined parameter estimates (β, on a logit scale) from competitive models to understand the relationship between survival and covariates.

2.5. Anti-predator behavior

I examined three aspects of anti-predator behavior for woodchucks that could vary with urbanization: vigilance behavior, distance from burrow during foraging bout, and FID. These behaviors also could covary within individuals. My observations for these components included both radio-marked and unmarked individuals, and thus I could not examine effects of sex.

2.5.1. Vigilance behavior and distance from burrow

     I recorded behavior during focal observations (Martin and Batesman, 2007) of woodchucks from June to October 2008. Each individual was observed only once. I located foraging woodchucks for observation by waiting at a burrow for an individual to emerge or by observing an individual already out foraging. In both cases, I started observations after the woodchuck had resumed foraging if I had disturbed it. Woodchucks generally do not react to people within vehicles (E. L. Watson, personal observation), therefore all observations were recorded from a vehicle parked >30 m from the focal animal. Observations were recorded by one of two observers (trained for consistency) using a window-mounted digital video camera (minimum 25x zoom) and a stopwatch. Only woodchucks in low vegetation were observed for ease of visibility. Observations lasted ≥8 min and were terminated if the woodchuck was flushed into the burrow or if the observation exceeded 45 min.

     During observations, I recorded local environmental covariates known to affect vigilance behavior by quietly speaking them into the camera's microphone every 20s. I recorded number of conspecifics within 10 m (Blumstein et al., 2004) and distance from the focal woodchuck to the nearest burrow. Distances were visually estimated according to categories (0-2, 2-4, 4-6, 6-10, 10-20, and >20 m) and accuracy of observers was tested throughout the season. I also recorded disturbances within 50 m (i.e., people walking, loud noises, cars, presence of predators) as they occurred during the observation. The burrow location was recorded with a handheld Global Positioning System (GPS) unit after the observation was terminated. Videos were later scored by one observer to estimate activity budgets using the same 20-s

intersample interval used to record environmental covariates at the time of the observation. Behaviors were classified from an ethogram based on one developed for woodchucks and yellow-bellied marmots (*Marmota flaviventris*, Armitage et al., 1996; Maher, 2006; Table 1).

2.5.2. Flight initiation distance

I evaluated the degree to which adult woodchucks were habituated to people by measuring flight initiation distance (FID) across the urbanization gradient from August to October 2008. To measure FID, I located a foraging woodchuck and positioned myself so that the woodchuck was in a straight line between me and the nearest burrow. I noted my initial location so that I could measure "start distance" (distance between predator and prey when approach begins; Blumstein, 2003). Once the individual detected me (as demonstrated by an alert posture), I noted its location relative to the burrow and began a slow, constant approach. I marked my location when the woodchuck began to flee, and continued to move toward the woodchuck with a steady pace until it reached the burrow. FID and start distances were recorded with a measuring tape and location of the burrow to which the woodchuck fled was recorded with a handheld GPS unit. I conducted all FID trials and wore similar clothing for each trial to avoid any biases. Only one trial was conducted for each individual.

2.5.3. Analysis of anti-predator behavior

To test for an effect of urbanization on vigilance behavior, distance from burrow during foraging bout, and FID, I used generalized linear models in SAS (PROC GENMOD - SAS Institute Inc., 2009) and evaluated candidate models using AIC. Vigilance behavior was analyzed as the proportion of sample intervals during which a woodchuck displayed low vigilance, medium vigilance, or high vigilance (Table 1). That is, these three behaviors were combined into one variable for analysis (vigilance). I arcsine transformed vigilance proportions prior to analysis. For vigilance behavior, I compared 16 models that included combinations of four predictors: urban land cover (urban), distance of woodchuck from burrow (DFB), presence of conspecifics (conspecifics), and the Julian date of the observation (date). DFB was calculated as the average distance for an individual across sample intervals from the simultaneous behavioral observations (using the center value of the distance categories). For analyzing DFB as a response variable, I evaluated 8 models that included combinations of urban, conspecifics, and date as predictors. For FID, I compared 15 models that included combinations of urban, DFB, the initial distance between me and the woodchuck (start), and date. I also examined parameter estimates (β) from competitive models to understand relationships between response variables and predictors.

I examined whether vigilance behavior varied within distance categories across the gradient. For each individual, I calculated the proportion of intervals that woodchucks spent vigilant while foraging at each distance category during behavioral observations, then averaged those proportions across individuals. I limited my

analysis to behavioral observations during which the focal woodchuck was not disturbed.

Independent of urbanization, I was interested in whether certain individuals might be risk-aversive, whereas others might be risk-takers. Thus, I examined covariation of vigilance behavior and FID for the subset of animals for which I had both types of behavioral data. Correlated behaviors are referred to as "behavioral syndromes" (Sih et al. 2004) and have been examined in a congener, yellow-bellied marmots (*Marmota flaviventris*; Blumstein et al. 2004)

3. Results

3.1. Survival rates

Survival estimates were based on 41 woodchucks (17 males, 24 females) distributed across the urbanization gradient (Fig. 1). Twenty-six woodchucks died (23 in the active season, 3 in the inactive season) during the 126-week study. Two individuals were relocated by homeowners and subsequently censored. The signal from one female, urban woodchuck was lost early in the 2008 active season, despite extensive searching. Because female woodchucks in urban areas have small home ranges (<3 ha, Chapter 2), and the missing woodchuck had never moved from her general capture site, I attributed her disappearance to a premature transmitter failure. During the last several months of the study, transmitters began to exceed their expected battery life and the remaining woodchucks ($n = 12$) also were censored due to transmitter failure.

Survival probability per two-week interval was higher during the inactive season than during the active season ($S_{inactive} = 0.997$, $SE = 0.004$; $S_{active} = 0.971$, $SE = 0.006$), and differences in survival rates increased with urbanization (Fig. 2). AIC rankings revealed three competitive models for explaining variation in survival rates of woodchucks (Table 2). All competitive models included season as a covariate and the top-ranked model included only season (Table 2). Another model that included urbanization, season, and an urban x season interaction was ranked second and close to the top model (Table 2). Although the second-ranked model was more complex than the top model (2 additional parameters), the second-ranked model reduced the deviance substantially. Thus, there was support for an effect of urbanization and an urbanization x season interaction on survival rates of woodchucks (Fig. 2). Survival was related positively to urbanization ($\beta_{urban} = 0.16$, $SE = 0.60$), but this effect was stronger for the inactive season than for the active season (($\beta_{inactive} = 2.15$, $SE = 1.09$; $\beta_{urban\ x\ season} = 3.37$, $SE = 2.31$). A model which included urbanization and season was competitive as well (Table 2). There was no support for an effect of sex on survival rates.

3.2. Causes of mortality

Of 26 woodchucks known to have died during the study (Fig. 3), 7 died from predation (26.9%), 5 died from vehicle collisions (19.2%), 2 died from conflict with a landowner (7.6%), 3 died during the inactive season (11.5%), and causes of 9 deaths were unknown (36%). Patterns in mortality causes were evident along the urbanization gradient (Fig. 3, Appendix A). Almost all mortalities from predation

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(86%) occurred in rural and suburban areas with <35% urban land cover. Mortalities

due to collisions with vehicles occurred only in urban and suburban areas. Mortalities

during the inactive season, presumably due to low body condition at the time of

immergence, occurred in more rural areas (<45% urban land cover). Causes of 9

mortalities could not be determined either because the carcass was too decomposed

by the time it was discovered, or because the woodchuck died in an inaccessible

burrow. Seven (78%) of these unknown mortalities occurred in areas with >80%

urban land cover.

3.3. Anti-predator behavior

Analyses of vigilance behavior and distance from burrow during foraging

bouts were based on observations of 41 individuals (14 radio-marked, 27 unmarked;

Fig. 1). On average, woodchucks spent 13.5% ($SE = 2.07$) of the observation time

engaged in vigilance behavior. There was no support for an overall, linear effect of

urbanization on vigilance behavior (Fig. 4). The only competitive model for

predicting vigilance behavior included date of the observation ($R^2 = 0.21$, Table 3).

Woodchucks were more vigilant in early season relative to late season ($\beta_{date} = -0.003$,

$SE = 0.0009$). Vigilance levels of 20-50% were common before 30 July, but vigilance

exceeded 10% only once in 15 (6.7%) observations after 30 July (Fig. 4). The second-

ranked model included urbanization, but urbanization did little to increase the log-

likelihood of the model relative to the top model without urbanization (Table 3).

During behavioral observations, woodchucks foraged within 7.5 m ($SE = 0.67$)

from the burrow on average. There was not strong support for an effect of

urbanization on foraging distance from burrows. The top-ranked model for predicting

DFB included date of the observation (Table 3), although the model did not explain a

substantial amount of variation (R^2 = 0.06, n = 41). Woodchucks foraged farther from

the burrow in late season relative to early season (β_{date} = 0.033, SE = 0.021). The

second-ranked model was the intercept-only model; however, the log-likelihood for

this model was considerably lower relative to the top model (Table 3). The third-

ranked model included urban only, but its log-likelihood was barely higher than the

intercept-only model (Table 3).

Based on those behavioral observations that were free from human

disturbance (n = 31), average vigilance levels decreased from 25% when woodchucks

foraged <2 m from the burrow to 7% when woodchucks foraged 10-20 m from the

burrow. Vigilance levels increased to an average of 16% when woodchucks foraged

>20m from the burrow (Fig. 5).

I conducted FID trials on 27 individuals (6 radio-marked, 21 unmarked; Fig.

1). The average FID across the gradient was 26.9 m (SE = 2.14). There was little

support for an effect of urbanization on FID. AIC rankings revealed 4 competitive

models that all included start distance as an important factor affecting flight initiation

distance. The top-ranked model included start distance and date (R^2 = 0.33, Table 3).

FID was related positively to start distance (β_{start} = 0.37, SE = 0.13) and negatively to

date (β_{date} = -0.20, SE = 0.13). Closely ranked with the top model was a model that

included start distance alone (Table 3). A model including distance to burrow in

addition to start and date also was competitive. Distance to burrow had a positive

effect on FID (β_{DFB} = 0.34, SE = 0.36; Table 3). There was support for effects of date

and distance to burrow on FID as the addition of each variable increased the model

log-likelihood compared to that of the start-distance-only model (Table 3). The final

competitive model included start distance plus urbanization; however, the small

difference in log-likelihoods between this model and the start-distance-only model

indicated little support for an effect of urbanization on FID (Table 3).

Flight initiation distance and vigilance behavior were correlated positively for

those woodchucks for which I had both types of data ($r = 0.83$, $P = 0.02$, $n = 7$).

Woodchucks that spent more time vigilant during behavioral observations also

flushed earlier when approached.

4. Discussion

As predicted, survival rates were higher for urban woodchucks than for rural

woodchucks. A similar pattern has been documented for several mammalian species

that persist in urban areas including raccoons (*Procyon lotor*; Prange et al., 2003),

white-tailed deer (*Odocoileus virginianus*; Etter, 2002), fox squirrels (*Sciurus niger*;

McCleery, 2008) and Virginia opossums (*Didelphis virginiana*; Kanda et al. 2009). In

addition, there was a strong effect of season on survival rates (inactive > active) for

woodchucks, a hibernating species, and an interaction between season and

urbanization so that differences in survival rates between urban and rural woodchucks

were greatest during the inactive season.

Results for survival rates paralleled variation in mortality causes across the

urbanization gradient. In rural areas, mortality during the inactive season was second

only to active-season predation as a cause of death. Mortalities during the inactive

season probably were due to starvation, as there was no evidence of predation at the hibernacula. In contrast, no urban woodchucks (>80% urban cover) died during the inactive season. Collisions with vehicles were a major cause of death for urban and suburban woodchucks, which is similar to the pattern for urban fox squirrels (McCleery et al., 2008) and juvenile opossums (Kanda et al. 2009). In contrast, mortality rates due to collisions with vehicles did not vary between urban and rural individuals for raccoons (Prange et al., 2003), skunks (*Mephitis mephitis;* Gehrt, 2005), and red foxes (Gosselink et al., 2007). In urban areas, home ranges of woodchucks are approximately 90% smaller than those in rural areas, roads often form home-range boundaries, and individuals generally avoid crossing roads with >2 lanes or those with considerable traffic (Chapter 2). However, distances moved by woodchucks increase during the early part of the active season (Ferron and Ouellet, 1989). Of the deaths attributed to vehicle collisions, 4 of 5 (80%) occurred in April and early May. Requirements of breeding might impose mortality risks for woodchucks in fragmented, urban regions.

Despite frequent radio-tracking, the cause of most (64%) urban woodchuck mortalities could not be determined because the carcass was either too decomposed, or the woodchuck had died in a burrow that was inaccessible. In contrast, a cause could not be determined for only two deaths in suburban and rural areas. Increased disease prevalence due to higher densities or altered spatial distributions of individuals has been documented for several urban wildlife species, and was the main cause of mortality for raccoons and skunks in Chicago (Prange et al., 2003; Gehrt, 2005) and red foxes living in urban areas in central Illinois (Gosselink et al., 2007). In

our study area, *Toxoplasma gondii* antibodies were found in sera from 14% of woodchucks, but only in areas with >70% urban land cover (Watson et al., *in review*). Potential effects of *T. gondii* include reduced body condition, neurological impairment, and increased predation risk (Berdoy et al., 2000; Bangari et al., 2007). Hence, some of the urban mortalities for which a cause could not be identified could have been disease-related.

Surprisingly, there was no effect of sex on survival rates of woodchucks. In general, male woodchucks have larger home ranges than females (Chapter 2). Larger home ranges and increased movements should translate into elevated mortality risk for male woodchucks either from predators in rural areas or vehicles in urban areas, but no differences in survival rates between males and females were detected.

There was no evidence of an overall effect of urbanization on vigilance behavior, distance from burrows during foraging, and flight initiation distance. In contrast, changes to anti-predator behavior in response to human disturbance have been documented for Olympic marmots (*Marmota olympus*; Griffin et al., 2007), gray squirrels (*Sciurus carolinensis*; Bowers and Breland, 1996), fox squirrels (McCleery, 2009), and several bird species (Cooke, 1980). This lack of response of anti-predator behaviors to urbanization suggests woodchucks are not strongly habituated to human disturbance in urban areas and may perceive humans to be a risk similar to natural predators. However, habituation to humans may be partial (Frid and Dill, 2002). Woodchucks living in urban areas must be tolerant of human disturbance to some degree to persist in such a highly disturbed landscape. Reactions by alpine marmots (*Marmota marmota*) to humans are less intense if they remain on predictable paths

such as hiking trails (Mainini, 1993). Woodchucks in urban areas likely are tolerant of humans walking on predictable, established paths such as sidewalks, but I was unable to capture this tolerance in my tests of flight initiation distance.

Although mean levels of vigilance behavior did not respond to urbanization in a linear fashion, vigilance levels might respond to urbanization in more complex ways. Vigilance levels were highly variable at the urban end of the gradient, ranging from 3% to 48%, whereas levels were constrained to <20% at the rural end (Fig. 4). Increased variability in vigilance behavior at the urban end of the gradient may reflect the variable nature of human disturbance levels in such environments. Some of my marked woodchucks occurred in areas adjacent to busy intersections, surrounded by high levels of traffic and regular pedestrian disturbance, whereas others were captured in isolated office parks or abandoned lots, where traffic and human disturbance was considerably reduced and sidewalks were rare (E. L. Watson, personal observation). Additionally, my results suggest that some woodchucks are risk-takers, whereas others are more risk-aversive. Woodchucks that spent more time vigilant during behavioral observations also fled more quickly from a human when approached, which implies individual variation in wariness that could reflect different disturbance levels to which individuals were exposed. This hypothesis that urbanization increases spatial variation in perceived predation risk for wildlife species deserves further study.

Date was included in the top models of all components of anti-predator behavior, and all responses showed a similar relationship that was independent of urbanization. Woodchucks were less vigilant, foraged farther from burrows, and tolerated closer approaches by humans later in the season. Hibernating sciurids gain

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considerable weight throughout the active season in preparation for hibernation, which could inhibit their ability to escape from predators (Trombulak, 1989; but see Blumstein, 1992). Despite this potential for increased risk related to constraints on running speeds, my results suggest woodchucks are actually willing to accept more risk later in the season. As hibernation approaches, it is likely that woodchucks are under more pressure to increase body condition, and they may reduce time spent engaged in anti-predator behaviors in favor of increased foraging time.

I predicted that urban woodchucks would exhibit reduced levels of anti-predator behavior in response to lower perceived risk, and that these behavioral adjustments would translate into higher over-winter survival rates resulting from increased foraging time and better body condition. Perceived risk can have strong effects on fitness (Creel and Christianson, 2007). Although I revealed variation in over-winter survival rates across the gradient, I found no evidence of variation in mean levels of anti-predator behavior. Why were over-winter survival rates higher for urban woodchucks? Food quality may be higher in urban areas than in rural areas. Although we did not examine resource levels across the urbanization gradient, resources in urban areas are typically abundant and rich due to artificial food sources such as managed lawns and gardens, which could lead to better body condition for urban woodchucks. For instance, a positive relationship between anthropogenic resources and body condition has been demonstrated for silver gulls (*Larus novaehollandiae*); males living in urban areas are heavier and have higher body condition than those in rural areas (Auman et al., 2008). Another possible explanation is variation in thermal conditions of the hibernacula across the urbanization gradient.

Although there were no obvious differences in the habitat selected for hibernacula, an increase in impervious surfaces created by urbanization can lead to a heat island effect, by which air and surface temperatures are warmer (1- 4°C) than those in the surrounding rural areas (Arnfield, 2003; Shochat et al., 2006). Warmer temperatures could translate into higher underground temperatures of hibernacula, which may explain the variation in over-winter survival rates across the urbanization gradient.

Survival rates and cause-specific mortality varied substantially for woodchucks across an urbanization gradient. Urban areas may act as refuges from natural predators for woodchucks, and local urban populations may even act as sources that supply rural populations (Kanda et al. 2009). However, urbanization also amplifies alternative real and perceived risks such as vehicles, disease, and human disturbance. My research provides insights into tradeoffs encountered by urban adapter species across an urbanization gradient, and evidence for lack of strong habituation to humans by an urban adapter. It is vital that we continue to examine how wildlife species are responding to urban environments and identify constraints to behavioral adjustments with consequences for fitness and persistence.

Chapter 1 meets the formatting requirements for *Biological Conservation.*

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6. Tables and Figures

Table 1

Ethogram used to classify behaviors observed for woodchucks across an urbanization gradient in Illinois.

Behavior	Definition
Low vigilance	Woodchuck is sitting on all four legs, alert with head lifted >3s
Medium vigilance	Woodchuck is on hind legs, scanning at medium height, and not chewing
High vigilance	Woodchuck is on extended hind legs, scanning at full height, and not chewing
Foraging alert	Woodchuck is sitting on all four legs, and lifting head up for <3s
Foraging	Woodchuck is eating with head down
Locomotion	Woodchuck is walking or running

Table 2

Ranking of known-fate survival models for woodchucks across an urbanization gradient in Illinois. Main effects included urbanization, sex, and season (active or inactive). $K =$ no. of explanatory variables $+ 1$, $\Delta AIC_c = AIC_c$ of model $-$ minimum AIC_c, and $\omega_i =$ Akaike weight. A 90% confidence set is presented.

Model	K	ΔAIC_c	ω_i	Deviance
S (season)	2	0	0.343	244.2
S (urban, season, urban x season)	4	0.1	0.321	240.3
S (urban, season)	3	1.1	0.193	243.3
S (urban, season, sex)	4	3.1	0.075	243.2

Table 3
Ranking of generalized linear models evaluating factors affecting anti-predator behavior of woodchucks in Illinois. Main effects included urbanization (urban), distance from burrow (DFB), date, presence of conspecifics, and start distance (start). K = no. of explanatory variables + 2, ΔAIC_c = AIC_c of model – minimum AIC_c, and ω_i = Akaike weight. A 90% confidence set is presented.

| Response variable, model	K	Log-likelihood	ΔAIC_c	ω_i
Vigilance behavior				
Date	3	12.08	0	0.456
Urban, date	4	12.13	2.37	0.139
Date, conspecifics	4	12.10	2.44	0.135
Date, DFB	4	12.10	2.45	0.134
Urban, date, DFB	5	12.14	4.96	0.038
Distance from burrow				
Date	3	-115.98	0	0.295
Intercept-only	2	-117.24	0.19	0.267
Urban	3	-117.00	2.05	0.106
Date, conspecifics	4	-115.88	2.28	0.094
Conspecifics	3	-117.19	2.42	0.088
Urban, date	4	-115.97	2.45	0.086
Flight initiation distance				
Start, date	4	-97.46	0	0.260
Start	3	-98.89	0.08	0.250
Start, date, DFB	5	-96.52	1.17	0.145
Urban, start	4	-98.41	1.91	0.101
Start, DFB	4	-98.87	2.82	0.064
Urban, start, date	5	-97.37	2.87	0.062
Urban, start, date, DFB	6	-96.29	4.04	0.035
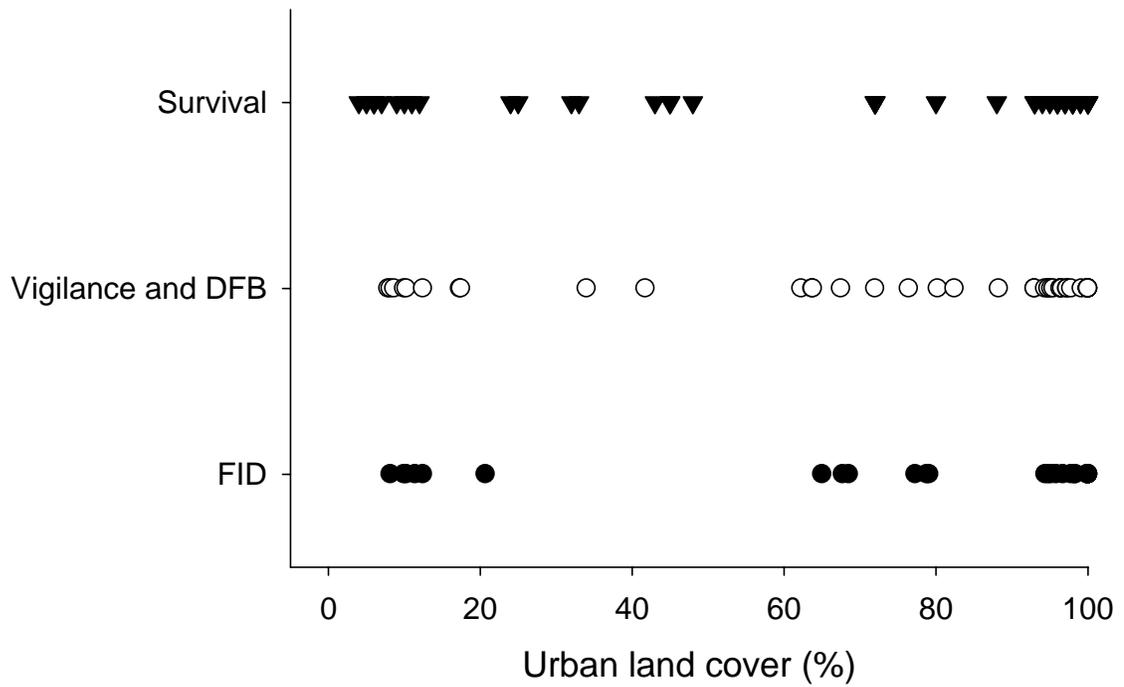
Fig. 1. Distribution of woodchucks across an urbanization gradient in Illinois. Distributions are presented for four response variables: survival, vigilance behavior, distance from burrow during foraging bout (DFB), and flight initiation distance (FID).
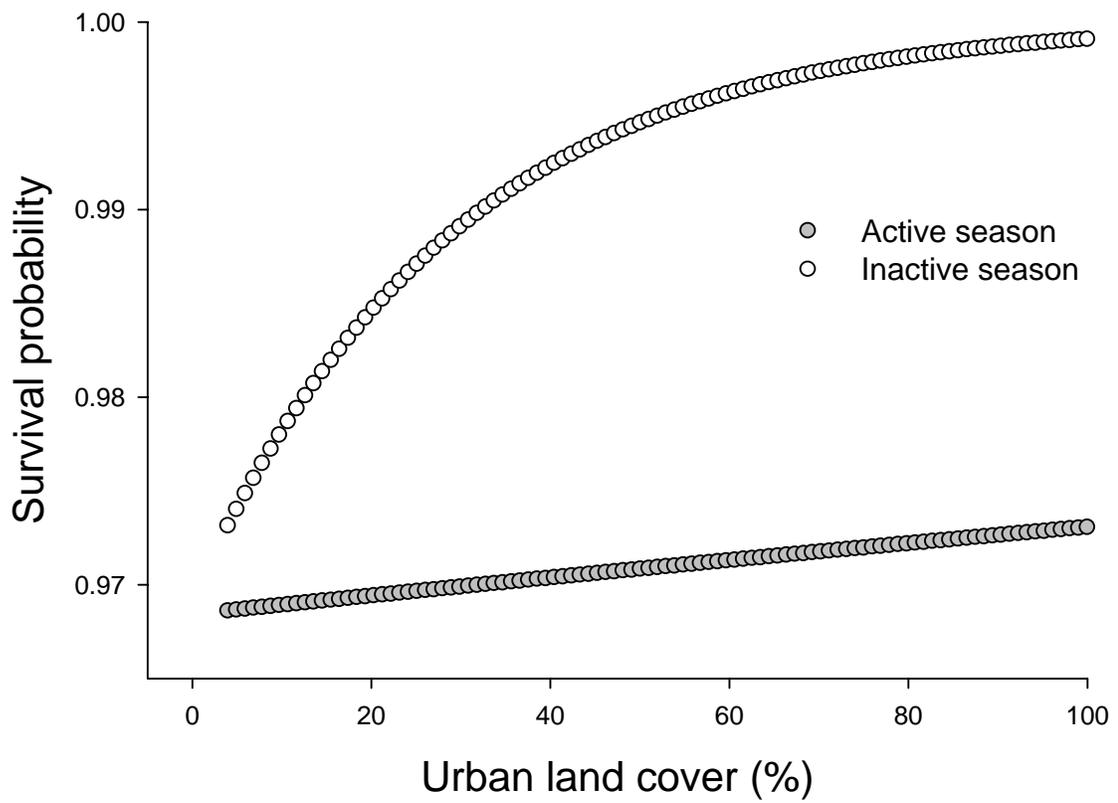
Fig. 2. Two-week survival probabilities for woodchucks during two seasons (active, inactive) across an urbanization gradient in Illinois. Estimates are from a highly supported model (survival = urbanization, season, urbanization x season).
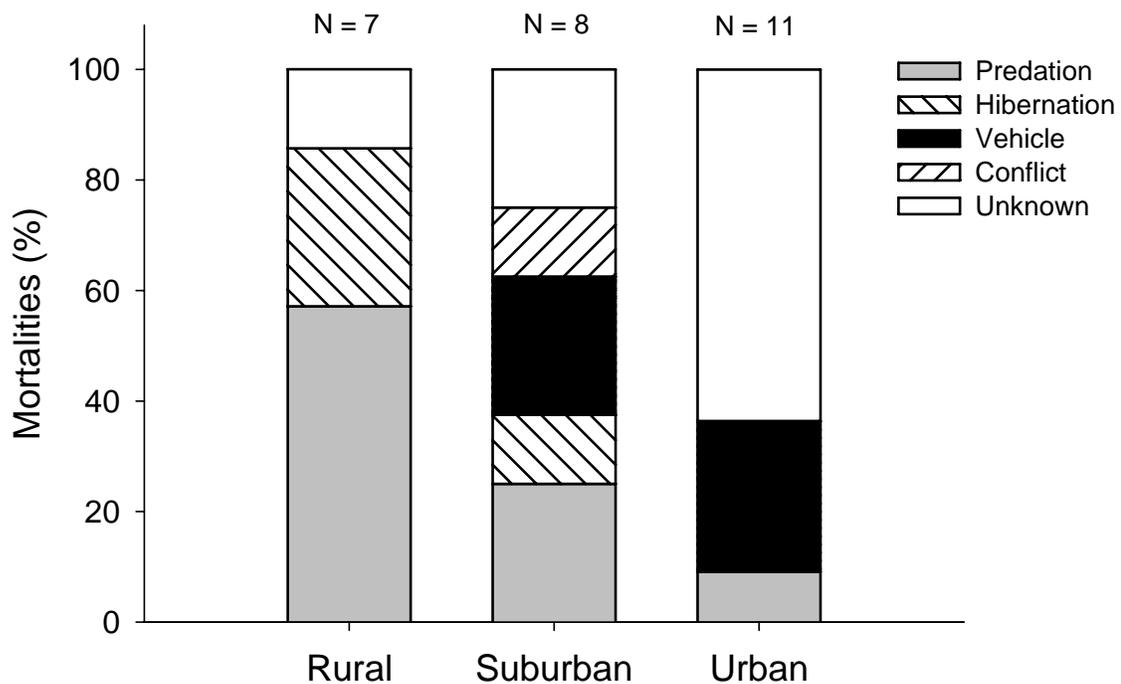
Fig. 3. Causes of mortalities of woodchucks categorized by location of individuals along the urbanization gradient. For this figure, rural was defined as 0-20% urban cover, suburban was defined as 20-80% urban cover, and urban as 80-100% urban cover.
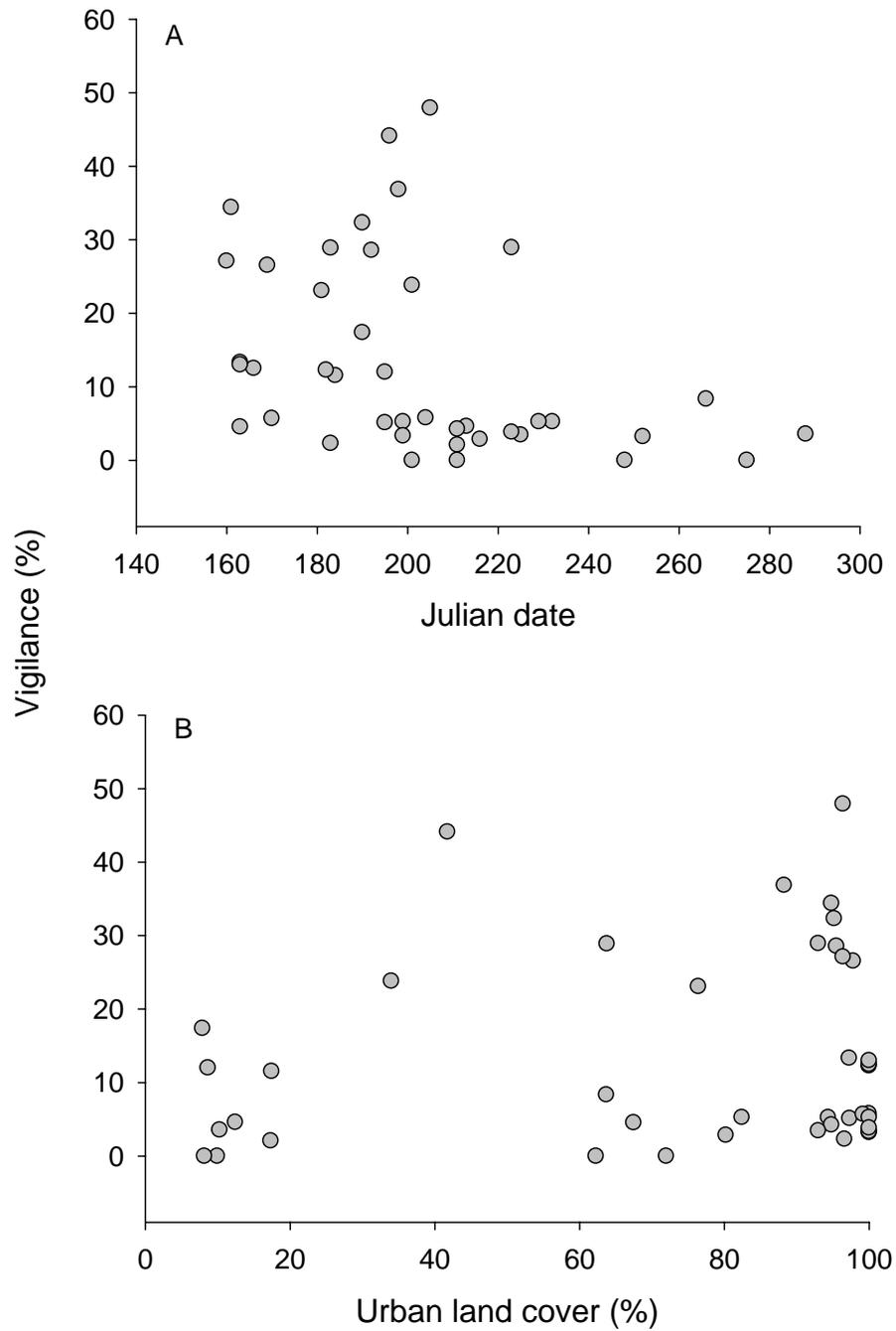
Fig. 4. A) Relationship between vigilance behavior and date for woodchucks across the urbanization gradient. Julian date 160 = 8 June 2008. Julian date 300 = 26 October 2008. B) Relationship between vigilance behavior and urbanization. Vigilance levels were clustered under 20% at the rural end of the gradient, whereas levels were highly variable at the urban end.

Fig. 5. Percent of observation woodchucks displayed vigilance behavior when foraging at various distances from the burrow, averaged across individuals. Error bars represent +1SE.

CHAPTER 2:

SPACE USE OF WOODCHUCKS ACROSS AN URBANIZATION
GRADIENT WITHIN AN AGRICULTURAL LANDSCAPE

1. Introduction

Urbanization is increasing at an alarming rate and further decreasing the
amount of suitable habitat available to wildlife species. In 2000, urban areas
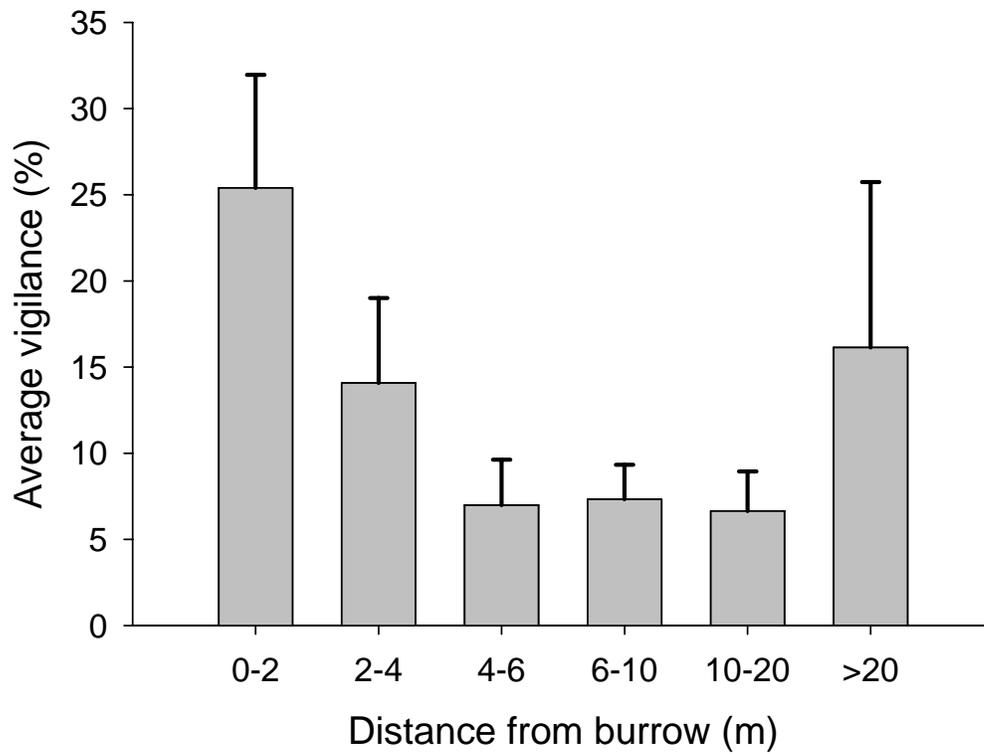represented >5% of the surface area of the United States and contained almost 80% of
the human population (U.S. Census Bureau 2001). Between 1990 and 2000,
expansion of urban boundaries into the rural countryside (i.e., urban sprawl) grew by
as much as 50% (DeStefano and DeGraaf 2003; Heimlich and Anderson 2001).
Humans also have dramatically altered the land outside of cities in many regions. For
example, much of the rural landscape in the Midwest has been converted for
agriculture resulting in vast areas of open cropland and few areas of natural habitat
(Gosselink et al. 2003; Mankin and Warner 1997; Warner 1994). Nevertheless,
urbanization still creates a novel footprint in such human-dominated landscapes.

As urbanization increases, remnant natural habitat is separated into patches
that may become isolated by human-made barriers such as roads, buildings, and
parking lots. Crossing high-traffic roads is risky, and collisions with vehicles can be a
major cause of mortality for some species (Forman et al. 2003; Kramer-Schadt et al.
2004; Tigas et al. 2002). Consequently, wildlife movements can be severely restricted
in urban areas thus impeding an individual's ability to disperse and find mates,
suitable habitat, and food resources (Ditchkoff et al. 2006). Urbanization also can

affect the abundance and distribution of food resources, which could then impact

space-use patterns of wildlife (Erlinge 1974; Isbell et al. 1998; Jepsen et al. 2002).

Food is typically abundant in urban areas due to artificial sources such as garbage or

managed vegetation (Ditchkoff et al. 2006; McKinney 2002). Individuals that utilize

these resources can exhibit reduced home ranges and altered spatial distributions

when compared to their rural counterparts (Prange et al. 2004). Concentration of

artificial food sources in urban areas also can increase spatial and temporal overlap of

individuals, which has ramifications for rates of disease transmission (Prange et al.

2003, 2004).

Studies examining movement behavior of mammals in relation to urbanization

have focused primarily on carnivores (Atwood et al. 2004; Prange et al. 2004; Riley

2006; Riley et al. 2003; Rosatte et al. 1991) and have emphasized changes in size or

spatial distribution of home ranges or core areas. Although patterns are emerging

from these studies, we still know relatively little regarding responses to urbanization

by other mammals such as herbivorous prey species. Like carnivores, prey may

respond to factors such as habitat fragmentation and changes in resource levels, but

prey also may be affected by landscape variation in predation risk created by

urbanization. Abundance of natural predators is generally lower in urban areas

(Gering and Blair 1999; McKinney 2002; Shochat et al. 2006), which should reduce

predation risk for prey species. Additionally, many mammalian species are multiple

central-place foragers that focus foraging activity around specific sites scattered

throughout their home ranges. This strategy requires risky movements from one

foraging site to another. Multiple central-place foragers could respond to changes in

predation risk across an urbanization gradient by adjusting aspects of space use such as number of foraging sites or distance between sites. These spatial adjustments may not be reflected in comparisons of home-range size alone.

Woodchucks (*Marmota monax*) are an excellent study species for investigating responses to urbanization because they occur in many environments but are considered to be "urban-adapters" (McKinney 2002). Woodchucks are diurnal herbivores that prefer vegetation common in urban areas such as grass, clover, and garden crops (Hoffmeister 2002; Kwiecinski 1998). Woodchucks are multiple central-place foragers that feed almost exclusively near burrows in which they hibernate, rear young, and escape from predators. Predators of woodchucks include coyotes (*Canis latrans*; Hofmann 2008; Kwiecinski 1998), which generally decrease in abundance with urbanization (Gosselink et al. 2003; Randa and Yunger 2006), and domestic dogs (Hofmann 2008; Kwiecinski 1998), which are typically leashed by owners in cities. Therefore, predation risk for woodchucks should be reduced in urban areas. Previous studies on woodchucks have emphasized spatial distribution, social organization, and habitat selection (Ferron and Ouellet 1989; Henderson and Gilbert 1978; Meier 1992; Merriam 1971), and woodchucks exhibit behavioral plasticity in relation to environmental heterogeneity (Bonenfant and Kramer 1996; Maher 2004, 2006, 2009; Swihart 1992). Despite the common occurrence of this species in urban areas, however, no studies have examined how woodchucks adjust to living in such highly human-altered landscapes.

I compared movements of adult woodchucks across an urbanization gradient within an agricultural landscape in central Illinois. I examined home-range size and

space use within home ranges including number of burrows used, average distance between burrows, and evenness of use among burrows. I predicted home-range size would decrease with urbanization because urban areas are fragmented by high-traffic roads that can be movement barriers for woodchucks (Woodward 1990), and urban areas provide concentrated food resources. I expected that number of burrows used would be related positively to home-range size. Hence, I predicted number of burrows used would decrease with urbanization but distance between burrows would remain constant across the gradient. That is, rural individuals would have larger home ranges but would reduce predation risk by establishing more burrows within their ranges. These predictions depend on the scaling relationship between number of burrows and home-range size and on how flexible space use is relative to perceived risk. I also predicted burrow use would be most aggregated for urban woodchucks that would favor burrows near concentrated food sources (i.e., managed lawns and gardens) present in urban areas. Alternatively, if aggregation patterns are more related to predation risk, burrow use would be most aggregated for rural woodchucks that should preferentially use burrows that are safer to reach. Finally, to gain general insights about space use by multiple central-place foragers, I also examined whether intensity of burrow use was related positively to spatial connectivity of burrows.

2. Methods

2.1. Study area and urbanization gradient

My research was conducted in a 700-km^2 study area located around the twin cities of Champaign and Urbana in east-central Illinois. The Champaign-Urbana metropolitan

area is a medium-sized, growing community (2007 population estimate: 220,923, a growth of 5% since 2000 census; U.S. Census Bureau 2009). The urban core is characterized by high densities of older buildings, impervious surfaces in the form of roads, sidewalks, and parking lots, and established trees. As distance from the urban core increases, the landscape becomes less forested, building density decreases in the form of newer residential subdivisions and office parks, and the landscape eventually grades into one of the most intensive regions of row crop agriculture in the United States (Mankin and Warner 1997). Because corn and soybeans are the dominant land cover outside of the urban centers, the rural landscape is almost completely absent of cover between the crop harvest in the fall and planting in the spring (Warner 1994). The rural landscape also is characterized by a low diversity of habitats including sparse forest fragments and fencerows.

I sampled woodchucks across an urbanization gradient defined by the amount of urban land cover within a 500-m buffer around the centroids of home ranges for individuals (details to follow). Digital orthophotographs from 2008 (for 34 woodchucks) and from 2005 (1 woodchuck outside of Champaign County) were used to manually classify land cover across the gradient (minimum resolution for both sets was 0.5 m). I delineated 5 main land-cover categories: developed, urban open space, urban forest, urban grassland, and rural (Table 4). To differentiate urban animals with home ranges without any natural habitat from those with home ranges that included natural habitat surrounded by developed land cover (urban grassland, urban forest), I considered urban land cover to include the categories of "developed" and "urban open space." I ground-truthed photographs during field visits and updated our

classifications when necessary. The urban endpoint of the gradient was characterized by high densities of buildings (average = 492.2 buildings/km^2), population, traffic and an average of 12.83 km of roads/km^2 whereas the rural endpoint of the gradient consisted of few homesteads (average = 8.92 buildings/km^2), minimal traffic, and an average of 1.10 km of roads/km^2.

2.2. Radiotracking

Woodchucks were livetrapped from May-November 2007 using single-door collapsible Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin; Model 207) following procedures approved by the University of Illinois' Institutional Animal Care and Use Committee, which met the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). I placed traps near active burrows and baited them with apples and peanut butter (Maher 2004; Swihart 1992). Traps were set in the early morning, checked every 2 hours, and closed by mid afternoon.

Each captured adult woodchuck ($\geq$ 1 year old; age determined by weight and pelage; Kwiecinski 1998) was transported to the College of Veterinary Medicine at the University of Illinois where a 32-g radio-transmitter (Model #M1240, Advanced Telemetry Systems, Isanti, Minnesota) was surgically implanted in the peritoneal cavity, generally within 3 hours of capture. I followed standard surgical procedures (Maher 2009; Van Vuren 1989) except medetomidine was used as the anesthetic rather than a xylazine-ketamine mixture. While woodchucks were anesthetized, I determined their sex and implanted passive-integrated transponders (PIT; Schooley et

al. 1993) in the interscapular region for long-term identification. I released

woodchucks at their burrows of capture after they had fully recovered. I tracked

woodchucks 2-4 times per week during 2 active seasons (2007 and 2008), and 3 times

per month during 2 hibernation seasons (2007-2008, 2008-2009). For each individual,

the active season began with the 1st location outside of the hibernaculum during

February-March and ended with the last location prior to settlement at the

hibernaculum in October-November. The average date of den immergence was 31

October in 2007 ($SE = 4.96$, $n = 33$) and 28 October in 2008 ($SE = 4.20$, $n = 19$). The

average date of den emergence was 10 March in 2007 ($SE = 4.51$, $n = 30$) and 11

March in 2008 ($SE = 4.18$, $n = 18$).

Radiolocations were obtained during the day by homing with a receiver and

handheld 3-element Yagi antenna. Most radiolocations (89%) were obtained when

woodchucks were in burrows because individuals spent much time underground, or

they often fled underground before they were observed. Each radiolocation was

recorded with a handheld Global Positioning System (GPS) unit.

2.3. Home-range size

For each individual, I estimated home-range size separately for each active

season with a 100% minimum convex polygon (MCP) model using Hawth's Analysis

Tools for ArcGIS (Beyer 2004) in ArcGIS9 (Environmental Systems Research Inc.

2006). Bootstrapped area-observation curves with 1,000 replications (Animal

Movement Extension to ArcView; Hooge and Eichenlaub 1997) indicated that about

25 locations were required to accurately estimate home-range size using the MCP

method. Hence, I excluded individuals from analysis if the number of radiolocations was <25.

Actual area used by an animal can be difficult to define for a multiple central–place forager like a woodchuck. Behavioral observations revealed that woodchucks rarely foraged >20m from a burrow, which suggests much of the area between burrows is used primarily for inter-burrow movement. Kernel-based home range estimators are generally favored over MCPs, but kernel methods do not work well if many radiolocations occur at the same place (Pattishall and Cundall 2008; Row et al. 2006; Seaman and Powell 1996). For my dataset that included multiple locations at particular burrows, kernel-based estimators substantially overestimated the amount of area used around burrows. Hence I used 100% MCPs as a means to estimate total spatial extent of a woodchuck's range, and then I evaluated space-use within home ranges in more detail by examining patterns of burrow use by this multiple central-place forager.

2.4. Space use within home ranges

I measured several aspects of space use within home-range areas including the number of burrow clusters used, average distance between burrow clusters, and evenness of use among burrow clusters. I defined a single burrow cluster to include all burrow entrances within 10 m of another entrance (Henderson and Gilbert 1978; Swihart 1992). To describe evenness of burrow use by individuals across the gradient, I used the Morisita Index (Morisita 1962; Veech 2005), defined as

$$I_M = N \times \frac{\Sigma x_j^2 - \Sigma x_j}{(\Sigma x_j)^2 - \Sigma x_j} \qquad (1)$$

where N = the number of burrow clusters used by an individual, and x_j = the number of radiolocations at a burrow cluster j for each cluster j = 1 to N. Values of $I_M > 1$ indicate a clumped distribution, and values of $I_M < 1$ indicate a regular distribution. I also measured the average distance between burrow clusters using Hawth's Analysis Tools for ArcGIS.

2.5. Analysis of home ranges and space use

Responses by woodchucks to urbanization were examined at 2 scales. The landscape scale was determined by the amount of urban land cover within a 500-m buffer centered on the centroid of a MCP for each individual (using data combined across years). The local scale was determined by the amount of urban land cover within each individual's combined-year MCP. I examined the response of home-range area at the landscape scale, and the responses of all other space-use variables at the local scale. Although urbanization measures for these 2 scales were correlated (r = 0.64, $P < 0.001$, n = 35), I thought that the landscape scale was more appropriate for examining broader constraints to home-range size, whereas urban land cover at the local scale would be more relevant to how a woodchuck used space within its established home range.

Because many woodchucks were sampled in 2 years, I used repeated-measures models and the maximum likelihood method (PROC MIXED - SAS Institute Inc. 2009) to test for an effect of urbanization on home-range size and each space-use variable at the appropriate scale. First, I determined the covariance structure of the data by fitting my global model for each response variable under

different covariance structures using the restricted maximum likelihood method. I identified the 1st-order autoregressive structure as the most appropriate for all responses by using Akaike's Information Criterion (AIC_c: corrected for small sample size; Burnham and Anderson 2002). AIC allows for simultaneous comparison of multiple models by ranking them based on goodness of fit and complexity. Models with a ΔAIC value < 2 are considered competitive (Burnham and Anderson 2002). Second, I evaluated 17 candidate models using maximum likelihood estimation and AIC. The candidate models included combinations of urban land cover (urban), sex, year, and number of locations as predictors plus interaction terms for urban x sex, and urban x year. I also examined parameter estimates (β) to understand the relationship between response variables and parameters included in competitive models.

2.6. Scaling of burrows and home-range size

To assess the scaling relationship between number of burrow clusters and home-range size, I conducted linear regression after transforming both variables (log_{10}-transform) to estimate the scaling exponent (i.e., slope coefficient). I estimated scaling exponents separately for woodchucks in 2007 and 2008.

2.7. Burrow use and connectivity

I was interested in whether frequency of use of burrow clusters could be explained by spatial connectivity of burrow clusters to other clusters within a home range for these multiple central-place foragers. For each individual, I calculated connectivity for an individual burrow cluster as the inverse of the average distance

between the cluster and all other clusters. I then correlated connectivity of burrow

clusters with the number of active-season locations at clusters. Because I wanted to

make inferences across individuals, I adopted a meta-analysis framework. I

transformed Pearson correlation coefficients (r) for individuals using a Fisher z

transformation and then calculated an unweighted mean z separately for 2007 and

2008 (Hedges and Olkin 1985). I constructed a 95% confidence interval (CI) of the

mean of the distribution for each year (Hedges and Olkin 1985) defined as

$$ \text{CI} = \bar{x} \pm 1.96 \frac{1}{\sqrt{N - 3K}} \tag{2} $$

where N = the total number of pairs in the correlation (total number of burrow

clusters across individuals) and K = the total number of individuals. I then back-

transformed z to get a confidence interval for r.

3. Results

Home-range and space-use analyses were based on data from 35 adult

woodchucks (12 males, 23 females) distributed across the urbanization gradient (Fig.

6). The average number of locations per individual per active season was 50 (SE =

1.98).

3.1. Home-range size

AIC rankings revealed 3 competitive models that all included urbanization,

sex, and the interaction between urbanization and sex as factors affecting home-range

size of woodchucks (Table 5). Two models were tied for the best model: 1 included

urbanization, sex, and the urban x sex interaction, whereas the other also included the locations covariate (Table 5). The model with locations had a lower log-likelihood, indicating the number of radiolocations obtained for an individual had a positive effect on home-range size ($\beta_{locations} = 0.06$, $SE = 0.04$). A 3rd model, which included year instead of locations, was competitive as well (Table 5). Home-range size was related negatively to urbanization for both males and females (Fig. 7), but the effect was stronger for males ($\beta_{urban} = -28.26$ for males, $\beta_{urban} = -3.88$ for females). During both years, home-range size was larger for males (2007: $\overline{X} = 13.29$ ha, $SE = 4.75$, $n = 8$; 2008: $\overline{X} = 17.1$ ha, $SE = 5.08$, $n = 9$) than for females (2007: $\overline{X} = 2.55$ ha, $SE = 0.66$, $n = 19$; 2008: $\overline{X} = 1.74$ ha, $SE = 0.46$, $n = 16$).

3.2. Number of burrow clusters

Woodchucks used an average of 10 burrow clusters ($SE = 0.70$), but number of clusters ranged from 1 to 25 clusters. The best approximating model describing the number of burrow clusters used by woodchucks included urbanization, sex, and locations (Table 6). A model including year was competitive as well and had a lower log-likelihood than the best model (Table 6). Number of burrow clusters was related negatively to urbanization ($\beta_{urban} = -1.47$, $SE = 1.94$). Males used an average of 12 clusters ($SE = 1.35$) in 2007 and 15 clusters ($SE = 2.04$) in 2008, whereas females used an average of 9 clusters ($SE = 1.00$) in 2007 and 8 clusters ($SE = 0.86$) in 2008. Number of burrow clusters was associated positively with number of locations ($\beta_{locations} = 0.118$, $SE = 0.04$).

3.3. Scaling of burrows and home-range size

Number of burrow clusters was related positively to home-range size in 2007 ($R^2 = 0.74$, $P < 0.001$, $n = 27$) and 2008 ($R^2 = 0.63$, $P < 0.001$, $n = 25$). However, the scaling exponent was not close to 1 in either year. The exponent was 0.26 ($SE = 0.03$) in 2007 and 0.25 ($SE = 0.03$) in 2008. Individuals with larger home ranges had more central places, but the relationship was not proportional.

3.4. Distance between burrow clusters

The average distance between burrow clusters ranged from 44 to 499 m with a mean of 190 m ($SE = 18.60$). The best model predicting distance between burrow clusters included urbanization and sex (Table 6). A model that also included the urbanization x sex interaction was competitive and had a lower log-likelihood (Table 6). Average distance between burrow clusters responded negatively to urbanization, but the effect was stronger for males than for females ($\beta_{urban} = -298.1$ for males, $\beta_{urban} = -141.4$ for females). The mean for average distance between burrow clusters was 308 m for males ($SE = 32.03$) and 131 m for females ($SE = 15.45$).

3.5. Evenness of burrow use

Woodchuck locations generally were aggregated among burrows within their home ranges (Fig. 8). The average Morisita index was 1.79 in 2007 ($SE = 0.08$) and 1.98 ($SE = 0.08$) in 2008. Variation in Morisita index was best explained by a model that included urbanization (Table 6). Morisita index increased with urbanization ($\beta_{urban} = 0.24$, $SE = 0.24$). That is, the aggregation patterns were stronger for more-

urban individuals. The intercept-only model was competitive as well, but had the highest log-likelihood of all of the competitive models (Table 6). Models including year or locations in addition to urbanization also were competitive but had lower log-likelihood values than the top model (Table 6) suggesting that these covariates had secondary effects on estimates of aggregation.

3.6. Burrow use and connectivity

The average correlation coefficient relating intensity of burrow use to connectivity was 0.18 for both 2007 ($n = 27$) and 2008 ($n = 25$). The 95% confidence interval of the mean correlation coefficient was $0.04 < r < 0.32$ in both years. There was a moderate, positive relationship between spatial connectivity and intensity of burrow use for these multiple-central place foragers (Fig. 8).

4. Discussion

Urbanization had substantial effects on space use of woodchucks within an already human-dominated, agricultural landscape. Home-range size of woodchucks in urban areas was approximately 10% of those in rural areas. This pattern is similar to that described for mammalian carnivores such as skunks (*Mephitis mephitis*; Rosatte et al. 1991), red foxes (*Vulpes vulpes*; Gosselink et al. 2003), raccoons (*Procyon lotor*; Prange et al. 2004), bobcats (*Lynx rufus*; Riley 2006), and coyotes (Atwood et al. 2004). Home-range size for woodchucks not only decreased with urbanization, home ranges appeared to be constrained in extremely urbanized areas (>80% urban land cover; see Fig. 7).

Movements of woodchucks likely were impeded by the dense network of high-traffic roads in urban areas. Roads act as movement barriers and increase mortality for many wildlife species (Baker et al. 2007; Brody and Pelton 1989; McGregor et al. 2008; Oxley et al. 1974; Rondinini and Doncaster 2002; Swihart and Slade 1984). Woodchucks living adjacent to suburban and urban highway interchanges readily crossed single-lane highway ramps, but attempts at crossing wider roads were rare and often resulted in mortality (Woodward 1990). In my study, home ranges of radio-marked urban woodchucks rarely included roads and those included in home ranges generally had 2 lanes but low levels of traffic. My data on survival rates indicate vehicle collisions are an important cause of mortality for woodchucks in urban areas (Chapter 2). The concentration of anthropogenic resources in urban areas also likely contributed to the decrease in home-range size by reducing the need for woodchucks to travel extensively in search of food (see also Prange et al. 2004).

The best model for predicting home-range size included urbanization, sex, and an urban x sex interaction. The effect of sex on home-range size was not surprising as home ranges of male woodchucks are known to be larger than those of females (Maher 2004; Swihart 1992). Male woodchucks had larger home ranges than females regardless of urbanization; however, urbanization had a much stronger effect on home ranges of males. Few studies have examined the interaction between urbanization and sex in relation to home-range size in mammals (but see Riley 2006). Sexual differences in urbanization effects should be considered, in addition to species-level responses, as they can have ramifications for key life-history requirements. For

example, adult male woodchucks extend their home ranges to find females during the breeding season (Ferron and Ouellet 1989). Barriers to these movements in urban areas could impede males from encountering females, which could reduce reproduction.

My estimates of home-range size generally were larger than averages previously reported for woodchucks, especially for males (1.6 ha – 4.0 ha for males; 0.6 ha – 1.6 ha for females; Maher 2004; Meier 1992; Swihart 1992). Home ranges at the urban end of the gradient were closer in size to those reported by other studies conducted in more natural landscapes (average size for home ranges of males with >80% urban land cover = 4.0 ha). A possible explanation for the differences in home-range size across studies is the fragmented nature of the landscape in central Illinois, even outside of urban areas. Given the dominance of row-crop agriculture in this area, preferred burrowing habitat such as woodland edges and fencerows (Swihart 1992) is sparsely distributed. Moreover, males in agricultural areas may be required to have larger home ranges to find mating opportunities because females are more dispersed and probably at lower densities.

Although I did not study juvenile woodchucks, habitat fragmentation in urban areas should have implications for this age class as well. Juvenile dispersal is common for woodchucks although degree of philopatry, timing of dispersal, and dispersal distances vary among populations (deVos and Gillespie 1960; Ferron and Ouellet 1989; Kwiecinski 1998; Maher 2004, 2009; Swihart 1992). High-traffic roads could reduce dispersal distances for juvenile woodchucks in urban areas and thus alter gene flow and population genetic structure.

I also observed variation across the urban-rural gradient in how adult woodchucks used space within home ranges, which is especially important for multiple central-place foragers. As home-range size increased in rural areas, woodchucks used more burrow clusters, but this relationship was not scaled proportionally. Hence, rural woodchucks did not compensate adequately and distances between burrow clusters increased in rural areas. Risk in rural areas should be relatively high due to a greater abundance of coyotes, and predation was the main cause of mortality for our radio-marked woodchucks in rural areas. My results indicate that risk is further elevated for rural woodchucks because they must travel longer distances to get from one burrow cluster to another. In contrast, urban woodchucks have fewer natural predators and shorter inter-burrow distances.

Although woodchucks generally favored certain burrows over others across the urbanization gradient, aggregation of burrow use increased with urbanization. The presence of concentrated, abundant food sources in urban areas likely contributed to aggregated spatial distributions of woodchucks. I did not measure resource abundance or distribution across the gradient, but food sources should be more concentrated in urban areas due to anthropogenic resources such as managed lawns and vegetation (Ditchkoff et al. 2006; McKinney 2002; Prange et al. 2004). Burrow use also could be more aggregated in urban areas if burrows within the home range are separated by anthropogenic barriers such as parking lots and small roads that impede movement. Burrows may be visited less frequently if woodchucks are reluctant to cross these semi-permeable barriers.

Within home ranges, frequency of use of a particular burrow was positively related to spatial connectivity of the burrow. Burrows that were centrally located and well connected may have been favored because they acted as stepping stones to other burrows and associated foraging areas and thus reduced predation risk during movements. Previous research demonstrates that locations of burrow clusters of woodchucks can be aggregated in space due to environmental characteristics such as soil type, drainage, slope, or vegetation (Henderson and Gilbert 1978; Merriam 1971; Swihart 1992). My study demonstrates that aggregation of use across burrows is related to simple connectivity of burrows independent of surrounding environmental traits. This result could generalize to other multiple central-place foragers that use burrows for refuge.

Woodchucks exhibited substantial behavioral plasticity by adjusting their movements in response to both physical and ecological changes in the landscape created by urbanization. My research provides novel insights into responses by an herbivorous mammal to urbanization and to factors affecting space use by multiple central-place foragers.

Chapter 2 meets the formatting requirements for the *Journal of Mammalogy*.

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6. Tables and Figures
Table 4
Definitions of land-cover categories used to digitize urban land cover from digital orthophotographs.

Land-cover category	Definition
Developed	Paved surfaces, buildings, and associated lawns and gardens
Urban open space	Maintained open areas (e.g., cemeteries, parks, golf courses)
Urban forest	Forest surrounded by developed land cover
Urban grassland	Unmaintained grass surrounded by developed land cover

Table 5

Ranking of repeated-measures mixed linear models evaluating factors affecting home-range size of woodchucks (*Marmota monax*) in Champaign-Urbana, Illinois, in 2007 and 2008. Main effects included urbanization, sex, number of locations, and year. K = no. of explanatory variables + 2, ΔAIC_c = AIC_c of model – minimum AIC_c, and ω_i = Akaike weight. Models with $\Delta AIC_c \leq 3$ are presented.

Model	K	Log-likelihood	ΔAIC_c	ω_i
Urban, sex, urban*sex	5	-152.95	0	0.318
Urban, sex, urban*sex, locations	6	-151.60	0	0.318
Urban, sex, urban*sex, year	6	-152.00	0.7	0.224
Urban, sex, urban*sex, locations, year	7	-151.35	2.3	0.101

Table 6

Ranking of repeated-measures mixed linear models evaluating factors affecting space use within home ranges by woodchucks (*Marmota monax*) in Champaign-Urbana, Illinois, in 2007 and 2008. Response variables included number of burrow clusters used, average distance between burrow clusters, and evenness of burrow cluster use. Main effects included urbanization, sex, number of locations, and year. K = no. of explanatory variables + 2, ΔAIC_c = AIC_c of model – minimum AIC_c, and ω_i = Akaike weight. Models with $\Delta AIC_c \leq 3$ are presented.

| Response variable, model	K	Log-likelihood	ΔAIC_c	ω_i
No. of clusters				
Urban, sex, locations	5	-142.10	0	0.484
Urban, sex, locations, year	6	-141.60	1.7	0.207
Urban, sex, urban*sex, locations	6	-142.00	2.5	0.139
Average distance between clusters				
Urban, sex	4	-290.85	0.0	0.312
Urban, sex, urban*sex	5	-289.75	0.4	0.256
Urban, sex, locations	5	-290.65	2.2	0.104
Urban, sex, year	5	-290.70	2.3	0.099
Urban, sex, urban*sex, year	6	-289.65	2.9	0.073
Urban, sex, urban*sex, locations	6	-289.70	3.0	0.070
Evenness of cluster use				
Urban	3	-45.60	0	0.198
Intercept-only	2	-47.05	0.5	0.154
Urban, year	4	-44.85	0.9	0.126
Urban, locations	4	-44.95	1.1	0.114
Urban, sex	4	-45.60	2.4	0.060
Urban, year, locations	5	-44.55	2.8	0.049
Urban, sex, urban*sex	5	-44.55	2.9	0.046
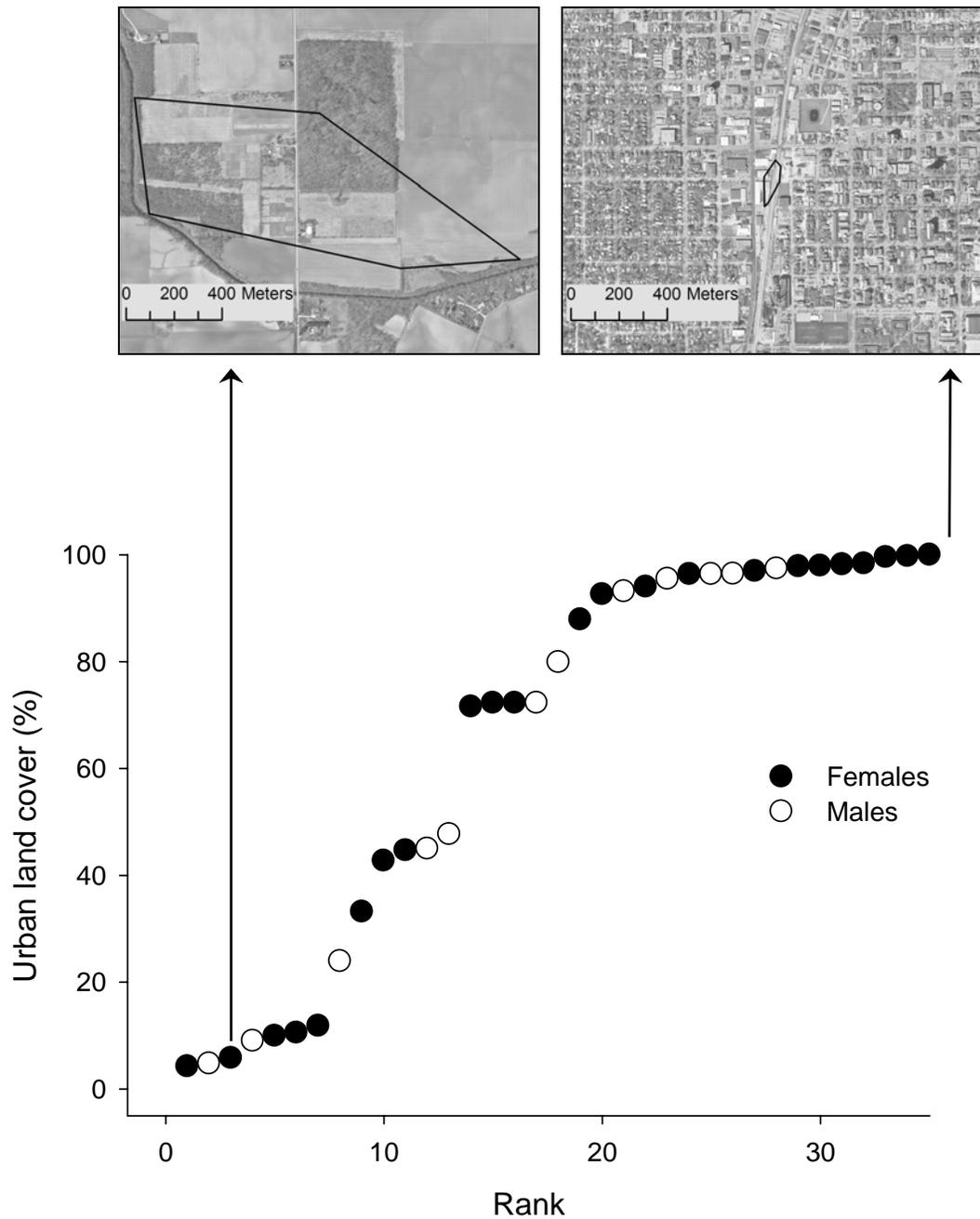
Fig. 6. Distribution of woodchucks (*Marmota monax*) across the urbanization gradient in east-central Illinois. Urban land cover was measured within a 500-m buffer centered on the centroid of each individual's home range. Individuals are ranked from rural to urban (left-to-right). Digital photographs illustrate the land cover for the home range of the most rural male and most urban female.
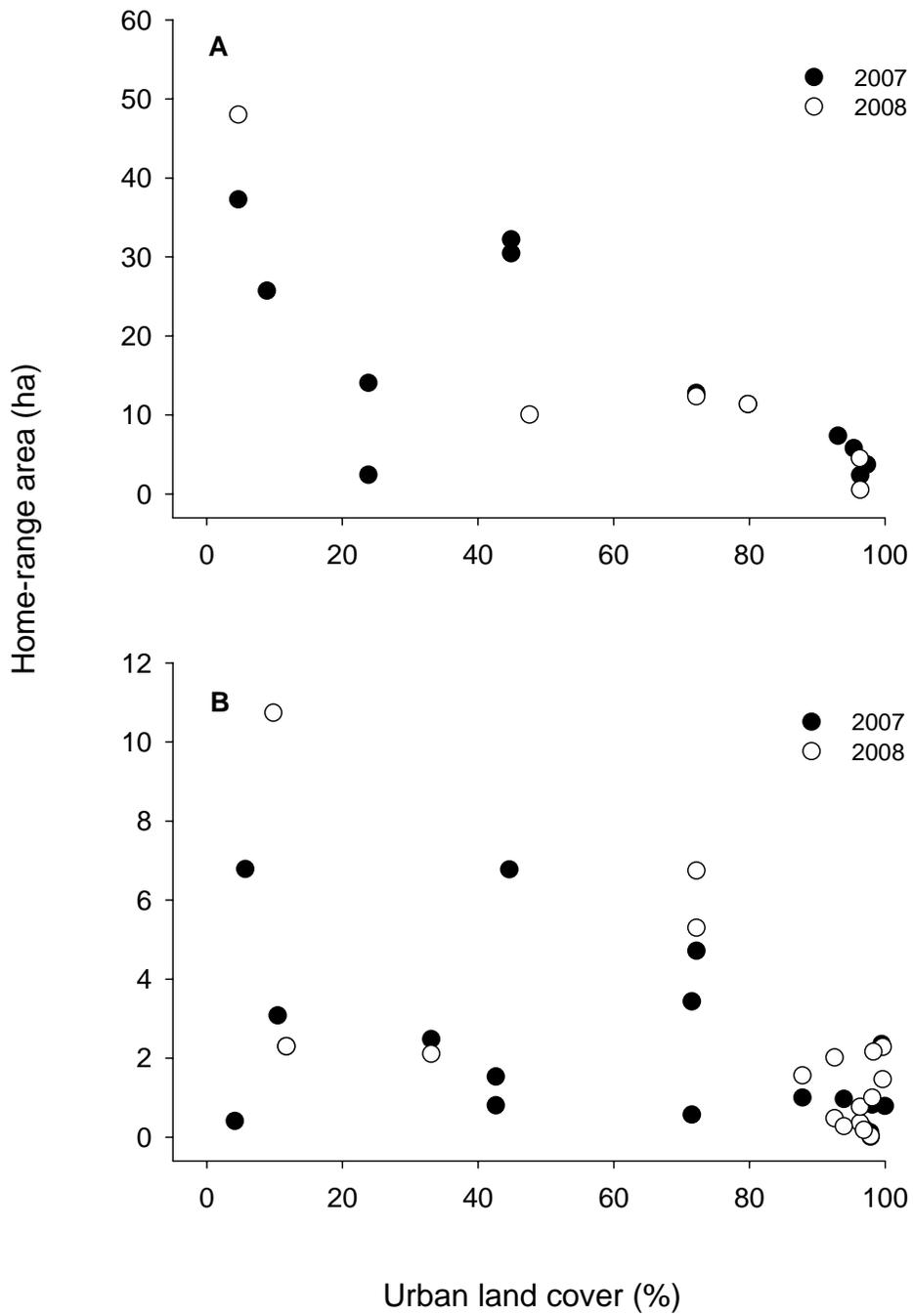
Fig. 7. Relationship between home-range area and urbanization for male (A) and female (B) woodchucks (*Marmota monax*) in 2007 and 2008. Note different scales on Y-axes for the 2 sexes.
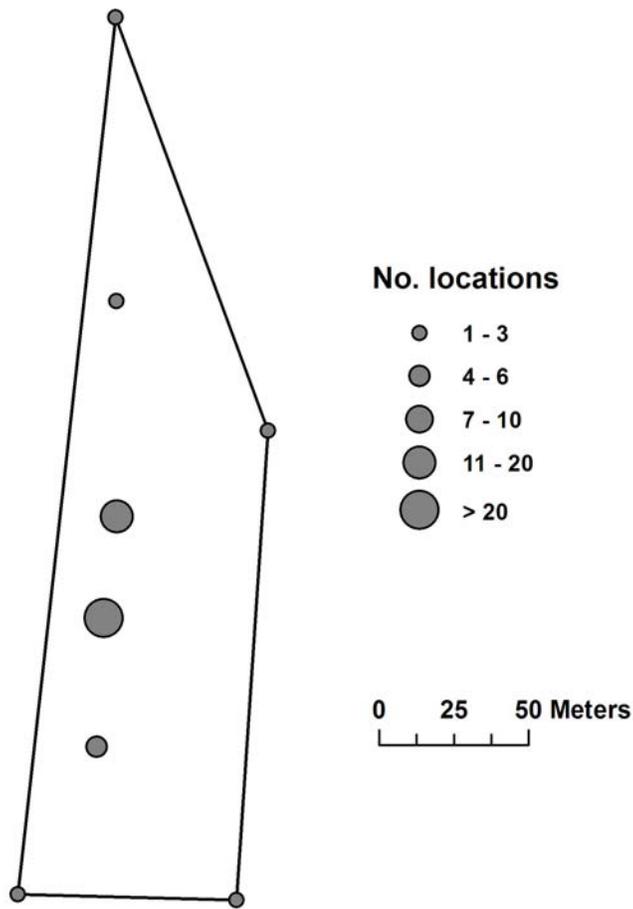
Fig. 8. Home range in 2008 of an urban, female woodchuck (*Marmota monax*) estimated using the minimum convex polygon method. Symbols represent burrow clusters. Symbol size indicates the number of locations at each burrow cluster during the active season based on radio-tracking data. The 2 most favored burrow clusters are the most connected to other clusters.

CHAPTER 3:

SUMMARY

Urbanization created spatial variation in real risk for woodchucks. Survival rates were related positively to urbanization and were higher during the inactive season. Moreover, the effects of urbanization on survival were greatest during the inactive season relative to the active season. For urban woodchucks, the main causes of mortality were collisions with vehicles and unknown reasons, whereas for rural woodchucks, the main mortality causes were predation and costs associated with hibernation. Anti-predator behavior did not vary with urbanization and woodchucks were not strongly habituated to people. Home-range size and space-use patterns varied substantially across the urbanization gradient. Urban woodchucks had smaller home ranges and used fewer burrows that were spaced closer together than did rural woodchucks. Aggregation of use among burrows increased with urbanization.

Because predators are reduced and food resources are abundant, urban areas may act as refuges for woodchucks, especially within an agricultural landscape where there is little remaining natural habitat. My results demonstrate that urbanization also can increase alternative real and perceived risks such as vehicles and human disturbance that could have numerous consequences for population dynamics and fitness. For example, woodchucks are polygynous, and males increase movements during the early spring to secure females for breeding (Ferron and Ouellet 1989). Movements of urban woodchucks were severely restricted by high-traffic roads that could impede males from finding mates during the breeding season, thus decreasing

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the reproductive rate or genetic diversity by forcing males to breed with nearby, closely related females.

One of the main constraints to living in urban areas could be the negative effects of the altered landscape on juveniles. Juvenile dispersal is common in woodchucks, although timing, distance, and degree of philopatry can vary between populations (deVos and Gillespie 1960; Ferron and Ouellet 1989; Swihart 1992; Maher 2009). Dispersal distances of juveniles in urban areas may be severely restricted which could reduce gene flow and alter population genetic structure. A major cause of mortality for adult woodchucks in urban areas was collisions with vehicles, and juveniles may be even more vulnerable to vehicle mortality due to their size and inexperience. Juveniles that attempt to cross high-traffic roads during dispersal may suffer high mortality rates resulting in reduced recruitment.

My results for anti-predator behavior indicated that woodchucks were not strongly habituated to humans, and perceived risk is still high for urban woodchucks despite the reduction of natural predators. Disturbance from humans, including traffic noise and pedestrians, could increase stress levels for urban woodchucks. Deleterious effects of prolonged stress include impaired reproduction, immune, and brain function (Sapolsky et al. 2000), and could affect fitness for woodchucks in urban areas.

My research gives valuable insight into responses to urbanization, and constraints to those responses by an urban-adapter species. Urbanization may buffer woodchucks from certain mortality risks present in rural areas, but my results suggest life in urban areas may not be dramatically better as there also may be serious consequences to living in this landscape. Further examination should be given to

juvenile dispersal and survival, stress levels, and reproductive success of woodchucks

across an urbanization gradient, as urbanization could be consequential for these

fitness-dependent factors.

Chapter 3 meets the formatting requirements for the *Journal of Mammalogy*.

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APPENDIX A: FATES OF MARKED WOODCHUCKS

Sex, date, and fates of radio-marked woodchucks across an urbanization gradient in east-central Illinois, based on the amount of urban land cover within a 500-m buffer around each individual's favored burrow. Date of mortality was estimated as the average of the last date the individual was located alive and the first date the mortality signal was heard. A cause of death was determined in the field or by necropsy, and was attributed to predation when the transmitter was discovered outside of the woodchuck, either alone or with evidence of a carcass nearby. Vehicle collision was determined as the cause of death when a carcass was found in or near a road, or if the necropsy results indicated massive trauma. The cause of death was presumed to be starvation during hibernation if the woodchuck never left the den after the inactive season.

Individual	Sex	Urban land cover	Date of mortality	Cause of mortality
H10	F	4%	05/21/2008	Predation
H2	F	5%	-	Censored
X1	F	6%	06/13/2009	Predation
Y1	M	6%	03/11/2008	Unknown
D2	M	7%	08/04/2007	Predation
J2	M	9%	-	Censored
H1	F	10%	05/15/2009	Predation
A1	F	11%	2007-2008	Hibernation
A2	F	12%	2007-2008	Hibernation
L1	M	24%	-	Censored
X2	M	25%	06/21/2009	Predation
X3	M	32%	06/10/2008	Predation
M1	F	33%	04/02/2009	Vehicle
C2	F	43%	06/26/2008	Conflict
T1	F	45%	05/08/2008	Vehicle
T2	M	45%	2008-2009	Hibernation
K1	M	48%	-	Censored
D1	F	72%	04/29/2008	Conflict
F1	F	72%	05/21/2009	Unknown
W2	M	72%	-	Censored
W3	F	72%	-	Censored
C1	M	80%	04/30/2008	Vehicle
S1	F	88%	-	Censored
P2	F	93%	-	Censored
E1	M	93%	-	Censored
U1	F	94%	-	Censored
K2	M	95%	04/14/2009	Predation
P5	F	96%	06/13/2009	Vehicle
P6	M	96%	-	Censored
W9	M	96%	06/22/2008	Unknown

Appendix A (cont.)

Individual	Sex	Urban land cover	Date of mortality	Cause of mortality
S3	F	97%	-	Censored
J3	M	97%	06/22/2008	Unknown
V1	F	98%	-	Censored
A4	F	98%	07/30/2008	Unknown
V2	F	98%	-	Censored
J4	F	98%	06/11/2008	Unknown
J5	M	99%	04/07/2008	Vehicle
F5	F	100%	-	Censored
J1	F	100%	08/21/2008	Unknown
O1	F	100%	05/31/2009	Unknown
R1	F	100%	08/26/2007	Unknown