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Evaluation Of Movements And Habitat Use Of Suburban Striped Skunks (Mephitis Mephitis) In The Northern Great Plains To Inform Rabies Management

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EVALUATION OF MOVEMENTS AND HABITAT USE OF SUBURBAN STRIPED SKUNKS (*MEPHITIS MEPHITIS*) IN THE NORTHERN GREAT PLAINS TO INFORM RABIES MANAGEMENT

by

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ABSTRACT

Few studies have investigated the ecology of urban striped skunks (*Mephitis mephitis*) despite their role as a primary rabies vector species paired with an ability to thrive in these landscapes. Our aim was to obtain baseline ecological information with an emphasis on spatial ecology of urban striped skunks in the Northern Great Plains region that is missing in the literature. This information, such as home range, nightly movements, habitat selection, and denning behavior is important for informing rabies management decisions such as the placement of oral rabies vaccine (ORV) baits. We used radio telemetry equipment to track 22 (4M, 18 F) skunks from September 2016–November 2016 and March 2017–November 2017 and monitored denning sites with trail cameras October 2016–July 2017. Size of home ranges estimated using kernel density estimation and least squares cross validation determined males ($\bar{x}$ = 4.36 km^2, SE ± 0.79) had larger home ranges than females ($\bar{x}$ = 1.79 km^2, SE ± 0.24). Female skunk home ranges differed by season with the largest home ranges found in summer 2017. However, rate of nightly movements (m/hr) among female skunks did not differ within seasons ($\bar{x}$ = 184.79 m/hr, SE ± 0.53). Moreover, we found no evidence that use-availability was associated with habitat type among female skunks. The strongest predictor of habitat use was distance to water sources with female skunks more likely to be found closer to this habitat type; however, we found no association of use with road factors and geographic location within the city. We observed communal denning in 3 winter den sites, which could amplify rabies transmission during these periods of inactivity. Targeting ORV efforts in areas near water and den sites may be warranted, but considering differences in urban skunk habitat selection studies, we caution that ORV baiting

programs may not be one-size-fits-all, and a framework for effective bait placement would be most successful should similar studies be conducted beforehand.

I. STRIPED SKUNK ECOLOGY AND RABIES MANAGEMENT IN URBAN LANDSCAPES: A REVIEW

INTRODUCTION

By 2025, it is estimated that 65% of the world's population will inhabit urban areas (Altizer and Bradley 2007). Increased densities of people and pets in urban landscapes may result in negative interactions with urban wildlife that thrive in these areas (Rosatte et al. 2010). Mesocarnivores, such as raccoons (*Procyon lotor*) or striped skunks (*Mephitis mephitis*), are more likely to establish permanent residency and flourish in urban environments, often surpassing survival, recruitment, and density estimates of their rural conspecifics (Prange et al. 2003, Rosatte et al. 2010). This amplifies the potential for zoonotic disease transmission, particularly rabies, which drives the need for urban wildlife management studies. Here we focus on the ecology of striped skunks in the Northern Great Plains, an important rabies reservoir species in North America, based on their susceptibility to the virus, wide geographic distribution, and ability to live among people and domestic animals.

Rabies lyssavirus belongs to genus *Lyssavirus*, family Rhabdoviridae, and can infect all mammals, generally through exposure from a rabid animal's saliva (MacInnes 1987). Rabies is a global viral disease afflicting humankind for thousands of years (Raczkowski and Trimarchi 2001), and is known for its serious physical and neurological symptoms (Jackson 2002) and highest case fatality rate of any infectious disease (Rupprecht et al. 2004). Worldwide, approximately 59,000 people die annually from rabies (World Health Organization 2015, Hampson et al. 2015) and millions are treated with post-exposure prophylaxis (PEP) annually (Bogel and Motschwiller 1986). In developed countries, however, rabies in humans and domestic animals is a rare occurrence due to more effective surveillance and vaccination programs.

Rabies remains an important zoonosis in North America because multiple wildlife hosts serve as virus reservoirs (Slate et al. 2005, Gilbert 2018). In the continental U.S., six distinct rabies variants circulate in four wild carnivore hosts: raccoons, striped skunks, arctic foxes (*Vulpes lagopus*) and gray foxes (*Urocyon cinereoargenteus*; Elmore et al. 2017). In mid-continental North America and California, there are 3 variants and foci of skunk rabies virus infection: North Central skunk (NCSK), South Central skunk (SCSK), and California skunk (CASK; Sterner et al. 2008, Blanton et al. 2012, Davis et al. 2013). The rabies virus enzootic in skunk populations in North Dakota is part of the NCSK cycle (Davis et al. 2013). However, the number of reported cases of rabies involving skunks in the Midwest itself pales in comparison to the northeast and mid-Atlantic states (Monroe et al. 2016) due to higher densities of raccoons in the region where raccoon rabies virus circulates, resulting in cross species transmission (CST; Gilbert 2018). Cross species transmission occurs when a rabies virus variant (e.g., raccoon) causes infection in a non-reservoir species for that variant (e.g., skunk; Wallace et al. 2014, Monroe et al. 2016). Some eastern states have reported an increased number in rabid striped skunks infected with raccoon variant rabies virus (Blanton et al. 2012). Of the non-reservoir animals reported with the raccoon rabies variant, skunks were most common (Wallace et al. 2014); however, it is unknown whether the raccoon variant could evolve towards independent transmission in skunks in these areas (Rupprecht et al. 2004). In the northeast and mid-Atlantic states, rabies in skunks is likely a result of direct transmission from raccoons (Guerra et al. 2003, Wallace et al. 2014).

Mesocarnivores that thrive in urban areas are of particular concern compared to other reservoirs. Raccoons are an example of this threat (Uhaa et al. 1992, Kemere 2002) due to their increased abundance and adaptability to residential areas (Prange et al. 2003), which may increase the risk of rabies transmission to people and domesticated animals (Winkler and Jenkins 1991). Moreover, human interaction with raccoons and deliberate increased contact with them (e.g., feeding) may further increase exposure risk (Bruggemann 1992). Though people may avoid skunks due to their ability to spray a noxious musk, they are similar to raccoons in that they are adaptable to urban areas, and their densities, though highly variable, may be greater in some urban landscapes (Prange et al. 2003).

Prior to the development of oral rabies vaccine (ORV) baits, it was reported that estimated expenditures for rabies prevention programs in the U.S. cost upwards of $300 million per year, most of which came from domestic animal vaccinations (Fishbein 1987). With the expansion of the raccoon rabies epizootic in the mid-Atlantic and northeastern states, management expenses have increased to ensure the protection of human health and safety (Chang et al. 2002). Approximately $13 million annually has been spent on ORV programs in North America (Sterner et al. 2009). Other increased costs associated with rabies epizootics include pet and livestock vaccinations, surveillance and monitoring, diagnostic testing, confinement of rabies-suspect domestic animals, abatement research, and human PEP. Up to approximately 36,000 courses of PEP are administered in the U.S. annually, but because there is no national reporting system for PEP in the U.S., a precise estimate in unknown (Christian et al. 2009). Slate et al. (2005) reported PEP use ranging between 20,000 to 40,000 people annually, at an estimated cost of $3,350 per treatment (Shwiff et al. 2003). Despite high initial expenses, PEP cost effectiveness in the U.S. has been estimated at saving billions of dollars per life saved

(Dhankhar et al. 2008). Fear likely drives overuse of PEP where rabies is present (Krebs et al. 1998); nonetheless, PEP has been very successful in preventing human rabies in the U.S. Since 2003, for example, there have been 37 human cases of rabies in the U.S., and these were linked primarily to infection from bats or related to international travel to areas with enzootic domestic dog (*Canis lupus familiaris*) rabies virus (Birhane et al. 2017).

RABIES MANAGEMENT

Early U.S. rabies management efforts focused on human vaccination, and in the 1920s, efforts transitioned to rabies control programs for domestic dogs, which was the source of human infections. Initial programs focused on vaccination, stray removal, leash laws, and dog rabies was generally controlled by 1960 (Rupprecht et al. 1995). By about this time, a greater number of wildlife species were diagnosed with rabies via skunks in the Midwest, foxes in Appalachia and the Northeast, and raccoons in the Southeast (MacInnes 1987). By 2005, a study of rabies surveillance in the U.S. reported that 92.5% of rabid animals were from wildlife species, with raccoons (37.5%) representing the most frequently reported species (Krebs et al. 2005).

Numerous methods have been used to combat rabies virus circulation in wild carnivores. Population reduction (PR) for raccoon rabies, for example, is a controversial lethal technique with mixed results in success (MacInnes 1988, Rosatte et al. 1986, 2001). However, Perry et al. (1989) suggested that PR by itself has been nearly impossible to reduce rabies vector populations to a point where rabies transmission ceases. Trap-vaccinate-release (TVR) is a technique that involves live-capture of mesocarnivores, injecting them intramuscularly with inactivated rabies vaccine, and releasing them at or near the point of capture. This technique, however, is time consuming and is ineffective for those animals displaying clinical signs of infection (Rosatte et al. 2001). Used alone, TVR has exhibited limited success with high costs (Hanlon et al. 1999, Rosatte et al. 2001). For example, both TVR and ORV were employed to mitigate a bat rabies epizootic resulting from spill-over into striped skunks and gray foxes near Flagstaff, Arizona from 2001–2009, but only TVR was effective on skunks (Leslie et al. 2006, Kuzmin et al. 2012). TVR was used to vaccinate approximately 500 raccoons in Central Park, New York City, New York, which contributed to the end of the rabies epizootic (Slavinski et al. 2012). TVR for striped skunks is valued for contingency actions in the U.S. among the mid-Atlantic states where a high frequency of raccoon rabies spillover into these mesocarnivores, potentially confounding local raccoon rabies elimination attempts (Slate and Rupprecht 2012).

More recently, the use of ORV baits has been most successful for large-scale management. For example, ORV, along with domestic dog vaccinations, have successfully controlled canine rabies in coyotes (*Canis latrans*) in south Texas, resulting in the U.S. becoming canine rabies free in 2007 (Velasco-Villa et al. 2008, Sidwa et al. 2005). In another example, the raccoon variant of rabies was eliminated from Long Island, New York in January 2009 (Elser et al. 2016). Vaccine-laden baits are distributed on the landscape and consumed by mesocarnivore reservoir species in order to decrease the susceptible fraction of the host population and disease incidence (Yang et al. 2013). Longer-term cost savings to offset PEP and other related expenses have been realized in areas with ORV targeting wild carnivores (Uhaa et al.1992, MacInnes and LeBer 2000, Kemere et al. 2002, Elser et al. 2016).

ORV has been used as a stand-alone technique or in combination with aforementioned methods. In an emergency response to raccoon rabies breaching an ORV barrier in the U.S. and entering Ontario, Canada, for example, a technique called point infection control (PIC) used a combination of PR, TVR, and ORV to help reduce the prevalence of rabies in this area (Rosatte et al. 2001). When Ohio's western ORV boundary was breached by rabid raccoons in 2004, a PIC-like procedure was implemented to extinguish further spread of rabies (Russell et al. 2005).

The United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services commenced cooperative ORV programs in 1997 aimed at raccoon rabies (Slate et al. 2009). This variant, located mainly along the East Coast of the United States, is a primary focus for the National Rabies Management Program due to the increased exposures to human and animal populations in that region paired with the relatively high incidence of raccoon variant rabies cases in the U.S. (Monroe et al. 2016). The concept of ORV was first conceived at the Centers for Disease Control (CDC) during the 1960s and demonstrated on red foxes in Europe in the early 1970s (Hanlon et al. 1999). Experimental ORV programs in the U.S. have demonstrated progress in controlling raccoon rabies via the distribution of 50 million vaccine baits in 15 states by 2003 (Rupprecht et al. 2004, Slate et al. 2005). In addition, ORV efforts reduced laboratory-confirmed animal rabies and PEP by 90% and 50%, respectively, where fox and raccoon rabies variants coexisted in Ontario, Canada (Nunan et al. 2002). In attempts to control raccoon rabies, baits have been distributed by fixed-wing aircraft in rural landscapes; bait stations, hand baiting, and helicopters have been used in suburban areas (Boulanger et al. 2006).

RABORAL V-RG® (V-RG; Merial Limited, Athens, Georgia, USA), a vaccinia-rabies glycoprotein recombinant vaccine, was licensed for use in the U.S. in 1997 (Maki et al. 2017). The vaccine is composed of a vaccinia virus vector and rabies virus glycoprotein RNA (Briggs 2002). Benefits of V-RG include effectiveness for immunizing raccoons (Rupprecht et al. 1986), safety for other vertebrate species (Hanlon et al. 1999), and restricted use of the vaccine is recommended by Brown et al. (2016). A newer rabies glycoprotein recombinant vaccine bait product (Ontario Rabies Vaccine Baits, ONRAB®, Artemis Technologies, Inc. Guelph, Ontario, Canada), has been successfully used to control raccoon rabies in Canada (Rosatte et al. 2009), and was subsequently determined safe and effective for skunks (Brown et al. 2014*a*). ONRAB® has also been demonstrated effective via oral route in raccoons and red foxes, so targeting multiple species of reservoir hosts is possible (Rosatte et al. 2009, Brown et al. 2012, 2014*b;* Gilbert et al. 2018). However, success of ORV baits for skunks in the U.S. is limited; the use of these baits is still considered experimental and there is currently no available licensed ORV product for skunks in the U.S. (Wohlers et al. 2018).

The host population density of rabies susceptible animals must be reduced to a level below which the disease can no longer spread, but not all animals need to be vaccinated (Bruggemann 1992). For example, a 50–75% vaccination rate was enough to eliminate fox rabies in parts of Europe (Wandeler 1991). Bait distribution densities may vary by area or species for best control results (Elmore et al. 2017, Freuling et al. 2013). Fixed-wing aircraft, helicopters, hand baiting, and bait stations dispensing a minimum of 75 baits/km^2 helped reduce the incidence of raccoon rabies in rural and suburban areas of Erie County, New York (Boulanger et al. 2008).

In a controlled laboratory experiment, Brown et al. (2014) demonstrated that 81% of skunks allowed to eat one ONRAB® bait survived a rabies challenge 247 days post-vaccination (Brown et al. 2014*a*). However, field tests on skunks yielded different results. Early ONRAB® field trials have been conducted in Ontario, Quebec, and New Brunswick, Canada, but bait densities and flight line spacing used generally followed methods to control raccoon rabies; rabies antibody prevalence in skunks ranged from 7 to 25% (Rosatte et al. 2009, Fehlner-Gardiner et al. 2012, Mainguy et al. 2012). ONRAB® baits were subsequently distributed via denser flight lines and high bait densities to better target skunk populations and immunization rates improved (20–34%; Rosatte et al. 2011*b*).

Hand baiting, bait stations, and helicopter distribution have been used for ORV control of raccoon rabies in suburban landscapes (Boulanger et al. 2008). Hand baiting is generally not practical across broad geographic areas due to high human labor involved (Johnston et al. 1988). Helicopters may be expensive, unavailable, or not suitable for small suburban areas with few green spaces. Bait stations are an alternative distribution technique that may improve cost savings or vaccination success in a suburban landscape (Boulanger et al. 2006, Smyser et al. 2015). Boulanger et al. (2008) compared use of a bait station to hand baiting and helicopter ORV baiting to control raccoon rabies in suburban areas within Buffalo, New York, USA; no significant difference was found between treatments and bait uptake. Berentsen et al. (2018) compared hand baiting with helicopter baiting in suburban Chattanooga, Tennessee, and found no difference in population immunity between the techniques. Combined aerial and ground ORV bait distribution, along with increased bait densities of up to 1,000 baits/km^2, helped to eliminate raccoon rabies from Long Island, New York by January 2009 (Elser et al. 2016).

The National Rabies Management Program incorporates natural barriers such as the Appalachian Mountains and large lakes into ORV baiting strategies to prevent raccoon rabies from expanding westward and northward (U.S. Department of Agriculture 2016). However, the Midwest presents a challenge for skunk rabies management given there are few natural barriers to strategically place baits paired with an expansive landscape where skunk rabies is enzootic. Moreover, per capita CST and human rabies prophylaxis appears lower in regions where skunk variants are enzootic (Christian et al. 2009, Wallace et al. 2014). Lastly, it appears that very high densities of baits may be necessary when targeting skunks for ORV, which is cost-prohibitive across broad landscapes. Therefore, ORV for elimination of NCSK remains a low priority of the National Rabies Management Program (Amy Gilbert, USDA APHIS National Wildlife Research

Center, personal communication). Instead, the program prioritizes the prevention of spread and elimination of skunk cases where spill-over of raccoon variant rabies virus into skunks exists.

Rabies management techniques are relatively more challenging in suburban landscapes compared to rural areas. In these areas, there are potentially elevated densities of reservoir hosts, higher opportunity for humans and domestic pets to contact vaccine baits, subsidized anthropogenic food sources which may render baits less enticing, and property rights and land use issues that may limit access to areas with high rabies incidence (Elvinger et al. 2001). In the case of raccoons, higher population densities in suburban landscapes (Prange et al. 2003) may lead to increased competition among conspecifics for a limited number of baits (Olson et al. 1999). Moreover, nontarget wildlife species may lead to increased competition in these areas. Striped skunks and Virginia opossums (*Didelphis virginiana*) are examples of mesocarnivores commonly found in urban habitats (Crooks 2002, Rosatte et al. 2010, Wright et al. 2012) that may compete for baits. Elevated skunk densities have been reported in urban Ontario, Canada (Rosatte et al. 1991, Broadfoot et al. 2001), but the literature appears equivocal as to whether skunk densities are consistently greater in urban areas (Rosatte et al. 1992, Gehrt 2004*a*). Larger average body mass on urban opossums compared to rural conspecifics suggests that urban areas provide more resources for this nontarget host (Prange and Gehrt 2004).

Multiple vaccines may be needed to eliminate rabies from an area due to CST if a given vaccine is not equally efficacious across multiple hosts such as targeted and spillover species (Muller et al. 2015). In Toronto, Canada, for example, the Arctic fox variant of rabies was eliminated in metropolitan red fox (*Vulpes vulpes*) populations in 1996 largely due to the implementation of ORV baiting effort (Rosatte et al. 2007). However, the virus still persisted in small foci due to the existence of skunks as a spill-over host paired with the lack of an effective ORV bait for skunks (Nadin-Davis et al. 2006, Rosatte et al. 2007).

Deciding where to place baits in large-scale urban landscapes remains a challenge for skunk rabies management (Slate et al. 2009). Placement and density of ORV baits is determined by studies that have investigated home range, habitat use, and population density information of the target species. For example, urban raccoons and red foxes have been studied extensively and thus have seen a successful decrease in the prevalence of rabies in ORV bait trials (Robbins et al. 1998, MacInnes et al. 2001, U.S. Department of Agriculture 2007). However, there has been relatively little research conducted on urban striped skunk ecology when compared to other urban wildlife species, especially in the Midwest and Central Plains where they are the primary rabies reservoir (Monroe et al. 2016). A thorough knowledge of skunk space use in urban areas is critical in determining rabies management strategies such as ORV, PR, or TVR. It is important to ascertain landscape heterogeneity and timing when planning the distribution of vaccine baits to control mesocarnivore rabies variants (Boyer et al. 2011). Rabies managers consider the location of documented rabies cases and the likelihood of the target species being found in specific habitat types where vaccine baits are to be distributed. This information may be used to concentrate sufficient densities of vaccine baits to where target animals are more likely to be found (Beasley et al. 2015, Robbins et al. 1998). This information may be used for PR and TVR efforts, as well.

STRIPED SKUNK ECOLOGY

The striped skunk is a mesocarnivore and one of the few members of the Mephitidae family endemic to North America (Wozencraft 2005). It has a widespread distribution from Southern Canada throughout the United States except for some arid regions in Utah, Nevada, and California (Verts 1967, Wade-Smith and Verts 1982, Kays and Wilson 2009). The most distinctive characteristic of striped skunks, besides their odorous musk, is the black and white coloration of their pelage. The characteristic striking contrast between black and white coloration exhibits an aposematic pattern, which warns potential predators of its distaste. Skunks are well known for their ability to project a noxious chemical spray, which is produced in their anal glands, for defense, but they typically use this as a last resort. Other defensive behaviors include stomping their front feet, tail raising, or charging (Larivière and Messier 1996, Kays and Wilson 2009). Skunks have relatively poor eyesight and most do not acknowledge approaching observers until they are within 5 meters (Verts 1967). Adult skunks range in weight from 1.2–5.3 kg and females are approximately 15% smaller than males (Verts 1967, Kays and Wilson 2009). During winter, skunks commonly lose more than half of their body weight due to inactivity (Hamilton 1937, Allen 1939, Verts 1967). Their legs are fairly short relative to their body size, which gives their gait a distinctive waddle.

Skunks are primarily insectivorous but will opportunistically consume small mammals, earthworms, fruits, vegetables, carrion, crustaceans, mollusks, garbage, domesticated cat food, and eggs of ground nesting birds (Hamilton 1936, Verts 1967). This presents a conflict of interest when skunks consume waterfowl eggs, causing bird enthusiasts and hunters to advocate for skunk control and removal (Larivière and Messier 1998*a*).

Skunks breed between February and March, and gestation is typically 59–77 days (Verts 1967, Kays and Wilson 2009). Litter sizes typically range from 1–10 kits and the young are born hairless, but their skin color still indicates the characteristic striped pattern. Musk is present at birth, but the kits lack the muscular coordination to accurately spray until they are older (Verts 1967). The young are reared in a natal den and weaned around 2 months of age (Kays and Wilson 2009). Many studies report high juvenile mortality and most kits do not survive their first year (Wade-Smith and Verts 1982, Fuller and Kuehn 1985, Kays and Wilson 2009). The typical life span of a free-ranging skunk is 2–3 years, and they rarely live past the age of 5 (Casey and Webster 1975). Common causes of skunk mortality include starvation, disease, fur harvest, vehicle collisions, farm machinery, and predation (Verts 1967, Britton et al. 2017).

Home ranges of striped skunks vary greatly based on region and habitat availability. However, most studies, both rural and urban, report home ranges between 1 and 3 km^2 for both males and females (Verts 1967, Greenwood et al. 1985, Greenwood et al. 1997, Bixler and Gittleman 2000). Seasonal home ranges are largest during spring, summer, and fall months (March–November) and significantly smaller during winter months due to inactivity (Rosatte et al. 2011*a*). For females, home ranges and general activity patterns vary with reproductive constraints (Larivière and Messier 1997).

Though skunks do tend to remain philopatric, long-range dispersal is not uncommon. Individuals have been visually observed travelling over 20 km in a single night (S. Larivière, Cree Hunters and Trappers Income Security Board, personal communication). Sargeant et al.

(1982) reported one male skunk that traveled in a straight-line distance of 119 km over the course of several months before he was found again.

Like many mammals, skunks will utilize dens when they are inactive both during the daylight hours and the winter months. Though they have strong digging capabilities, most dens they inhabit are not initially excavated by skunks themselves, but rather by other mammals such as badgers (*Taxidea taxus*), red foxes, and, most commonly, woodchucks (*Marmota monax*) (Allen and Shapton 1942, Verts 1967). They will opportunistically use anthropogenic structures as a foundation for their dens, especially when resources are available in urban settings (Larivière and Messier 1998*a*). Many factors are associated with skunks choosing a den site, but previous research suggests that skunks choose locations more in response to the landscape and habitat type surrounding the den, not site-specific or local habitat characteristics (Hwang et al. 2007). Skunks tend to avoid cropland when choosing denning sites and often select sites in forest or edge habitat (Larivière and Messier 1998*b*, Bixler and Gittleman 2000).

Previous studies have shown that skunks not only share dens with other skunks, but with other species, including raccoons (Verts 1967). Skunks often den communally to promote thermal conservation as they enter torpor (Mutch and Aleksiuk 1977). Though several females have been found in a single den, male skunks typically den alone or with other females, but are fairly intolerant of other males (Gehrt 2004*b*, 2005, Theimer 2016, 2017). Some studies have suggested that while communal denning may benefit individuals in the winter, it may also facilitate the spread of infectious diseases (Houseknecht 1978, Rosatte et al. 1986). This presents a potential risk to pets and humans in relatively close contact with urban skunks. However, most of the ecological inquiry conducted with this species has been with rural populations.

URBAN SKUNK STUDIES

I present reviews of North American studies pertaining to urban and rural home range, movement, and habitat selection in striped skunks in Tables 1–3, but here present pertinent urban skunk studies. Ruffino (2008) explored home ranges and habitat selection of skunks in the Houston, Texas metropolitan area. Skunks showed a strong preference for short grass areas, but quickly migrated to areas with more cover once temperatures dropped. Skunks would not remain dormant for significant amounts of time but, instead, fasted for a few days if temperatures temporarily dropped below 7° C. Although Ruffino (2008) contributed insights into urban skunk ecology, a warmer Texas climate may preclude representativeness when compared to northern skunk populations.

An urban skunk study in Flagstaff, Arizona, USA was conducted by Weissinger et al. (2009) and followed by denning ecology studies (Theimer et al. 2016, Theimer et al. 2017). Though Flagstaff is located in the desert southwest, the climate is more temperate due to higher elevation, and this study area receives snowfall during winter months (Theimer et al. 2016). These studies used a combination of radio-collars and automated cameras to determine home ranges, nightly movements, seasonal movements, and potential inter- and intraspecific interactions, which could potentially lead to rabies transmission. Striped skunks were followed from January 2004 through December 2005. Mean nightly rates of movement for both sexes varied significantly across seasons and peaked during the months of May and July, the post-breeding months. The researchers found that both males and females frequently crossed the urban-rural interface for days or weeks at a time. Cameras were placed at known denning locations and nocturnal locations where skunks were frequently found during their nightly excursions. They documented both concurrent and sequential use of these sites by skunks, domesticated animals, and other wildlife species. These interactions, combined with the movements across the urban-rural interface, allow for inter- and intraspecies transfer of rabies within an urban setting (Weissinger et al. 2009, Theimer et al. 2017).

Gehrt (2005) monitored and compared survival of urban and rural skunks in the Chicago, Illinois area. Out of 73 skunks radio collared, 30 mortality events were recorded (17 urban, 13 rural). Most mortalities occurred during the winter months and disease or poor physical condition was the most common cause of death for these urban skunks. Conversely, rural skunks, mostly succumbed to vehicle collisions, followed by disease or poor physical condition. The skunks were also monitored for general physical condition and experienced significant weight loss from autumn to spring, especially the rural skunks. The results of this study suggest that skunks endure significant stress during winter, and this is likely a contributing factor to low survival rates (Gehrt 2005).

Rosatte et al. (2011*a*) studied urban skunk ecology in Scarborough, Ontario, Canada. In this study, 28 skunks were fitted with radio collars and tracked between July 1986 and July 1987. In addition to tracking home range, researchers followed a subsample of skunks from dusk until dawn to record nightly movements. Annual home range sizes ranged between 0.1 and 5.0 km^2 and nightly movements ranged between 0.1 km and 3.0 km. Skunks utilized field habitat more frequently than residential or industrial habitats. Skunks generally stayed in their winter dens from early December to early March, and communal winter denning was recorded on several occasions. Though multiple females denned together or a female denned with a male, the researchers never recorded an instance where two males occupied the same den. In January, a few skunks moved denning sites in what researchers attributed to breeding activities (Rosatte et al. 2011*a*).

CONTRIBUTION TO CURRENT LITERATURE

In short, only a handful of studies have investigated urban skunk ecology despite their frequency in these settings and importance as a rabies reservoir. In addition to filling gaps in knowledge in urban skunk ecology, this study serves as a pilot for possible future skunk research and management efforts. Though widespread ORV efforts may never occur in the Northern Great Plains where the NCSK variant is endemic, this study will contribute to the body of knowledge for combating spillover cases of the raccoon variant in skunks among mid-Atlantic states. This is a critical step in the National Rabies Management Program's goal of preventing further spread of and, eventually, elimination of the raccoon variant altogether. In addition, the purpose of this study was to obtain baseline ecological information on urban skunks to help inform disease management decisions, particularly bait distribution and placement in relation to multiple landscape attributes should an ORV bait be approved for use in skunks in the U.S and be warranted for small-scale distribution in urban landscapes.

Using Rosatte et al. (2011*a*) as a baseline for inquiry, we were specifically interested in home range, nightly movements, a more extensive investigation of habitat selection, and documenting denning behaviors of urban striped skunks in the Northern Great Plains. This project is a mutual endeavor between the University of North Dakota (UND) and the United States Department of Agriculture Wildlife Services and will benefit all concerned by providing new information regarding urban skunk ecology. The primary objectives of this study were to:

1. Estimate annual and seasonal skunk home range size in urban areas of Grand Forks, North Dakota and/or East Grand Forks, Minnesota.

2. Evaluate habitat selection by urban skunks within individual home ranges (third-order selection per Johnson [1980]).
3. Determine anthropogenic (e.g., person, housing, and road densities) and other factors (e.g., weather, sex) that may influence resource use.
4. Investigate skunk movements (e.g., nightly, winter, dispersal) and denning behavior (e.g., winter period, communal denning).

STUDY AREA

Though the NCSK variant of rabies is endemic to the Northern Great Plains, few studies have been conducted in this area; therefore, the city of Grand Forks provided an opportunity to explore urban skunk ecology in the midst of the NCSK variant range. Grand Forks, North Dakota, USA (47°55′31″N 97°1′57″W) is a city approximately 5,200 ha in size located along the eastern edge of North Dakota in the Red River Valley. In April 1997, the Red River flooded and caused approximately $3.6 billion worth of damage to the cities of Grand Forks, North Dakota and East Grand Forks, Minnesota (Todhunter 1998). To protect residents and structures from future flooding events, 2,200 acres surrounding the Red River was transformed into a natural open space surrounded by intermittent berms and walls to contain water in the event of another catastrophic flood. This natural area provides habitat, denning locations, and a travel corridor for many wildlife species, including skunks.

The city itself is surrounded by primarily agricultural fields and flat prairie with a few shelterbelts, which block wind and prevent erosion, between fields. The human population of Grand Forks is approaching 60,000, and is growing due to urban sprawl, especially in the southern part of the city (US Census Bureau 2010). Habitat types include highly urban, suburban, industrial, and fragmented green areas flanking rivers and coulees.

Prior to the commencement of field efforts, project staff collected anecdotal information from local wildlife and law enforcement officials, a nonprofit animal welfare organization, and hobbyists who might inform relevant information on Grand Forks urban skunks. Based on that information and previous literature, sampling protocols were developed in an attempt to distribute trapping effort while maximizing trap success. Trapping was conducted during the summer months (June–August 2016, May–August 2017) and radio-collared skunks were tracked during spring (March–May 2017), summer (June–August 2017), and fall (September–November 2016 and 2017). Home range, nightly movement, and habitat selection data were collected during that time and later analyzed using modern geographic information systems and statistical software. Denning locations were located opportunistically and monitored using trail cameras. In the subsequent chapter, we present results from these efforts.

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Table 1. A review of North American home range sizes for adult striped skunks (*Mephitis mephitis*), including authors and year study was published, location, habitat type (urban vs. rural), estimator type, home range by sex, and overall home range. Sample sizes in parentheses.

Study	Location	Rural or Urban	Home Range Estimation Method	Male	Female	Overall
Shirer and Fitch 1970	Northeastern KS	Rural	MCP	0.12 (1)	0.18, 0.37 (2)	0.22 (3)
Bailey 1971	Northwestern OH	Rural	MCP	0.31 (5)		
Storm 1972	Northwestern IL	Rural	MCP	5.06 (2)	3.74 (5)	2.84 (7)
Greenwood et al. 1997	Stutsman County, ND	Rural	MCP	2.8 (8)	1.2 (9)	1.6 (17)
Goldsmith 1981	Northeastern TN	Rural	MCP	0.16 (5)	0.24 (9)	0.21 (14)
Rosatte and Gunson 1984	Southern Alberta	Rural	MCP	2.9 (14)	2.5 (14)	2.7 (28)
Greenwood et al. 1985	Griggs County, ND	Rural	MCP	3.08 (15)	2.42 (24)	2.67 (39)
Rosatte 1986	metropolitan Toronto	Urban	MCP	0.83 (4)	0.51 (5)	0.65 (9)
Rosatte et al. 1991	metropolitan Toronto	Urban	MCP			0.51 (57)
Larivière and Messier 1998*b*	Southcentral Saskatchewan	Rural	KDE/MCP	12.06/ 11.63 (5)	4.31/3.74 (21)	5.80/5.26 (26)
Bixler and Gittleman 2000	Blount County, Tennessee	Rural	MCP	1.20 (9)	0.88 (6)	1.08 (15)
Larivière and Messier 2001	Prairie Pothole Region of SC Saskatchewan	Rural	MCP		2.3 (5)	
Rosatte and Larivière 2003	Southern Ontario	Rural	MCP			1.0-3.0
Ruffino 2008	Houston, TX	Urban	MCP	2.55 (5)	1.26 (15)	1.58 (20)
Weissinger et al. 2009	Flagstaff, AZ	Urban	KDE	1.3; 0.7 (19)	1.1; 0.4 (21)	0.87 (40)
Rosatte et al. 2011*a*	Scarborough, Ontario, Canada	Urban	MCP	0.5 (4)	0.3 (3)	0.9 (7)

Table 2. A review of North American nightly movement studies for adult striped skunks (*Mephitis mephitis*), including authors and year study was published, location, habitat type (urban vs. rural), rate of movement (m/hr), or distance traveled (meters/night).

			Rate of Movement (m/hr)			Distance Traveled (m/night)		
Study	Location	Urban/ Rural	Male	Female	Overall	Male	Female	Overall
Greenwood et al. 1985	Griggs County, ND	Rural				3,300	2,600	3,051
Greenwood et al. 1997	Stutsman County, ND	Rural	250	221	234	2,010	1,806	1,896
Phillips et al. 2004	Barnes/Wells County, ND	Rural			390/342			2,196.7/ 2,357.1
Weissinger et al. 2009	Flagstaff, AZ	Urban			140			
Neiswenter et al. 2010	Tom Green County, TX	Rural			280			
Rosatte et al. 2011*a*	Scarborough, Ontario, Canada	Urban						100–3,000

Table 3. A review of North American habitat selection studies for adult striped skunks (*Mephitis mephitis*), including authors and year study was published, location, habitat type (urban vs. rural), data collection technique, statistical analysis used, and habitat selection.

Authors	Location	Urban/Rural	Type of Data	Analysis	Selected	Less Selected
Rosatte et al. 1991	Toronto	Urban	Trapping data	Chi-square and ANOVA	Fields	
Rosatte et al. 1992	Scarborough, Ontario, Canada	Urban	Trapping data	Paired t-tests	Field, Industrial, Commercial	Forested-park, Groomed-grass
Larivière and Messier 2000	Prairie Pothole Region of SC Saskatchewan	Rural	Telemetry locations	Compositional analysis	Wetland, woodland	Cropland
Bixler and Gittleman 2000	Blount County, Tennessee	Rural	Telemetry locations	Correlation	Forest-field edge	Forest, Field
Broadfoot et al. 2001	Scarborough, Ontario, Canada	Urban	Trapping data	Model selection	Industrial	Field
Larivière and Messier 2001	Prairie Pothole Region of SC Saskatchewan	Rural	Telemetry locations	Compositional analysis	Woodland	Cropland
Phillips et al. 2003	Barnes/Wells County, ND	Rural	Telemetry locations	Compositional analysis	Agricultural-wetland edge	Pastureland, roads
Prange and Gehrt 2004	northeastern Illinois	Urban	Trapping data & roadkills	Model selection	Rural	Suburban, Urban
Ruffino 2008	Houston, Texas	Urban	Telemetry locations	Chi-squared	Short grass fields	
Rosatte et al. 2011	Scarborough, Ontario, Canada	Urban	Telemetry locations	Friedman ANOVA	Field	Industrial, Field/Industrial, Residential

SPATIAL ECOLOGY OF URBAN STRIPED SKUNKS (MEPHITIS MEPHITIS) IN THE NORTHERN GREAT PLAINS: A FRAMEWORK FOR FUTURE ORAL RABIES VACCINATION PROGRAMS

INTRODUCTION

Rabies remains an important zoonosis in North America and is perpetuated by multiple terrestrial wildlife vectors including raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and gray foxes (*Urocyon cinereoargenteus*; Slate et al. 2005, Elmore et al. 2017, Gilbert 2018). In mid-continental North America and California, there are 3 enzootic variants of skunk rabies virus that account for approximately 25% of rabid wild animal cases reported annually in the U.S. (Sterner et al. 2008, Blanton et al. 2012, Davis et al. 2013, Monroe et al. 2016, Birhane et al. 2017). Striped skunks are habitat generalists and are widely distributed throughout North America, thriving in rural, urban, and peri-urban environments (Rosatte et al. 2010*b*, Rosatte et al. 2011). While the risk level posed by striped skunks to humans and domestic animals in urban areas is unclear (Ragahaven et al. 2016), their role as a major spillover recipient of raccoon rabies infections places striped skunks as a species of importance for national rabies management efforts (Wallace et al. 2014, Gilbert 2018, Wohlers et al. 2018). An understanding of the spatial ecology of urban and peri-urban striped skunks is critical for effective disease management. Spatial ecology of striped skunks has been well documented for rural areas in the U.S. (Verts 1967, Shirer and Fitch 1970, Bailey 1971, Greenwood et al. 1997) and Canada (Rosatte and Gunson 1984, Larivière and Messier 1998*b*), however, few studies have addressed urban striped skunk ecology (Rosatte et al. 2001, 2011, Gehrt 2005, Weissinger et al. 2009), and fewer still have addressed urban habitat selection (Broadfoot et al. 2001, Prange and Gehrt 2004, Ruffino 2008, Rosatte et al. 2011). In one study conducted in metropolitan Toronto, Ontario, Canada, striped skunks tended to use agricultural or field areas over residential or industrial areas (Rosatte et al. 2011), but differences exist among habitat selection studies based on geographic location.

Efforts to control rabies in striped skunks have been met with challenges in field and laboratory settings (Charlton et al. 1988, Rupprecht et al. 1995, Grosenbaugh et al. 2007, Wohlers et al. 2018). The U.S. Department of Agriculture Animal Plant and Health Inspection Service Wildlife Services National Rabies Management Program (NRMP) has implemented oral rabies vaccination (ORV) bait distribution programs targeting the raccoon rabies variant in 16 states, while Texas distributes ORV baits for coyote (*Canis latrans*) and gray fox (U.S. Department of Agriculture 2016). While ORV has been relatively successful in regional raccoon, gray fox, and coyote immunization (Slate et al. 2009), population immunity levels in striped skunks suggests marginal impact of traditional NRMP ORV methods for this species, and there is not currently a licensed ORV product for skunks in the U.S. (Lawson et al. 1989, Wohlers et al. 2018). Managers must consider skunk spatial ecology for rabies management efforts; for example, placement and density of ORV baits is determined by studies that have investigated movement patterns, home range, habitat use, and population density information of targeted species (Adkins and Stott 1998, Weissinger et al. 2009, Rosatte et al. 2010*b*).

Although not all striped skunks den communally, the benefits of doing so include conserving body heat and energy during winter months, even in southern latitudes (Theimer et al. 2016, Theimer et al. 2017*b*). However, the proximity of individual skunks during communal denning may exacerbate spread of infectious disease, especially rabies (Verts 1967, Houseknecht

1978, Rosatte et al. 1986, Theimer et al. 2017*b*). It has been theorized that communal denning contributes significantly to peak rabies outbreaks during late-spring or early-summer, which may include a combination of overwintered infections and transmission during copulation activities in February and March (Verts 1967, Rosatte 1984, Pepin et al. 2017). Females skunks often den communally, but males are more likely to move from den to den and breed with as many females as possible, thus exacerbating rabies spread (Gehrt 2004, Theimer et al. 2016).

Factors related to striped skunk spatial ecology, including denning behavior, may interact to alter contact rates and the probability of disease transmission (Totton et al. 2002). Knowledge of these factors, however, are often unknown or assumed to be similar to those previously reported in other geographic areas (Weissinger et al. 2009). Moreover, there is little information on urban striped skunks in the Northern Great Plains. Thus, decisions regarding optimal ORV bait placement in large-scale urban landscapes remains unclear in many areas given a paucity of studies.

We investigated the urban spatial ecology of striped skunks to inform rabies management and to fill gaps in knowledge for this region. Specifically, we 1) estimated annual and seasonal home ranges among male and female skunks and differences in seasonal home ranges among female skunks; 2) estimated nightly movements by male and female skunks and differences in seasonal nightly movements among female skunks; 3) evaluated habitat selection and anthropogenic factors that may explain habitat use by female skunks; and 4) evaluated denning behavior. Based on previous literature, we predicted differences in seasonal home ranges. We also predicted differences in habitat use, with skunks using agricultural or field areas over residential or industrial areas, and that urban characteristics such as road density and distance to water and roads would be related to use.

STUDY AREA

This study was conducted from June 2016 to November 2017 in the cities of Grand Forks, North Dakota and East Grand Forks, Minnesota (Fig. 1*a*). Grand Forks (47°55′31″N 97°1′57″W) is a city approximately 5,200 ha in size with a population of approximately 57,000 people (3rd largest in the state) and located along the eastern edge of North Dakota in the Red River Valley (United States Census Bureau 2011). East Grand Forks, Minnesota is a city adjacent to Grand Forks on the East side of the Red River approximately 1,500 ha in size with a population of 8,600 people. Originally comprised of riparian areas and tall-grass prairie, the Red River Valley region has been anthropogenically modified and transformed into an agricultural mosaic with areas of urban development (Seabloom et al. 2011). Average annual rainfall is 53 cm and the area is characterized by hot summers and cold winters (Seabloom et al. 2011). The landscape of Grand Forks and East Grand Forks during the time of this study consisted primarily of urban housing (39%), commercial businesses (19%), green park areas (14%), and industrial sites (14%) adjacent to agricultural fields (13%) on the city's periphery (Fig. 1*b*).

METHODS

Capture and Handling

Trapping and handling protocols followed the general guidelines of the American Society of Mammalogists (Sikes et al. 2011) and University of North Dakota's (UND) Animal Welfare Assurance Number A3917-01 and Institutional Animal Care and Use Committee Protocol Number 1605-1. Skunks were live captured during June–August 2016 and May–August 2017 in cage traps (Model 105SS, Tomahawk Live Trap Co., Hazelhurst, Wisconsin) baited with a combination of sardines, large marshmallows, anise or fish oil, canned cat food, or commercial baits (Marsayada's Nosey [Minnesota Trapline Company, Pennock, Minnesota] and Caven's Hiawatha Valley Predator Bait [Minnesota Trapline Company, Pennock, Minnesota]). We distributed trap efforts by randomly placing a grid of 1 km^2 cells over a digital orthophoto of the Cities of Grand Forks and East Grand Forks, resulting in 83 possible trap units. Using this map, along with ground truthing, we removed 8 cells from sampling due to safety considerations and a paucity of trap locations. Among remaining trap units, we randomly selected cells for initial trapping efforts. In each cell, two locations were initially set a minimum of 100 meters apart in sets of 2 (4 traps total) and targeted preferred skunk habitat while considering the possibility of trap tampering. Typically, we set 20–50 traps per trap night. If no adult skunks were captured after 3 trap nights, the traps were moved to another location within the same cell at a minimum of 100 m away for an additional 3 trap nights. However, we limited adult skunk captures to a maximum of 3 adults per grid cell annually to maximize representation of the entire study area. To supplement sample size, we opportunistically attempted to trap skunks at specific locations based on tips from animal control officers or landowner's complaints. We set traps each afternoon and closed them each morning to help prevent nontarget captures. We released nontarget species and skunk kits upon capture; adult skunks were covered within cage traps with a tarp and transported, without sedation, to UND for sample processing.

We chemically immobilized adult skunks with an intramuscular hand-injection of 0.5 ml 5:1 mixture of ketamine:xylazine (10–16 mg/kg ketamine and 2–8 mg/kg xylazine; Grimm et al. 2011); once immobilized, we applied an ophthalmic ointment to each eye and monitored breathing and pedal reflex. We applied a unique identifying Monel 1005-1 metal ear tag (National Band and Tag Company, Newport, Kentucky) in each ear. We collected biological samples from skunks for subsequent storage and reporting elsewhere. For example, we extracted the first upper premolar tooth (PM1) using a 2 mm feline dental elevator and rongeur pliers to collect age data. For rabies titer and genetic analysis purposes, we drew blood from the jugular vein. Sera were separated from whole blood and shipped to Kansas State University Rabies Laboratory for quantitation of rabies virus neutralizing antibodies by standard rapid fluorescent focus inhibition test (Yager and Moore 2015). We sent teeth to Matson's Laboratory for aging analysis to the nearest year using annuli count method. We fitted skunks with small mammal M1820 VHF radio transmitter collars (Advanced Telemetry Systems, Isanti, Minnesota) operating on 151 MHz. During recovery, the individual was placed on its side inside the trap to facilitate breathing, loosely covered with a tarp, and transported back to point of capture or a safer location nearby.

Tracking

To maximize battery limits, we set collars to turn on at 1600 hours and checked for signals on both newly released skunks and other collared skunks while setting traps the following day. Project staff conducted tracking efforts during September–November 2016 and March–November 2017 between 1900 and 0600 hours. Initially, we randomly distributed tracking efforts among all active radio-collared skunks and subsequently spent more effort focused on individuals lacking a sufficient number of locations. Using an R-1000 telemetry receiver (Communications Specialists, Orange, California), omni-directional roof antennae and a handheld, 3-element folding yagi antenna (Advanced Telemetry Systems, Insanti, Minnesota), project staff attempted to locate each skunk a minimum of twice per week either via triangulation or visual location. Researchers commenced nightly telemetry searches by visiting areas based on previous fixes and expanded the search up to a 6 km radius for a minimum of 30 min. If a skunk could not be located within 30 minutes, efforts were abandoned to search for a different skunk. We made efforts to obtain at least 3 bearings no less than 20° and no more than 30 minutes apart from elevated positions (Kenward 2001, White and Garrott 1990).

We collected GPS points using a Garmin eTrex 20x (Garmin, Olathe, Kansas), and estimated bearings of strongest signals with a Suunto MC-2G USGS Mirror Compass (Suunto Oy, Vantaa, Finland). If we obtained a visual on the individual skunk, we either marked the spot with a GPS point or, if the location was not accessible, used Google Maps (Google LLC, Mountain View, California) to acquire location coordinates. Researchers recorded these data, along with date, time, general location, skunk and collar frequency. Triangulated points were estimated using Locate III (Nams 2006; Pacer Computer Software, Tatamagouche, Nova Scotia, Canada) software and rejected if error polygon > 1 hectare (0.01 km^2; White and Garrott 1990). An accuracy assessment indicated that error in triangulated locations from project staff was similar to those of other urban wildlife studies (~0.09 km ± 0.01 SE from actual collar location; Kauhala and Tiilikainen 2002, Bartolommei et al. 2012, Gehrt et al. 2013).

Movements and Home Range

Nightly movements

To assess nightly movements, we randomly selected a subset of radio-collared skunks and monitored them from sunset until sunrise or when the collars turned off at 0600. We tracked these skunks a minimum of two nights per season and twice per month, with locations taken every hour (minimum = 5 points per night, range = 5–10 points), an interval considered biologically independent (Lair 1987, McNay 1994). Project staff conducted longer, 3-hour initial searches for skunks selected for nightly movement data collection before abandoning efforts for another skunk. We followed 2–3 skunks per night. We analyzed 332 (n = 49 M, 283 F) locations for male (n = 4) and female (n = 19) skunks between September–November 2016 and again March–November 2017. To estimate straight-line distance between consecutive nightly position fixes for each skunk, we used the adehabitatLT package in R (R Version 3.3.1, www.r-project.org, accessed 07 April 2017). To obtain mean nightly rate of travel (m), we divided the distance between successive position fixes by the elapsed time and then averaged these across all movements in a single night for a given skunk (Weissinger et al. 2009). As our sample contained primarily female skunks, we hypothesized that nightly rate of movement, like home range size, would be influenced by annual reproductive cycle and, thus, coincide with n = 3 seasons: 1) spring (March–May; breeding, post-breeding and parturition), 2) summer (June–August; rearing, weaning, and kit dispersal), and 3) fall (September–November; increased foraging and subsequent decrease in activity due to cooling temperatures; Verts 1967, Rosatte et al. 1991, Weissinger et al. 2009).

Size of Home Range

We calculated 95% contours of annual home ranges (km^2) using a kernel density estimation (KDE) approach and three bandwidth methods (local convex hull [LoCoH], least squares cross validation [LSCV], and H reference [Href]) using the adehabitatHR package in R

(R Version 3.3.1, www.r-project.org, accessed 18 April 2017). LoCoH calculates a convex hull around a single point based on its nearest neighbors and forms a home range estimation by combining the hulls to create a density map (Getz et al. 2007). Conceptually, KDE for point features such as telemetry locations entails fitting a density function that distributes the weight of each location over an area, and then sums across these densities at each spatial location to create a smoothed surface (Zheng et al. 2004). The height and width of each distribution is determined by a bandwidth (h) which provides the smoothing parameter of the home range. Href uses a default or reference bandwidth based on the estimates of the variances in the x, y locational data, but this technique may over-smooth point data, resulting in relatively large home ranges (Worton 1995). In comparison, LSCV seeks to minimize integrated square error between true and estimated distributions by adjusting bandwidth accordingly. We selected LSCV for home range estimates and seasonal comparisons because it appeared to best represent our data, given a limitation of 15 minimum telemetry fixes per skunk.

City Longitude

Habitat composition is not consistent throughout the city (Fig. 2). For example, the eastern portion of our study area had proportionally more green and residential areas, and skunk movements further east may be limited by the Red River as a natural barrier. However, while there is some evidence that rivers may act as barriers for gene flow among SCSK skunks in the central Great Plains (Barton et al. 2010), it remains unclear how larger rivers may physically impede skunks from crossing larger rivers. In the western edge of the Grand Forks, industrial and commercial areas predominate and are immediately adjacent to agricultural field areas which do not restrict skunk movements further west. Therefore, we divided our skunk sample into $n = 2$ longitudinal groups to examine differences in longitude by home ranges and nightly movements.

We used ArcGIS (ArcGIS 10.4, ESRI, Redlands, California) geographic information system (GIS) software and the Center to Point tool to determine the centroid of the city limits shapefile available at City of Grand Forks GIS Services Open Data Warehouse (http://www.gfgis.com/data/, accessed 4 March 2018). We bisected the city vertically through the centroid and categorized skunk location data accordingly.

Habitat Classification

We considered two land cover layers for habitat analysis and conducted accuracy assessments on both to ascertain the most accurate for habitat selection among skunks within our study area. The first layer, 2011 National Land Cover Database (NLCD; Homer et al. 2015), included 11 available habitat types which we subsequently reclassified into open water (e.g., rivers, ponds, streams), green areas (e.g., parks, forested, developed open, cemeteries), developed (e.g., houses, businesses, roads, factories), and agricultural crops. The second layer was comprised of zoning areas made available by the City of Grand Forks GIS Services Open Data Warehouse (http://www.gfgis.com/data/, accessed 22 March 2018) which are updated monthly. Grand Forks zoning layer contained 66 unique zone categories which we subsequently reclassified into 4 habitat types: green (e.g., parks, open lawns, ditches, cemeteries), residential (e.g., houses, trailer parks), industrial/commercial (e.g., malls, restaurants, campus, small businesses, train yards, industrial parks, factories), and agricultural/field. We compared both layers individually against a reference true color aerial photo from May 2017 available from City of Grand Forks GIS Services Open Data Warehouse. We then constructed 100% minimum convex polygons (MCP) around individual skunks' telemetry locations and then conducted an accuracy assessment of 350 random points within those boundaries. We performed Kappa analysis, which yields a $\widehat{K}$ statistic measuring agreement between actual and expected land-cover classification and reference data sets by chance (Congalton and Mead 1983). Values of $\widehat{K}$ ranging from 0.4–0.8 suggested that moderately accurate, non-random, classifications and those > 0.8 indicate highly accurate (Jensen 2005). Overall accuracy from the Grand Forks zoning layer was assessed at 85% ($\widehat{K}$ = 0.79) and NLCD was assessed at 76.6% ($\widehat{K}$ = 0.65). Therefore, we selected the Grand Forks zoning layer for subsequent habitat selection analyses.

Habitat Selection

We used 100% MCP to estimate the available habitat for each skunk because we were interested in including the total area potentially used by each animal based on bounded telemetry fixes (White and Garrott 1990, Berentsen et al. 2013; Fig. 2. We generated an equal number of random locations within the MCP as hypothetical skunk telemetry fixes. We then classified recorded skunk fixes as "used" and those containing randomly generated points as "available" to create a binary response. Therefore, our habitat study design generally follows a third order, within home range structure as outlined by Johnson (1980); however, while we consider the use of MCP as a reasonable bound for habitat selection estimation, we do not consider it an estimate for home range (Walter and Fisher 2016).

Statistical Analyses

Nightly Movement and Home Range

To test for differences in nightly movements and size of home range by effects of season and longitude from City of Grand Forks centroid, we used general linear mixed effects models (Zuur 2009) with individual female skunk treated as a random effect to address issues associated with autocorrelation and uneven sample sizes (Gillies 2006). A small sample size of male skunks precluded feasibility of sex as a covariate. We used Fall 2016 as the baseline for estimating seasonal effects and western Grand Forks as the baseline for longitude. We analyzed $\log_{10}$-

transformed nightly movement and home range estimates to meet the assumptions of residual normality. We used R and package lme4 (R version 3.3.2, https://www.r-project.org/, accessed 10 May 2017) to estimate models with main effects. We did not consider our analyses of home range and nightly movements as model selection problems because our goal was to test the effects of all of the included factors and not simply to produce a single or set of models that yielded the optimal prediction of home range size.

Habitat Selection

We conducted analysis by estimating a population-level resource selection function (RSF) using a mixed-effects logistic regression model with habitat type, relationship to roads (distance and density), and distance to water resources as fixed effects and individual female skunk as a random effect. We used ArcGIS (ArcGIS 10.4, ESRI, Redlands, California) software and the Line Density and Point Distance tools to calculate road density (km^2) and distance to roads and water (m). Our primary interest was the influence of habitat type, and logistic regression can provide an unbiased method for ranking and for comparing relative probability of use (Keating and Cherry 2004, Johnson et al. 2006). Using R (Version 3.3.2, www.r-project.org, accessed 28 May 2018) and scripts from the Manual of Applied Spatial Ecology (Walter and Fischer 2016), we developed and compared multi-factor models using a model selection approach based on Akaike's information criterion corrected for small sample sizes (AIC_c) as described by Burnham and Anderson (2002). We used female skunk locations as a binomial response (i.e., actual used vs. random "available" locations) and constructed a set of 10 candidate models that included combinations of the following predictor variables of interest: habitat type, distance of skunk locations to closest road (km), distance of skunk locations to closest water resource (km), and road density (km/km^2), a global model that included all covariates, and a null, intercept only model. We again used individual female skunk as a random effect in our mixed-effects logit analysis to address issues associated with autocorrelation (Gillies et al. 2006). We assessed multicollinearity using variance inflation factor (VIF; Zuur et al. 2010), but no covariates scored a VIF $\geq$ 3.0; therefore, we did not remove predictor variables of interest from analyses. We based parameter estimates on fitting the top model and estimated model fit by comparing residual deviances to null deviances.

Denning

To examine the presence of skunks and non-target species with an emphasis on assessing communal denning, we located winter and natal dens opportunistically and placed Reconyx HyperFire HC600 trail cameras (Reconyx, Holmen, Wisconsin) near den entrances to monitor activity. Our camera traps consisted of a 3.1-million-pixel camera with a glass, multi-element lens, and an infrared with 18.3-m illumination range. At each den site, we mounted cameras on tripods or metal poles 2–5 m from den entrances. We positioned the cameras approximately 0.5 m above the ground and set both sensitivity of the passive infrared motion and heat sensor and picture quality to high. When possible, we adjusted cameras to face north or south to avoid overexposure of photos near dawn or dusk. To balance our desire to reduce consecutive photographs of unique skunks with the risk of missing animals, we set the photographic interval to 5 min (Koerth and Kroll 2000). We identified each site with unique den characteristics within the camera's field of view. To facilitate skunk identification in photographs, we cleared low vegetation within a 2-m radius of the den entrance. We checked photographic data a minimum of once per month and cameras operated continuously for up to 270 days (median = 125, range = 14–270) until a minimum of 10,000 photographs were recorded, after which visible species were tallied. We did not attempt to identify individual skunks due to logistics and because similarity in physical characteristics may cause difficulty in identifying individuals (Theimer et al. 2017*a*).

RESULTS

Trapping

We captured 138 skunks (95 kits, 29 adults [6 M, 23 F], 16 recaptures) over 3,070 trap nights (0.009 adults/trap night) during the study (Table 4, Fig. 3. We physically examined immobilized skunks and all were apparently healthy. Overall, our capture success rate was 0.04 skunks per trap night and for adult, uncollared skunks was 0.009 skunks per trap night. By year, we caught 84 skunks (59 kits, 15 adults [3 M, 12 F], 10 recaptured adults) over 1,744 trap nights in 2016 and 56 skunks (36 kits, 14 adults [3 M, 11 F], 6 recaptured adults) over 1,326 trap nights in 2017. We captured and collared 1 adult skunk opportunistically based on a tip from the City of Grand Forks Animal Control Officer, but efforts to capture skunks in East Grand Forks, Minnesota were unsuccessful. We set traps in all habitat types including 8% (*n* = 31) in agricultural/field, 18% (*n* = 75) in green, 38% (*n* = 156) in industrial/commercial, and 26% (*n* = 106) in residential areas (Table 5, Fig. 3). Proportions of habitat type available within the city limits of Grand Forks included 13% agriculture/field, 14% green, 33% industrial/commercial, and 39% residential areas. We captured and radio collared skunks in agriculture/field (*n* = 2), green (*n* = 3), industrial/commercial (*n* = 19), and residential areas (*n* = 5; Table 5). In general, however, most (*n* = 23 [4 M, 19 F]) trapping success occurred on the urban/rural interface northwestern portion of our study area (Fig. 3).

Of adult skunks caught and fitted with VHF radio collars, we lost 12 (41%) due to various events. Four females disappeared from the study area, 2 males experienced vehicle mortality, and 1 male slipped its collar before we were able to collect sufficient data. We were able to collect sufficient data based on a minimum of 15 telemetry fixes from 22 (4M, 18F) skunks. During tracking efforts, we lost 5 skunks (1 M, 4 F) due to loss of signal (2 F, 1 M), a suspected predation event (1 F), and a vehicle mortality (1 F; Table 6, Table 7).

Nightly Movements and Home Range

We obtained ≥5 telemetry fixes per night for 19 individual skunks (4 M, 15 F; Table 6). Mean number of points taken per skunk night and mean time tracked in minutes was 6.6 (± 0.21 SE) and 443.98 (± 10.2 SE), respectively. Mean nightly movement (m/hr) of female and male skunks was 184.79 (± 19.6 SE) and 281.26 (± 43.79 SE), respectively. Rate of nightly movements among female skunks did not differ ($P > 0.05$) within season or longitude (Table 8).

We calculated and compared 95% seasonal and annual size of home range of urban skunks based on LoCoH and KDE (LSCV and Href) methods (Table 9). We selected LSCV for further analysis because LoCoH was unable to estimate size of home range for all seasons due to inadequate sample size and because Href appeared to over-smooth our data (Table 9). Mean home range for male skunks was 4.36 km^2 (SE ± 0.79) and 1.79 km^2 (SE ± 0.24) for females. Size of female skunk home range differed within season ($F_{3,28} = 6.01$, $P = 0.003$; Table 8) with the greatest size observed during summer when compared to other seasons. However, female skunk home range did not differ ($P > 0.05$) by longitude (Table 8).

Habitat Selection

Four out of 10 logistic regression models for use-availability had combined weight of at least 90% (Table 10), but top model fit was modest with a null deviance of 2,620.1 and a residual deviance of 2,572.9. In the single, top-ranked model (AIC = 1,288.07.1, 2nd ranked model: ΔAIC = 0.19), use was best explained by distance to water ($\hat{\beta} = -1.90$, SE = 0.29). A unit increase in distance to water was associated with an 85% decrease in the predicted odds of use (OR = 0.15, 95% CI [0.08–0.27]).

Denning Behavior

We located 12 den sites and set up trail cameras at 7 of these locations (3 winter, 4 natal dens; Fig. 4). We did not monitor 5 denning locations due to concerns of camera theft, damage, or lack of property access. All dens were anthropogenically sourced and most were located where skunks burrowed underneath standing structures, like sheds. All three winter den locations yielded evidence of communal denning with other skunks, rabbits (*Sylvilagus floridanus, Lepus* spp.), and a domesticated kitten. We noted a minimum of 3 and maximum of 6 different skunks at a single communal den site. Natal dens were typically occupied by a single female and her litter of kits, though several other species were observed visiting den entrances such as domestic dogs and cats, rabbits, Norway rats (*Rattus norvegicus*), red squirrels (*Tamiasciurus hudsonicus*), woodchucks (*Marmota monax*), and other skunks (Table 11). We did not tally non-target species and it is unclear how many of these animals gained entry to skunk dens.

DISCUSSION

Our research has contributed to understanding factors that have implications for ORV bait placement in urban or peri-urban landscapes while filling gaps in knowledge regarding striped skunk ecology in the Northern Great Plains. Specifically, we collected and analyzed information pertaining to striped skunk home range, nightly movements, habitat selection, and denning behavior, important factors for informing rabies mitigation efforts such as bait placement (Adkins and Stott 1998, Weissinger et al. 2009, Rosatte et al. 2010*b*). While elements of this framework were available in limited urban areas of North America, such as Flagstaff, Arizona (Weissinger et al. 2009) and Toronto, Ontario, Canada (Rosatte et al. 2011), this information was lacking in the Great Plains, where enzootic skunk rabies persists and striped skunks are the most common terrestrial reservoir.

Our capture success rate and sex ratio skewed toward females, and this was comparable to those reported in other striped skunk studies (Verts 1967, Bixler 2004). Female-biased sex ratios are common in populations of striped skunks and were likely driven by strong male biased dispersal during spring months (Bailey 1971, Sergeant et al. 1982, Greenwood et al. 1985, Larivière and Messier 1998*b*). During this time, males have been reported traveling up to 100 km from their original capture site (Sargeant et al. 1982). Though some studies have increased capture success, especially for male skunks, in March and April, the effort to collar male skunks may confound urban spatial ecology or ORV related research if they disperse from the study area and aerial reconnaissance is unavailable (Larivière and Messier 1998*b*).

We lost radio telemetry signals on several collared skunks throughout our study, and while we suspect we lost some to dispersal or vehicle collisions, their ultimate fates are unknown. Project staff made considerable effort to locate missing skunks but were met with little success given time constraints and the unavailability of aircraft with an omnidirectional VHF antenna. We opportunistically surveyed for road killed skunks for evidence of radio collars and ear tags, but this method was unsuccessful in locating missing collared animals.

Of the three home range estimators, we selected LSCV for analysis of size of home range because insufficient telemetry fixes precluded use of LoCoH and because Href appeared to overestimate size of home ranges, in some cases, predicting areas of over 20 km^2. We recognize that the use of MCP as a home range boundary is controversial, but it is still widely used for this purpose, and we include these estimates to compare to previous studies and because of our desire to use MCP for habitat selection analysis. In general, urban skunk studies reported size of home ranges notably smaller than the overall mean size of home ranges for males (2.68 km^2) and females (1.04 km^2) in our study. For example, MCP estimates of urban striped skunks in Scarborough, Canada averaged 0.51 km^2 (Rosatte et al. 1991) and those from metropolitan Toronto, Canada averaged 0.5 km^2 for males and 0.3 km^2 for females (Rosatte et al. 2011). Reported size of home range using LSCV for urban striped skunks in Flagstaff, Arizona were 1.3 km^2 for males and 1.1 km^2 for females (Weissinger et al. 2009). Conversely, rural skunk studies reported size of home ranges larger than their conspecifics in urban areas, and this is common among mesocarnivores in general (Bozek et al. 2007, Šálek et al. 2015). For example, size of home range using MCP for rural skunks have been reported as 2.9 km^2 for males and 2.5 km^2 for females (Rosatte and Gunson 1984); 5.0 km^2 for males and 3.7 km^2 for females (Storm and Verts 1966); and as high as 11.63 km^2 for males and 3.74 km^2 for females (Larivière and Messier 1998*b*). Average male skunk size of home range in our study was nearly double that of females similar to previous research on both urban and rural skunks (Storm and Verts 1966, Larivière and Messier 1998*b*, Weissinger et al 2009, Rosatte et al. 2011).

We reported size of home range differing by season in our study. Size of home range was largest in summer 2017 (3.18 km^2) and smallest in the fall of 2016 (0.94 km^2), which conflicts with Rosatte et al. (2011) in which skunks were reported to have larger home range during the fall months and did not differ between summer or spring. Larivière and Messier (1998*b*) reported no difference in size of home range across seasons, including the winter months. Weissinger et al. (2009) reported larger size of home range March–August (1.3 km^2 for males, 1.1 km^2 for females) than September–February (0.7 km^2 for males, 0.4 km^2 for females), but direct comparisons to this study are difficult as the report categorizes seasons more broadly. Size of home range in our study was smaller in spring (1.58 km^2) in comparison to summer which is to be expected as females were raising young and may have had reduced movement (Verts 1967). Based on photographic evidence, kits emerged from den sites in early June and literature suggests that weaning will occur by late-July, allowing females to travel greater distances with their kits (Allen 1939, Rosatte et al. 2010*a*). However, it was surprising that home ranges in Fall 2016 were approximately half the size of those in Fall 2017. We note a larger sample size in Fall 2017 when compared to Fall 2016, but otherwise are unclear why this difference occurred.

Overall, size of home range estimates in our urban study area were consistent with those reported for rural areas, and we suspect this is because most of our study skunks were trapped and tracked near the periphery of city limits, a reflection of our inability to capture a larger sample of skunks in the city's interior. We hypothesize that these skunks living in the city's peri-urban areas may be attempting to transition from rural to urban areas. Anecdotal evidence from city animal control officers suggest that striped skunks are generally unwelcome within the city, and if found, are quickly dispatched or relocated outside of city limits. However, translocation of skunks is illegal in North Dakota without a joint permit from the State Board of Animal Health and North Dakota Game and Fish Department, and it is unknown whether these activities, if occurring, could potentially slow the process of immigration into the city. Alternatively, striped skunks may simply prefer peripheral urban habitat in the Northern Great Plains.

Rates of nightly movement within our study did not differ between seasons but were highest during the summer months, however, a small sample size of male skunks precluded comparisons with other studies. For example, Weissinger et al. (2009) found that nightly rate of travel did not vary across sexes but did find variance across seasons in that summer (May–July) movements were greater than those in fall (August–October) and winter (November–February). The average rate of nightly movement in our study was double (200 m/hr) that of Weissinger et al. (2009; 100 m/hr). Skunks crossing from urban to rural areas, as reported by our study and Weissinger et al. (2009), have the potential to transport diseases into highly populated areas. In contrast, Rosatte et al. (2011) concluded that, based on average nightly travel distances, urban skunks in Scarborough, Ontario, Canada traveled more during September and October than in March and November, not including the winter months. A paucity of urban skunk nightly movement studies precludes further comparisons. Evidence of decreased mobility rates during the spring and fall months in this study may indicate smaller containments areas, which could decrease cost and increase effectiveness of rabies management tactics (Rosatte et al. 1997).

We found no evidence that home range size or nightly movements of female skunks differed by longitude when separating skunks by eastern and western halves of the city. We may have expected that bounding effects of the Red River which divides Grand Forks, North Dakota from East Grand Forks, Minnesota would reduce home range size or possibly nightly movement when compared to unbounded western city skunks. While limited evidence suggests that rivers may act as barriers for gene flow within the south central skunk variant of rabies (Barton et al. 2010), it remains unclear to what extent rivers act as physical barriers for striped skunks within our study area. We may have also expected variation by longitude due to differing habitat types within Grand Forks, especially near the extreme eastern and western boundaries. Thus, it also remains unknown why home ranges were similar throughout our study area.

We also found no evidence that use of habitat by female skunks was associated with habitat type, which was contrary to our prediction. Supporting literature suggests that industrial areas were considered “hubs” for subpopulations of urban skunks (Broadfoot and Rosatte 2001). The industrial habitat in our study area contained edge habitat, and we assume these areas were abundant in arthropods and small mammals, the preferred food types of striped skunks (Verts 1967, Greenwood et al. 1999, Seabloom 2011). Buildings, equipment, and other structures provide cover, long-term denning opportunities and, unlike residential areas, are often abandoned during nighttime when skunks are most active. As resource selection is driven by available food and cover and may change depending on region, crop type, insecticide use, and type of cover nearby, the avoidance of agricultural/field habitat is inconsistent throughout the literature. For example, Rosatte et al. (2011) reported that urban skunks were found in field and residential habitats more frequently than all other habitat types, especially industrial areas. Conversely, other studies suggest avoidance for cropland habitat (Larivière and Messier 2000, Castillo et al. 2012) or no general selection of habitat type (Wade-Smith and Verts 1982, Bixler and Gittleman 2000). Given inconsistencies in skunk habitat selection among geographical areas, ORV efforts for targeting vaccine baits to specific areas may be confounded unless specific habitat selection studies occur prior to management efforts. Should no differences in habitat use be discerned, ORV managers may consider other available evidence prior to management efforts. For example, although we found no statistical evidence that skunks selected industrial areas, it was clear that these areas were the most productive for catching skunks. Therefore, targeting these areas for ORV efforts would appear warranted within our study area.

To our knowledge, this study is the first to investigate resource selection in skunks beyond habitat type as we incorporated road density, distance to road, and water as additional factors. The model indicated that skunk locations were more likely to be closer to water bodies in comparison to randomly generated points within our MCP boundaries. We found that skunks were more likely to be closer to water bodies perhaps because areas near water are an important source of food and water (Phillips et al. 2003). ORV efforts may be enhanced by targeting these areas for bait placement. Road covariates were not associated with land use. However, we treated roads as a homogenous landscape feature given that incomplete available data precluded differentiating roads within our study area based on degree of use, width, and speed limits. The majority of our skunks were generally found near roads with minimal nighttime traffic and speed limits ranging from 40mph to 65 mph.

Our pilot efforts on skunk denning suggested that VHF radio telemetry signals were poor to nonexistent when skunks entered certain types of dens and, thus, presented a challenge in data collection and precluded meaningful conclusions about denning behavior beyond simple observations. However, we verified communal denning in all three of the winter denning sites and, in some cases, denning with other species. We note that long North Dakota winters offer skunks extreme wind and some of the coldest temperatures in the U.S. (Chiu et al. 2014), so we suspect that communal denning behavior remains important for some skunks given these conditions. However, we note that communal denning also occurs in lower latitudes (Theimer et al. 2016). Based on photographic evidence, both collared and un-collared skunks emerged occasionally from the winter communal dens throughout December–March, but we did not attempt to identify sex or identity. We presume that some interactions during February and early March were reproductive related (Verts 1967, Wade-Smith and Richmond 1978). However, it remains unknown how these conditions may affect rabies spread within this region.

MANAGEMENT IMPLICATIONS

Our study provides a better understanding of the spatial ecology of urban skunks and provides the first evaluation of habitat selection by skunks in an urban area of the agricultural Midwest. This information will allow managers to better focus efforts on areas more likely to be used by skunks for ORV bait distribution in urban areas. Our data indicated that urban ORV bait distribution may best be suited near water, however, we remind the reader of the difficulties we experienced obtaining sufficient sample sizes for some of our sampled skunks. Future studies may benefit from GPS collars to increase sample size and movement data in and around urban areas to further refine bait placement. Considering the differences in habitat selection studies on urban skunks, it appears that ORV baiting programs are not “one-size-fits-all” and a framework for bait placement would be most successful if applied differently depending geographical area.

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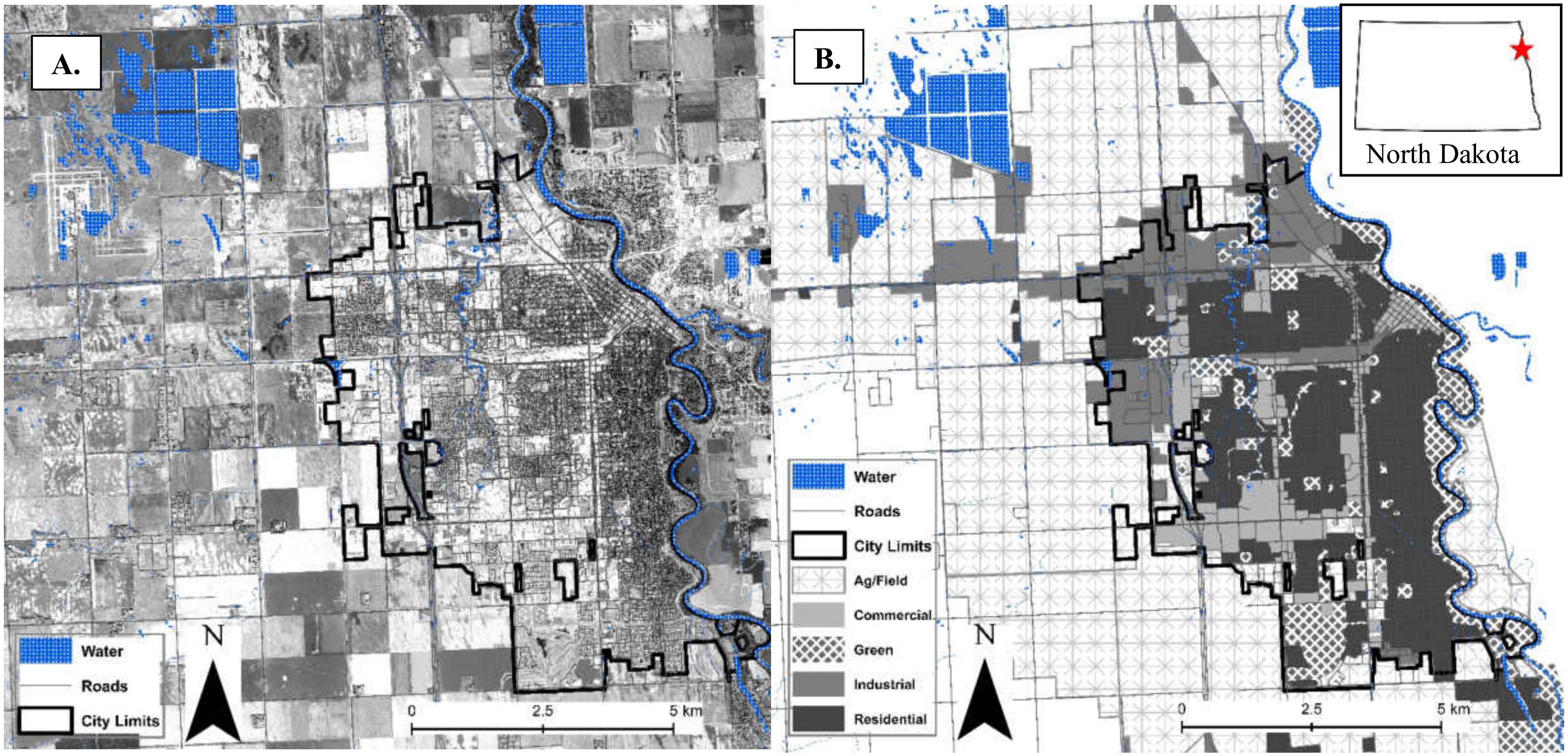

Figure 1. Study area maps depicting aerial photo (A) and available land cover classifications (B) within Grand Forks, North Dakota, USA, 2016–2017.

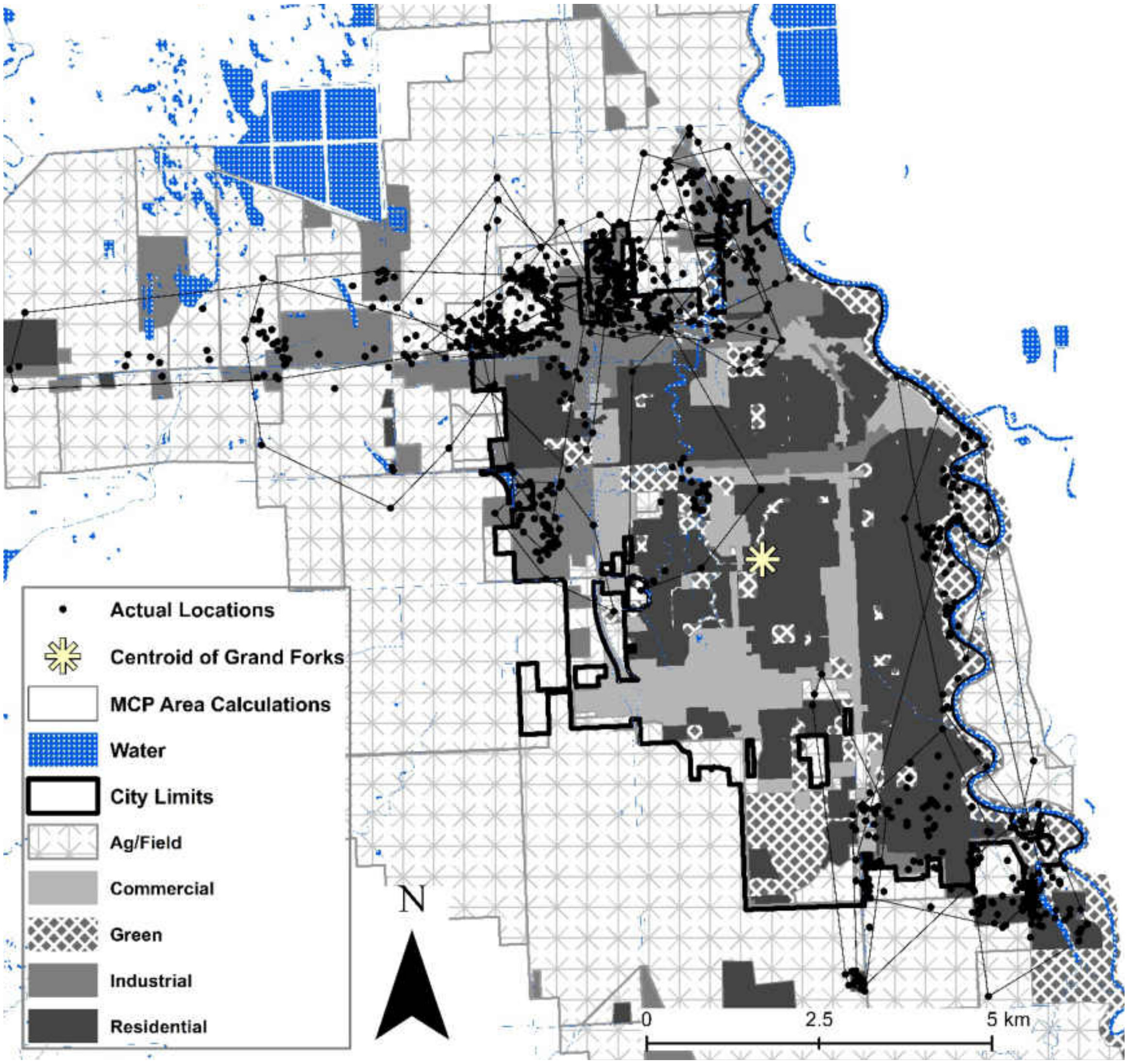

Figure 2: Data used to assess habitat selection, including telemetry locations and minimum convex polygon (MCP) boundaries used by striped skunks (*Mephitis mephitis*), along with water and habitat types available in Grand Forks, North Dakota, USA, 2016–2017.

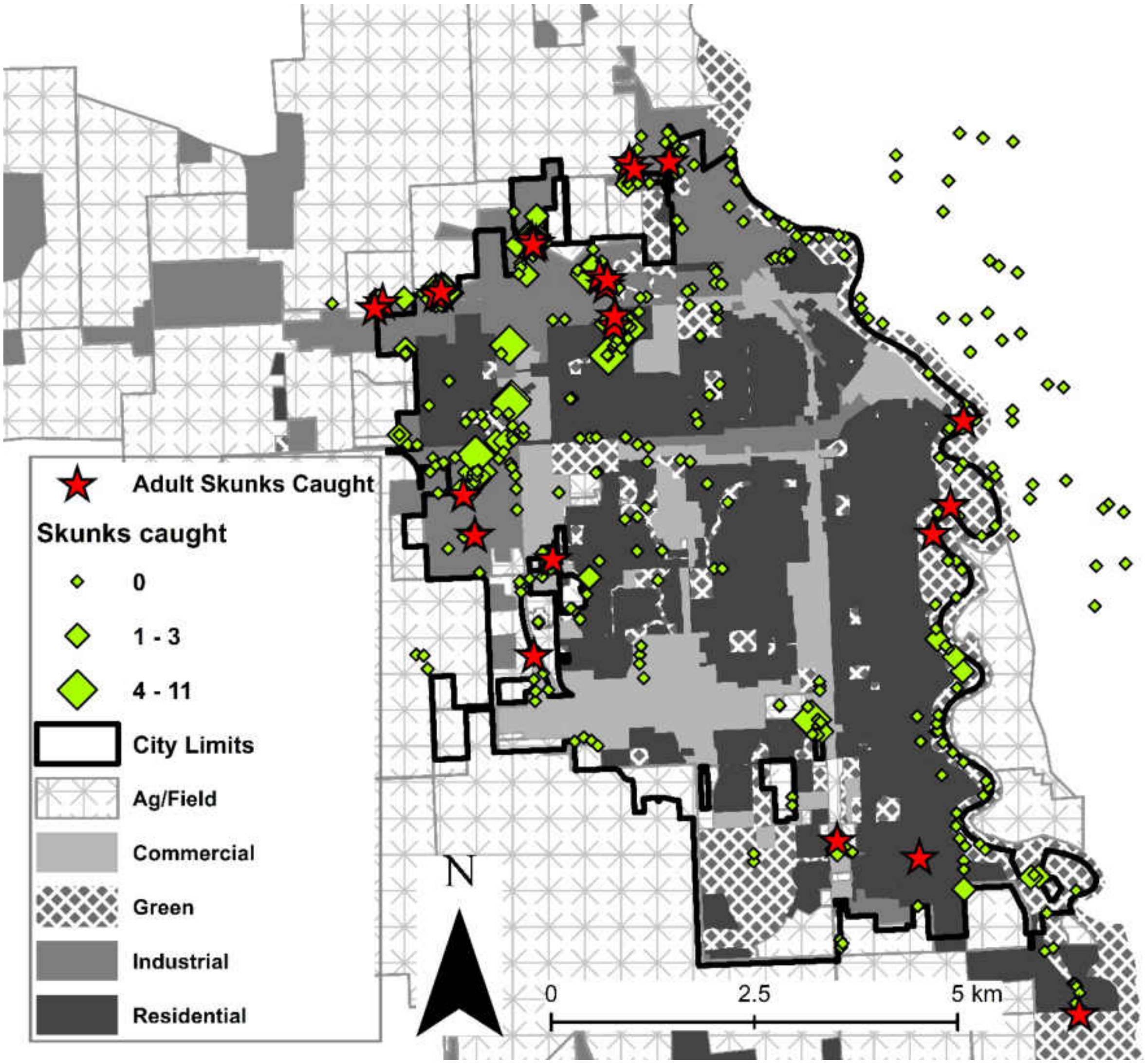

Figure 3. Trapping success of urban striped skunks (*Mephitis mephitis*) displayed visually by habitat type. Trap locations with associated capture success (green diamonds) and red stars indicate locations of adult striped skunks fitted with radio collars. Trapping was conducted from June–August 2016 and May–August 2017 in Grand Forks, North Dakota, and East Grand Forks, Minnesota, USA, 2016–2017.

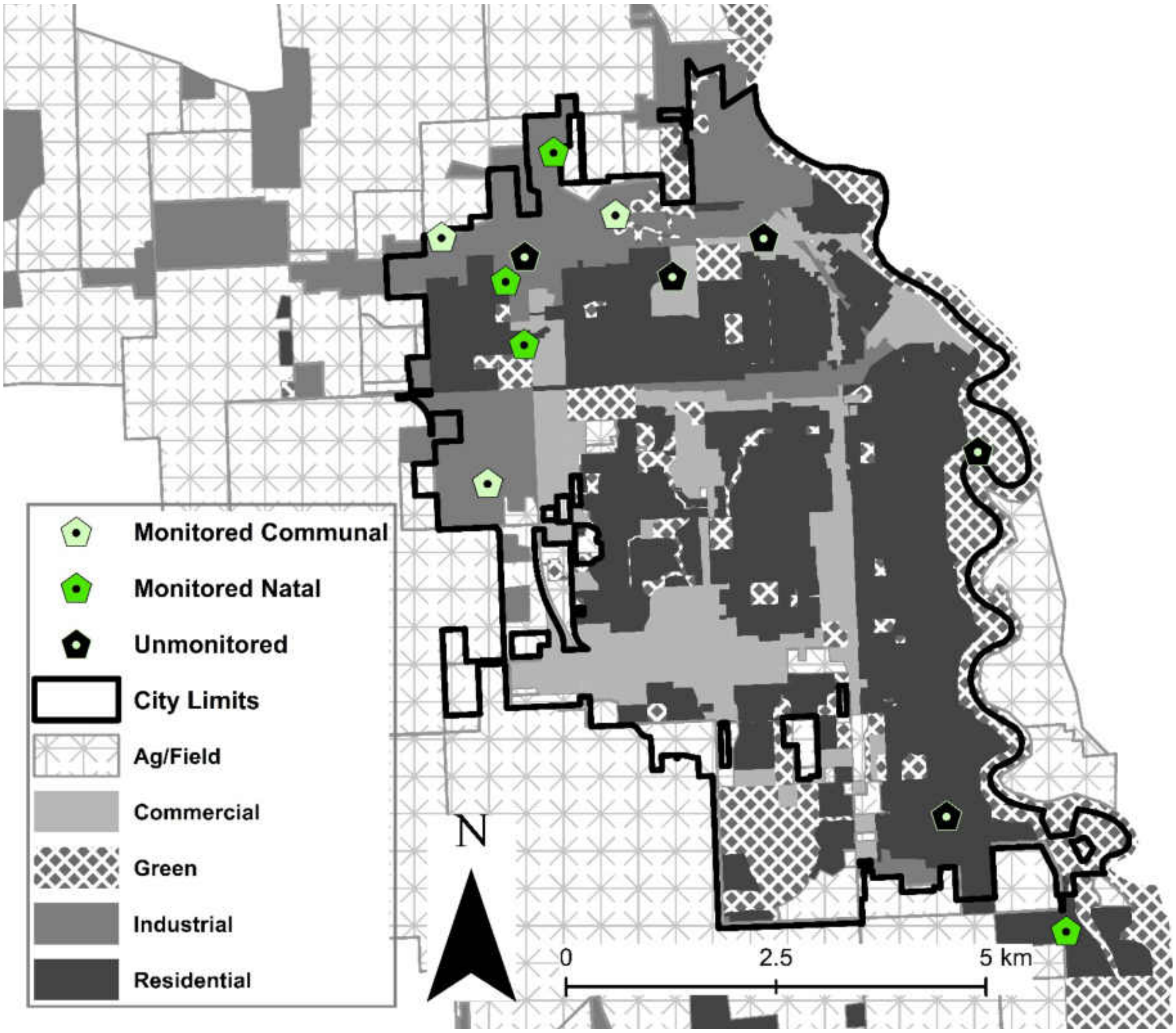

Figure 4. Denning locations of urban striped skunks (*Mephitis mephitis*) displayed visually by habitat type. Reconyx HyperFire HC600 trail cameras were placed near the entrances of monitored denning sites (red and blue) in Grand Forks, North Dakota, and East Grand Forks, Minnesota, USA, 2016–2017.

Table 4. Trapping success of urban striped skunks (*Mephitis mephitis*). Trapping was conducted from June–August 2016 and May–August 2017 in Grand Forks, North Dakota, and East Grand Forks, MN, USA, 2016–2017.

	Grand Forks, ND		East Grand Forks, MN	Total
Year	2016	2017	2017	
Trap Nights[a]	1,744	1,128	198	3,070
Adult Captures	15 (3M, 12F)	14 (3M, 11F)	0	29 (6M, 23F)
Recaptured Collared Adults	10	6	0	16
Skunk kits	59	36	0	95
Total skunks[b]	84	56	0	138
Capture rate[c]	0.86	1.24	0.00	0.94

[a] a single trap set for a single night
[b] sum of adult captures, recaptured collared adults, and skunk kits
[c]number of adult skunks captured per 100 trap nights

Table 5. Trapping success of urban striped skunks (*Mephitis mephitis*) described by habitat type. Sample sizes are listed in parentheses. Trapping was conducted from June–August 2016 and May–August 2017 in Grand Forks, North Dakota, USA, 2016–2017.

	Habitat type				
	Green	Residential	Industrial	Commercial	Ag/Field
Percentage of Trap Locations (*n* = #)	18% (75)	26% (106)	38% (156)	9% (38)	8% (31)
Percentage of Habitat	14%	39%	14%	19%	13%
Skunks Caught	9	38	78	2	10
Adult Skunks Caught	3	5	18	1	2
Trap nights[a]	492	694	1220	236	230
Capture rate[b]	0.61	0.72	1.5	0.42	0.87

[a] a single trap set for a single night
[b] number of adult skunks captured per 100 trap nights

Table 6. Seasonal (≥5 telemetry fixes/night) nightly movement estimates (meters/hour) for individual urban striped skunks (*Mephitis mephitis*), Grand Forks, North Dakota, USA, 2016–2017.

		Season			
Skunk ID	Location	Fall 2016	Spring 2017	Summer 2017	Fall 2017
32 [a]	W			252.53	
41 [a]	W			73.91, 253.48	
51	W			296.59	
62 [a]	W			261.59, 256.3	265.13
82	E		298.09	244.67	412.71, 92.49
100	E				53.46, 144.71
111	W	224.22			[b]
122	W	195.35	344.97, 75.75	510.26, 216.43, 270.52	
162	W				124.13, 129.97
171	E			528.27, 350.88	
181	W	150.64, 97.73	116.59, 20.08	241.38	
214	W	37.89, 58.51	[b]		
223 [a]	W	[b]	509.95	377.18	[b]
230	W		109.27, 80.54	108.45, 101.89	
241	W			253.2	131.2
263	W	152.76, 37.91	70.56, 193.1, 397.81	[c]	
281	W				189.06, 101.19
293	W			202.6, 190.95	
302	E		179.18	25.06	
Mean		119.38	199.66	250.81	164.41
SE		27.22	44.41	28.32	33.03

[a] male skunks
[b] lost telemetry signal
[c] mortality

Table 7. Seasonal (≥15 telemetry fixes/season) and annual (≥30 telemetry fixes) 95% isopleths for size of home range (km^2) by least squared cross validation (LSCV) estimator for individual urban striped skunks (*Mephitis mephitis*), Grand Forks, North Dakota, USA, 2016–2017.

		Season				
Skunk ID	Location	Fall 2016	Spring 2017	Summer 2017	Fall 2017	Annual
12	W			3.11	2.70	2.59
32[a]	W				3.65	
41[a]	W			5.91	4.58	6.35
51	W			2.75	2.06	1.01
62[a]	E			2.51	3.31	4.18
82	E	1.69	1.11	2.25	6.51	2.71
100	E			1.49	0.68	1.48
111	W	1.34	0.73	2.45	[b]	1.00
122	W	1.36	0.43	5.79	1.03	1.31
140	W			4.69	0.50	2.63
162	W				2.27	
171	E			2.90	0.76	1.07
181	W	0.22	0.22	0.92	0.70	0.69
202	W	2.41	1.59	[c]		2.42
214	W	0.12	[b]			
223[a]	W	[b]	2.38	8.17	[b]	6.00
230	W	0.17	0.16	1.74	0.53	0.90
241	W				1.77	2.46
263	W	0.21	6.01	[c]		1.74
281	W				2.05	
293	W			1.82	0.45	0.93
302	E			1.20	2.38	2.00
Mean		0.94	1.58	3.18	2.11	2.3
SE		0.31	0.69	0.53	0.41	0.39

[a] male skunks
[b] lost telemetry signal
[c] mortality

Table 8. General linear mixed effects analysis discerning differences in female striped skunk (*Mephitis mephitis*) nightly movements and size of home range using LSCV by season and longitude from City of Grand Forks centroid, North Dakota, USA, 2016–2017. (A) degrees of freedom, F-value, and *P*-values from analysis of season on $\log_{10}$ transformed nightly movements (m) and size of home range (km^2) followed by (B) comparison of back-transformed least-squares means and confidence intervals.

		Nightly Movements			Home Range		
(A)	Fixed Effects	df	F	*P*	df	F	*P*
	Season	3,34	1.84	0.16	3,28	6.01	0.003
	Longitude	1,14	0.06	0.81	1,16	0.03	0.86
(B)	Treatments	Mean	Lower	Upper	Mean	Lower	Upper
	Season						
	Fall 2016	92.07	47.26	179.38	0.55[a]	0.27	1.11
	Spring 2017	138.13	83.31	229.01	0.70[ac]	0.34	1.46
	Summer 2017	204.63	130.61	320.58	2.46[bc]	1.41	4.31
	Fall 2017	130.05	75.62	223.67	1.36[cb]	0.79	2.32
	Longitude						
	East	141.01	78.70	252.66	1.10	0.50	2.42
	West	130.47	93.13	182.78	1.03	0.67	1.56

[a–c] Means with contrasting letter (within a column) indicate contrasting means within sex or season ($P < 0.05$).

Table 9. Seasonal and annual means for 95% isopleths for size of home range (km^2) by estimator (Least Squares Cross Validation [LSCV], Local Convex Hull [LoCoH], H reference [Href]) and a boundary estimator (100% minimum convex polygon [MCP]) for habitat selection analysis in urban striped skunks (*Mephitis mephitis*), North Dakota, USA, 2016–2017.

	Fall 2016 (*n* = 8)		Spring 2017 (*n* = 8)		Summer 2017 (*n* = 15)		Fall 2017 (*n* = 17)		Annual (*n* = 18)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
LSCV	0.94	0.29	1.58	0.69	3.18	0.53	2.11	0.41	2.30	0.34
LoCoH	0.66	0.13	N/A	N/A	1.51	0.27	N/A	N/A	2.05	0.37
Href	2.78	0.52	6.70	1.67	10.34	2.40	5.49	1.19	9.86	2.28
MCP	1.11	0.19	1.43	0.41	2.67	0.51	1.36	0.27	4.05	0.56

Table 10. Binary logistic regression models for effects of habitat type, distance to road, distance to water resource, and road density on habitat use by female striped skunks (*Mephitis mephitis*) in Grand Forks, North Dakota, USA from pooled radio telemetry locations collected during 2016–2017. Model rank, variables, number of estimable parameters (*K*), log-likelihood (log [L]), Akaike's Information Criterion (AIC_c), ΔAIC_c, and Akaike weights (ω_i) for 10 logistic regression models.

Rank	Model Variables	*K*	Log (L)	AIC_c	ΔAIC_c	ω_i
1	Water distance[a], skunk ID[b]	3	-1,288.07	2,582.2	0.00	0.341
2	Road density[c], water distance, skunk ID	4	-1,287.16	2,582.3	0.19	0.310
3	Road density, road distance[d], water distance, skunk ID	5	-1,286.80	2,583.6	1.47	0.163
4	Water distance, habitat type, skunk ID	6	-1,286.44	2,584.9	2.78	0.085
5	Road density, water distance, habitat type, skunk ID	7	-1,286.02	2,586.1	3.95	0.047
6	Road distance, water distance, habitat type, skunk ID	7	-1,286.31	2,586.7	4.52	0.036

7[e]	Road density, road distance, water distance, habitat type, skunk ID	8	-1,285.94	2,588.0	5.81	0.019
8	Habitat type, skunk ID	5	-1,305.84	2,621.7	39.56	0.000
9	Road density, skunk ID	3	-1,307.92	2,621.9	39.71	0.000
10[f]	Skunk ID	2	-1,310.05	2,624.1	41.95	0.000

[a] Distance of skunk location to nearest water resource

[b] Individual skunks (random effect)

[c] Road density per km^2 at skunk location

[d] Distance of skunk location to nearest road

[e] Global model

[f] Random intercept only model

Table 11. Characteristics of striped skunk (*Mephitis mephitis*) den sites monitored by trail cameras and the animals that visited them, North Dakota, USA, 2016–2017.

Habitat Type	Skunk ID	Den Structure	Natal[a]/ Winter[b]	Wildlife present	Domestic animals present	Animals at site simultaneously[c]
Residential	263	Shed	Natal	Red squirrel, American robin	>1 Cat	Skunk, cat
Residential	82	Shed	Natal	Red squirrel, cottontail, mice, robin, raccoon	Cat	Cat
Industrial	181, 230	Dock	Winter	Woodchuck, mice, cottontail	>1 Cat	Skunk, cat
Green	263, 111,	Wood pile	Winter	Cottontail, Norway rat, red squirrel,	>1 Cat	Skunk
Industrial	214	Concrete slab	Winter	Cottontail, white-tailed jackrabbit,	None	Skunk, rabbit
Residential	-	Shed	Natal	Raccoon, mink	>1 Cat	Skunk, raccoon, cat
Industrial	181	Shed	Natal	Cottontail, woodchuck	>1 Cat, >1 Dogs	Skunk, cat, woodchuck

[a] Natal dens had females with kits.

[b] All winter dens had multiple adult skunks denning together (communal denning).

[c] Indicates instances when multiple animals were either captured in the same photograph (<2 m from each other) or photographed within 5 min of each other.

Table 12. A review of North American home range sizes for adult striped skunks (*Mephitis mephitis*), including authors and year study was published, location, habitat type (urban vs. rural), estimator type, home range by sex, and overall home range. Sample sizes in parentheses.

Study	Location	Rural or Urban	Home Range Estimation Method	Male	Female	Overall
Shirer and Fitch 1970	Northeastern KS	Rural	MCP	0.12 (1)	0.18, 0.37 (2)	0.22 (3)
Bailey 1971	Northwestern OH	Rural	MCP	0.31 (5)		
Storm 1972	Northwestern IL	Rural	MCP	5.06 (2)	3.74 (5)	2.84 (7)
Greenwood et al. 1997	Stutsman County, ND	Rural	MCP	2.8 (8)	1.2 (9)	1.6 (17)
Goldsmith 1981	Northeastern TN	Rural	MCP	0.16 (5)	0.24 (9)	0.21 (14)
Rosatte and Gunson 1984	Southern Alberta	Rural	MCP	2.9 (14)	2.5 (14)	2.7 (28)
Greenwood et al. 1985	Griggs County, ND	Rural	MCP	3.08 (15)	2.42 (24)	2.67 (39)
Rosatte 1986	metropolitan Toronto	Urban	MCP	0.83 (4)	0.51 (5)	0.65 (9)
Rosatte et al. 1991	metropolitan Toronto	Urban	MCP			0.51 (57)
Larivière and Messier 1998*b*	Southcentral Saskatchewan	Rural	KDE/MCP	12.06/ 11.63 (5)	4.31/3.74 (21)	5.80/5.26 (26)
Bixler and Gittleman 2000	Blount County, Tennessee	Rural	MCP	1.20 (9)	0.88 (6)	1.08 (15)
Larivière and Messier 2001	Prairie Pothole Region of SC Saskatchewan	Rural	MCP		2.3 (5)	
Rosatte and Larivière 2003	Southern Ontario	Rural	MCP			1.0-3.0
Ruffino 2008	Houston, TX	Urban	MCP	2.55 (5)	1.26 (15)	1.58 (20)
Weissinger et al. 2009	Flagstaff, AZ	Urban	KDE	1.3; 0.7 (19)	1.1 ; 0.4 (21)	0.87 (40)
Rosatte et al. 2011*a*	Scarborough, Ontario, Canada	Urban	MCP	0.5 (4)	0.3 (3)	0.9 (7)
This Study (Schneider 2018)	Grand Forks, ND	Urban	KDE/MCP	4.36 /7.94 (3)	1.79/3.27 (15)	2.22/4.05 (18)