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# NIGHTLY AND SEASONAL MOVEMENTS, SEASONAL HOME RANGE, AND FOCAL LOCATION PHOTO-MONITORING OF URBAN STRIPED SKUNKS (*MEPHITIS MEPHITIS*): IMPLICATIONS FOR RABIES TRANSMISSION

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**ABSTRACT:** We followed radio-collared striped skunks (*Mephitis mephitis*) from January 2004–December 2005 in two urban areas of Flagstaff, Arizona, USA to determine seasonal patterns of movement and home-range size. We also used automated cameras to determine the potential for inter- and intraspecific interaction at skunks' diurnal resting sites and nocturnal focal locations. We found no difference between sexes in nightly rates of travel or in size of seasonal home range. Nightly rates of travel were greatest in the postbreeding months (May–July) and smallest from November to February, consistent with larger home ranges (95% kernel estimates) from March–August and smaller home ranges from September–February. Sixty-three percent of monitored males and 38% of monitored females crossed the urban–wildland interface, in at least one direction on at least one night, and some remained outside the urban area for days or weeks, indicating that skunks could act as vectors of disease across the urban–wildland interface. We recorded co-occurrence of skunks with domestic cats (*Felis domesticus*), raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), and other skunks at focal locations and diurnal retreats used by skunks, suggesting these areas are potential sites for both inter- and intraspecific rabies transmission and could be targeted by wildlife managers during trapping or vaccination programs.

**Key words:** *Mephitis mephitis*, photo-monitoring, rabies, radio telemetry, spillover, striped skunk, urban.

## INTRODUCTION

Wildlife species are currently the primary rabies reservoirs in the United States, with over 90% of all rabies cases from 2000–2005 occurring principally in raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), and some insectivorous bats (Blanton et al., 2006). Nearly one-third of all US rabies cases from 2000 to 2005 occurred in skunks (Blanton et al., 2006), in part due to spillover infections during epizootics (Guerra et al., 2003). Most cases of rabies in skunks in Arizona occur in the southern and south-eastern area of the state (Krebs et al., 2005), and the skunks are infected with the south-central skunk rabies virus variant (Hass and Drago, 2006). However, a spillover event was documented in 2001 when intraspecific rabies transmission of a

variant commonly associated with an insectivorous bat (*Eptesicus fuscus*) was spread, and temporally maintained, in the striped skunk population in Flagstaff, an urban area in northern Arizona, USA (Krebs et al., 2002; Engeman et al., 2003; Leslie et al., 2006). Between September 2004 and September 2005, an additional six skunks, one gray fox, and one domestic cat (*Felis domesticus*) were confirmed infected by the same bat strain in the Flagstaff area (Leslie et al., 2006).

Although landscape patterns of rabies spread have been successfully modeled using relatively coarse population and geographic data (e.g. Broadfoot et al., 2001; Smith et al., 2002; Russell et al., 2004), understanding the dynamics at smaller spatial scales often requires more-specific knowledge of host behavior (MacDonald and Voigt, 1985). Movement patterns, areas of use, and population

density of host species can interact to alter contact rates and the probability of disease transmission (White et al., 1995; Totton et al., 2002), but these factors are often unknown or must be assumed to be the same as that previously documented in other geographic areas. For example, skunk movements, home-range estimates, and denning ecology are better documented for rural areas in the mid-western United States (e.g., Shirer and Fitch, 1970; Weller and Pelton, 1987; Greenwood et al., 1997) and in parts of southern Canada (e.g., Rosatte and Gunson, 1984). Much less is known about skunks in urban areas (Rosatte et al., 1990; 1991; 2001) and other regions, such as the southwestern US, where skunks act either as reservoirs for the rabies virus or as rabies vectors during spillover events (Gordon et al., 2004; Guerra et al., 2003; Krebs et al., 2005).

Our study was designed so we could better understand the movements and seasonal home ranges of skunks in Flagstaff, Arizona, USA, a moderately sized city representative of many in the western US and Canada that are set within a matrix of relatively wild land with extensive areas of urban–suburban–wildland interface. Studies of red foxes (*Vulpes vulpes*) and gray foxes have suggested that animals use urban and wildland areas for different activities, foraging in one and sheltering in the other, thereby potentially varying the pattern of disease transmission across the urban–wildland interface (Harrison, 1997; Saunders et al., 1997). In addition, seasonal differences in activity and movement could also alter the likelihood of disease transmission (Gremillion-Smith and Woolf, 1988; Altizer et al., 2006). Therefore, we used radio telemetry to determine seasonal patterns of skunk movement and home-range size so we could better understand the potential for disease spread in the urban areas of Flagstaff. Because urban areas often harbor multiple animal species that could act as carriers of rabies through spillover infections during epizootics (Guerra et al., 2003; Gordon et

al., 2004), we also used photo-monitoring of selected focal sites to assess the potential for contact between individual skunks and between skunks and domestic and other wild animal species that could potentially contract the disease.

## MATERIALS AND METHODS

### Study area

Flagstaff, Arizona, USA (35°11'N, 111°39'W) is a city with a human population of approximately 60,000, roughly 1,600 ha in size, surrounded by extensive ponderosa pine (*Pinus ponderosa*) forest in the transition zone (1,981–2,438 m elev.) between the Upper-Sonoran and Canadian zones in northern Arizona (Epple and Epple, 1995). The high elevation creates a seasonal climate, with the roughly 56 cm of annual precipitation falling primarily as winter snow and summer monsoonal rains. We focused on two areas of Flagstaff's urban matrix, a 5.6-km<sup>2</sup> area in the eastern portion of the city and a 5.5-km<sup>2</sup> area in the western portion of the city. Each area was primarily residential, with some commercial development, and was bounded by public open space and greenbelt connectivity corridors within the city's corporate boundary.

### Trapping and radio collaring

We live-trapped and radio-collared (Telemetry Solutions VHF radio collars, Concord, California, USA) skunks during winter 2003–2004 and continued trapping and collaring opportunistically for the next 1.5 yr to maintain approximately twenty active radio collars on skunks throughout the 2-yr study. We set live-traps (Tomahawk Live Trap Models 106 and 108, Tomahawk, Wisconsin, USA) baited with sardines, peanut butter, or both along presumed skunk travel corridors (alleys and culverts) and near structures reported by local residents to be used by skunks. Traps were set in the evenings and checked and closed the following morning (Larivière and Messier, 1996; Rosatte et al., 2001). All nontarget domestic and wild animals were released on-site unharmed. Captured skunks were injected intramuscularly with a 5:1 mixture of ketamine HCL (100 mg/ml; Fort Dodge Laboratories, Fort Dodge, Iowa, USA) and xylazine HCL (100 mg/ml; Mobey Corporation, Animal Health Division, Shawnee, Kansas, USA). Skunks received approximately 0.7 ml (15 mg/kg skunk body weight) of chemical immobilization agent, which provided approximately 20–30 min of surgical-level anesthesia.

Immobilized, skunks were fitted with a uniquely tuned radio collar and a uniquely numbered, self-piercing, 1×3 mm nickel–copper ear tag (#1005-1, National Band and Tag Company, Newport, Kentucky, USA) in each ear.

### Radio tracking

We located radio-collared animals with an ATS model R3000 radio receiver (Advanced Telemetry Solutions, Isanti, Minnesota, USA) and an omnidirectional, vehicle-mounted whip antennae and handheld, directional, 3-element Yagi antenna (Advanced Telemetry Solutions). We determined the skunks' urban locations by homing-in and used triangulation when skunks had traveled into the surrounding nonurban areas. We determined three to six locations per night on 2–3 nights per week from 6 January 2004 through 22 March 2005, and once per night (randomized either early in the tracking period [6:00 PM–11:00 PM] during the middle night hours [11:00 PM–1:00 AM], or late in the tracking period [1:00 AM–7:00 AM]) from 22 March 2005 to 16 December 2005.

### Nightly and seasonal movements

Between 6 January 2004 and 22 March 2005, we analyzed 2,890 locations for 21 female and 19 male skunks at roughly 2-hr intervals during the night to obtain three to six positions per night. We used ArcView 3.3 (ESRI, Redlands, California, USA) and the Animal Movement (Hooge and Eichenlaub, 2000) and X-tools extensions to determine the straight-line distance between consecutive-position fixes within a night for each skunk. We calculated a rate of travel for each movement by dividing the distance between successive position fixes by the elapsed time and then averaged these across all movements for a given skunk within a night (two to five movements) to obtain a mean nightly rate of travel. We tested whether mean nightly rates of travel differed across season or between sexes using an analysis of variance (ANOVA) followed by Tukey's HSD post hoc tests. We hypothesized that movements would differ among four major portions of the annual cycle: 1) a breeding period from March through April; 2) a postbreeding and parturition period from May through July; 3) a rearing, weaning, and dispersal period from August through October; and 4) an overwintering period characterized by reduced movements with the onset of lower temperatures and accumulated snowfall from November through February (Schowalter and Gunson, 1982; Pybus, 1988; Rosatte et al., 1991). Statistical analyses were calculated with JMP®

Statistical Software (SAS, Cary, North Carolina, USA).

### Seasonal home range

We used all locations ( $n=2,218$ ) collected between 6 January 2004 and 15 December 2005 to determine 95% kernel estimates (using least squares cross-validation to determine the smoothing factor  $h$ ) of home-range size using ArcView 3.3 and the Animal Movement and X-tools extensions and Animal Movement and Hawth's Tools extensions with ArcGIS 9.0 (ESRI) (Hooge and Eichenlaub, 2000, Rodgers et al., 2005). We calculated kernel estimates over two 6-mo time periods to obtain an estimate for spring–summer and fall–winter home range sizes (spring–summer=March–August; fall–winter=September–February) and compared those kernel estimates using ANOVA. Home-range size reached an asymptote at roughly 25 locations. To control for the potential that variation among individuals could confound our seasonal comparisons, only individuals with  $\geq 25$  locations in both time periods (eight males and 10 females) were used for these analyses. Unfortunately, this restriction precluded us from comparing all four seasons, as we were able to do for seasonal rates of movement, and we instead compared the period of relatively high rates of movement (late spring, summer, early fall) to the period of low rates of movement (late fall, winter, early spring).

### Photo-monitoring

To assess potential for inter- and intraspecific contact, we set automated 35 mm and digital cameras triggered by Trailmaster Models 500 and 1500 passive infrared detectors (Goodson & Associates, Lenexa, Kansas, USA) at 21 known diurnal retreats and nocturnal focal locations determined from the radio-tracking of animals during this study. Cameras were placed opportunistically at each site for a total of 5–12 days. Sites were monitored in autumn 2004 and spring, summer, and autumn 2005. Diurnal retreats were below-ground locations used by skunks for cover during the day. These sites included locations such as decks, outbuildings, crawlspaces, and rock piles. Radio-collared skunks were repeatedly located at these sites during both regular nocturnal tracking sessions and diurnal position fixes. Focal locations were above-ground areas with resources that skunks were documented utilizing during nocturnal forays, including locations where pet food or water was made available, either intentionally or unintentionally, by local residents; areas under bird feeders with spilled bird seed; and vegetable gardens. Cameras were triggered by

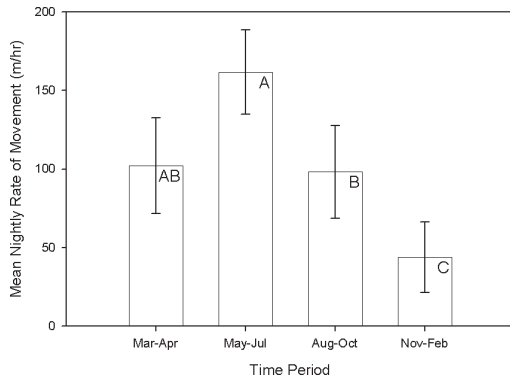


FIGURE 1. Mean ( $\pm 95\%$  CI) nightly rates of movement for 40 radio-collared striped skunks (19 male, 21 female) across four seasons (1: March–April, 2: May–July, 3: August–October, 4: November–February) in urban Flagstaff, Arizona, USA from 6 January 2004–22 March 2005. Bars with the same letter are not significantly different at  $P < 0.05$ .

animal movements into or out of an obvious opening at diurnal retreats, or across the area surrounding the available resource(s) at focal locations. Visitation was categorized as either sequential, if different animals were recorded using the same site on different nights or at different hours within a night, or simultaneous, if animals were recorded either in the same photo or in different photos taken within 5 min of each other. In many cases, individual cats, raccoons, and skunks could be differentiated either by the presence of radio collars (skunks) or by unique pelage patterns–body size combinations.

This protocol was approved by the Northern Arizona University Institutional Animal Care and Use Committee under Protocol #03-097. No animals died as a result of the research methods used during this study.

## RESULTS

We radio-collared 40 adult skunks (19 males and 21 females) during the course of this study. Of those, one was found dead with an arrow through its neck, one was killed by a vehicle on a roadway, four lost their collars, five had collars fail, and two had collars removed early because they had caused abrasions on the animal's necks.

### Nightly rate of travel and seasonal home-range size

Nightly rate of travel varied significantly across seasons, but we detected no sex-by-

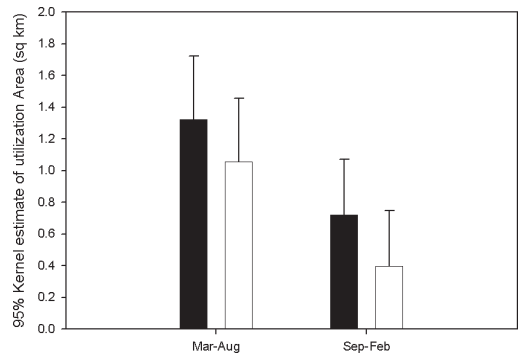


FIGURE 2. Mean ( $\pm 95\%$  CI) 95% kernel estimates of area ( $\text{km}^2$ ) utilized by radio-collared male (solid bars) and female (open bars) striped skunks in Flagstaff, Arizona, USA from 6 January 2004–15 December 2005.

season interaction or difference between the sexes (overall  $F_{7,51} = 7.2$ ,  $P < 0.0001$ ; season  $F_{3,51} = 13.9$ ,  $P < 0.0001$ ; sex  $\times$  season  $F_{3,51} = 1.5$ ,  $P = 0.22$ ; sex  $F_{1,51} = 0.31$ ,  $P = 0.58$ ). Travel rates were highest during the postbreeding season corresponding to the summer months of May, June, and July while rates were lowest during the winter months of November, December, January, and February (Fig. 1).

Seasonal home-range size, determined by 95% kernel estimates, varied across time periods, but we found no sex-by-time-period interaction or difference in seasonal home-range size between sexes (overall  $F_{3,35} = 4.4$ ,  $P = 0.01$ ; time-period  $F_{1,35} = 10.8$ ,  $P = 0.002$ ; sex  $\times$  season  $F_{1,35} = 0.02$ ,  $P = 0.88$ ; sex  $F_{1,35} = 2.4$ ,  $P = 0.13$ ; Fig. 2). Seasonal home-range sizes were larger in spring–summer (March–August,  $1.3 \text{ km}^2$  [ $\pm 0.8$ ] for males and  $1.1 \text{ km}^2$  [ $\pm 0.5$ ] for females), concurrent with increased nightly rates of travel; and smaller in fall–winter (September–February) for both sexes ( $0.7 \text{ km}^2$  [ $\pm 0.6$ ] for males and  $0.4 \text{ km}^2$  [ $\pm 0.4$ ] for females) when nightly rates of travel were also reduced.

Of the 40 skunks we studied, eight males and 10 females had contiguous home ranges during one of the two time periods (March–August or September–

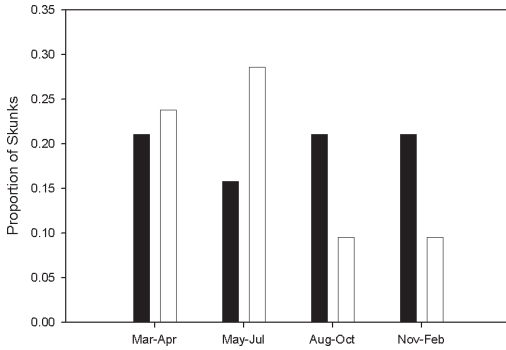


FIGURE 3. Proportion of radio-collared male (solid bars) and female (open bars) skunks using nonurban habitat surrounding the urban matrix of Flagstaff, Arizona, USA across four time periods from 5 January 2004–15 December 2005.

February). For the spring–summer set, 95% kernel estimates of area overlap were 25% among males, 33% among females, and 26% among male–female pairs. For animals followed in fall–winter, overlap was 9% for males, 25% for females, and 26% for male–female pairs.

#### Movements across the urban–wildland interface

From 6 January 2004 to 22 March 2005, 20 of 40 radio-collared skunks crossed the urban–wildland interface in at least one direction on at least one night (Fig. 3). Fourteen of these (32% of males, 38% of females) moved back and forth across the urban–wildland interface within a night. Nineteen skunks were never recorded outside of the urban matrix. Females were found utilizing nonurban wildland areas more often from March–July than from September–February, and males utilized these wildland areas relatively steadily throughout the year. We also documented relatively infrequent, but recurring, events when individuals left the urban radio-tracking areas for multiple nights or several weeks, then later returned to the urban tracking areas.

#### Photo-monitoring

The 21 photo-monitoring locations were spread across both eastern and western

portions of the city, with four of these on the border or well-within intervening wildlands (Fig. 4). We documented both sequential and simultaneous use by skunks, other wildlife, and domestic animals at 16 of the 21 sites used by skunks as either diurnal retreats or nocturnal focal locations (Table 1). At one site, we recorded at least four different skunks, one raccoon, and one domestic cat within a single night, while at another we recorded four different skunks and at least two different raccoons within a night.

#### DISCUSSION

Daily and seasonal movements, home-range size, and other behavioral patterns have important implications for inter- and intraspecific contact rates and, therefore, the spread of diseases such as rabies (Rosatte and Gunson, 1984; Gremillion-Smith and Woolf, 1988; Rupprecht and Smith, 1994; White et al., 1995; Altizer et al., 2006). Home-range sizes have been estimated for skunks using a variety of methods and with varying research goals, making comparisons across studies difficult. Several previous radio-telemetry studies in rural areas reported home ranges larger than those we documented (5 km<sup>2</sup> for males, 3.7 km<sup>2</sup> for females [Storm and Verts, 1966], 2.9 km<sup>2</sup> for males, 2.5 km<sup>2</sup> for females [Rosatte and Gunson, 1984], 3 km<sup>2</sup> for males, 2.4 km<sup>2</sup> for females [Greenwood et al., 1985]), although Bixler and Gittleman (2000) reported home ranges similar in size to those we found. In contrast, home ranges for skunks in urban Toronto, Canada (0.51 km<sup>2</sup>; [Rosatte et al., 1991]) were more similar to the home ranges we found for skunks during the fall–winter. Our nightly rates of travel are most-directly comparable to those of Greenwood et al. (1997), who used similar methods to calculate movements of skunks inhabiting rural areas in South Dakota, USA from March through July. Skunks in our study moved roughly half the distance/hr during

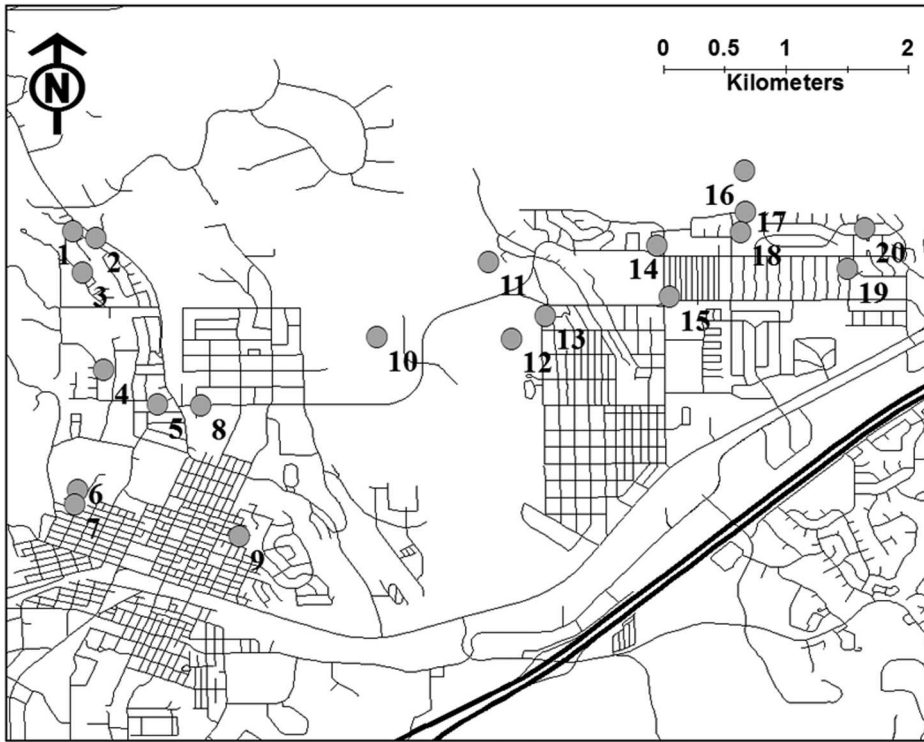


FIGURE 4. Photo-monitoring locations in Flagstaff, Arizona, USA used by skunks as diurnal refugia, nocturnal resting sites, and for food and water resources. Site number 21 was located east of Flagstaff's city limits.

similar periods of the year compared to those in South Dakota (140 m/hr versus 232 m/hr, respectively). Taken together, the results of these studies suggest that urban skunks have smaller home ranges, and move less distance, than those in rural areas, perhaps because of greater availability of food resources in urban environments.

The seasonal patterns of fluctuations in movements, home-range size, and home-range overlap we documented were similar to several other studies that documented reduced activity and extended periods in dens during winter months and more-extensive movements during spring and summer (Shirer and Fitch, 1970; Bixler and Gittleman, 2000). More extensive movements in spring were reflected in greater home-range overlap, although our measures of overlap were undoubtedly conservative given that we did not have all animals in the study area radio-collared

and, therefore, uncollared animals likely had home ranges overlapping the animals we compared. This seasonal shift in behavior has been argued to drive the pattern of rabies occurrence typically exhibited by skunks in the United States and Canada (Gremillion-Smith and Woolf, 1988; Krebs et al., 2005). The spring peak in rabies occurrence has been hypothesized to result from rabies transfer in communal winter dens, followed by a variable incubation period for the virus before expression (Rosatte, 1984; Gremillion-Smith and Woolf, 1988). Data for rabies occurrence in skunks in Flagstaff are consistent with this pattern, with 18 of 23 cases reported between the months of January and May with a peak in March. Peaks in rabies occurrence in the late fall and winter have been attributed to increased contact between skunks during the fall dispersal of naive, susceptible juveniles (Gunson et al., 1978; Rosatte, 1984). Patterns of rabies

TABLE 1. Characteristics of photo-monitoring locations and the animals recorded visiting them. Locations were classified as having recorded more than one unique individual skunk (based on size, pelage, etc.) using the site during the period monitored, as well as any other wild or domestic species that were recorded using the site. The last column indicates instances when multiple animals were at the site simultaneously, either captured in the same photograph (<2 m from each other) or photographed within 5 min of each other. Numbers in the first column refer to locations of sites shown in Figure 4.

Site	Cover type	Attraction	>1 Skunk present	Wildlife present	Domestic animals present	Animals at site simultaneously
1	Outbuilding	Pet food intentionally available	Yes	Raccoon, gray fox	Cat	Skunk, raccoon, gray fox
2	Outbuilding	None	No	None	Cat	None
3	Deck	Water	No	Raccoon	Cat	None
4	None	Water, spilled bird seed	Yes	Raccoon	Cat	Skunk, raccoon, cat
5	Outbuilding	Garden	Yes	Gray fox	None	Skunk, gray fox
6	Outbuilding	None	Yes	Cottontail	Cat	Skunk, cottontail
7	Deck, outbuilding	None	No	Gray fox	Cat	Skunk, gray fox, cat
8	Outbuilding	None	Yes	None	Cat	None
9	Outbuilding	Garden	Yes	None	None	Skunk
10	Outbuilding	None	No	None	None	None
11	Rock outcrop	None	No	None	Cat, dog	None
12	Under stadium	Pet food intentionally available	Yes	Raccoon	>1 Cat	Skunk, raccoon, cat
13	Outbuilding	None	No	None	Cat	Skunk, cat
14	Outbuilding	None	No	None	None	None
15	Outbuilding	Spilled bird seed	Yes	None	None	Skunk
16	Rock outcrop	None	No	None	None	None
17	Outbuilding	None	No	None	None	None
18	Deck	Garden	No	Raccoon	Cat	Skunk, raccoon, cat
19	Deck	None	Yes	Raccoon	>1 Cat	Skunk, cat
20	Outbuilding	Garden	No	None	Cat, dog	None
21	Building foundation	Pet food intentionally available	Yes	Raccoon	>1 Cat	None

occurrence in Flagstaff suggest a very-weak peak, if any, in the fall, with four of 23 cases reported in October and November. Hass and Dragoo (2006) likewise failed to find a fall peak in their study of rabies in skunks in southern Arizona. Interestingly, the single cases of bat-variant rabies in gray fox and domestic cat in Flagstaff were both reported in September, suggesting that spillover events may be more likely after the increased activity and greater movements of skunks during spring and summer.

One- and two-way movements across the urban-wildland interface within a night were commonly exhibited by half of the monitored skunks in this study, while some individuals moved into the wildlands and did not return to the urban area over a period of several nights to

weeks. Most studies of skunks have focused on either urban (Rosatte et al., 1991) or rural areas (Schowalter and Gunson, 1982; Greenwood et al., 1997; Bixler and Gittleman, 2000; Rosatte et al., 2001) in the mid-western and eastern states of the US and Canada. Skunk movements across the interface could impact rabies management in two ways: First, skunks moving across the interface could act as vectors by transporting disease either into or out of the urban matrix, especially during increased movements during the spring-summer months. Second, animals that leave the urban matrix for extended periods could be missed during trap-vaccinate-release or oral rabies vaccine programs, lending further support for treatments to be



implemented over large areas, as has been done in previous treatment programs (Rosatte et al., 1992; 2007).

Although several skunks traveled into the wildlands separating the eastern and western urban study areas, we only documented one animal moving between these two areas. The rarity of this type of movement was unexpected, given that distances between the urban areas were within the range of distances that skunks moved within either urban study area. Genetic analysis of the rabies variants involved in the 2001 outbreak indicated a temporal movement of virus from the eastern to the western sections of the city, which was hypothesized to be caused either by animal movements along travel corridors or by human translocation (Leslie et al., 2006). Given the lack of regular movement of radio-collared skunks between eastern and western urban areas in our study, spread of the disease in Flagstaff due to human translocation seems more likely and suggests that outbreaks in the area could be relatively spatially limited in the absence of human translocation. However, we lack data on relative densities of skunks during our study period compared to outbreak periods, so we cannot rule out that higher skunk densities during the outbreak, changes in behavior of infected animals, or both could have led to greater interchange among areas during outbreak periods.

The potential for intraspecific transfer of rabies among skunks, and for spill-over into other species, depends on the probability that animals come in contact, but contact rates are rarely known (White et al., 1995; Totton et al., 2002). Our photo-monitoring of focal locations indicated that this potential is relatively high within the urban environment, with skunks appearing together with other skunks or other wild or domestic species in the same photo, or in photos only minutes apart, at approximately half of the sites we monitored. Given that each site was monitored for only 1–2 wk,

our results likely underestimate the potential for these types of contact. Based on relative frequency of co-occurrence at our focal monitoring sites, the potential for spillover from skunks to other species was greatest for raccoons, gray foxes, and domestic cats. Experimental trials have indicated that raccoons appear relatively resistant to skunk rabies variants (Hill et al., 1993), and rabies has not yet been recorded in raccoons in the Flagstaff area; however, little is known about raccoon susceptibility to bat-rabies variants. In contrast, gray foxes with the same bat-rabies variant found in skunks were recovered in the area, suggesting spill-over between these species. Domestic cats had the greatest potential to interact with skunks, appearing simultaneously with skunks at nearly one-third, and recorded as present at two-thirds, of the locations. A domestic cat was also recently confirmed with the same rabies variant found in Flagstaff skunks. Cats in Arizona are not required to be licensed or to have rabies vaccinations, yet they are the domestic species most-often documented with rabies in the US (Krebs et al., 2005). A recent model by Gordon et al. (2004) demonstrated that spill-over to this species can increase dramatically during rabies epizootics.

Although the co-occurrence of skunks with conspecifics or other species, such as we documented, can suggest the potential for rabies transfer, that potential depends on how often animals in close proximity interact in ways that transfer the virus. Observation of raccoons attracted to a garbage dump in Ontario, Canada recorded raccoons biting each other roughly once every three nights, while skunks and raccoons never interacted and rarely approached within 2–3 m of each other (Totton et al., 2002). Conversely, Flagstaff homeowners reported audible skunk–raccoon interactions at backyard feeding sites, and we documented skunks and raccoons within 1 m of each other at several monitored sites. However, given that rabies infection can potentially alter

an animal's behavior (Greenwood et al., 1997), any observation of uninfected animals may not accurately reflect the probability of rabies transfer.

The sites at which multiple individuals or species were recorded varied, including skunk resting sites under buildings or decks as well as sites where food was intentionally or unintentionally made available to animals. Although the locations of some of these sites would have been unknown without radio-telemetry, many were known by the human residents of the area to be visited by skunks and other animals. As a result, public surveys designed to identify areas where skunks and other wildlife congregated could reveal locations that could act as foci for trap-vaccinate-release or oral vaccine programs, an opportunity for effective use of "citizen science" (Dobson, 2000).

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#### LITERATURE CITED

- ALTIZER, S., A. DOBSON, P. HOSSEINI, P. HUDSON, M. PASCUA, AND P. ROHANI. 2006. Seasonality and

- the dynamics of infectious diseases. *Ecology Letters* 9: 467–484.
- BIXLER, A., AND J. L. GITTLEMAN. 2000. Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *Journal of Zoology* 251: 525–533.
- BLANTON, J. D., J. W. KREBS, C. A. HANLON, AND C. E. RUPPRECHT. 2006. Rabies surveillance in the United States during 2002. *Journal of the American Veterinary Medical Association* 229: 1897–1911.
- BROADFOOT, J. D., R. C. ROSATTE, AND D. T. O'LEARY. 2001. Raccoon and skunk population models for urban disease control planning in Ontario, Canada. *Ecological Applications* 11: 295–303.
- DOBSON, A. 2000. Raccoon rabies in space and time. *Proceedings of the National Academy of Sciences* 97: 14041–14043.
- ENGEMAN, R. M., K. L. CHRISTENSEN, M. K. PIPAS, AND D. L. BERGMAN. 2003. Population monitoring in support of a rabies vaccination program for skunks in Arizona. *Journal of Wildlife Diseases* 39: 746–750.
- EPPLE, L. E., AND A. O. EPPLE. 1995. A field guide to the plants of Arizona. The Globe Pequot Press, Guilford, Connecticut. 347 pp.
- GORDON, E. R., A. T. CURNS, J. W. KREBS, C. E. RUPPRECHT, L. A. REAL, AND J. E. CHILDS. 2004. Temporal dynamics of rabies in a wildlife host and the risk of cross-species transmission. *Epidemiology and Infection* 132: 515–524.
- GREENWOOD, R. J., A. B. SARGEANT, AND D. H. JOHNSON. 1985. Evaluation of mark-recapture for estimating striped skunk abundance. *Journal of Wildlife Management* 49: 332–340.
- , W. E. NEWTON, G. L. PEARSON, AND R. G. SCHAMBER. 1997. Population and movement characteristics of radio-collared striped skunks in North Dakota during an epizootic of rabies. *Journal of Wildlife Diseases* 33: 226–241.
- GREMILLION-SMITH, C., AND A. WOOLF. 1988. Epizootiology of skunk rabies in North America. *Journal of Wildlife Diseases* 24: 620–626.
- GUNSON, J. R., W. J. DORWARD, AND D. B. SCHOWALTER. 1978. An evaluation of rabies control in skunks in Alberta. *Canadian Veterinary Journal* 19: 214–220.
- GUERRA, M. A., A. T. CURNS, C. E. RUPPRECHT, C. A. HANLON, J. W. KREBS, AND J. E. CHILDS. 2003. Skunk and raccoon rabies in the eastern United States: Temporal and spatial analysis. *Emerging Infectious Diseases* 9: 1143–1158.
- HARRISON, R. L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. *Journal of Wildlife Management* 61: 112–122.
- HASS, C. C., AND J. W. DRAGOO. 2006. Rabies in hooded and striped skunks in Arizona. *Journal of Wildlife Diseases* 42: 825–829.
- HILL, JR., R. E., K. E. SMITH, G. W. BERAN, AND P. D. BEARD. 1993. Further studies on the suscepti-

- bility of raccoons (*Procyon lotor*) to a rabies virus of skunk origin and comparative susceptibility of striped skunks (*Mephitis mephitis*). *Journal of Wildlife Diseases* 29: 475–477.
- HOOG, P. N., AND B. EICHENLAUB. 2000. Animal movement extension to ArcView, version 2.0. Alaska Science Center, Biological Science Office, US Geological Survey, Anchorage, Alaska.
- KREBS, J. W., H. R. NOLL, C. E. RUPPRECHT, AND J. E. CHILDS. 2002. Rabies surveillance in the United States during 2001. *Journal of the American Veterinary Medical Association* 221: 1690–1701.
- , E. J. MANDEL, D. L. SWERDLOW, AND C. E. RUPPRECHT. 2005. Rabies surveillance in the United States during 2004. *Journal of the American Veterinary Medical Association* 227: 1912–1925.
- LARIVIÈRE, S., AND F. MESSIER. 1996. Immobilization of striped skunks with Telazol®. *Wildlife Society Bulletin* 24: 713–716.
- LESLIE, M. J., S. MESSENGER, R. E. RHODE, J. SMITH, R. CHESHIER, C. HANLON, AND C. E. RUPPRECHT. 2006. Bat-associated rabies virus in skunks. *Emerging Infectious Diseases* 12: 1274–1277.
- MACDONALD, D. W., AND D. R. VOIGT. 1985. The biological basis of rabies models. In *Population dynamics of rabies in wildlife*, P. J. Bacon (ed.). Academic Press, London, England, pp. 71–108.
- PYBUS, M. J. 1988. Rabies and rabies control in striped skunks (*Mephitis mephitis*) in three prairie regions of western North America. *Journal of Wildlife Diseases* 24: 434–449.
- RODGERS, A. R., A. P. CARR, L. SMITH, AND J. G. KIE. 2005. HRT: Home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- ROSATTE, R. C. 1984. Seasonal occurrence and habitat preference of rabid skunks in southern Alberta. *Canadian Veterinary Journal* 25: 142–144.
- , AND J. R. GUNSON. 1984. Dispersal and home range of striped skunks, *Mephitis mephitis*, in an area of population reduction in Southern Alberta. *Canadian Field-Naturalist* 98: 315–319.
- , M. J. POWER, AND C. D. MACINNES. 1990. Rabies control for urban foxes, skunks and raccoons. In *Proceedings of the 14th vertebrate pest conference*, L. R. Davis and R. E. Marsh (eds.). University of California, Davis, California, pp. 160–176.
- , ———, AND ———. 1991. Ecology of urban skunks, raccoons, and foxes in metropolitan Toronto. In *Proceedings: Wildlife conservation in metropolitan environments: National Institute for Urban Wildlife—A national symposium on urban wildlife*, L. Adams and D. Leedy (eds.). Columbia, Maryland, pp. 31–38.
- , ———, ———, AND J. B. CAMPBELL. 1992. Trap-vaccinate-release and oral vaccination for rabies control in urban skunks, raccoons and foxes. *Journal of Wildlife Diseases* 28: 562–571.
- , ———, AND ———. 2001. Density, dispersion, movement and habitat of skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) in metropolitan Toronto. In *Wildlife 2001: Populations*, D. McCullough and R. Barrett (eds.). Elsevier Applied Science, London and New York, pp. 932–944.
- , R. TINLINE, AND D. JOHNSTON. 2007. Rabies control in wild carnivores. In *Rabies*. Academic Press, San Diego, California, pp. 595–634.
- RUPPRECHT, C. E., AND J. S. SMITH. 1994. Raccoon rabies: The re-emergence of an epizootic in a densely populated area. *Virology* 5: 155–164.
- RUSSELL, C. A., D. L. SMITH, L. A. WALLER, J. E. CHILDS, AND L. A. REAL. 2004. *A priori* prediction of disease invasion dynamics in a novel environment. *Proceedings of the Royal Society, London B*, 271: 21–25.
- SAUNDERS, B., P. C. L. WHITE, AND S. HARRIS. 1997. Habitat utilization by urban foxes (*Vulpes vulpes*) and the implications for rabies control. *Mammalia* 6: 497–510.
- SCHOWALTER, D. B., AND J. R. GUNSON. 1982. Parameters of population and seasonal activity of striped skunks, *Mephitis mephitis*, in Alberta and Saskatchewan. *Canadian Field-Naturalist* 96: 409–420.
- SHIRER, H. A., AND H. S. FITCH. 1970. Comparison from radio tracking of movements and denning habits of the raccoon, striped skunk, and opossum in northeastern Kansas. *Journal of Mammalogy* 51: 491–503.
- SMITH, D. L., L. BRENDAN, L. A. WALLER, J. E. CHILDS, AND L. A. REAL. 2002. Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. *Proceedings of the National Academy of Sciences* 99: 3668–3672.
- STORM, G. L., AND B. J. VERTS. 1966. Movements of a striped skunk infected with rabies. *Journal of Mammalogy* 47: 705–708.
- TOTTON, S. C., R. R. TINLINE, R. C. ROSATTE, AND L. L. BIGLER. 2002. Contact rates of raccoons (*Procyon lotor*) at a communal feeding site in rural eastern Ontario. *Journal of Wildlife Diseases* 38: 313–319.
- WELLER, D. M. G., AND M. R. PELTON. 1987. Denning characteristics of the striped skunks in Great Smokey Mountain National Park. *Journal of Mammalogy* 68: 177–179.
- WHITE, P. C. L., S. HARRIS, AND G. C. SMITH. 1995. Fox contact behaviour and rabies spread: A model for the estimation of contact probabilities between urban foxes at different population densities and its implications for rabies control in Britain. *Journal of Applied Ecology* 32: 693–706.

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