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## Original Article

# Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore

Maureen H. Murray and Colleen Cassady St. Clair

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

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Many species living in developed areas adjust the timing of their activity and habitat selection to avoid humans, which may reduce their risk of conflict, including vehicle collisions. Understanding the behavioral adaptations to vehicles exhibited by species that thrive in urban areas could improve the conservation of many species that are threatened by road-caused mortality. We explored these behaviors using the seasonal distribution of 80 road-killed coyotes (*Canis latrans*) collected by civic employees and by comparing the activity patterns (step lengths) and road crossings made by 19 coyotes fitted with GPS collars with 3-h fix rates, 7 of which were killed in vehicle collisions. Coyotes were collected on roads most often in spring and fall, which corresponded to the most rapid changes in day length in our northern study area and when collared road-killed coyotes were more active during rush hour. Among collared coyotes, those that were killed on roads were most active and crossed roads most frequently at dusk. By contrast, surviving animals were most active and crossed roads most often near midnight year round and surprisingly, exhibited less avoidance of roads than did road-killed coyotes. Our results suggest that risk of vehicle collision is lower for coyotes that restrict the times at which they cross roads but some coyotes do not or cannot. Such behavioral flexibility to adapt to the timing of human activity relative to exogenous cues such as dawn and dusk may contribute to differences both among and within wildlife species in rates of coexistence with humans.

**Key words:** behavioral flexibility, *Canis latrans*, movement, roads, survival, urban adaptation, vehicle collisions.

## INTRODUCTION

Urbanization is currently the fastest growing type of land use globally, with accompanying increases in the density of human infrastructure and disturbance that can contribute to loss of biodiversity (Angel et al. 2011; Murphy and Romanuk 2014). One problematic type of infrastructure is road networks (Hansen et al. 2005), which can have many negative effects on wildlife, including habitat loss, barriers to movement, and road mortality (reviewed by Trombulak and Frissell 2000; Benítez-López et al. 2010). For some species, road mortality can be significant enough to cause population decline (e.g., Hells and Buchwald 2001). For humans, vehicle collisions with species such as large ungulates cause ~200 human fatalities (Langley et al. 2006) and ~8.4 billion USD in damage and injuries (Bissonette et al. 2008; Huijser et al. 2008) annually in the USA. Road mitigation, such as fencing and crossing structures (reviewed by Glista et al. 2009) can reduce rates of wildlife mortality but could be advanced with a better understanding of the behavioral adaptations exhibited

by species that thrive in human-dominated landscapes with high road densities.

Species that tolerate high densities of people are known as urban adapters and exploiters (McKinney 2002) and many are increasing in cities around the world. Urban adapters include several species of carnivores (reviewed by Bateman and Fleming 2012) that are typically generalists with high behavioral flexibility (McKinney 2002; Lowry et al. 2013). For these species, persistence in human-dominated landscapes appears to require a complex mix of behaviors that makes use of available habitat while avoiding negative encounters with people and vehicles, often by exhibiting more nocturnal behavior than their rural counterparts. This suite of behaviors appears to characterize urban foxes (*Vulpes vulpes*; Baker et al. 2007), urban bobcats (*Felis rufus*; Riley et al. 2003), and wolves (*Canis lupus*) near human settlements (Ciucci et al. 1997). Wary wildlife may also reduce their risk of collision by preferentially avoiding roads with higher traffic volumes, which has been observed in moose (*Alces alces*; Seiler 2005), wolves (Whittington et al. 2005), elk (*Cervus elaphus*; Preisler et al. 2006), and grizzly bears (*Ursus arctos*; Northrup et al. 2012). Avoiding traffic in space or time may allow wildlife to avoid humans at fine scales while continuing to persist in

Address correspondence to M. Murray. E-mail: mhmurray@ualberta.ca.

fragmented areas. Although avoidance of human activity in time or space appears to be variable among both populations (above) and individuals (e.g., Knopff et al. 2014), no study has determined the effect of that flexibility on the risk of road mortality.

Individual variation in the ability to adjust behavior to avoid overlap with people might be especially important at higher latitudes where there are pronounced seasonal changes in human activity in relation to day length and light levels. Several studies have found that wildlife–vehicle collisions peak in fall and spring and at dusk and dawn (e.g., Lagos et al. 2012; reviewed by Steiner et al. 2014). These patterns in road mortality have been hypothesized to coincide with periods of high movement rates, including dispersal (e.g., foxes [Baker et al. 2007] and Eurasian badgers [*Meles meles*; Grilo et al. 2009]), mating (e.g., roe deer [*Capreolus capreolus*; Lagos et al. 2012] and Egyptian mongoose [*Herpestes ichneumon*; Grilo et al. 2009]), and migration (e.g., moose [Lavsund and Sandegren 1992]). These life-history explanations do not appear to explain all seasonal peaks in vehicle collisions, which sometimes do not correspond to periods of high movement (Neumann et al. 2012) and vary by region (Steiner et al. 2014). A more general explanation for this variation might be achieved by comparing the movement and road-crossing behavior of individuals that were or were not killed in vehicle collisions within a single species and region.

We studied seasonal vulnerability to vehicle mortality and individual variation in responses to roads in urban coyotes (*Canis latrans*), an opportunistic midsized canid with increasing prevalence in cities across North America (Riley et al. 2003; White and Gehrt 2009; Lukasik and Alexander 2011). Urban coyotes typically have higher survival rates (Gehrt and Riley 2010) and usually exhibit more nocturnal activity cycles than rural coyotes, which are typically crepuscular (Grinder and Krausman 2001; Riley et al. 2003). Among urban coyotes, there appears to be considerable variation among individuals in the size of home ranges, the use of developed areas (Riley et al. 2003; Gese et al. 2012), and the probability of being killed from a collision with a vehicle (Gehrt and Riley 2010). Although more than two-thirds of the mortalities of urban coyotes may be caused by vehicle collisions (Gehrt and Riley 2010), coyotes often cross major roads and can occupy areas that are highly fragmented by human infrastructure (Tigas et al. 2002; Riley et al. 2003).

We hypothesized that urban coyotes adjust their activity to reduce overlap with people as a means of reducing risk but that the degree of this adjustment would vary among individuals. We predicted that, in general, coyotes that exhibit more overlap with humans in space or time would experience higher rates of conflict. Specifically, we predicted that coyotes that were more active and more likely to cross roads when or where traffic volumes were highest would be more likely to be killed by vehicles. We also predicted that this variation among individuals would be most pronounced in the seasons—spring and fall—when day length changes most quickly.

## MATERIALS AND METHODS

### Study area and road characteristics

We studied coyote movement in Edmonton, Alberta, Canada (pop: 870 000) one of the northernmost major cities in North America (53.5472°N, 113.5006°W) where day length varies from 7.5 h in December to 17 h in June (National Research Council of Canada 2014). Reports of coyote sightings by the public in Edmonton have increased steadily over the past 20 years (Cox R, personal

communication) and now occur almost daily. Collisions between coyotes and vehicles are reported almost weekly throughout the year (Melnick K, City of Edmonton, personal communication). The city contains several large and contiguous riparian natural areas that may facilitate animal movement, but these are bisected in several locations by highways that contain up to 7 lanes of traffic.

To examine the road-crossing behavior of coyotes (below), we designated major roads as those with at least 4 lanes of traffic because these roads likely pose the greatest barrier to movement (Riley et al. 2006) and because they were typically at least 5 km long, making it likely that coyotes crossed rather than circumvented them when successive GPS locations occurred on either side. Traffic volume on these roads peaks at 0800 and 1700 h and does not vary significantly with season (AAWDT 2013). We designated morning and evening rush hours as being 0500–0800 h and 1700–2000 h because these time periods contain 41% of daily traffic flow (AAWDT 2013) and because they maximize the seasonal changes in day length.

### Road mortality

To determine the annual distribution of coyote–vehicle collisions in our study area, we requested mortality records from the City of Edmonton collected in 2013–2014. We received the total number of coyote mortalities for each month, which we binned into 4 seasons based on changes in day length. We defined winter as November–January (day length [mean  $\pm$  standard deviation {SD}] = 8.1  $\pm$  0.5 h/day, change in day length = 2.3  $\pm$  0.7 min/day), spring as February–March (11.9  $\pm$  2.1 h/day, 4.1  $\pm$  0.1 min/day), summer as May–July (16.4  $\pm$  0.5 h/day, 2.2  $\pm$  0.7 min/day), and fall as August–October (12.7  $\pm$  2.1 h/day, 4.0  $\pm$  0.1 min/day). We then tested whether collisions were more frequent during the spring and fall relative to summer and winter using a *G* test of independence.

### Coyote capture and collaring

Coyotes were captured from 2009 to 2012 in areas within city limits where coyote presence was previously reported, and where dogs were prohibited, using 4-coil padded foot-hold traps (No. 3, Victor Soft Catch Coil-spring; Animal Trap Co., Lilitz, PA) and physically restrained using catch poles. Once captured, coyotes were sexed, aged as either subadults (<1 year old) or adults ( $\geq$ 1 year old) using degree of tooth wear (Bowen 1982), weighed, ear tagged, assessed for body condition, and fitted with a GPS collar. We programmed the GPS collars to collect fixes every 3 h that, depending on the collar, were stored until the collar was retrieved (Lotek 3300S, 2 coyotes), were remotely downloaded (Lotek 4400S, 3 coyotes), or were sent to us daily over the cell phone network (Lotek Wildcell, 14 coyotes). We calculated movement metrics for each of our collared animals (below) and related these metrics to whether or not the animal was killed by a vehicle collision during the study period.

### Spatial and temporal analyses

We tested whether coyotes killed in vehicle collisions were more likely to overlap with human activity in their activity and road crossings by creating steps between consecutive 3-h GPS locations. Using these steps, we calculated 2 movement metrics for each 3-h period of the day: *step length* (i.e., the distance between successive GPS locations) and the number of *road crossings*. We inferred the locations and times of road crossings by intersecting each 3-h step with major roads using a Geographic Information System (ArcMap

v10.1, Redlands, CA). We then compared the mean values for step length and proportion of steps crossing roads across season and coyote fate (i.e., for coyotes that were and were not killed on roads).

To compare step length across seasons, we used a 2-factor Anova with a weighted means analysis for unequal sample sizes and log-transformed step length to normalize its distribution. Because we did not have 12 months of GPS data per coyote, we calculated the average log-transformed step length for at least 5 coyotes in each survival category per season. We used circular statistics (Oriana 4; Kovach Computing Services) to compare the step lengths and the relative frequency of road crossings at different times of the day and how this pattern differed between seasons. We tested for skewness in the distributions of both crossing frequency and step lengths over the diel cycle using Moore's modified Rayleigh test (Zar 1999) for uniform circular distributions and tested for differences in the mean time of crossings using a Watson's  $U^2$  test. Finally, we determined whether the diel timing of road crossings was correlated with step lengths and compared this relationship between seasons. To increase sample sizes within groups, we condensed the 4 calendar seasons into 2 seasons based on day length and defined summer as 22 March–21 September when day length was longer than average (day length  $\pm$  SD =  $15.2 \pm 1.7$  h) and winter as 22 September–21 March when day length was shorter than average (day length =  $9.4 \pm 1.7$  h).

We furthered our spatial analysis of road crossings by testing whether surviving coyotes exhibited more avoidance of roads or traffic in space or time relative to coyotes that were killed in collisions. To do so, we compared each coyote movement step with available steps that started at coyote locations using logistic regression (i.e., step selection function; Fortin et al. 2005; Roever et al. 2010). For each used step, we generated 10 available steps randomly using the same distribution of step lengths and turning angles as the used steps made by collared coyotes. At each used or available step, we measured whether the step did or did not cross a major road (0/1). If a step did cross a road, we measured the relative traffic volume at the time of crossing (% of daily traffic flow) and the traffic volume of the road section that was crossed (average number of cars per hour). Traffic information for each hour of day and on individual road sections were provided by the City of Edmonton (AAWDT 2013). Using these data from used and available steps, we calculated selection ratios (used in category/<sub>available</sub> in category; Manly et al. 2002).

We evaluated the importance of avoiding roads or traffic in time versus space using the characteristics of used and available road crossings. We used logistic regression to distinguish between used and available steps by road-killed and surviving coyotes and tested whether road-killed coyotes crossed roads 1) more frequently, 2) when traffic volume was higher, and/or 3) where traffic volume was higher (Table 1). We compared used and available steps using a generalized linear mixed model that included coyote ID as a random effect to account for nonindependence of steps made by the same individual (Pinheiro et al. 2012). We then calculated Nagelkerke's  $R^2$  as a measure of model fit.

Lastly, we compared the likelihood of collision for coyotes of different age, sex, or body condition classes and for coyotes with larger home ranges (see Murray et al. 2015 for methods details) using a  $G$  test of independence.

## RESULTS

We received reports of 80 coyotes collected on roads from vehicle-caused mortalities from 2013 to 2014, and we captured and collared

19 coyotes. The collared coyotes were monitored for an average of 5 months (range: 1–10 months) and we collected on average six hundred and thirty-nine 3-h GPS locations per coyote (range: 161–1867 fixes). Seven of the 19 collared coyotes were killed in vehicle collisions during the study period; the other 12 were presumed not to have died from vehicle collisions (hereafter, “survived”).

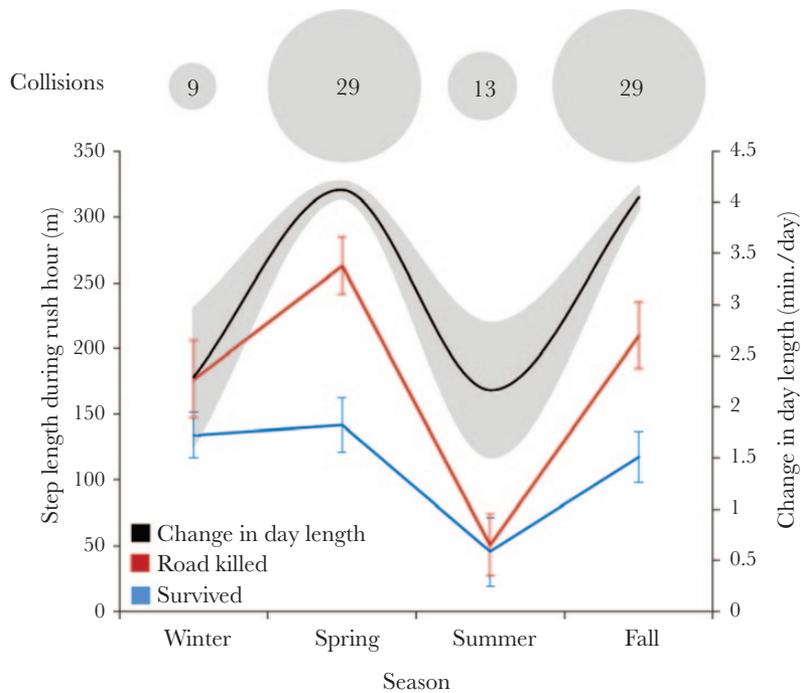
Of the 80 reports of coyotes killed on roads, 73% were collected in spring or fall, significantly more than the other seasons ( $G = 14.0$ , degrees of freedom [df] = 1,  $P < 0.01$ ; Figure 1). These 2 seasons also exhibited larger average changes in day length ( $t = 4.39$ , df = 1,  $P < 0.01$ ). Although there were no differences among seasons in the average step length during rush hour for all coyotes (mean  $\pm$  SD =  $123.81 \pm 38.34$  m/h [spring and fall],  $103.89 \pm 44.07$  m/h [summer and winter]; 2-factor Anova  $F_{1,1} = 0.86$ ,  $P = 0.19$ ; Figure 1), road-killed coyotes were significantly more active during rush hour in the spring and fall ( $231.21 \pm 64.86$  m [spring and fall],  $115.02 \pm 56.28$  m/h [summer and winter]; 2-factor Anova  $F_{1,1} = 4.74$ ,  $P = 0.036$ ; Figure 1). Five of the 7 road-killed collared coyotes were also collected in spring and fall.

A similar interaction between season and coyote fate characterized the diel patterns of coyote step lengths. In summer, surviving coyotes had 3 times longer step lengths at night with peaks near midnight (Moore's  $R^* = 2.35$ ,  $P < 0.001$ ), but there was no similar difference in the summer step lengths of coyotes that were road killed (Moore's  $R^* = 0.55$ ,  $P = 0.62$ ; Figure 2). In the winter, coyotes of both fates were slightly, but not significantly, more active at night (survived:  $R^* = 0.94$ ,  $P = 0.39$ ; road killed:  $R^* = 0.29$ ,  $P = 0.75$ ; Figure 2).

Corresponding to their more even diel patterns of activity, road-killed coyotes were more likely to cross roads throughout the day (Moore's  $R^* \leq 1.65$ ,  $P \geq 0.57$ ; mean crossing time  $\pm$  95% confidence interval:  $19:34 \pm 4:32$  [summer];  $17:22 \pm 3:49$  [winter]), whereas the surviving coyotes crossed roads mainly late at night (Moore's  $R^* \geq 9.58$ ,  $P < 0.001$ ;  $23:17 \pm 1:36$  [summer];  $23:14 \pm 1:03$  [winter]; Figure 3). On average in both summer and winter, road-killed coyotes crossed roads most frequently at dusk (summer: average time of sunset = 20:04, peak crossings = 20:00; winter: average time of sunset = 17:17, peak crossings = 17:00). Because of this alignment with dusk, in winter road-killed coyotes crossed roads most often when traffic volume was 57% higher than when they crossed roads in the summer and 343% higher than when surviving coyotes crossed roads (Watson's  $U^2 = 23.56$ ,  $P = 0.034$ ).

The likelihood of a coyote being killed in a collision was best predicted by crossing roads during the day when traffic was higher compared with crossing roads more frequently overall or crossing roads with higher traffic loads (Table 1). Surviving coyotes avoided crossing roads at the times when traffic volume was higher and neither group selected nor avoided roads with higher traffic loads (Figure 4). Surprisingly, road-killed coyotes exhibited more avoidance of crossing roads than surviving coyotes. Surviving coyotes crossed roads in proportion to their availability and 2.2  $\pm$  0.8 times more often than road-killed coyotes (Figure 4).

We did not find any relationship between the fate of our 19 collared coyotes and any other metric by which we could categorize them. Specifically, coyotes that were road killed were not of different age and sex classes (road killed: 2 adult males, 3 adult females, and 2 subadult males; survived: 2 adult males, 7 adult females, 2 subadult males, and 1 subadult female;  $G = 1.70$ , df = 3,  $P = 0.64$ ). Similarly, road-killed coyotes were not more likely to have ectoparasites that were visible at capture (road killed: 3 diseased, 4 apparently healthy; survived: 4 diseased, 8 apparently healthy;  $G = 0.171$ ,



**Figure 1** Seasonal values for step lengths during rush hour for road-killed (red) and surviving (blue) coyotes ( $\pm$ SD as error bars), average change in day length (black line  $\pm$  SD in gray outline), and civic reports of coyote mortality from vehicle collisions (relative size of gray circles and the numbers within them). Mortalities were summarized monthly by the City of Edmonton in 2013 and 2014 were categorized as winter (November–January), spring (February–April), summer (May–July), and fall (August–October). Step lengths were derived from the meters traveled between consecutive 3-h GPS fixes.

$df = 1$ ,  $P = 0.68$ ). Finally, road-killed coyotes were no more or less likely to exhibit large home ranges that overlapped with other animals and which might be indicative of transient social status (road killed: 4 residents, 3 transients; survived: 7 residents, 5 transients;  $G = 0.003$ ,  $df = 1$ ,  $P = 0.96$ ).

## DISCUSSION

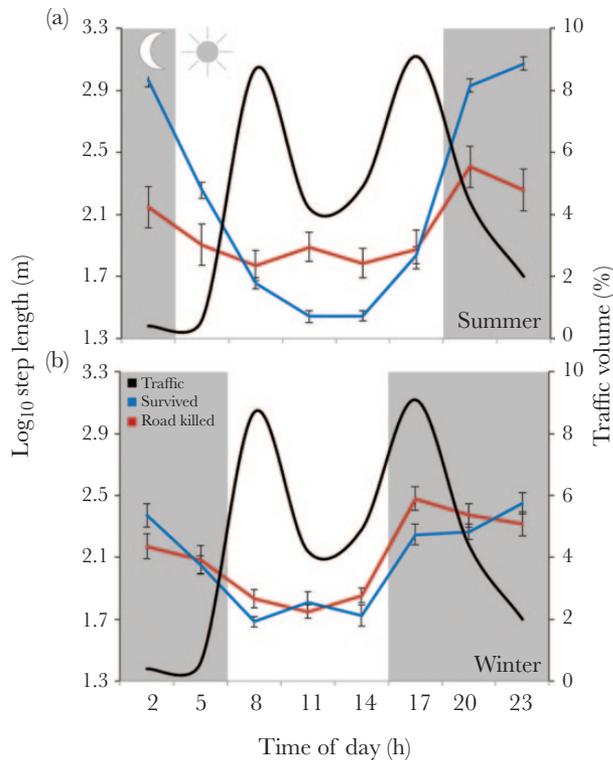
In this study, we tested the hypothesis that coyotes adjust their activity to reduce overlap with people in time and/or space as a means of reducing risk of conflict and that this behavior varies among individuals. Our results support our prediction that conflict, as measured by road kill, is higher for coyotes that overlap with humans, as measured by traffic volume, in time but not in space. The importance of avoiding overlap in time was also supported by our analysis of a database of 80 road-caused mortalities, in which we found that road-killed coyotes were more likely to be killed on roads in spring and fall when coyotes were more active during rush hour. We found that road-killed coyotes were most active and crossed roads most often at dusk, whereas surviving coyotes were active and crossed roads much later at night, especially in summer. In addition to overlapping with rush hour, the timing of dusk changed most rapidly in spring and fall.

The shift by surviving coyotes to more nocturnal activity cycles is one of several behavioral changes exhibited by wildlife in other human-dominated landscapes. For example, areas with high densities of humans or their infrastructure are associated with more nocturnal activity by several carnivores, including wolves (Boitani 1982; Ciucci et al. 1997; Zimmermann et al. 2014), grizzly bears (Kaczensky et al. 2006; Northrup et al. 2012), leopards (*Panthera*

*pardus*; Odden et al. 2014), and coyotes (Grinder and Krausman 2001; Riley et al. 2003). Such shifts to nocturnal activity have been interpreted as avoidance by animals of activity at times with high traffic volumes (reviewed by Ditchkoff et al. 2006; Lowry et al. 2013), but existing studies of this relationship report population-level changes. For example, urban foxes in the UK preferentially cross roads at night when traffic is lower (Baker et al. 2007), and urban barn owls (*Tyto alba*) are more likely to be killed on roads when traffic is high (Grilo et al. 2012).

Inferring a causal relationship between nocturnal activity and vehicle mortality requires knowledge of variation in and consequences of this shift within a population. Our data provide both components; peaks in both activity and road crossings late at night characterized surviving coyotes, whereas peaks for activity and crossings at dusk, and corresponding more often with rush hour, characterized road-killed coyotes. It is especially interesting that the surviving coyotes did not avoid crossing roads overall and did so over twice as often as coyotes killed in collisions. These differences among individuals suggest that temporal avoidance of high traffic volume is not only important but also complex. Most coyotes were killed on roads in spring and fall and so vulnerability might be higher in these periods. Coyote vulnerability to collision could be higher in spring and fall because there is a rapid change in the relationship between traffic volume and the exogenous cue of provided by dusk.

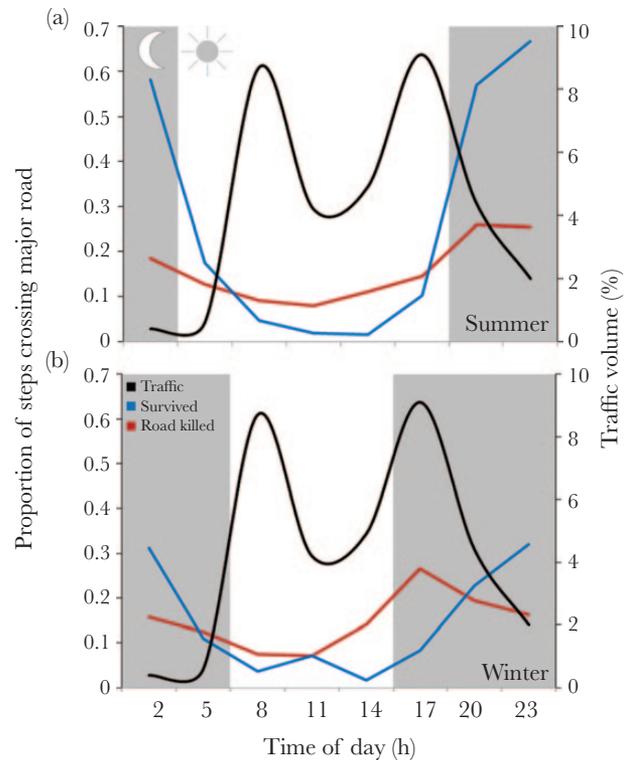
The seasonal changes in the timing of activity and road crossings suggest that some coyotes, like many other species (e.g., Georgii 1981; sensu Hill et al. 2004), vary their activity based on day length. Darkness may be a fairly reliable cue for human disturbance more generally, for example, to minimize the risk of encountering people in natural areas (Arnberger 2006) or being seen in backyards.

**Figure 2**

Diel distribution of activity as measured by step lengths for coyotes that were killed in vehicle collisions (red;  $n = 7$ ) or presumed to have survived (blue;  $n = 12$ ) in summer (22 March–21 September; a) and winter (22 September–21 March; b). Blue and red lines show the weighted average of log-transformed step lengths between GPS locations taken every 3 h and error bars show SD. Black lines show percent of daily traffic flow over time, provided by the City of Edmonton. Gray areas indicate times after sunset and before sunrise.

However, natural cues for the timing of activity such as daylight can become mismatched and unreliable as predictors of travel risk in locations where the timing of sunset and sunrise, but not traffic, vary throughout the year. Even in the absence of people, many mammalian species are nocturnal owing to a combination of evolutionary, sensory, and ecological factors (Gerkema et al. 2013).

The ubiquity with which dusk serves as an exogenous cue for biological activity makes its interaction with postindustrial human activity a potential ecological trap (sensu Gates and Gysel 1978; Robertson et al. 2013). For wildlife, the lack of a consistent relationship between the timing of traffic volume and the cues of dawn and dusk may impose the need for behavioral flexibility to successfully avoid traffic, particularly at higher latitudes where changes in day length are more pronounced and where many of the studies of vehicle collisions have been conducted. For example, studies of roe deer in more northern countries (e.g., Scotland, Netherlands, and Denmark) found peaks in collisions in spring (April and May) or fall (October), whereas studies in more southern countries (e.g., Italy, Slovenia, and Germany) found no such pattern (Steiner et al. 2014). Others have speculated that the ability for wildlife to avoid high traffic volumes is compromised by the rapid changes in this relationship in spring and fall (Hardy and Seidler 2014). In some species, these peaks may also stem from higher movement rates associated with breeding, dispersal, and migration (e.g., Lavsund and Sandegren 1992; Grilo et al. 2009), but those do not appear to provide a compelling explanation for coyotes.

**Figure 3**

The timing of road crossings made by coyotes that were killed in vehicle collisions (red;  $n = 7$ ) or presumed to have survived (blue;  $n = 12$ ) in summer (22 March–21 September; a) and winter (22 September–21 March; b). Blue and red lines show the weighted average proportion of coyote movement steps between successive 3-h GPS locations that crossed major roads. Black lines show percent of daily traffic flow over time, provided by the City of Edmonton. Gray areas indicate times after sunset and before sunrise.

Coyote dispersal typically occurs most between November and April (Gese et al. 1996; Way 2007) and their home ranges tend to be either smaller during the breeding season in early spring (Gese et al. 1988) or similar among seasons (Gehrt et al. 2009). Thus, for coyotes and potentially many other species, the spring and fall peaks in road mortality may be more associated with the rapid changes in overlap in those seasons between rush hour and twilight.

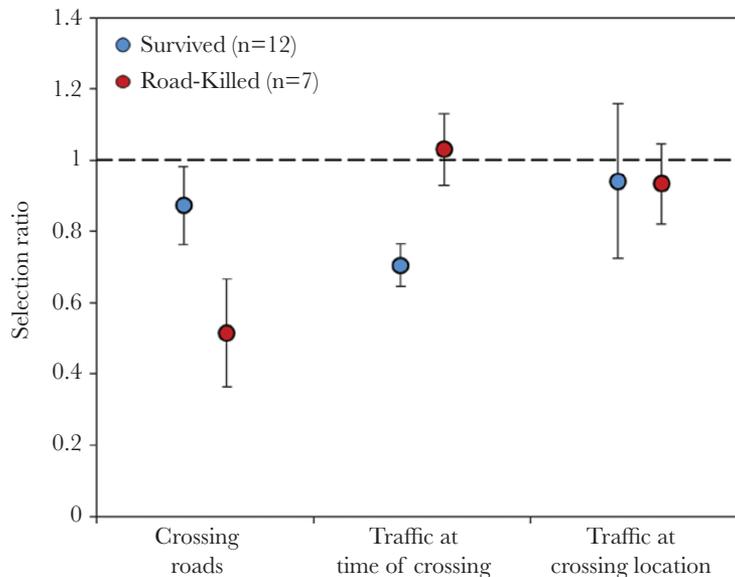
The ability for some coyotes to restrict the timing of their road crossings suggests high behavioral flexibility in this species, which may generalize to other urban-adapted wildlife. Previous studies have shown that urban coyotes tend to be more nocturnal than rural coyotes, which tend to be crepuscular (Grinder and Krausman 2001; Riley et al. 2003). Our study highlights the importance of variation in this behavior among urban individuals. In our study, the coyotes that shifted their activity patterns to be more nocturnal, especially in summer, crossed roads late at night when traffic was consistently lower and also exhibited higher rates of subsequent survival. Interestingly, our data do not suggest that this difference was associated with age, sex, or body condition, but such flexibility could potentially drive further behavioral changes in urban wildlife because plasticity itself is partly heritable (e.g., Nussey et al. 2005). Perhaps because of this flexibility, some animals appear to learn to associate times late at night with lower traffic volume, either through experience (e.g., Nielsen et al. 2013) or taught to offspring by parents (e.g., Mazur and Seher 2008), and these are the ones that survive. Regardless of cause, the

**Table 1**

**Outputs for models comparing the 1) frequency, 2) timing, and 3) locations of road crossings made by road-killed and surviving coyotes including standardized beta coefficients ( $\beta$ ) and Nagelkerke's  $r^2$  as an estimate of model fit. For hypothesis 1,  $n = 11518$  used steps and 115 180 available steps. For hypotheses 2 and 3,  $n = 2314$  used steps across roads and  $n = 28481$  available steps across roads**

Hypothesis	$r^2$	Model covariates	$\beta \pm SE$	$\chi^2$	$P$
1) Road-killed coyotes cross roads more <i>frequently</i>	0.12	Intercept	$-2.88 \pm 0.32$	-9.14	<0.01
		Killed in collision	$0.16 \pm 0.54$	0.43	0.65
		Step crossed road	$-1.3 \pm 0.29$	-6.21	0.02
		Crossed road $\times$ killed	$0.54 \pm 0.51$	-1.06	0.28
2) Road-killed coyotes cross roads <i>when</i> traffic is higher	0.35	Intercept	$-2.98 \pm 0.31$	-9.50	<0.01
		Killed in collision	$-0.45 \pm 0.50$	-0.91	0.37
		Traffic (time of crossing)	$-0.45 \pm 0.03$	-16.47	<0.01
		Traffic (time) $\times$ killed	$1.52 \pm 0.26$	10.45	<0.01
3) Road-killed coyotes cross roads <i>where</i> traffic is higher	0.11	Intercept	$-2.89 \pm 0.32$	-9.10	<0.01
		Killed in collision	$-0.54 \pm 0.51$	-1.05	0.29
		Traffic (crossing location)	$0.02 \pm 0.03$	0.53	0.60
		Traffic (location) $\times$ killed	$-0.14 \pm 0.07$	-2.06	0.06

SE, standard error.

**Figure 4**

Selection ratios for the 3-h movement steps of 19 coyotes fitted with GPS collars, 7 of which were killed in vehicle collisions during the study period (road killed, red) and 12 that were not (survived, blue). The selection ratios were calculated using (value of used steps/value of available steps) for the following metrics: the proportion of used and available steps *crossing roads*; the percent of daily *traffic at time of crossing* occurring during each 3-h step that crossed a road (traffic); and the *traffic at crossing location* measured as the number of cars per hour at the road section crossed by the step.

behavioral flexibility that enables some coyotes to delay activity, and associated road crossing, until late at night may partly explain why coyotes and other species are able to thrive in urban areas.

Other authors have successfully identified spatial hot spots of wildlife–vehicle collisions for the purposes of advancing mitigation (Ramp et al. 2005) and we advance that framework by suggesting that identifying hot spots in time could be just as important. In particular, we have shown that an overlap between high traffic volume and activity may explain patterns of vehicle-caused mortality for urban coyotes when measured at the level of both individuals and populations. These relationships suggest that animals may be misled by changing relationships between traffic volume and dusk, but some animals reduce their risk of mortality by concentrating their activity late at night when traffic volumes are consistently low.

Managers could address the vulnerability stemming from mismatch in light cues in several ways. For example, they could add devices that detect and signal the arrival of either vehicles (via headlights; e.g., DeerDeter 2015) or wildlife (via thermal cameras; e.g., Crosstek 2012). Managers could also encourage populations of urban wildlife to become more nocturnal (Lowry et al. 2013). Hazing programs (e.g., Humane Society of the United States 2009) of carnivores that are active during the day might be one way to accelerate a shift to nocturnal activity for many species, potentially encouraging wildlife movement and survival while decreasing the probability of vehicle collisions and encounters with people. However achieved, an increased emphasis on temporal segregation of humans and wildlife might support complementary approaches based on spatial segregation, ultimately fostering greater coexistence of humans and wildlife.

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**Handling editor:** Bob Wong

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