Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality

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Traffic collisions can be a major source of mortality in wild populations, and animals may be expected to exhibit behavioral mechanisms that reduce the risk associated with crossing roads. Animals living in urban areas in particular have to negotiate very dense road networks, often with high levels of traffic flow. We examined traffic-related mortality of red foxes (*Vulpes vulpes*) in the city of Bristol, UK, and the extent to which roads affected fox activity by comparing real and randomly generated patterns of movement. There were significant seasonal differences in the number of traffic-related fox deaths for different age and sex classes; peaks were associated with periods when individuals were likely to be moving through unfamiliar terrain and would have had to cross major roads. Mortality rates per unit road length increased with road magnitude. The number of roads crossed by foxes and the rate at which roads were crossed per hour of activity increased after midnight when traffic flow was lower. Adults and juveniles crossed 17% and 30% fewer roads, respectively, than expected from randomly generated movement. This highly mobile species appeared to reduce the mortality risk of minor category roads by changing its activity patterns, but it remained vulnerable to the effects of larger roads with higher traffic flows during periods associated with extraterritorial movements. **Key words:** aversive behavior, carnivora, dispersal, extra-territorial movements, habitat fragmentation, risk-sensitive behavior, urbanization. [Behav Ecol 18:716–724 (2007)]

Roads exert a wide range of ecological effects, including the mortality risk posed by vehicles (Slater 1994; Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000; Erritzoe et al. 2003; Jaeger et al. 2005), which can lead to local declines and changes in population structure (Fahrig et al. 1995; Mumme et al. 2000; Aresco 2005; Gibbs and Steen 2005). Consequently, traffic may exert a significant yet recent selective pressure, with individuals adopting movement patterns to minimize the risk posed by vehicles (Shine et al. 2004; Whittington et al. 2004; Andrews and Gibbons 2005; Jaeger et al. 2005). Road characteristics known to affect mortality rates and movement behavior include road width, traffic volume, and traffic speed (Rolley and Lehman 1992; Romin and Bissonette 1996; Clarke et al. 1998; Jones 2000; Goossem 2001; Dyer et al. 2002; Cleverenger et al. 2003; Kaczensky et al. 2005), although these components are generally highly correlated, that is, major roads are wider, carry higher volumes of traffic, and at higher speeds.

At an interspecific level, larger species are less likely to be at risk because body size affects the speed with which species can traverse roads (Jaarsma et al. 2006). Similarly, roadside characteristics that affect driver visibility may significantly influence the risk of collision (Romin and Bissonette 1996; Cleverenger et al. 2003; Malo et al. 2004; Saeki and Macdonald 2004). Conversely, as roads are an evolutionarily recent phenomenon, some species may display maladaptive responses to traffic, for example, “freezing” (Mazerolle et al. 2005).

At an intraspecific level, factors such as age, sex, reproductive status, and social status may affect the number of times individuals have to cross roads due to foraging, reproductive, or territorial activities. These factors may also affect an individual’s ability to process proximate cues and take appropriate action when a road is encountered, for example, juvenile animals may be less capable of judging vehicle speeds and/or avoiding vehicles once on the road because their sensory and motor skills are still developing. One corollary of this is that juveniles that are less wary may be less likely to survive to adulthood, such that traffic mortality would act as a selective mechanism leading to increased “road awareness” in older age classes. Similar age-related changes in the degree of awareness could also arise as a consequence of learning.

At the most basic level, animals can minimize the risk posed by traffic by configuring their home range to avoid or minimize contact with roads per se (McLellan and Shackleton 1988; Brody and Pelton 1989; Thurber et al. 1994; Tigas et al. 2002), although this becomes increasingly difficult as road density, body size, and animal density increase and/or fragments of natural habitats decrease in size (Tigas et al. 2002). For example, in very dense urban road networks, individuals may be able to align home-range boundaries along major roads, thereby reducing or eliminating the need to cross the busiest roads, but they still have to traverse smaller roads regularly (Rondinini and Doncaster 2002). Alternatively, animals may adjust movement within range boundaries, for example, limiting the number of times that roads are crossed and/or rapidly crossing roads as they are encountered (Shine et al. 2004; Andrews and Gibbons 2005).

Such within-range adjustments may be evident from comparisons of real and simulated patterns of movement (Rondinini and Doncaster 2002; Whittington et al. 2004). Relatively few such studies have been undertaken, however, possibly because of the problems associated with collecting fine-scale...
high-resolution movement data from free-ranging animals. Furthermore, studies have tended to focus on the conservation implications of major roads within blocks of natural or seminatural habitats (Roobitaille and Laurence 2002; Kramer-Schadt et al. 2004). Less attention has been focused on the effects of dense networks of minor roads carrying relatively small volumes of traffic and on species that are not of conservation concern. However, common species can represent useful models to identify factors that may influence the mortality risk faced by rarer taxa and how the behavior of species that do not seem to be detrimentally affected by roads compares with those that are. Urban-dwelling species may, therefore, be useful model organisms as they occupy a habitat dominated by major and minor category roads, yet are often highly successful and tolerant of human observers. Furthermore, urban areas are becoming increasingly important in the wider landscape as they expand to support the increased demand for housing, thereby further impinging on and fragmenting natural habitats (McKinney 2002; Tigas et al. 2002) including conservation reserves (Ramp et al. 2006). Conversely, urban areas may represent potential refuges for some species (e.g., kit fox Vulpes macrotis mutica; Cypher and Frost 1999).

The red fox (Vulpes vulpes) is widely distributed throughout towns and cities in southern Britain (Harris and Rayner 1986; Wilkinson and Smith 2001) and is becoming increasingly common in urban areas in other countries (Willingham et al. 1996; Adkins and Stott 1998; Marks and Bloomfield 1999; Hofer et al. 2000; Tsukada et al. 2000). It is a highly agile medium-sized carnivore (adult mass 4–8 kg; Harris and Lloyd 1991) that is able to traverse roads rapidly and that avoids foraging on roads and roadside verges (Saunders et al. 1997). Nevertheless, traffic mortality is a major cause of death (Harris and Smith 1987), although seasonal variation in patterns of traffic-induced mortality and the effects of different categories of road are not known.

In this study, we use data from a long-term study in Bristol, UK, to examine the effect of roads on mortality patterns and ranging behavior of foxes. We address the following specific hypotheses. First, more foxes will be killed per unit length on higher category roads because mortality risk will increase with traffic load and speed. Second, traffic-induced mortality will be higher at those times of year when foxes are more active and range more widely. Specifically, traffic-induced mortality will be higher for 1) adult males in winter due to extraterrestrial movements associated with mating activities (White et al. 1996; Baker et al. 2004); 2) juveniles, particularly males, in autumn and winter due to dispersal movements away from the natal territory (Harris and Trewella 1988); and 3) adult females in spring and summer due to the increased energetic burden associated with the provisioning of cubs, which may increase their likelihood of making extraterrestrial movements (Baker, Harris, et al. 2001). Third, at a general level, foxes will show avoidance of crossing roads due to the associated mortality risks. Fourth, this avoidance behavior will have a temporal component associated with 1) the age- and sex-specific changes in behavior during the annual reproductive cycle highlighted above and 2) changes in traffic flow during the course of each period of nocturnal activity. Fifth, this avoidance will be more pronounced in older individuals due to learned behavior and/or selection against road-naive juveniles. Data on the recovery of fox carcasses for necropsy are used to quantify age, sex, and seasonal differences in the number of animals killed on roads and the relative mortality rate per unit length of different road types (hypotheses 1–2).

Radio tracking data from foxes living in one suburb within the city are compared with randomly generated movement data to test for age, sex, and seasonal differences in the number of roads crossed and the rate of road crossings per hour of activity on a nightly basis (hypotheses 3–5).

METHODS

Pattern of fox mortality

Seasonal trends in traffic-related mortality were derived from carcasses collected during 1977–1989 throughout the city of Bristol, UK. At the onset of this study, the continuous urban area covered approximately 116 km², with a human population of 510 000 people (Harris 1981). Requests were made annually through the local media that resident householders report fox carcasses for collection and the cleansing departments of the 3 local authorities, who were responsible for removing animal carcasses reported to them, were also contacted. Only those foxes recovered dead on roads have been included in the current analyses. For aging purposes, all animals were assumed to have been born on April 1 (Harris and Trewella 1988). The terms juvenile and adult refer to animals aged <12 months and ≥12 months, respectively.

Chi-squared tests were used to compare 1) the number of animals recovered dead in each season assuming an equal distribution and 2) the number of animals recovered dead on each road type compared with the number expected based on the total length of that road type. Seasons were spring, March–May; summer, June–August; autumn, September–November; winter, December–February. In declining order of magnitude, 4 road types were utilized: 1) motorways (6 lane highway i.e., 3 lanes of traffic in either direction, national speed limit 70 mph/113 km h⁻¹); 2) A-category roads (2 lanes with 30 or 40 mph speed limit [48–64 km h⁻¹] or 4 lanes with 40 or 50 mph [64–80 km h⁻¹] limit); 3) B-category roads (2 lanes, predominantly 30 mph/48 km h⁻¹ speed limit); and 4) C-category (2 lanes, 30 mph/48 km h⁻¹ speed limit) and other lower category (1 or 2 lanes, 30 mph/48 km h⁻¹ limit, some small not surface dressed) roads combined (Department of Transport 1994). In terms of function, motorways are primarily intercity routes but also convey traffic into urban areas; A-roads are the major thoroughfares throughout the city; B-roads principally connect A-roads; and C/unclassified roads are minor thoroughfares that permeate industrial and residential suburbs. For some analyses, motorways and A-roads were combined due to the scarcity of the former within the city limits. Road lengths were measured from a scale map using a digitizer. Lengths of all motorways, A-, and B-category roads were measured directly. The total length of lower category roads was extrapolated from 130 randomly selected 0.25 km² grid squares. Post hoc groupings were identified as outlined by Siegel and Castellan (1988).

Movement study

Radio tracking was undertaken within a 1.5 km² residential suburb (>1000 houses per km²) in the northwest of the city during March 1990 to June 1994 prior to an outbreak of sarcoptic mange (Sarcoptes scabiei). During this period, fox density ranged from 10 to 37 adults per km² (Baker et al. 2000; Baker, Newman, and Harris 2001); average annual territory size varied from 18 to 29 ha (Baker et al. 2000). The study area consisted mainly of residential houses and associated gardens; other habitats present were a cemetery and sports fields (Saunders et al. 1997). The site was bordered by A-category roads to the north, east, and south and by a B-category road to the west; all roads within the study area were C-category or unclassified. Animals were captured in cage traps in residential gardens (Baker, Harris, et al. 2001), sexed, weighed, aged by incisor wear (Harris 1978), and ear...
Tagged (Rototags, Dalton Supplies Ltd, Henley-on-Thames, Oxon, UK). Animals >6 months old were fitted with fixed radio collars (<250 g) manufactured at the University of Bristol; animals <6 months were fitted with expanding radio collars (Robertson and Harris 1996; Robertson et al. 2000). Animals were handled by physical restraint or sedated with ketamine hydrochloride.

Tracking was conducted on foot using a 3-element handheld antenna and CE12 receiver (Custom Electronics of Urbana, IL). Individual foxes were followed by a single person continuously for an 8-h period from 20.00 to 04.00 GMT, which reflects the peak movement activity of foxes in the study area (White et al. 1996) and coincides with changing traffic flows (Figure 1). Up to 4 animals were followed on a single night, but a maximum of 2 animals from the same social group were monitored simultaneously to minimize disruption of behavior. Locational fixes were recorded every 5 min. At each fix, animals were assigned to a 25 × 25-m grid cell and classified as active or inactive based on fluctuations in the signal received. Only nights where all 97 fixes had been collected were analyzed.

The observed absolute number of roads crossed in each tracking session (night) was determined by plotting each location sequentially within the software TRACKEr (Campnotus AB, Radio Location Systems AB, Huddinge, Sweden) overlaid on a 1:5000 scale map. We calculated the rate of road crossing per hour of activity by dividing the absolute number of roads crossed by the amount of time the fox was active.

The expected number of roads crossed per night was estimated from randomly generated patterns of movement (hereafter, “simulated” movement) using the random walk model developed by White and Harris (1994). Ten simulated nights were generated for every night of real data. In each simulation, the first location was taken as the initial position in the corresponding observed data. A series of consecutive locations equal to the number of active fixes in the observed data was then generated. Movements from each location were generated by applying a randomly selected distance moved and bearing in accordance with the sex and age of the animal and the position of the location within the home range. Foxes are likely to show differences in movement in relation to, for example, physical development and reproductive condition. In addition, patterns of movement within and outside core areas are markedly different, the former being associated with smaller interfix distances and more frequent turning. Therefore, sets of observed distances and bearings moved between successive locations were obtained from the radio tracking data for each 1) sex and 2) age class within 3) each season and for movements 4) within and 5) outside core areas (Table 1). There was no significant difference in distances and bearings moved before and after midnight, so data were not stratified at this level. Core areas were defined as 50% kernel density isopleths (Worton 1989); optimal smoothing parameters for kernel isopleths for each animal in each season were calculated using the method outlined by Wray et al. (1992). For each simulated movement, a distance and bearing were randomly and independently selected from the corresponding set of observed distances and bearings (summarized in

### Table 1
Average distance and relative bearing moved between successive 5-min movements used in the simulation of random seasonal movement patterns

<table>
<thead>
<tr>
<th>Season</th>
<th>Age</th>
<th>Sex</th>
<th>n</th>
<th>Distance moved (m)</th>
<th>Relative bearing (°)</th>
<th>n</th>
<th>Distance moved (m)</th>
<th>Relative bearing (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>Adult</td>
<td>♂</td>
<td>1468</td>
<td>77.1 ± 72.1</td>
<td>−2.5 ± 80.0</td>
<td>1662</td>
<td>57.8 ± 68.5</td>
<td>−6.2 ± 84.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>1907</td>
<td>73.9 ± 77.4</td>
<td>4.3 ± 82.7</td>
<td>1619</td>
<td>44.8 ± 63.0</td>
<td>−1.98 ± 81.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>138</td>
<td>44.4 ± 45.9</td>
<td>14.0 ± 95.5</td>
<td>747</td>
<td>5.2 ± 10.9</td>
<td>5.2 ± 69.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>20</td>
<td>30.7 ± 29.7</td>
<td>36.0 ± 87.8</td>
<td>157</td>
<td>14.8 ± 45.6</td>
<td>−8.6 ± 88.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>1208</td>
<td>90.0 ± 84.5</td>
<td>0.2 ± 84.8</td>
<td>1756</td>
<td>70.0 ± 73.3</td>
<td>24 ± 87.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>1677</td>
<td>71.7 ± 67.2</td>
<td>2.5 ± 83.5</td>
<td>1391</td>
<td>58.8 ± 73.3</td>
<td>−0.6 ± 86.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>1899</td>
<td>49.1 ± 62.7</td>
<td>−1.4 ± 94.8</td>
<td>2328</td>
<td>25.7 ± 50.0</td>
<td>0.5 ± 94.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>977</td>
<td>48.3 ± 60.3</td>
<td>3.0 ± 89.3</td>
<td>1453</td>
<td>32.7 ± 48.5</td>
<td>0.5 ± 94.8</td>
</tr>
<tr>
<td>Autumn</td>
<td>Adult</td>
<td>♂</td>
<td>1059</td>
<td>80.0 ± 71.3</td>
<td>−2.3 ± 79.1</td>
<td>1291</td>
<td>60.9 ± 70.4</td>
<td>1.1 ± 83.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>1117</td>
<td>80.1 ± 87.0</td>
<td>0.9 ± 88.3</td>
<td>1165</td>
<td>53.2 ± 53.1</td>
<td>3.5 ± 90.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>351</td>
<td>54.8 ± 62.2</td>
<td>−0.8 ± 85.3</td>
<td>646</td>
<td>33.1 ± 42.3</td>
<td>−7.9 ± 81.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>95</td>
<td>38.9 ± 40.6</td>
<td>−8.6 ± 96.8</td>
<td>137</td>
<td>22.1 ± 28.2</td>
<td>3.9 ± 93.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>858</td>
<td>87.5 ± 82.7</td>
<td>7.6 ± 77.5</td>
<td>1353</td>
<td>65.7 ± 77.5</td>
<td>2.6 ± 85.1</td>
</tr>
<tr>
<td>Winter</td>
<td>Adult</td>
<td>♂</td>
<td>661</td>
<td>66.5 ± 70.9</td>
<td>0.2 ± 74.2</td>
<td>612</td>
<td>58.7 ± 75.0</td>
<td>−1.6 ± 76.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>352</td>
<td>42.9 ± 52.4</td>
<td>5.2 ± 69.3</td>
<td>355</td>
<td>26.4 ± 32.5</td>
<td>2.5 ± 78.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>126</td>
<td>89.2 ± 79.4</td>
<td>2.7 ± 68.9</td>
<td>120</td>
<td>64.7 ± 65.6</td>
<td>−5.4 ± 88.8</td>
</tr>
</tbody>
</table>
Table 1) and applied to the current position; if the movement resulted in the new position lying outside the home range, the movement was recalculated. Home ranges were defined as 100% minimum convex polygons (Saunders et al. 1993).

Due to small sample sizes for juvenile animals, for statistical analyses, seasons were merged as 1) spring and summer (juveniles are wholly or partially nutritionally dependent on adults and have not yet started to disperse) and 2) autumn and winter (dispersal and mating periods). However, due to the inherent differences in the ranging behavior of adults and juveniles in some seasons (Saunders et al. 1993; White and Harris 1994; Robertson et al. 2000), simulated data were created separately for each season before being combined.

We used mixed-effects models fitted by REML within Brodgar (Highland Statistics Ltd, Newburgh, UK) to determine the effects of sex, age, season, and data type (observed or simulated) on 1) the number of roads crossed and 2) the rate of road crossings per hour of activity throughout the whole 8-h tracking period; if foxes were showing avoidance of roads, the observed number of roads crossed would be significantly lower than predicted by the simulated data. We also used mixed models to determine the effects of sex, age, season, and the time of night (20.00–00.00 GMT, hereafter termed “before midnight,” vs. 00.00–04.00 GMT, hereafter termed “after midnight”) on 3) the number of roads crossed and 4) the rate of road crossings per hour of activity; time of night corresponded to half-nights (4-h periods) of tracking. If foxes were avoiding crossing roads when the volume of traffic was highest, the number of roads crossed per 4-h period and the rate at which roads were crossed per hour of activity would be higher after midnight, when traffic volumes were lower (Figure 1). In these models, a full or half-night was the basic unit of analysis; sex, age, season, time of night, and data type were treated as nominal fixed variables; individual foxes were treated as random effects; and fox × year × season was the repeated effect to account for repeated measurements of specific individuals over time. A first-order autoregressive covariance structure was employed due to potential dependence in the data between successive measurements over time. Because we were interested in the relative influence of different parameters and the direction of this influence, rather than deriving specific “best” models, we entered all the fixed effects and their interactions together into the models, thereby avoiding the potential pitfalls of stepwise techniques for model selection (Whittingham et al. 2006).

All figures quoted are mean ± standard error.

**RESULTS**

Pattern of fox mortality

Significantly more adult males were recovered dead in winter than in any other season ($\chi^2 = 34.26$, $P < 0.001$, $n = 263$; Figure 2), with 25% of recoveries occurring in January alone. There was no seasonal difference in the number of adult females recovered dead ($\chi^2 = 3.72$, $P = 0.293$, $n = 242$). Both juvenile males ($\chi^2 = 54.76$, $P < 0.001$, $n = 336$) and juvenile females ($\chi^2 = 48.80$, $P < 0.001$, $n = 254$) were significantly less likely to be recovered in spring and most likely to be recovered in summer. Recoveries of juvenile females, but not juvenile males, declined in autumn and winter.

Significantly more foxes were recovered dead on higher magnitude roads relative to the number expected given their total length in all age and sex categories (adult males: $\chi^2 = 358.67$, $P < 0.001$; adult females: $\chi^2 = 402.98$, $P < 0.001$; juvenile males: $\chi^2 = 492.71$, $P < 0.001$; juvenile females: $\chi^2 = 252.98$, $P < 0.001$; Figure 3). Combining data for all individuals, the mean number of animals recovered per km per year was 0.34, 0.21, and 0.04 for motorways/A-roads, B-roads, and C/unclassified roads, respectively.

Movement study

Fifty-two foxes ($30^\text{M}, 22^\text{F}$) were radio tracked for 75 animal seasons ($n = 411$ nights: Table 2). Seventeen ($7^\text{M}, 10^\text{F}$), 28 ($20^\text{M}, 8^\text{F}$), and 7 ($3^\text{M}, 4^\text{F}$) animals were tracked as an adult only, as a juvenile only, and as both a juvenile and adult,

<table>
<thead>
<tr>
<th>Season</th>
<th>Juvenile</th>
<th>Adult</th>
<th>Juvenile</th>
<th>Adult</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring/summer</td>
<td>22 (61)</td>
<td>9 (76)</td>
<td>11 (31)</td>
<td>12 (89)</td>
<td>54 (257)</td>
</tr>
<tr>
<td>Autumn/winter</td>
<td>4 (24)</td>
<td>6 (68)</td>
<td>2 (7)</td>
<td>9 (55)</td>
<td>21 (154)</td>
</tr>
<tr>
<td>Total</td>
<td>26 (85)</td>
<td>15 (144)</td>
<td>13 (38)</td>
<td>21 (144)</td>
<td>75 (411)</td>
</tr>
</tbody>
</table>

Figures are the number of animal seasons. Figures in parentheses are the number of nights’ data collected.
respectively. Animals were tracked for between 1 and 26 nights in spring/summer and between 1 and 28 nights in autumn/winter.

Data type (real or simulated), age, and the interaction between age and season significantly affected the number of roads crossed per night and the number of roads crossed per hour active (Table 3, Figure 4); no other factors alone or in combination were significant. Overall, foxes crossed 20% fewer roads than expected from the simulated data (17.1 ± 0.7 vs. 21.3 ± 0.6; n = 411 nights) with adults and juveniles crossing 17% (19.5 ± 0.8 vs. 23.5 ± 0.8; n = 288 nights) and 30% (11.3 ± 0.9 vs. 16.1 ± 0.9; n = 123 nights) fewer roads than simulated, respectively.

Age, season, time of night, and the interactions between age and season, season and time of night, sex and age, and sex and season significantly affected the absolute number of roads crossed per half-night and the rate at which foxes crossed roads per hour of activity (Table 4, Figure 5). Adults crossed significantly more roads per half-night and at a higher rate than juveniles. Significantly more roads were crossed in each half-night during spring/summer compared with autumn/winter (Table 4a), but the higher rate of road crossing in spring/summer was not sufficiently different to show up as significant in the pairwise analysis (Table 4b). Significantly fewer roads were crossed in the 4-h period before (6.6 ± 0.3; n = 411 half-nights) compared with after (10.5 ± 0.4; 720

Figure 4
Observed (shaded) and simulated (unshaded) mean (a) number and (b) hourly rate of road crossings per night for individuals of different sex and age categories in different seasons.

Table 3
Fixed effects for the mixed models relating to (a) the number of roads crossed by individual foxes per night derived from real and simulated data and (b) the rate of road crossings per hour during the night

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>ANOVA</th>
<th>Coefficient ± SE</th>
<th>df</th>
<th>t</th>
<th>P</th>
<th>Class</th>
<th>Mean ± SE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>Age (Ad)</td>
<td>$F_{1,20} = 11.6$, $P = 0.002$</td>
<td>13.3 ± 3.10</td>
<td>29</td>
<td>4.30</td>
<td>&lt;0.001</td>
<td>Ad: Ad: Sp/su 3.5</td>
<td>19.5 ± 0.8</td>
<td>288</td>
</tr>
<tr>
<td></td>
<td>Data type (Sim)</td>
<td>$F_{1,718} = 42.4$, $P &lt; 0.001$</td>
<td>4.34 ± 1.22</td>
<td>718</td>
<td>3.57</td>
<td>&lt;0.001</td>
<td>Juv: Sp/su 1.8</td>
<td>17.1 ± 0.7</td>
<td>411</td>
</tr>
<tr>
<td></td>
<td>Age (Ad) × season (Au/wi)</td>
<td>$F_{1,11} = 6.0$, $P = 0.028$</td>
<td>−10.31 ± 3.75</td>
<td>14</td>
<td>−2.75</td>
<td>0.016</td>
<td>Juv: Au/wi 1.5</td>
<td>21.3 ± 0.6</td>
<td>411</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td></td>
<td>9.28 ± 2.05</td>
<td>718</td>
<td>4.52</td>
<td>&lt;0.001</td>
<td>Juv: Au/wi 1.5</td>
<td>16.7 ± 1.0</td>
<td>123</td>
</tr>
<tr>
<td>(b)</td>
<td>Age (Ad)</td>
<td>$F_{1,20} = 21.3$, $P &lt; 0.001$</td>
<td>2.05 ± 0.43</td>
<td>29</td>
<td>4.82</td>
<td>&lt;0.001</td>
<td>Ad: Au/wi 3.5</td>
<td>1.4 ± 0.1</td>
<td>123</td>
</tr>
<tr>
<td></td>
<td>Data type (Sim)</td>
<td>$F_{1,718} = 55.1$, $P &lt; 0.001$</td>
<td>0.72 ± 0.19</td>
<td>718</td>
<td>3.72</td>
<td>&lt;0.001</td>
<td>Juv: Au/wi 3.2</td>
<td>2.9 ± 0.1</td>
<td>411</td>
</tr>
<tr>
<td></td>
<td>Age (Ad) × season (Au/wi)</td>
<td>$F_{1,11} = 10.2$, $P = 0.007$</td>
<td>−1.54 ± 0.47</td>
<td>14</td>
<td>−3.28</td>
<td>0.005</td>
<td>Juv: Au/wi 3.2</td>
<td>3.7 ± 0.1</td>
<td>411</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td></td>
<td>1.44 ± 0.29</td>
<td>718</td>
<td>4.93</td>
<td>&lt;0.001</td>
<td>Juv: Au/wi 1.5</td>
<td>1.5 ± 1.2</td>
<td>92</td>
</tr>
</tbody>
</table>

Results are shown relative to the reference categories (data type: real; age: juvenile; season: spring/summer).

Notes
- Ad, adult; Juv, juvenile; Sim, simulated data; Sp/su, spring/summer; Au/wi, autumn/winter.
- Figures indicate mean ± standard error (SE) number of roads crossed per night (model a) or mean ± SE number of roads crossed per hour active (model b); n indicates number of nights.

Figure 4
Observed (shaded) and simulated (unshaded) mean (a) number and (b) hourly rate of road crossings per night for individuals of different sex and age categories in different seasons.
Results are shown relative to the reference categories (age: juvenile; sex: male; season: spring/summer; time of night: before midnight).  

Figures indicate mean ± standard error (SE) number of roads crossed per night (model a) or mean ± SE number of roads crossed per hour active (model b); n indicates number of half-nights.

n = 411 half-nights) midnight (Table 4a), but again the higher rate of road crossing was not sufficiently different to show up as significant in the pairwise analysis (Table 4b).

**DISCUSSION**

The seasonal pattern of traffic-induced mortality observed largely reflects the known behavior of adult and juvenile foxes. The peak in the number of adult males recovered in winter correlates with their extraterritorial movements in relation to extrapair mating strategies (Zimen 1984; White et al. 1996; Baker et al. 2004) rather than a simple increase in activity associated with increased hours of darkness. For example, males are active for 9.5 h each day during winter compared with 8.2 h during spring (Saunders et al. 1993), an increase of 16%. In comparison, there was a 2.1-fold increase in the number of animals recovered dead, implying that off-range movements pose a much greater risk than simple changes in activity levels. However, there was no increase in the number of adult females recovered during spring, when lactating individuals also make extraterritorial movements (Baker, Harris, et al. 2001). The low number of juveniles recovered in spring and the subsequent increase in summer mirrors their developing pattern of ranging behavior (Robertson et al. 2000). The different patterns of recovery of males and females in autumn and winter are consistent with the male bias in dispersal (Harris and Trewella 1988).

Overall, therefore, peaks in the number of recoveries were associated with periods when foxes were likely to be moving more per se (Saunders et al. 1993) and, in particular, through unfamiliar terrain. For adult males and dispersing juveniles, this novel ground was off the individual’s territory; for animals <6 months old, it was on the natal territory as the area they ranged over increased (Robertson et al. 2000). These data,
therefore, indicate marked costs to dispersal and extrapair mating movements.

The number of recoveries per unit length declined consistently with decreasing road magnitude across all age-sex categories. This is likely to relate directly to the risks associated with crossing wider roads carrying larger volumes of traffic at greater speeds. However, foxes killed on busier roads may be more likely to be reported, which could exacerbate between-season comparisons of the number of each sex-age class recovered if there were inherent biases in the types of road on which that subgroup of animals was killed. Yet, given the effort expended both on advertising the study and the assistance of organizations responsible for the collections of carcasses both within the city limits and on motorways, it is unlikely that such biases are present in our data set. Thus, we believe our results reflect real differences in behavior.

Overall, adults crossed more roads than juveniles, reflecting their generally longer activity periods and larger home ranges (Saunders et al. 1993; Robertson et al. 2000). However, adults also showed seasonal differences, crossing more roads in spring/summer than in autumn/winter, associated with the provisioning of nutritionally dependent cubs (Baker et al. 1998). The number of roads crossed by adult males during autumn/winter was greater than for females and reflects the increased home-range size and increased activity of males associated with mating (White and Harris 1994; Baker et al. 2004).

Yet, both adult and juvenile foxes crossed significantly fewer roads than expected based on simulated movement patterns, indicating a negative effect of roads on fox movement patterns. The lack of any significant interaction between data type and age indicates that there was no evidence that individuals “learnt” to avoid roads more as they got older and/or that road-naive individuals perished as juveniles. Indeed, juveniles showed a greater degree of avoidance, crossing 30% fewer roads than expected compared with 17% for adults.

The percentage of reduction in the frequency of road crossing shown by these foxes is much higher than in other studies of similar species in natural or seminatural environments, where road density is much lower. For example, Whittington et al. (2004) estimated that gray wolves (Canis lupus) crossed roads, trails, and railway lines 10% less often than expected in Jasper National Park, Canada. At first glance, the magnitude of this aversion may appear surprising in the context of the relative ease with which foxes can traverse minor category roads and the low volume of traffic present. Data collected by the local city council in winter 2002 on the busiest road within any of the fox territories indicated an average traffic flow of just 39 cars h⁻¹ (range 2-119) during 20.00-04.00 GMT (total ~300 vehicles in 8-h period), traveling at an average speed of 40 km h⁻¹ (road 4 in Figure 1). Even these relatively low levels of traffic flow can significantly affect fox behavior, however. For example, the mortality risk for a fox-sized animal crossing a road with a traffic flow of 10 vehicles h⁻¹ has been estimated as 0.03%, increasing to 0.25% with a flow of 100 vehicles h⁻¹ (Jaarsma et al. 2006). The foxes in the present study crossed an average of 6.55 and 10.53 roads before and after midnight, respectively, in the presence of traffic flow rates of 73 and 6 vehicles h⁻¹, providing strong evidence of temporal adaptation of movement patterns to avoid road traffic.

Such levels of avoidance of crossing roads could significantly reduce food intake rates and ultimately lower reproductive success. However, fox populations attain their highest densities in urban areas (Harris 1981; Harris and Rayner 1986) with no evidence for reduced reproductive output in dominant breeding females. One possible explanation for this apparent contradiction could be the abundance and spatial distribution of key food resources in urban areas. Red foxes are opportunistic predators, and although they consume small rodents, birds, invertebrates, and fruit in urban areas (Saunders et al. 1993), the major dietary component of the animals in this study was food deliberately supplied by resident householders (Baker et al. 2000). All of these food types are available in abundance in residential gardens (Ansell 2004), especially those at the rear of houses. Commonly, back gardens of houses on 3 or 4 adjoining roads are all connected such that foxes are able to move between many contiguous gardens without having to cross any roads. Blocks of houses, therefore, represent “superrich” foraging patches that animals do not have to leave often to meet their daily nutritional needs. Thus, foxes can easily confine large periods of activity to single blocks of houses, thereby only crossing roads to a limited degree with minimal impact on the rate at which they can acquire food.

Superabundant resources may also help to reduce the effects of roads on urban-dwelling species by allowing dominant animals to establish territories or home ranges within the boundaries formed by major roads. As resource density declines, ranges would have to increase in size to fulfill the requirements of resident individuals. At a critical point, this would necessitate that they spanned major roads and that

Figure 5
Mean (a) number and (b) hourly rate of road crossings per 4-h tracking period; before midnight shaded and after midnight unshaded.
animals had to cross those roads regularly for, for example, territorial defense. Consequently, traffic mortality may be increasingly important in low-productivity habitats, associated with low-density populations, as range size increases relative to the dispersion of major roads (see also Grinder and Krausman 2001).

In summary, the foxes in this study showed a high degree of aversion to crossing minor category roads although moving through novel areas. In particular, dispersing juveniles and cuckolding males had to cross major roads that tended to be utilized as territorial boundaries (Saunders et al. 1993), giving rise to significant costs to these behaviors. Yet, such extraterritorial movements are integral to facilitating connectivity within and between populations. Consequently, major roads in urban areas appeared to be acting as both a barrier to movement and as a potentially significant source of mortality for those animals likely to contribute to gene flow. Although unlikely to affect abundant species such as the red fox, increased mortality rates for animals undertaking these key processes may be more significant for less abundant and more widely dispersed species.

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REFERENCES


