

# The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision mortality



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## ABSTRACT

As human populations increase, roads are expanded and traffic increases, leading to more opportunities for animal–vehicle collisions. Roadkill is a serious threat to animal populations, and has the potential to drive threatened populations extinct. Despite this widespread damage, what makes a species' particularly vulnerable to being hit by vehicles is not well understood and mitigation attempts have been largely unsuccessful. Previous studies have found that animals are more likely to be killed in certain areas (hot-spots) and that species are killed at differential rates. While there have been some suggestions that variation in roadkill rate is correlated with life history traits, such as body size and diet, most of these studies have been on a small scale and therefore are not necessarily generalizable. We aimed to explain variation in roadkill vulnerability on a larger scale by performing a formal comparative analysis of published roadkill data from around the world. Focusing on birds and mammals, we compiled data on rates that species were struck and killed, then sought to identify the life history and natural history correlates of vulnerability. We found that diet explained a significant amount of variation in the rate of roadkill, with omnivorous mammals and herbivorous birds having the highest rates within their respective classes. Mitigation attempts should target these especially vulnerable types to increase efficiency and efficacy.

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## 1. Introduction

Human activity is a driving force behind the many environmental problems, including the currently high rate of extinctions (Vito-usek et al., 1997; Brodie et al., 2012). Roads create many problems, and road ecology is a rapidly expanding field (Coffin, 2007). Importantly, road systems are expanding rapidly in previously undeveloped areas (van der Ree et al., 2011). When they are built, roads cause immediate habitat loss. After this initial blow however, roads begin exerting a variety of other ecological effects. Road noise causes a decline in the reproduction success of the great tit (*Parus major*) (Halfwerk et al., 2011). Traffic noise drives bats and forest birds away from loud roads (Zurcher et al., 2010; Schaub et al., 2008; Goodwin and Shriver, 2010). The creation of roads also increases the edge habitat present in an ecosystem, allowing destructive edge species, such as brown-headed cowbirds (*Molothrus ater*) and raccoons (*Procyon lotor*), access into previously secluded core habitat (Howell et al., 2007; Donovan et al., 1997). In addition to creating physical edges, roads act as a barrier to movement between patches of habitat, leading to fragmentation. This has been observed in mammals of all sizes, reptiles, amphibians, birds, and insects (Coffin, 2007).

Perhaps the most graphic indication of how roads affect wildlife is the occurrence of roadkill, a consequence of animal–vehicle collisions. While clearly affecting animals on an individual level (as well as vehicle owners and drivers), vehicular collision mortality can also have deleterious effects at the population level, as seen in common wombats (*Vombatus ursinus*). Roger et al. (2011) developed a predictive population viability analysis model for wombats that showed that roadkill, when combined with other natural threats, could cause a significant decrease in population to the point of population inviability. In other words, road mortality can be the tipping factor sending a vulnerable population towards extinction.

Despite the negative effects and large scale of animal–vehicle collisions, this problem remains poorly understood. Some patterns have been identified but these are often specific to a species, population, or geographic location. In general, rates of roadkill tend to increase with traffic volume (Gunson et al., 2011), and with speed limit (Chambers et al., 2010). In addition, areas where roads intersect with favorable habitat for a particular species create roadkill “hotspots” that have much higher rates of roadkill for that species than the surrounding area (Clevenger et al., 2003; Jaeger et al., 2005; Gomes et al., 2009). It has also been shown that species are killed at different rates, indicating that some species may be more inherently vulnerable to being struck by a vehicle (McClure, 1951; Taylor and Goldingay, 2004; Ford and Fahrig, 2007; Brockie et al., 2009; Grilo et al., 2009; Barthelmeß and Brooks, 2010).

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While illustrative, a shortcoming of previous studies is that most have been conducted on a relatively small scale (i.e., by surveying only one section of road). This prevents their results from being generalizable. We aimed to fill this knowledge gap by performing a comparative analysis of a wide range of published roadkill data to explain interspecies variation in roadkill vulnerability on a large scale. We aimed to create generalizable results that could help aid future mitigation efforts.

Previous studies have suggested that certain life history variables (especially diet and body mass) may be important in explaining a species' vulnerability to roadkill (Ford and Fahrig, 2007; Barthelmess and Brooks, 2010; Møller et al. 2011). For our study, we wished to test these factors, as well as other life history variables that could have an effect on roadkill vulnerability. Our selected factors and their hypothesized effect on an animal's interaction with a motor vehicle are as follows:

1. Diet may have an effect on roadkill vulnerability, possibly due to feeding strategies, as suggested by Ford and Fahrig (2007) and Barthelmess and Brooks (2010).
2. Body mass was also suggested as an important factor by these same two studies, which found that medium sized mammals are killed more often on roads.
3. Scavengers may be attracted to carcasses, and by feeding on them may be hit themselves.
4. Flight initiation distance (the distance an individual flees from an approaching threat—Ydenberg and Dill, 1986; Blumstein, 2003) was included because animals that flee early may have a better chance of escaping a car as suggested by Møller et al. (2011).
5. Maximum sprint speed may permit animals to better escape and we hypothesized that mammals that run swiftly may be killed less often.
6. Time of activity (nocturnal, diurnal or crepuscular) may have an effect based on suggestions from a previous study (Sullivan, 2009).
7. Larger brains have been associated with spatial learning ability (Sherry et al., 1992; Healy and Krebs, 1996), and may thus give animals a better capability to avoid being hit by cars.
8. Longevity has been correlated with learning ability, so animals that live longer under natural conditions may be better able to learn to avoid cars (Rushton, 2004).
9. Since maternal care allows offspring to learn correct behavioral responses (Kedar et al., 2000), longer duration of maternal care may provide individuals with a better chance to learn from parents how to avoid cars.
10. Alternatively, an extended period of parental care is a mechanism creating groups, and if grouped animals are more vulnerable due to multiple animals being killed in a single incident, then we might see such species hit more frequently.
11. We predicted that social animals may have higher road mortality rates due to this potential grouping effect.
12. Finally, showy sexual dimorphisms (excessively long tails, large antlers, etc.) often confer a handicap (Zahavi, 1975) on the owner, which may impede an animal's attempt to escape an oncoming car.

We reviewed published roadkill data and analyzed these variables aiming to find which of these 12 factors best explained roadkill vulnerability. If any of these life history or natural history factors were associated with roadkill vulnerability, we might then be able to generate novel insights for targeted mitigation efforts.

## 2. Materials and methods

We focused on mammals and birds and gathered data by searching ISI Web of Science and Google Scholar for published roadkill studies using the terms 'roadkill' and 'road mortality' on 18 August 2011. The references of each paper located were also searched. We only included studies that reported animals identified down to the species level as well as the total length of road surveyed. Data from each study were summarized in a spreadsheet and organized by species. Data from 10 studies were used in the final analyses because these studies reported the total distance of road surveyed. Our data included 80 mammal species and 99 bird species. The total number of each species killed and the total length of road surveyed were combined across studies and divided to calculate the rate of roadkill for each species. Mammal and bird data were analyzed separately.

We created a list of life history traits to permit us to evaluate our 12 hypotheses (sources are provided in the appendices), and added the relevant information for each species to our database. These variables were: (1) diet (carnivore, omnivore, herbivore or insectivore); (2) body mass (g); (3) whether the species scavenge food; (4) flight initiation distance (in m); (5) maximum running speed (mammals only, in m/s); (6) time of activity (nocturnal, diurnal, crepuscular); (7) brain mass (g); (8) longevity (years); (9, 10) length of maternal care (days till fledging for birds, length of lactation in days for mammals); (11) sociality (social versus solitary, as provided in species descriptions which were based on whether the animal lived in groups or alone); and (12) sexual dimorphism (present/absent). Any study on roadkill can be affected by species' detectability because smaller animals are harder to see and/or identify properly after being struck by a vehicle. We controlled for detectability by including body size (in g) as a covariate in all analyses. We performed two complimentary analyses to test whether our variables were associated with the rate of roadkill.

First, using species values, we fitted a series of general linear models in SPSS v. 20 (IBM, Inc. 2011, New York, New York). Rate of roadkill and body mass were log-10 transformed to eliminate outliers and to achieve a more normal distribution. Our basic model included body mass, diet, and whether or not a species was reported to scavenge. We used this as the base model because we had a complete set of data for all species, and a previous study had indicated that these variables may be important (Ford and Fahrig, 2007). Scavenge was included as a separate variable from diet type because both carnivores and omnivores may scavenge at roadkills and this could enhance their vulnerability. We then used a forward addition procedure where we systematically added each of our other variables to the model one at a time. We added each variable singly because information on some of the factors was not available for all species, and including all of the variables at once would reduce the dataset to an unnecessarily small subset of complete data that was inadequate to properly evaluate any of the hypotheses. Variables that were not significant ( $p \geq 0.05$ ) when added to the basic model were excluded from further analysis.

Second, using the 'final' models developed from the forwards stepwise procedure, we fitted phylogenetic general least squares models (Garland and Ives, 2000) using the "caper" package in R (R Development Core Team, 2013). This analysis incorporated phylogenetic relationships to account for the similarity between close relatives. We obtained a supertree for mammals from Bininda-Emonds et al. (2007) and for birds from Jetz et al. (2012). These were trimmed, using Mesquite (Maddison and Maddison, 2011) for mammals and the website accompanying Jetz et al. (www.bird-tree.org) for birds, to include only the species in our dataset. We fitted the PGLS with these trees, as well as with trees with branch

lengths set to 1 (a transformation that assumes a punctuated rate of evolution).

We expected there to be fewer carnivores than herbivores based solely on energetic constraints (Heal and Maclean, 1975). If there were fewer carnivores to begin with, there will be fewer incidents of carnivore roadkill. To account for this, we calculated a confidence interval for the mean rates of roadkill of carnivores and herbivores and compared these to expected rates based on theoretical trophic level energetics. Our null hypothesis, based on trophic constraints, was that the carnivore mean should be 10% of the herbivore mean.

Finally, we tested whether the any variation in rate of roadkill was explained by phylogenetic signal, or “the tendency for related species to resemble each other more than they resemble species drawn at random from the tree” (Blomberg and Garland, 2002). The “caper” package in R was used to calculate a Pagel’s lambda maximum likelihood value for the rate of roadkill in birds and mammals. Using likelihood ratio tests, these values were compared to lambda set to one and zero. A value not significantly different from zero indicated no phylogenetic signal, while a value significantly different from zero and not significantly different from one indicated the presence of phylogenetic signal.

### 3. Results

#### 3.1. Mammals

Our study included 8028 individual records of mammalian roadkill tallied over a total of 3,972,437 km. Data came from 11 studies across 3 continents (Australia: Brockie, 2007; Hobday and Minstrell, 2008; North America: McClure, 1951; Oxley et al., 1974; Caro et al., 2000; Cleverger et al., 2003; Dodd et al., 2004; Smith-Patten and Patten, 2008; Barthelmess and Brooks, 2010; and South America: Cáceres et al., 2010). The records included 80 species from 32 families (Table A1 and Fig. A1).

Our final general linear model included rate of roadkill as the dependent variable and body mass, diet, scavenge and sociality as independent variables ( $R^2 = 0.200$ ,  $p = 0.010$ ,  $N = 80$  species). In the GLM, diet explained a significant amount of variance (partial eta squared = 0.118,  $p = 0.027$ ) as did body mass (partial eta squared = 0.088,  $p = 0.010$ ) and sociality (partial eta squared = 0.062,  $p = 0.032$ ). Scavenge was not significant (partial eta squared = 0.033,  $p = 0.121$ ). None of our other tested variables explained significant variation in the rate of roadkill when added to the basic model: longevity (partial eta squared = 0.003,

$p = 0.695$ ,  $N = 62$ ), brain mass (partial eta squared = 0.002,  $p = 0.793$ ,  $N = 39$ ), running speed (partial eta squared = 0.106,  $p = 0.175$ ,  $N = 23$ ), sexual dimorphism (partial eta squared = 0.004,  $p = 0.598$ ), or maternal care (partial eta squared = 0.0002,  $p = 0.899$ ,  $N = 80$ ).

The phylogenetic general least squares models were built identically, with one model having estimated branch lengths from the supertree, the other having branch lengths set to 1. In the model using supertree branch lengths, no variables were significant. In the model with branches set to 1, omnivores were killed significantly more than carnivores (Table 1).

In two out of three models, omnivores were killed significantly more than carnivores (GLM:  $p = 0.003$ , PGLS:  $p = 0.086$  and PGLS with branches set to 1:  $p = 0.024$ ), with omnivores having the highest rate of roadkill mortality and carnivores the lowest (Fig. 1). To test our trophic hypothesis for the decreased carnivore vulnerability, we calculated confidence intervals for each mean in order to examine the overlap between the carnivore mean, 10% of the herbivore mean and the herbivore confidence interval. The carnivore mean was within the herbivore confidence interval, as was the 10% mark (Fig. 1a). This indicates that the carnivore mean was not significantly different from the herbivore mean. In other words, carnivores are not being killed significantly less than herbivores, as would be expected based on abundance.

The maximum likelihood value for Pagel’s lambda was 0.129. This value was not significantly different from 0 ( $p = 0.393$ ), and significantly different from lambda = 1 ( $p < 0.0001$ ). This implies no phylogenetic signal in the rate of mammalian roadkill.

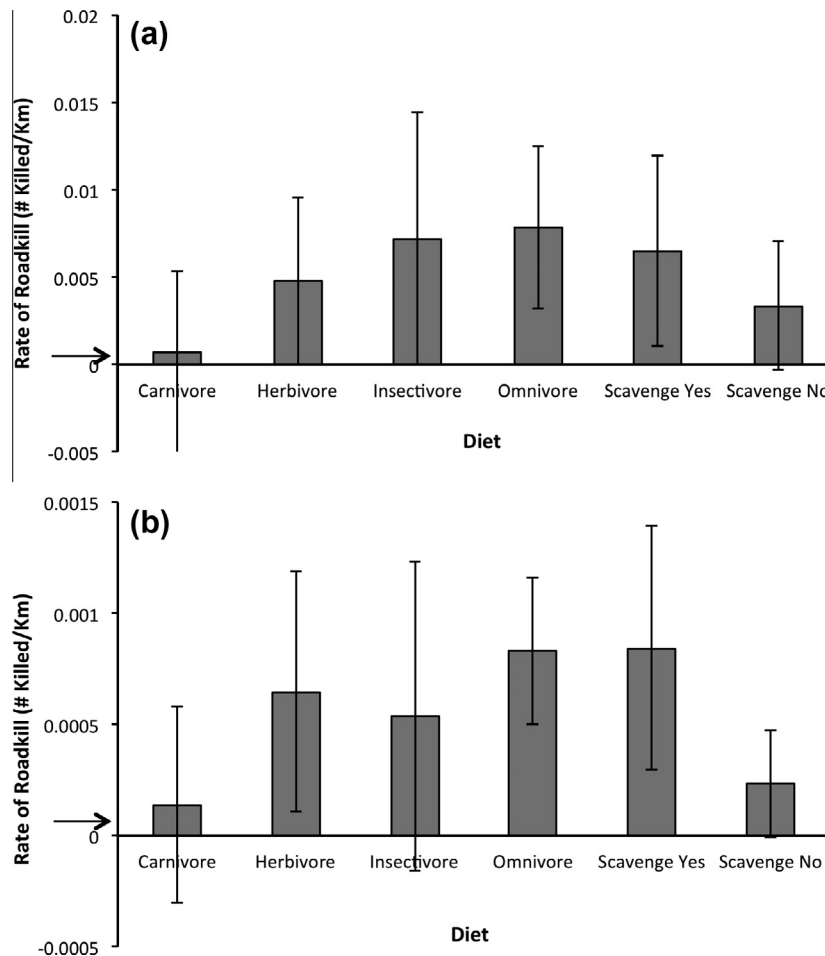
#### 3.2. Birds

There were a total of 2,236 bird mortalities tallied over 8,489,886 km of surveyed roads. Data came from 4 studies across 2 continents (North America: Cleverger et al., 2003; McClure, 1951; Australia: Brockie, 2007; Hobday and Minstrell, 2008). The records included 99 species from 32 families (Table A2 and Fig. A2).

Our base GLM was not significant ( $R^2 = 0.040$ ,  $p = 0.601$ ,  $n = 99$  species). Additionally, none of the other tested variables were significant when added to the base model: brain mass (partial eta squared = 0.02,  $p = 0.495$ ,  $N = 31$ ), longevity (partial eta squared = 0.014,  $p = 0.321$ ,  $N = 76$ ), sociality (partial eta squared = 0.011,  $p = 0.355$ ,  $N = 86$ ), night activity (partial eta squared = 0.009,  $p = 0.382$ ,  $N = 91$ ), FID (partial eta squared = 0.076,  $p = 0.147$ ,  $N = 34$ ), sexual dimorphism (partial eta squared = 0.005,  $p = 0.489$ ,  $N = 99$ ), maternal care (partial eta squared = 0.001,  $p = 0.846$ ,  $N = 84$ ).

**Table 1**  
Summary of analyses that studied variation in roadkill rates across diet type. We report parameter estimates, standard error and  $p$ -values for each variable for mammals (a) and birds (b). Significant  $p$ -values ( $p < 0.05$ ) are bold. In all cases, values contrast mortality rates with carnivores because in both mammals and birds, carnivores were killed at the absolutely lowest average rates.

Analysis	Body mass	Omnivore	Herbivore	Insectivore	Scavenge
<b>a</b>					
GLM	0.281 ± 0.106, <b><math>p = 0.010</math></b>	0.947 ± 0.305, <b><math>p = 0.003</math></b>	0.579 ± 0.353, $p = 0.105$	0.537 ± 0.426, $p = 0.212$	0.536 ± 0.342, $p = 0.121$
PGLS	0.304 ± 0.210, $p = 0.152$	0.493 ± 0.283, $p = 0.086$	0.405 ± 0.667, $p = 0.545$	0.496 ± 0.936, $p = 0.598$	0.337 ± 0.364, $p = 0.358$
PGLS Branches = 1	0.247 ± 0.202, $p = 0.225$	0.626 ± 0.272, <b><math>p = 0.024</math></b>	0.302 ± 0.648, $p = 0.642$	0.392 ± 0.887, $p = 0.660$	0.353 ± 0.340, $p = 0.303$
<b>b</b>					
GLM	0.071 ± 0.125, $p = 0.570$	0.288 ± 0.216, $p = 0.186$	0.401 ± 0.263, $p = 0.131$	0.206 ± 0.354, $p = 0.562$	0.315 ± 0.231, $p = 0.176$
PGLS	0.364 ± 0.281, $p = 0.199$	1.213 ± 0.442, <b><math>p = 0.007</math></b>	1.456 ± 0.513, <b><math>p = 0.006</math></b>	0.808 ± 0.622, $p = 0.198$	0.667 ± 0.498, $p = 0.184$
PGLS Branches = 1	0.294 ± 0.220, $p = 0.184$	1.027 ± 0.372, <b><math>p = 0.007</math></b>	1.289 ± 0.429, <b><math>p = 0.004</math></b>	0.437 ± 0.443, $p = 0.327$	0.489 ± 0.362, $p = 0.180$



**Fig. 1.** Average rates of roadkill across diet type in mammals (a) and birds (b). Bars represent 95% confidence intervals; arrows identify 10% of the herbivore mean.

In a PGLS model fitted with the basic variables, we found that herbivores and omnivores were killed significantly more than carnivores ( $p = 0.006$  and  $p = 0.007$ , respectively, see Table 1b and Fig. 1b). Scavenge and body mass were not significant ( $p = 0.184$  and  $p = 0.199$ ). When branches were set to 1, only herbivores were killed significantly more than carnivores ( $p = 0.037$ ). No other variables were significant.

Carnivores again had the lowest rate of roadkill, but the mean was slightly higher than 10% of the herbivore mean, and both were within the confidence interval calculated for herbivores (Fig. 1b). Carnivores, while killed the least, were killed more often than trophic level abundance could account for.

The Pagel's lambda maximum likelihood for bird rates of roadkill was 0. Compared to lambda = 0 this was not significantly different ( $p = 1.0$ ). When compared with lambda = 1, the difference was significant ( $p < 0.0001$ ). These values show a complete absence of phylogenetic signal in the rate of avian roadkill.

#### 4. Discussion

Taken together, our results show that after controlling for body size, diet type has a significant effect on a species' vulnerability to being struck and killed by a vehicle. Omnivorous mammals appear to be especially vulnerable, more so than any other diet type, while carnivores had the lowest absolute rate of roadkill. These results were largely consistent across the different phylogenetic and non-phylogenetic analyses. Despite having the lowest absolute

rate of roadkill, carnivores seemed to be hit more often than expected based on their estimated 'trophic' abundance. This indicates that carnivorous mammals also are particularly vulnerable to vehicular collision. In birds, diet was only significant when phylogenetic information was taken into account. Herbivorous and omnivorous birds were especially vulnerable and were killed at significantly higher rates than carnivores. Carnivores again had the lowest absolute rate of roadkill, but they were killed at higher rates than expected based on trophic considerations and thus they too are especially vulnerable to vehicular collisions.

Additionally, social mammals were killed less often than solitary ones, contrary to our original hypothesis that predicted that grouped animals would be more vulnerable due to the higher concentration of animals in the path of a car. Instead it is possible that groups of animals may benefit from increased vigilance, and therefore avoid cars better. A similar result is seen in Møller et al. (2011), which found that socially breeding birds were less prone to becoming roadkill. However, this result was not consistent across our analyses, and was only significant in the GLM.

Most previous studies have focused on patterns related to the road itself (e.g., speed limit, traffic volume, or the terrain the road passes through), rather than species-specific life history traits (Clevenger et al., 2003; Brockie, 2007; Smith-Patten and Patten, 2008; Hobday and Minstrell, 2008; Gomes et al., 2009; Gunson et al., 2011). We have shown that species-specific life history traits are also an influential factor in the occurrence of roadkill. Our results suggest that diet predisposes individuals of a species to be particularly vulnerable to being struck and killed by vehicles. The ab-

sence of any phylogenetic signal in the rate of roadkill confirms that the phylogeny of a species at level analyzed, and with the species included, does not foretell vulnerability; it is still possible that a detailed comparison of within class variation (e.g., within rodents or carnivores) might reveal that closely-related species are similar and that these similarities are due to some phylogenetic constraints. Nonetheless, this points towards the importance of species-specific traits in predicting roadkill vulnerability. Rather than being structured by family or genus, conservation and mitigation efforts should be organized based on groupings by other traits shown to be good predictors of vulnerability, especially diet type.

It should be stated that there are shortcomings associated with a review using previously published data. We were only able to use the data included in papers, which was not always consistent. As a result, we were not able to address a few of the common biases associated with roadkill studies. For instance, there is always error associated with sampling methods, carcasses decomposing, being removed by scavengers or humans before observation, or with animals dying only after moving some distance from the road (Slater, 2002; Prosser et al., 2008; Teixeira et al., 2013). Because few of the published studies recorded the date of each roadkill, we were not able to address issues of seasonality, a potentially important issue since it is possible that breeding season may be a factor in vulnerability (as suggested by Møller et al., 2011). Additionally, we were not able to use species density estimates, because the studies were conducted at different points in time and did not include this information. However, the comparison with trophic level estimates mitigates this somewhat. Finally, roadkill tends to become worn and unrecognizable after lying on the road. Small carcasses tend to dissipate more quickly and are more difficult to detect (Slater, 2002), which could lead to a bias in detection. To combat this, we used only data that confidently identified the specimen to the species level, and added body size to the model to check for skew towards larger animals due to their relative ease of detection. No skew was found, indicating that our data is without size bias.

What might explain diet specific vulnerability? Diet type tends to be associated with a suite of life history factors, such as range size, mobility and speed (Gittleman and Harvey, 1982; Mace et al., 1983) and perhaps it is diet that holds together this syndrome of vulnerability. Future research could identify the specific mechanism(s) associated with diet that drive vulnerability. For instance, it could emerge from sensory adaptations specific to a diet type.

What are the implications of these results for roadkill mitigation? There are two ways to reduce roadkill mortality: modifying human driver behavior and modifying animal behavior (Hedlund et al., 2004; Mastro et al., 2008). Changing driver behavior includes measures such as reducing speed limits, adding signs to roads, and educational outreach programs (Mastro et al., 2008). Changing habitat suitability and animal behavior involves repelling or blocking them from roadways. This has been attempted by adding fences to roads, using chemical deterrents, and adding whistles to cars (Knapp et al., 2004). Studies have shown that fencing is the only strategy which has had decent success in keeping animals away from roads, and that signs and reduction of speed limit are effective ways of changing human behavior (Danielson and Hubbard, 1998; Hedlund et al., 2004; Knapp et al., 2004; Sullivan, 2009, 2011).

Our results suggest that there are potentially novel mitigation strategies to reduce roadkill by altering animal behavior. For instance, previous studies have shown that kangaroos (*Macropus* spp.) are killed more often in areas where there is lush green grass on the roadside, suggesting that these herbivores are attracted to food (Klöcker et al., 2006). As a result, it may be possible to repel the most vulnerable animals by removing food that is specifically attractive to them from the roadside. This strategy has been at-

tempted with moose (*Alces alces*), but the implementation was not particularly efficient or cost effective (Rea, 2003). However, removing seeds, grasses, and fruits that attract herbivorous birds could reduce their apparently high incidence of roadkill. To repel carnivores from roads, it may be possible to employ strategies used to repel carnivores from livestock. These include chemical repellents, as well as fear inducing visual and acoustic stimuli (Smith et al., 2000; Darrow and Shivik, 2009). Given the length of roads to be 'protected', perhaps such methods would be most economically applied in previously identified carnivore roadkill hotspots. Omnivores, however, present a special dilemma. In general, their dietary plasticity make it infeasible to remove all attractive elements from roads. Thus, other means would have to be found to repel omnivores from roads. While scavengers were not especially vulnerable, removing potential carcasses efficiently is a method to reduce scavenger-related mortality. Because diet type is associated with vulnerability, these strategies could be implemented on a geographically broader scale than simply at hotspots.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.08.016>.

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