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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 (hotspots) 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.

1. Introduction

Human activity is a driving force behind the many environmental problems, including the currently high rate of extinctions (Vitousek 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 ($p \geqslant 0.05$) 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.birdtree.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