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Diet and body size of North American mammal road mortalities

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Abstract

Previous studies suggest roadkill may not be evenly distributed among species or within species due to life history characteristics. We examine published data on mammalian roadkill surveys conducted in North America for a relationship between diet type, body size and roadkill frequency. Eight studies with comparable methods are used in the analysis for a combined survey mileage of 224,354 km that includes 3.101 individuals killed from 38 species. Carnivores were less likely to be found in roadkill surveys than omnivores or herbivores. After controlling for diet type, a peaked relationship was found between body size and roadkill frequency with the model predicting the highest roadkill for body sizes of about 1.06 kg. These results may be explained by both biological factors and sampling methods.

Keywords: Roadkill; Wildlife; Life history; Highway; Accidents

1. Introduction

Roads affect wildlife populations through habitat loss, habitat degradation (e.g. from traffic emissions and invasive species), decreased landscape connectivity due to road avoidance, and mortality due to collisions with vehicles (roadkill). Population level effects of roadkill can exceed natural rates of mortality and cause populations to decline (Forman et al., 2003). Efforts have been made by land management agencies to mitigate these various effects of roads, with a particular focus on reducing roadkill for both wildlife conservation and human safety concerns (Clevenger et al., 2003; Rea, 2003; Dodd et al., 2004). The identification of potential across-species patterns in roadkill frequency will help managers direct their efforts towards wildlife populations that are most susceptible to roadkill and help inform the development of standardized protocols for collecting roadkill data (Cramer and Bisonnette, 2006).

Previous studies have used roadkill surveys to track changes in population size (Ghert, 2002; Baker et al., 2004) and to find spatial and temporal patterns in the distribution of roadkill (Haxton, 2000; Baker et al., 2004; Taylor and Goldingay, 2004; Ramp et al., 2005). Few empirical studies have addressed potential links

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between species attributes and the relative frequency of roadkill across-species. Theoretical studies suggest that variation in roadkill frequency can be explained, in part, by characteristics such as sex, age, road avoidance behavior, dispersal distance, population density, or activity period (van Langevelde and Jaarsma, 2004; Jaeger et al., 2005; Jaarsma et al., 2006). Empirical studies support this. For instance, Carr and Fahrig (2000) found that a more mobile anuran species had higher a roadkill frequency than a less mobile species. Coulson (1997) found a male bias in roadkill carcasses for five marsupial species and Steen et al. (2006) found that female turtles are more susceptible to road mortality than males. Warren (1936) observed that most of the Gunnison's prairie dogs (*Cynomys gunnisoni*) he found in a roadkill survey were 'young animals'. These studies suggest that some life history variables can be used to explain variation in roadkill frequency both within and across species.

Body size and diet preference are useful starting places to explore patterns in interspecies variation in roadkill frequency because both of these variables likely affect the probability of roadkill (predictions summarized in Table 1) and species' information is readily obtained from published records. Furthermore, these attributes are associated with a broad array of biological phenomena that may help in the prediction of road effects on wildlife. The purpose of this study is to determine if interspecies variation in roadkill frequency can be predicted from diet and body size for mammals in North America using published records of roadkill surveys.

There are several possible ways in which diet could be related to roadkill frequency. First, diet is related to population density with herbivores occurring at higher population densities than carnivores and omnivores occurring at intermediate population densities for species with otherwise similar life history characters (Peters, 1983). Therefore, herbivores could have a higher roadkill frequency than omnivores, and omnivores could have a higher roadkill frequency than carnivores since roadkill frequency should increase with population density. Alternatively, since carnivores are more vagile (i.e. greater home ranges/dispersal distances) than herbivores of the same body size (Sutherland et al., 2000), and increasing vagility increases the probability that an animal will encounter a road, carnivores could show a higher roadkill frequency than omnivores, and omnivores could have a higher roadkill frequency than herbivores. If both of these hypotheses are correct, they could cancel out and result in no effect of diet on roadkill frequency, or omnivores could show either the lowest or the highest road kill frequency.

We considered five possible shapes of the relationship between body size and roadkill frequency: (1) positive-linear; (2) negative-linear; (3) no relationship; (4) U-shaped; (5) peaked. The relationship with roadkill frequency could be positive-linear because: larger animals are harder for motorists to avoid than smaller animals (Jaarsma et al., 2006); larger animals move over larger areas (Sutherland et al., 2000), increasing the likelihood that a larger animal will encounter a road compared to smaller animals; larger animals are less habitat specific than smaller animals (Ziv, 2000), so they are more likely to cross habitat edges near roads (Forman

Table 1
Predicted linear effects of species' characters on roadkill frequency

Species character	Factor affecting roadkill frequency	Relationship between species character and factor	Predicted effect of species character on roadkill frequency	Source of effect
Body size	Population density	−	−	Biological
	Habitat specificity	−	−	Biological
	Velocity	+	−	Biological
	Driver avoidance	+	−	Driver
	Vagility[a]	+	+	Biological
	Body surface area	+	+	Biological
	Detectability[b]	+	+	Sampling method
	Carcass durability	+	+	Sampling method
Diet	Population density	Herbivores occur at higher densities than carnivores	Roadkill increases with increasing density	Biological
	Vagility[a]	Carnivores are more vagile than herbivores	Roadkill increases with increasing vagility	Biological

[a] Refers to home range size and dispersal distance.
[b] Refers to ease of detection by researchers.

et al., 2003); and the carcasses of larger animals are more likely to be detected by researchers conducting roadkill surveys because they are easier to see and they take longer to decompose than smaller animals (Slater, 2002). In contrast, body size could have a negative-linear effect on roadkill frequency because: populations of larger animals occur at lower densities than smaller animals so, as body size increases, there are simply fewer animals available to be killed (Peters, 1983); larger animals are more actively avoided by motorists than smaller animals; and larger animals move more quickly than smaller animals, so they spend less time traversing across a road, which reduces the chance of their being struck by a vehicle (van Langevelde and Jaarsma, 2004). If some or all of the positive and negative effects occur, they could cancel each other out, resulting in no relationship between body size and roadkill frequency. Alternatively, if negative effects outweigh positive effects at smaller body sizes and positive effects outweigh negative effects at larger body sizes, the minimum roadkill frequency will occur at an intermediate body size (U-shaped relationship). The reverse of this last prediction would result in the maximum roadkill frequency occurring at an intermediate body size (peaked relationship).

2. Method

The *Web of Science* was searched on December 15, 2006 for papers using the combination of terms: (traffic or road or highway) and (mortality or roadkill) and (wildlife or mammal). We also looked in the references of the papers that came from this search for other appropriate studies as well as papers cited by Forman et al. (2003). We only analyzed studies that involved a distance-based sampling effort, which usually involves an observer driving in a motor vehicle over a length of road and visually scanning for carcasses. Some roadkill studies, usually involving large mammals, use accident insurance or transportation department records to summarize the roadkill numbers within a given area (Finder et al., 1999; Weir, 2002; Biggs et al., 2004); however, we could not translate this information into a per distance sampling effort to make these results comparable to distance-based sampling designs. Three types of records are excluded after pooling records from appropriate studies:

- domestic species, because our interest is in wildlife;
- imprecisely identified species (e.g. "mice", "skunk", "rat"), because we could not ascertain the body size from this type of description;
- species for which, we only had a single occurrence after pooling all studies, because we wanted to reduce the variability in roadkill frequency explained by the design or location of a single study.

It is assumed that each kilometer of road surveyed is independent; e.g. a 5 km road surveyed twice has equal sampling effort to a 10 km road surveyed once. This assumption allowed simplification of the sampling effort among studies because not all authors reported the actual frequency with which they sampled each stretch of road. In this way, aspects of our data are not entirely independent because animals killed on a stretch of road are less likely to be 'replaced' as re-sampling of that stretch of road is repeated, especially for species occurring at low population densities.

We used published records of body sizes and diet preferences from Burt (1980) – Table 2. In most studies, the sex of the carcasses is not reported and we use the midpoint of the given range for both sexes combined as the value for body size. We categorized diet preference as herbivore, omnivore or carnivore. The response variable, roadkill frequency, is the number of animals of each species killed per 1000 km surveyed, averaged across all studies containing that species.

An ANCOVA is performed using diet type as a categorical predictor variable (herbivore, omnivore, carnivore) and body size as a continuous predictor variable and included squared-terms for body size. We log transformed both roadkill frequency and body size (Sokal and Rolf, 1995). [1]

[1] All statistical procedures were conducted with the GLM function in SPSS v12.0.2 (SPSS Inc., Chicago, Illinois).

Table 2
Life history summary for species used in this study

Species	Body size (kg)	Diet[a]	Roadkill from all studies	Number of studies represented (max. 8)
Canis latrans	15.500	o	19	3
Castor canadensis	20.250	h	2	1
Clethrionomys gapperi	0.027	h	6	1
Scurius carolinensis	0.530	h	23	2
Cynomys gunnisoni	0.900	h	56	1
Dasypus novemcinctus	5.600	o	41	1
Didelphis virginiana	4.950	o	91	4
Erethizon dorsatum	8.600	h	72	1
Lepus americanus	1.350	h	97	2
Lepus californicus	2.200	h	504	3
Lepus townsendii	3.350	h	202	3
Marmota monax	3.350	h	105	2
Martes americana	0.960	c	15	1
Mephitis mephitis	4.500	o	179	8
Microtus pennsylvanicus	0.050	h	6	1
Mustela vison	3.520	c	7	2
Ondatra zibethicus	1.360	h	84	5
Peromyscus sp.[b]	0.020	h	42	1
Procyon lotor	10.600	o	53	4
Rattus norvegicus	0.240	o	25	4
Scalopus aquaticus	0.100	o	4	2
Sciurus griseus	0.680	h	3	1
Sciurus niger	0.950	h	76	4
Sigmodon hispidus	0.160	h	11	1
Spermophilus beecheyi	0.730	h	53	1
Spermophilus columbianus	0.580	h	26	1
Spermophilus franklinii	0.500	h	27	2
Spermophilus lateralis	0.223	o	12	1
Spermophilus tridecemlineatus	0.200	o	302	2
Spilogale putorius	0.680	o	55	2
Sylvilagus floridanus	1.350	h	728	4
Sylvilagus nuttallii	1.000	h	8	1
Tamias minimus[c] *Source*: from Burt (1980).	0.040	h	10	2
Tamias striatus	0.100	h	44	2
Tamiasciurus hudsonicus	0.220	h	109	2
Taxidea taxus	8.500	c	2	1
Urocyon cinereoargenteus	4.500	c	3	2
Vulpes vulpes	5.600	c	3	1
Zapus princeps	0.030	h	3	1

[a] o = omnivore; h = herbivore; c = carnivore.
[b] Includes *P. maniculatus* and *P.leucopus*.
[c] Includes "western chipmunk" (McClure, 1951).

3. Results

The analyses are based on 38 species from eight studies with a combined mileage of 224,354 km and a record of 3,101 individuals killed. Table 2 summarizes the final database and Table 3 presents meta-data of the studies. We excluded two outliers from the ANCOVA analysis after reviewing uncentered leverage values and Cook's distances (i.e. records with values exceeding 0.3 are excluded for both). These outliers were the only two ungulate species in the dataset, with 2 records for mule deer and 6 records for white-tailed deer.

We found a statistically significant ($R^2 = 0.379$) model relating diet and body size to roadkill frequency (Tables 4 and 5). A post-hoc analysis of the ANCOVA with a Bonferronni correction for multiple comparisons indicates that carnivores had a significantly lower roadkill frequency than either herbivores ($p = 0.003$) or omnivores ($p = 0.004$). Herbivores and omnivores did not significantly differ in roadkill frequency ($p = 1.000$).

Table 3
Meta-data of the studies used

Study	Province/state where study took place	Month/year surveyed (start–finish of survey)	Distance surveyed (km)	Total number of mammal species detected[a]	Total roadkill/ 1000 km surveyed[a]
Caro et al. (2000)	CA	07/1997–09/1999	21372	9	10
Clevenger et al. (2003)	AB	09/1997–08/2000	65253	14	5
Dreyer (1937)	IL to MA	06/1935–07/1935	4104	7	4
McClure (1951)	NB	01/1941–04/1944	120725	16	13
Oxley et al. (1974)	ON	06/1975–09/1975	5171	9	74
Scott (1938)	IW	05/1936–05/1937	4738	14	73
Warren (1936)	CO	06/1935–07/1935	1223	4	56
Wilkins and Schmidlym (1980)	TX	1975–1976	1768	10	88

[a] After exclusions.

Table 4
ANCOVA table for the effect of diet and body size on roadkill frequency

Source	Type I sum of squares	DF	Mean square error	F	p
Corrected model	12.414	4	3.104	6.646	<0.0001
Intercept	0.057	1	0.057	0.122	0.730
Diet	5.731	2	2.866	6.136	0.005
Log_{10} body size (kg)	2.205	1	2.205	4.722	0.037
Log_{10} (body size (kg))^2	4.478	1	4.478	9.589	0.004
Error	15.411	33	0.467		
Total	27.882	38			
Corrected Total	27.825	37			

Table 5
Parameter estimates for the effect of diet and body size on roadkill frequency per 1000 km. Omnivore is set as the reference category for diet

Parameter	B[a]	Standard error[a]	B[b]	Lower 95% confidence interval[b]	Upper 95% confidence interval[b]
Intercept	0.544	0.231	1.723	1.077	2.755
Diet = carnivore	−1.329	0.377	0.265	0.123	0.570
Diet = herbivore	−0.038	0.271	0.963	0.555	1.669
Log_{10} body size (kg)	0.093	0.169	1.097	0.779	1.546
Log_{10} (body size (kg))^2	−0.468	0.151	0.626	0.460	0.852

[a] Prior to back transformation.
[b] After back transformation.

Results of a Levene's test indicates that error variances were homogeneous across diet types ($p = 0.444$). After controlling for diet type, there was a peaked (negative quadratic) relationship between body size and roadkill frequency (Table 4 and Fig. 1). Roadkill frequency was highest at a body size of 1.06 kg (i.e. back transformed from $\log_{10}$ 0.0607 kg).

4. Discussion

The results support the prediction that carnivores have a lower roadkill frequency than herbivores or omnivores. We also found support for the fifth possible shape for the relationship between body sizes and roadkill frequency: roadkill frequency increased with body size up to a given point i.e. 1.06 kg, and then decreased as body size increased past this point. These results have implications for the design and interpretation of distance-based roadkill studies and for our understanding of road effects on wildlife.

We found that carnivores are killed less frequently than herbivores or omnivores. This may be explained by the fact that carnivore populations normally persist at lower densities than populations of other animals with

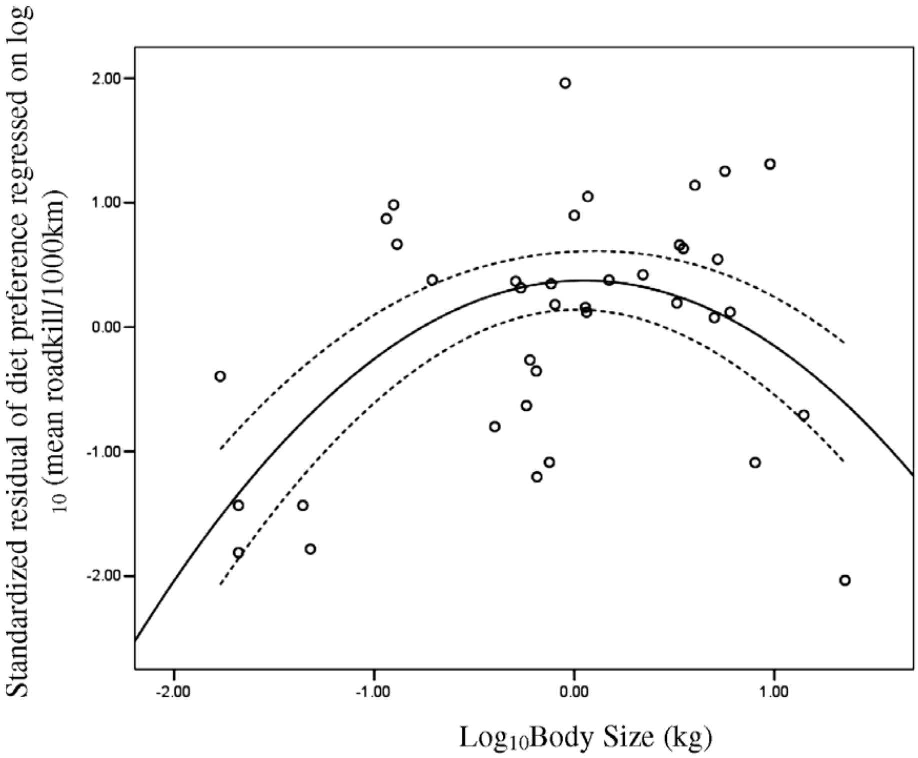

Fig. 1. The effect of mean roadkill per 1000 km versus body size. *Note*: Residuals from the effect of diet on roadkill frequency are plotted on the *Y*-axis to illustrate the effect of body size when diet type is controlled for. The solid line represents the best-fit model and the dashed lines represent the 95% confidence interval.

similar body size (Peters, 1983; Damuth, 1993). Sutherland et al. (2000) found that omnivores and herbivores had similar vagilities as a function of body size, and that these vagilities were lower than that of carnivores. Combined, these results support the prediction that species' population densities affect roadkill more than their vagilities.

We can only speculate on the cause of the peaked relationship between body size and roadkill frequency. We suggest that the competing positive and negative-linear effects change in relative importance as body size increases, specifically at around 1.06 kg. At this body size, high mobility and large population size may combine to maximize roadkill. At smaller body sizes, mobility effects limit density effects to produce fewer roadkill than expected from population densities, whereas at larger body sizes population density may have a more limiting effect on roadkill than vagility.

The positive relationship between roadkill frequency and body size for smaller animals may also be caused, at least in part, by an increase in detectability with body size. None of the studies incorporated into our dataset accounted for this potential bias by either increasing their search effort for smaller animals or by testing the probability of detecting carcasses whose location was known by a second party. Furthermore, all of the studies we reviewed searched for carcasses from a moving vehicle. Slater (2002) found that searching on foot was more efficient at detecting the carcasses of small animals than observing carcasses from a moving vehicle. Slater (2002) also found that removal of carcasses by scavengers affected detectability of roadkill carcasses, with shorter removal times for smaller species (<0.150 kg) and longer staying times for larger items or less palatable items like hedgehogs (*Erinaceus europaeus*). We found only one distance-based roadkill study that tested the reliability of detecting carcasses (Taylor and Goldingay, 2004).

The two outliers excluded from the final model were both ungulate species and the only ungulates found in this review. It is not surprising that ungulates showed up as outliers in our analyses for at least two reasons. First, carcasses of these species are systematically targeted for removal from highways by transportation departments in many jurisdictions (Weir, 2002; Knapp et al., 2004). Second, some of the studies we found only surveyed medium and small mammal species (Caro et al., 2000; Clevenger et al., 2003). For these reasons, including ungulates in our analysis would underestimate the actual roadkill frequency for this body size and diet type. At the same time, we caution that although our results suggest the relationship between body size and roadkill frequency is peaked, we have no data for species larger than about 30 kg and do not want to offer speculation beyond the data we present here.

Interpretation of our results should be weighted by at least five caveats. First, the use of a literature search engine to find suitable studies likely excluded a relevant body of 'gray literature.' Second, we included studies dating back to the 1930's when traffic patterns in North America were different than they are at the end of the century when the most recent study in our dataset was published (Forman et al., 2003). Vehicle speed, traffic density, and road density have all increased over the past century and these factors may affect long-term roadkill patterns and wildlife population densities. Third, the studies we looked at were from a variety of North American regions, and population dynamics for the same species varies throughout the continent (Badgley and Fox, 2000). Fourth, differences among studies in driving speed of the sampling vehicle, number of observers, and training of the observers could influence the detectability of carcasses between studies. Lastly, our final dataset is relatively small to produce unequivocal conclusions. For example, our dataset includes only 5 carnivore species and, overall, the 38 species used in our study represent about 10% of the number of non-volant mammal species in North America.

5. Conclusion

A statistically significant amount of variation in roadkill frequency can be explained by diet type and body size. We attribute the significant effect of diet on roadkill frequency to population density, where carnivore populations are normally less dense than herbivore or omnivore populations of similar body size. We speculate that processes having a positive effect on the relationship between body size and roadkill (i.e. vagility, detectability) become less important than processes that have a negative affect on this relationship (i.e. population density, body surface area, driver avoidance) as body size increases past about 1.0 kg; however, we cannot separate biological effects from sampling bias effects. These results leave us with many unanswered questions and we urge researchers performing distance-based surveys for roadkill carcasses to address potential sources of bias in their sampling design, especially when looking at multi-species responses to road mortality.

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