

FLÁVIO ZANCHETTA FERREIRA

PREDICTING ROAD MORTALITY RISK USING LIFE TRAITS OF BIRDS AND MAMMALS

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Ecossistemas, para a obtenção do título de Mestre.

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RESUMO

Estradas são estruturas ubíquas na paisagem, e a colisão da fauna com veículos pode afetar as populações, influenciando sua persistência no longo prazo. Entretanto, algumas espécies são mais suscetíveis a serem atropeladas do que outras. Ademais, muitas espécies que ainda não foram estudadas ou detectadas em amostragens rodoviárias podem ser afetadas pela mortalidade em rodovias. Para ajudar a entender por que espécies são atropeladas a diferentes taxas é útil examinar a relação entre seus traços e o risco de atropelamento. Nós desenvolvemos modelos baseados em traços utilizando random forest regression para avaliar o papel de uma ampla variedade de traços das espécies nas taxas de atropelamento de aves e mamíferos. Utilizamos então esses modelos para prever o risco para todas as espécies de aves e mamíferos brasileiras. As taxas de atropelamento de aves foram melhor explicadas pela massa corporal, amplitude de habitat, longevidade e idade de maturidade sexual, enquanto as taxas de atropelamento de mamíferos foram melhor explicadas pelo comportamento de alimentação, área de vida, amplitude de habitat, massa corporal, amplitude de dieta e idade de maturidade sexual. Aves com mais de 2 kg e generalistas de habitat foram positivamente correlacionadas com altas taxas de atropelamento. Rápido amadurecimento sexual e curta longevidade foram também associados à alta vulnerabilidade ao tráfego. Mamíferos carniceiros, com áreas de vida pequenas e médias, generalistas em habitat e dieta, com massa corporal entre 3kg e 45 kg, e rápida maturidade sexual foram mais suscetíveis a altas taxas de atropelamento. Nós identificamos 16 aves e 14 mamíferos potencialmente vulneráveis à mortalidade em rodovias. Nosso modelo contribui para melhor compreender as características biológicas que tornam as espécies particularmente vulneráveis ao atropelamento. Nós argumentamos que a avaliação do risco de atropelamento deve focar não apenas nas características da estrada e da paisagem, mas também utilizar o conhecimento disponível acerca dos traços das espécies para gerar informação mais precisa para avaliações de impacto ambiental.

Palavras-chave: História de vida. Random forest. Traço funcional. Atropelamento. Trait-based

ABSTRACT

Roads are a ubiquitous feature in landscape, and wildlife-vehicle collision can affect populations influencing their long-term persistence. However, some species are more likely to be killed than others. Moreover, many species that are still unstudied or are not detected on road surveys might be affected by road mortality. To help understand why species are road-killed at distinct rates, it is useful to examine the relationship between their traits and the road-kill risk. We developed trait-based models using random forest regression to assess the role of a wide range of species' traits on road-kill rates for bird and mammal species. We then used these models to predict risk for all bird and mammal species in Brazil. Bird road-kill rates were best explained by body mass, habitat breadth, lifespan and maturity age, whereas mammal road-kill rates were best explained by feeding behavior, home range, habitat breadth, body mass, diet breadth and maturity age. Birds with more than 2 kg and habitat generalists were positively related to high road-kill rates. Short maturity age and lifespan were also associated with high vulnerability to traffic. Mammals exhibiting scavenging feeding behavior, small and intermediate home range sizes, being habitat and diet generalists, with body masses between 3 kg and 45 kg, and earlier maturity age were more susceptible to high road-kill rates. We found that 16 bird and 14 mammal species are potentially vulnerable to road mortality. Our model contributes to a better understanding of the biological characteristics that make species particularly vulnerable to road-kill. We argue that road-kill risk assessment should focus not only on road and landscape related features, but also use the available knowledge on species traits to provide more accurate information for environmental impact assessments.

Keywords: Life-history traits. Random forest. Functional trait. Road-kill. Trait-based.

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PRIMEIRA PARTE

1 INTRODUÇÃO

Colisões com veículos são um dos impactos mais conspícuos das estradas (COFFIN 2007), reduzindo a abundância de populações e limitando a dispersão para muitas espécies. Entretanto, nem todas as espécies são igualmente afetadas pelos riscos associados a estradas (FAHRIG & RYTWINSKI 2009). A abundância local (FORD & FAHRIG 2007; SANTOS et al. 2016) e a detectabilidade de carcaças (SANTOS et al. 2011; TEIXEIRA et al. 2013) são dois fatores capazes de influenciar a variabilidade nas taxas de atropelamento. Por exemplo, espécies pequenas podem ser subestimadas em amostragens em estradas devido à dificuldade de se detectá-las (SLATER 2002). No entanto, as taxas de atropelamento podem contrastar entre espécies com abundâncias locais e detectabilidade similares. Duas espécies - anta (Tapirus terrestris) e o cachorro-do-mato (Cerdocyon thous) – com densidades populacionais semelhantes na região do Pantanal brasileiro (0,4 ind./km²) (DESBIEZ et al. 2010) apresentaram diferenças significativas em suas taxas de atropelamento: 0,01 ind./km/ano e 0,24 ind./km/ano, respectivamente (SOUZA et al. 2014). Alguns estudos demostram que traços das espécies relacionados a hábitos ecológicos, comportamentais ou de história-de-vida (e.g. tipo de dieta, especialização de hábitat, sociabilidade, idade de maturidade) podem afetar as taxas de atropelamento (e.g. FORD & FAHRIG 2007; BARTHELMESS & BROOKS 2010; RYTWINSKI & FAHRIG 2011). Por exemplo, SANTOS et al. (2016) identificou que Passeriformes que forrageiam em substratos baixos de áreas florestadas são mais afetados por mortalidade associada às estradas do que espécies que forrageiam no solo ou no ar, possivelmente devido à baixa altura de voo. Mamíferos herbívoros e onívoros aparentam ser significativamente mais atropelados do que carnívoros (COOK & BLUMSTEIN 2013). Espécies generalistas capazes de se locomover por muitos ambientes são mais propensas a cruzar um estrada e serem atingidas (NÚÑEZ-REGUEIRO et al. 2015). Ademais, a percepção do risco associado à estrada pode ser influenciada pelos traços das espécies. Por exemplo, espécies noturnas podem não perceber as estradas como uma ameaca devido ao baixo tráfego de veículos e, portanto, estarem mais suscetíveis ao atropelamento (e.g. GRILO et al. 2012). Em contraste, espécies regularmente expostas a ameaças antropogênicas como a

caça podem estar mais alertas ao risco associado a humanos e exibir um comportamento de evitação da estrada (LAURANCE et al. 2006).

Embora estudos tenham avaliado as relações entre os traços e as taxas de mortalidade, grande parte focou apenas em algumas poucas características; portanto, a importância relativa de diferentes aspectos ecológicos, comportamentais e de história-de-vida para o risco de mortalidade nas estradas não foi suficientemente investigada (veja COOK & BLUMSTEIN 2013 para uma exceção). Em países onde a expansão viária deve ocorrer em grandes escalas nos próximos anos como no Brasil, o entendimento de uma ampla variedade de traços é crucial para guiar ações de planejamento e mitigação. Nas últimas duas décadas o Brasil passou por um enorme progresso social e econômico, levando a um aumento de 20% na malha rodoviária (DNIT 2015). Entretanto, a maioria dos estudos sobre atropelamentos no país limita-se à região sul (e.g. COELHO et al. 2008; BAGER & ROSA 2011; TEIXEIRA et al. 2013), onde a densidade rodoviária é, em média, 0,6 km/km² e a maioria das áreas naturais já foram modificadas ou destruídas (RIBEIRO et al. 2009). As regiões central e norte do Brasil, apesar de terem uma densidade rodoviária muito menor (0,1 km/km². DNIT 2015), compreendem o bioma Cerrado e Amazônico, que passaram por grandes mudanças de cobertura do solo durante as últimas décadas (MYERS et al. 2000; LAURANCE et al. 2001; KLINK & MACHADO 2005). O entendimento sobre o risco potencial associado a projetos atuais e futuros é crítico para preservar essas regiões de interesse para a conservação em escala global (BRIENEN et al. 2015).

Métodos comparativos são ferramentas amplamente utilizadas para avaliar os mecanismos que direcionam as respostas das espécies aos efeitos ambientais e ameaças (e.g. DAVIDSON et al. 2009; GONZÁLEZ-SUÁREZ et al. 2013). Ao examinar quais características das espécies aumentam a vulnerabilidade a distúrbios ambientais, as análises baseadas nos traços das espécies podem ajudar a prever suas respostas às mudanças ambientais e identificar riscos potenciais para espécies não-estudadas ou não-detectadas. Neste trabalho nós avaliamos o papel de uma ampla variedade de traços das espécies nas taxas de atropelamento de aves e mamíferos. Utilizando modelos, nós determinamos quais fatores influenciam a mortalidade em estradas para espécies com estimativas empíricas. Posteriormente, os modelos foram utilizados para prever o risco para o restante das espécies de aves e mamíferos brasileiros que não foram estudadas ou detectadas. Nosso estudo oferece um melhor entendimento sobre os fatores intrínsecos de risco para espécies brasileiras e pode contribuir para identificar espécies potencialmente vulneráveis para as quais a mortalidade viária não foi ainda quantificada.

2 CONCLUSÃO

Nossos resultados mostram que o atropelamento não é distribuído aleatoriamente entre espécies e que a vulnerabilidade de aves e mamíferos às estradas é afetada, em parte, por diversos traços ecológicos, comportamentais e de história de vida. As evidências deste trabalho mostram que há uma complexa interação entre traços e o risco de atropelamento, envolvendo massa corporal, amplitude de habitat e dieta, idade de maturidade sexual, entre outros.

Algumas limitações necessitam consideração em futuras pesquisas, tais como a falta de dados sobre os traços das espécies, limitações de técnicas de imputação (PENONE et al. 2014) e problemas inerentes ao método de amostragem de atropelamentos em estradas (SANTOS et al. 2011; TEIXEIRA et al. 2013). Embora apenas uma parte da variabilidade nos traços de aves e mamíferos tenha sido abordada neste trabalho, foi possível delinearmos relações ecológicas consistentes com outros trabalhos (e.g. FORD & FAHRIG 2007; RYTWINSKI & FAHRIG 2012), apesar de serem necessárias mais pesquisas, em especial, para certos traços (e.g. COOK & BLUMSTEIN 2013).

Eventualmente, combinando-se o conhecimento acerca do papel dos traços com características das estradas e paisagens, pode-se fornecer informações mais precisas para avaliações de impacto ambiental. A análise dos traços de espécies ajuda a detectar espécies potencialmente em risco, o que é crucial para planejar medidas mitigatórias. Pesquisas futuras devem focar em elucidar algumas controvérsias existentes entre grupos para refinar o papel dos traços no risco de atropelamento e possibilitar a ações de conservação direcionadas.

REFERÊNCIAS

BAGER, A.; ROSA, C.A. Influence of Sampling Effort on the Estimated Richness of Road-Killed Vertebrate Wildlife. **Environmental Management**, Amsterdam, v. 47, n. 5, p. 851-858, 2011.

BARTHELMESS, E.L.; BROOKS, M.S. The influence of body-size and diet on road-kill trends in mammals. **Biodiversity and Conservation**, New York, v. 19, n. 6, p. 1611-1629, 2010.

BRIENEN, R.J.W.; et al. Long-term decline of the Amazon carbon sink. **Nature**, London, v. 519, n. 7543, p. 344-348, 2015.

COELHO, I.P.; KINDEL, A.; COELHO, A.V.P. Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. **European Journal of Wildlife Research** New York, v. 54, n. 4, p. 689-699, 2008.

COFFIN, A.W. From roadkill to road ecology: A review of the ecological effects of roads. **Journal of Transport Geography**, Amsterdam, v. 15, n. 5, p. 396-406, 2007.

COOK, T.C.; BLUMSTEIM, D.T. The omnivore's dilema: diet explains variation in vulnerability to vehicle collision mortality. **Biological Conservation**, Amsterdam, v. 167, p. 310-315, 2013.

DAVIDSON, A.D; et al. Multiple ecological pathways to extinction in mammals. **PNAS**, San Diego, v. 106, n. 26, p. 10702-10705, 2009.

DESBIEZ, A.L.J.; BODMER, R.E.; TOMAS, W.M. Mamalian densities in a neotropical wetland subject to extreme climatic events. **Biotropica**, Hoboken, v. 42, n. 3, p. 372-378, 2010.

FAHRIG, L.; RYTWINSKI, T. Effects of roads on animal abundance: an empirical review and synthesis. **Ecology and Society**, Wolfville, v. 14, n. 21, p. 1-19, 2009.

FORD, A.T.; FAHRIG, L. Diet and body size of North American mammal road mortalities. **Transportation Research Part D**, London, v. 12, n. 7, p. 498-505, 2007.

GONZÁLEZ-SUÁREZ, M.; GÓMEZ, A.; REVILLA, E. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes **Ecosphere** v. 4, n. 6, p. 1-16, 2013.

GRILO, C.; ET AL. Individual spatial responses towards roads: implications for road mortality risk. **PLoS ONE** v. 7, n. 9, 2012.

KLINK, C.A.; MACHADO, R.B. Conservation of the Brazilian Cerrado. **Conservation Biology**, Hoboken, v. 19, n. 3, p. 707-713, 2005.

LAURANCE, W.F.; et al. The future of the Brazilian Amazon. **Science**, Washington, v. 291, n. 5503, p. 438-439, 2001.

LAURANCE, W.F.; et al. Impacts of roads and hunting on central African rainforest mammals. **Conservation Biology**, Hoboken, v. 20, n. 4, p. 1251-1261, 2006.

MYERS, N.; et al. Biodiversity hotspots for conservation priorities. Nature, London, v. 403, n. 333, p. 853-858, 2000.

NÚÑEZ-REGUEIRO, M.M.; et al. Spatial patterns of mammal occurrence in forest strips surrounded by agricultural crops of the Chaco region, Argentina. **Biological Conservation**, Amsterdam, v. 187, p. 19-26, 2015.

RIBEIRO, M.C.; et al. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, Amsterdam, v. 142, n. 6, p. 1141-1153, 2009.

RYTWINSKI, T.; FAHRIG, L. Reproductive rate and body size predict road impacts on mammal abundance. **Ecological Applications**, Hoboken, v. 21, n. 2, p. 589-600, 2011.

RYTWINSKI, T.; FAHRIG, L. Do species life history traits explain population responses to roads? A meta-analysis. **Biological Conservation**, Amsterdam, v.147, p. 87-98, 2012.

SANTOS, S.M.; CARVALHO, F.; MIRA, A. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. **PLoS ONE** v. 6, n. 9, 2011.

SANTOS, S.M.; et al. Avian trait-mediated vulnerability to road traffic collisions. **Biological Conservation**, Amsterdam, v. 200, p. 122-130, 2016.

SLATER, F.M. An assessment of wildlife road casualities - the potential discrepancy between numbers counted and numbers killed. **Web Ecology**, Göttingen, v. 3, n. 1, p. 33-42, 2002.

SOUZA, J.C.; CUNHA, V.P.; MARKWITH, S.H. Spatiotemporal variation in human-wildlife conflicts along highway BR-262 in the Brazilian Pantanal. **Wetlands Ecology Management**, New York, v. 23, n. 2, p. 227-239, 2014.

TEIXEIRA, F.Z.; et al. Vertebrate road mortality estimates: Effects of sampling methods and carcass removal. **Biological Conservation**, Amsterdam, v. 157, p. 317-323, 2013.

SEGUNDA PARTE

Predicting road mortality risk using life traits of birds and mammals

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Abstract: Wildlife-vehicle collisions are recognized as one of the major causes of mortality for many species. However, some species are more likely to be killed than others, and there are a large number of species for which the risk of collision with vehicles is still unknown. Thus, by understanding which species traits better explain road-kill rates, we can predict the vulnerability of unstudied or undetected species to roads. We developed trait-based models using random forest regression to assess the role of a wide range of species' traits on road-kill rates for birds and mammals. We then used these models to predict the risk of being road-killed for all bird and mammal species in Brazil. Bird road-kill rates were best explained by body mass, habitat breadth, lifespan and maturity age, whereas mammal road-kill rates were best explained by feeding behavior, home range, habitat breadth, body mass, diet breadth and maturity age. Birds with more than 2 kg, short maturity age and lifespan and habitat generalists were positively related to high road-kill rates. Mammals exhibiting scavenging feeding behavior, small and intermediate home range sizes, habitat and diet generalists, with body mass between 3 kg and 45 kg, and earlier maturity age were more susceptible to high road-kill rates. We found that 16 bird and 14 mammal unstudied or undetected species can be potentially vulnerable to road mortality. Our results contribute to a better understanding the biological drivers that make species particularly vulnerable to road traffic collisions. Therefore, we argue that research to evaluate road-kill risk should use not only road-related and landscape features but also available knowledge on species traits to provide more accurate information for environmental impact assessments.

Keywords: life-history traits, random forest, functional trait, roadkill, trait-based

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Introduction

Roads are an increasingly prevalent feature in global landscapes (Laurance & Balmford 2013), which intensifies the concerns about their impacts on wildlife and conservation efforts (lbisch et al. 2016). Wildlife-vehicle collisions are one of the most visible roadrelated impacts (Coffin 2007), reducing population abundance and limiting dispersal for many species, which can decrease genetic diversity and threaten population viability (e.g., Fahrig & Rytwinski 2009; Borda-de-Água et al. 2014; Grilo et al. 2016). However, not all species are equally affected by road-associated risks (see Fahrig & Rytwinski 2009). Variability in road-kill rates may be attributed to differences in collision risk associated to local abundance (Ford & Fahrig 2007; Santos et al. 2016). Moreover, variation may also occur due to methodological issues associated with detectability of carcasses (Santos et al. 2011; Teixeira et al. 2013). For example, detectability of road-kills is mainly influenced by species body size, due to the greater difficulty in detecting small species (Slater 2002) (i.e. small-sized road-kills can be underestimated). However, previous studies have shown that species with similar local abundances and comparable detectability rates may have contrasting road-kill estimates. Lowland tapir (Tapirus terrestris) and crab-eating fox (Cerdocyon thous) with similar observed population densities in the Brazilian Pantanal region (0.4 ind./km²) (Desbiez et al. 2010) showed significant differences in their road-kill rates: 0.01 ind./km/year for the lowland tapir and 0.24 ind./km/year for the crab-eating fox (Souza et al. 2014). Variability in road-kill rates among species may also be explained by species' traits related to ecological habits, behavior or life-history traits (e.g. diet type, habitat specialization, sociality, maturity age) that in turn influence the probabilities of encountering and crossing roads. Several studies have shown how some of these species' traits influence road-kill incidence (e.g. Ford & Fahrig 2007; Barthelmess & Brookes 2010; Rytwinski & Fahrig 2011). Passeriformes that forage on foliage or bark and inhabit woodlands are also more frequently affected by road-associated mortality than ground and aerial foragers, possibly due to their lower flight heights (Santos et al. 2016). Herbivorous and omnivorous mammals are hit significantly more often by vehicles than carnivores (Cook & Blumstein 2013). Habitat generalists, which are capable of moving through many environments, are more likely to cross a road and be hit by vehicles (Núñez-Regueiro et al. 2015). Traits may also influence how species perceive the road as a threat and try to avoid them. For example, nocturnal species may not perceive the road as a threat due to low traffic volume and thus be more disposed to be road-killed (e.g. Grilo et al. 2012). Alternatively, species exposed to regular anthropogenic threat from hunting or poaching may be more aware of the humanassociated risks and therefore show road avoidance behavior (Laurance et al. 2006).

Most of these previous studies focused on only a few traits and thus the relative importance of different ecological, behavioral and life-history aspects on the risk of road-related mortality have not been thoroughly investigated (but see Cook & Blumstein 2013). Analyzing a wide range of traits and determining which are the most important to predict the risk of being road-killed can be useful for management and conservation efforts. In countries where road expansion is likely to occur at a large scale in coming years, such as Brazil, this understanding is crucial to guide road planning and mitigation, as knowing which species are most likely to be affected by road structures enables the design of specific mitigation measures, for example. Brazil has been under an economic and social progress in the last two decades which has led to a 20% growth of the road network (DNIT 2015). Most studies on road-kills in Brazil have been limited to the southern region (e.g. Coelho et al. 2008; Bager & Rosa 2011; Teixeira et al. 2013) where road density is on average 0.6 km/km² and most of the natural areas have either been destroyed or heavily modified (Ribeiro et al. 2009). Although the central and northern regions of Brazil have a much lower road network density (0.1 km/km². DNIT 2015), these regions comprise the Cerrado and Amazon biomes, which have been undergoing rapid land cover change for the past decades (Myers et al. 2000; Laurance et al. 2001; Klink & Machado 2005). Knowledge on the potential risk associated to current and future road projects is important to preserve these regions that are of conservation interest at a global scale (Brienen et al. 2015).

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Comparative methods are powerful tools to assess the mechanisms underlying the response of species to environmental effects and threats (e.g. Davidson et al. 2009; González-Suárez et al. 2013). By examining which species' characteristics increase vulnerability to environmental disturbances, these trait-based approaches can help forecast species responses to environmental changes and identify potential risks for unstudied or undetected species. In this paper, we developed trait-based models to assess the role of a wide range of species' traits on road-kill rates for bird and mammal species. We first determined which factors influence mortality for species with empirical estimates road and subsequently used these models to predict risk for the remaining bird and mammal species that occur in Brazil without road-kill estimates (unstudied or undetected species). Our study offers insights into the key intrinsic risk factors for Brazilian wildlife, and can contribute to identify potentially vulnerable species for which road mortality has not yet been quantified.

Methods

Road-kill data of birds and mammals in Brazil

Road-associated mortality rates for Brazilian terrestrial birds and mammals were collected from unpublished databases (made available by individual researchers contacted via the Lattes http://lattes.cnpq.br), platform from grey literature sources (technical reports, proceedings of scientific conferences, Master and PhD theses), and from Brazilian and international peerreviewed journals. Published sources were located using the following keywords in English and their translations to Portuguese: ("road-kills" OR "road mortality") AND ("mammals" OR "birds" OR "vertebrates"). We considered only road-kill rates from studies in which systematic surveys had been conducted at least once a week and for a minimum period of three months to reduce the sampling bias towards large species, as they tend to last longer on the road, and because correction rates were not available for surveying intervals longer than a week. We applied and adapted correction for detectability as suggested by Santos et al. (2011) to further reduce bias from detection rates that differ among species. The correction consists of multiplying the observed road-kill rate for a factor based on the species group and the survey frequency adopted on the study, which varied from once a week to once per day. For short survey intervals (ranging from twice to 16 times a day) no correction was applied (see Supporting Information for details on the values used and how survey frequency was calculated). Both corrected and uncorrected rates were tested in models. Road-kill rates were calculated for each species as the number of individuals killed per kilometer of the road surveyed and per year (ind./km/year). When a species was surveyed in multiple studies, we calculated the road-kill rate for each species independently. We also estimated the study location using the surveyed road midway point to obtain the geographic coordinates. Brazilian species classification and nomenclature were defined based on the Annotated Checklist of the Birds of Brazil (Piacentini et al. 2015) which recognizes 1919 bird species, and the Annotated Checklist of Brazilian Mammals (Paglia et al. 2012) which accounts for 701 mammal species. We excluded species from our analysis when nomenclature from trait databases differed from the Brazilian checklist and no matching synonyms were available.

Traits of birds and mammals

We initially identified 12 species' traits as potentially important to predict the vulnerability of species to road-kill. Using available published databases, we found sufficient data for nine of these traits for birds and for all 12 for mammals (Table 1). Data were not available for all Brazilian species for all variables, as it is often the case in comparative studies (González-Suárez et al. 2012). Therefore, we used a nonparametric imputation method based on random forest algorithm (Penone et al. 2014) to estimate missing values. This imputation method is based on random forest that uses the empirical values for each species (i.e. data from other traits) to predict the variables with missing data (see Stekhoven and Bühlmann 2012 for details). Since this imputation approach results in slightly different values each time it is run, we imputed ten datasets for each taxa and used these in subsequent analyses to capture uncertainty in the imputation process, fitting one model per estimated dataset.

Data analysis

The role of species traits on the road-kill rates was explored using random forest regression trees (Breiman 2001). Random forest is a machine learning technique that uses bootstrapped data samples to generate multiple classification or regression trees from which the importance of the predictors is defined (Breiman 2001). Birds and mammals were analyzed separately to reflect their intrinsic differences and variation in data availability. We fitted a random forest model with 2000 trees, which was enough to stabilize the model, for each imputed version (resulting in a total of ten forest per taxa) of all species with empirical estimates of road mortality (hereafter empirical dataset) using the Random Forest R package ('randomForest' - Liaw & Wiener 2002). Each model included the selected trait variables and considered the survey interval and the geographic coordinates (longitude and latitude) of the road surveyed as study-control predictors. We assessed overall model performance using the variance explained, and calculated the importance of each variable to identify the best predictors of roadkill rates. Variable importance was estimated by permuting all observed values within each variable across observations and evaluating the effect on model performance (changes in variance explained). The permutation of important variables decreases significantly the model performance whereas the permutation of less important variables should have little effect on the model performance.

To predict the vulnerability of species for which road mortality data are currently not available (unstudied or undetected species dataset), we fitted a second set of random forest models for each imputed version of the empirical dataset, excluding the predictors survey interval, latitude and longitude. These new models were then used to predict the relative vulnerability to road traffic of the remaining bird and mammal species that occur in Brazil without road-kill estimates.

Results

Road-kill data

We located 71 studies that reported road mortality rates in Brazil. From these, 43 met our criteria of minimum frequency and period of survey. The region with more studies was the southern Brazil (n=21) followed by the northern and central regions (n=12 and 10, 10)respectively) (Supporting Information). We estimated 417 road-kill rates for 170 bird species and 366 road-kill rates for 75 mammal species. The surveyed bird and mammal species accounted for 9% and 10.5% of the total Brazilian diversity, respectively. The smoothbilled ani (Crotophaga ani) was the most frequently reported bird (18 studies), having also the highest road-kill rate (8.33 ind./km/year). Among mammals, the crab-eating fox was the most frequently reported (27 studies). The highest road-kill rate for mammals was 12.71 ind./km/year for capybara (Hydrochoerus hydrochaeris). In both taxa, we detected high within-species variability in estimated road-kill rates. For example, the tropical kingbird (Tyrannus melancholicus) road-kill rates ranged from 0.015 to 5.106 ind /km/year and the Brazilian guinea pig (Cavia *aperea*) varied from 0.004 to 5.89 ind./km/year. Among surveyed species, four birds and seven mammals are listed as near threatened, and five mammals as vulnerable on the IUCN Red List (IUCN 2016).

Life traits that explain road-kill rates for birds and mammals

Brazilian species with observed road-kill rates had available information on trait databases. Only three traits had missing data and were imputed: maturity age (73.5% missing for birds and 17.5% missing for mammals), home range size (26.5% missing for mammals) and lifespan (73.5% missing for birds and 2.7% missing for mammals). The correction for detectability on observed road-kill rates produced the same results as without the correction for both taxa.

Both bird and mammal models were accurate to predict the combination of species' traits that make species more vulnerable to traffic. The mean of squared residuals for bird and mammal models was 27% (0.27±0.003 for birds and 0.277±0.001 for mammals). Our models were able to explain 58% of the observed variance in

road mortality rates for birds and 45% for mammals. When the survey descriptors (geographic coordinates and survey interval) were excluded, the variance explained dropped to 21% and 10%, respectively.

The variables with a contribution higher than 25% to explain bird road-kill rates, in decreasing order, were: longitude, survey interval, body mass, habitat breadth, latitude, lifespan and maturity age (Fig. 1). Variables with a contribution higher than 25% to explain mammal road-kill rates, in decreasing order, were: latitude, feeding behavior, longitude, home range, habitat breadth, body mass, diet breadth and maturity age (Fig. 1)

Species traits had a variable relationship with road-kill rates (Fig. 2). Birds in high longitudes and low latitudes, with more than 2 kg, and habitat generalists were more likely to have high road-kill rates. Short lifespan and maturity age were also associated with high vulnerability to traffic (Fig. 2). Mammals in high latitudes and longitudes, exhibiting scavenging feeding behavior, small and intermediate home range sizes, and being habitat and diet generalists were positively associated with high road-kill rates.

Additionally, mammals with body mass between 3 kg and 45 kg, and earlier maturity age were found to be more vulnerable to vehicle collision.

Predictions of road mortality risk for unstudied or undetected species

Predictions were made for 1624 species of birds and 572 mammal species. We predicted the highest average bird road-kill rate as 0.138 ind./km/year (median 0.013 ind./km/year) with the speckled rail (Coturnicops notatus), the yellow-hooded blackbird (Chrysomus icterocephalus), and the ivory-billed araçari (Pteroglossus azara) among the top three predicted to be most affected by road mortality (Suporting Information). The highest average mammal road-kill rate predicted was 0.069 ind./km/year (median 0.022 ind./km/year) with the Vanzolini's bald-faced saki (Pithecia irrorata), the golden-faced saki (Pithecia pithecia), and the Hoffmann's two-toed sloth (Choloepus hoffmanni) among the top three most affected. We detected 16 bird species among the 10% most affected species listed on the IUCN Red List: three as near threatened, five as vulnerable, five as endangered, and three

as critically endangered (Supporting Information). The 10% most affected mammals included 14 species listed on the IUCN Red List: eight as data Deficient, and six as vulnerable (Supporting Information).

Discussion

Our results reinforce the idea that road-kill is not randomly distributed among species and the vulnerability of birds and mammals to roads is affected to some extent by diverse ecological, behavioral and life-history traits. Previous studies have associated some species traits to the risk of collisions with vehicles such as body mass, diet type and sociality (e.g. Ford & Fahrig 2007; Cook & Blumstein 2013). However, our results provide evidence that vulnerability to traffic is better described as a complex combination of predictors, which also include habitat breadth, diet breadth, maturity age, lifespan, and feeding behavior. Interestingly, we also found that several traits explained vulnerability to traffic for both bird and mammal species such as body size, habitat specialization

and maturity age. However, our study showed that the importance of some traits varied between taxa. The context in which the species is located and the interval of road survey were also important to explain road-kill rates. Although we observed the same patterns of longitude for birds and mammals, we found differences in their intensity. Latitude had contrasting effects in explaining the road-kill rates for each taxon. Based on our models, we predicted that 16 bird and 14 mammal threatened species that had not been studied or detected might be particularly vulnerable to road mortality.

In general, we observed that species with weights above 3 kg had higher risk of being road-killed. This is in line with Rytwinski and Fahrig (2011) that found a positive correlation between body mass and mobility for mammals. In fact, large body sized species tend to be more mobile and have large home ranges (Lindsted et al. 1986; Ofstad et al. 2016), which increases the chances to interact with roads. However, Santos et al. (2016) found that the risk of birds being road-killed declines as the body size increases. We analyzed a wider range of bird species than Santos et al. (2016) (93.5% were Passeriformes), which can be one explanation for the differences between results.

Our findings show that habitat generalists seemed to be more prone to road mortality than specialists. Studies have shown that species that are reluctant to cross open grounds generally avoid crossing roads due to low availability of cover, and therefore have lower likelihood of being road-killed (Develey & Stouffer 2001; Rytwinski & Fahrig 2012). Moreover, the high availability of resources and refuge in road verges can attract habitat and diet generalist species and increase their risk of being hit by vehicles (Ruiz-Capillas et al. 2012).

The early maturity age seemed to increase the risk of collision in both birds and mammals. Since early maturity age and body size are correlated (Blueweiss et al. 1978, Hendriks 2007) and show contrasting effects regarding vulnerability to road traffic road-kill, we hypothesized that a complex combination of perception of risk indirectly associated to biological features may explain the road-kill rates. However, maturity age for birds in particular must be considered carefully as most data were imputed. Additional studies considering empirical estimates will be necessary to clarify this relationship.

We also found factors that explain the vulnerability to traffic collisions only for birds or for mammals. Apparently, the higher chance of being hit by a vehicle is related with the attraction to roads due to the presence of carcasses. Interestingly, bird scavenging had little impact in the model. The ability of birds to escape in time to avoid collisions may explain differences between bird and mammal scavengers.

Although diet specialization had a high contribution in our model, diet type (here expressed as trophic level) was not important to explain road-kill rates as found by previous studies (Ford & Fahrig 2007; Cook & Blumstein 2013). In fact, diet generalists might be more capable of foraging on anthropic habitats, such as road verges, and thus would be more prone to cross roads (Barrientos & Bolonio 2009). Since diet breadth was not tested in other studies, we cannot make direct comparisons; nonetheless, our findings suggested that the degree of diet specialization is more informative to predict road-kill likelihood than trophic level.

Another contrasting result was the little support found for mammal sociality to explain road-kill rates (see Cook & Blumstein's 2013). These authors hypothesized a grouping effect observed in social animals would lead to higher road mortality as more animals might be on the road. However, sociality typically involves engaging in cooperative parental and help care, which contributes to experience sharing among individuals and could reduce the risk of vehicle collision (Laland 2004).

Our model was able to predict that 30 threatened bird and mammal species are likely to be at risk or become vulnerable if a new road infrastructure is implemented. For example, the boa nova topaculo (*Scytalopus gonzagai*) and the buffy saki (*Pitheca albicans*) are endangered bird and mammal species, respectively, predicted to be vulnerable to road-kill. The boa nova topaculo occurs in the Atlantic forest, which has been highly deforested (Ribeiro et al. 2009), while the buffy saki occurs in the Amazon forest, which is currently undergoing a severe deforestation process (Fearnside 2017). Additionally, the IUCN lists these species under several threats such as ecosystem degradation and hunting. Therefore, additional mortality due to collision with vehicles, even if relatively small fractions of the population are removed, might have a significant impact on their populations' viability in the medium term.

In this study, we found some limitations that should be considered for future research. Missing data is a common problem in datasets unlikely to be easily overcome. Data imputation methods may be helpful, but some limitations (e.g. handling variable correlation) need consideration (Penone et al. 2014). Road-kill surveys may be spatially biased, generating nonrepresentative sampling which can potentially affect results. The differential detectability is a recurrent problem in road surveys and studies have shown that small species may be removed from roads in less than 24 hours (Teixeira et al. 2013). The correction we have applied to observed road-kill rates does not consider intervals shorter than one day (Supplementary Material), which may underestimated the road-kill rates of small-sized species.

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Surprisingly, predictions for trait importance and their effects on the risk of road-kill did not vary between corrected or uncorrected rates as suggested by Santos et al. (2011). The criteria we adopted for minimum survey interval may have contributed to reduce differences between methods, since intervals of one week or shorter significantly reduce bias for medium- and large-sized birds and mammals (Bager & Rosa 2011). Finally, our study comprised only part of the existing variability in bird and mammal traits due to the diversity sampled in road surveys, limiting the accuracy to make predictions for a large number of species.

Nevertheless, we were still able to find relationships in line with other studies (e.g. Ford & Fahrig 2007; Rytwinski & Fahrig 2012), despite some inconsistencies (e.g. Cook & Blumstein 2013). Validation of our model would enable verifying if predicted species are under road mortality risk. Intensifying the survey effort in the studied areas will enable us to check if undetected species are being road-killed as predicted or not (Santos et al. 2016). Surveying areas where studies have not yet been done will enable us to confirm the predictions for non-studied species.

Our results contribute to a better understanding of the biological drivers that make species particularly vulnerable to road traffic collisions. Several studies show evidences that road characteristics (e.g. traffic, size, and design) and landscape features (e.g. vegetation type, and degree of fragmentation) have a significant role in explaining road-kill rates (e.g. Saeki & Macdonald 2004; Santos et al. 2013). Therefore, we argue that research to evaluate road-kill risk should use not only road-related and landscape features but also available knowledge on species traits to provide more accurate information for environmental impact assessments. The trait-based approach also helps to detect species potentially at risk, which is crucial to plan mitigation measures for new infrastructures. Future research should focus on elucidating some controversy found among studies to refine the role of traits and enable group-specific conservation actions.

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Literature Cited

Bager A, Rosa CA. 2011. Influence of Sampling Effort on the Estimated Richness of Road-Killed Vertebrate Wildlife. *Environmental Management* **47**:851-858.

Barrientos R, Bolonio L. 2009. The presence of rabbits adjacent to roads increases polecat road mortality. *Biodiversity Conservation* **18**:405-418.

Barthelmess EL, Brooks MS. 2010. The influence of body-size and diet on road-kill trends in mammals. *Biodiversity Conservation* **19**:1611-1629.

Borda-de-Água L, Grilo C, Pereira HM. 2014. Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using agestructured models. *Ecological Modelling* **276**:29-37.

Breiman L. 2001. Random Forests. *Machine Learning* **45**:5-32.

Brienen RJW, et al. 2015. Long-term decline of the Amazon carbon sink. *Nature* **519**:344-350.

Blueweiss L, Fox H, Kudzuma V, Nakashima D, Peters R, Sams S. 1978. Relationships between body size and some life history parameters. *Oecologia* **37**:257-272.

Clevenger AP, Chruszcz B, Gunson KE. 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation* **109**:15-26.

Coelho IP, Kindel A, Coelho AVP. 2008. Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *European Journal of Wildlife Research* **54**:689-699.

Coffin AW. 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography* **15**:396-406.

Cook TC, Blumsteim DT. 2013. The omnivore's dilema: diet explains variation in vulnerability to vehicle collision mortality. *Biological Conservation* **167**:310-315.

Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G. 2009. Multiple ecological pathways to extinction in mammals. *PNAS* **106**:10702-10705.

Desbiez ALJ, Bodmer RE, Tomas WM. 2010. Mamalian densities in a neotropical wetland subject to extreme climatic events. *Biotropica* **42**:373-378.

Develey PF, Stouffer PC. 2001. Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. *Conservation Biology* **15**:1416-1422.

DNIT (Departamento Nacional de Infraestrutura de Transportes).2015. Sistema nacional de viação. Brasília, DF.

Fahrig L, Rytwinski T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* **14**:21.

Fearnside, PM. 2017. Brazilian politics threaten environmental policies. *Science* **353**:746-748.

Ford AT, Fahrig L. 2007. Diet and body size of North American mammal road mortalities. *Transportation Research Part D* **12**:498-503.

González-Suárez M, Lucas PM, Revilla E. 2012. Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology* **81**:1211-1222

González-Suárez M, Gómez A, Revilla E. 2013. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes *Ecosphere* **4**:76.

Grilo C, Ascensão F, Santos-Reis M, Bissonette JA. 2011. Do wellconnected landscapes promote road-related mortality? *European Journal of Wildlife Research* **57**:707-716.

Grilo C, et al. 2012. Individual spatial responses towards roads: implications for road mortality risk. *PLoS ONE* **7**:9.

Grilo C, et al. 2016. Heterogeneous road networks have no apparent effect on the genetic structure of small mammal populations. *Science of the Total Environment* **565**:706-713.

Hendriks AJ. 2007. The power of size: a meta-analysis reveals consistency of allometric regressions. *Ecological Modelling* **205** 196:208.

Ibisch PL, Hoffmann MT, Kreft S, Pe'er G, Kati V, Biber-Freudenberger L, DellaSala DA, Vale MM, Hobson PR, Selva N. 2016. A global map of roadless areas and their conservation status. *Science* **354**:1423-1427.

IUCN 2016. The IUCN Red List of threatened species. Version 2016-3. http://www.iucnredlist.org. Downloaded on 22 November 2016.

Jones KE, et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**:2648-2648.

Klink CA, Machado RB. 2005. Conservation of the Brazilian Cerrado. *Conservation Biology* **19**:707-713.

Laland KN. 2004. Social learning strategies. *Learning & Behavior* **32**:4-14.

Laurance WF, Cochrane MA, Bergen S, Fearnside PM, Delamônica P, Barber C, D'Angelo S, Fernandes T. 2001. The future of the Brazilian Amazon. *Science* **291**:438-439.

Laurance WF, Croes BM, Tchignoumba L, Lahm SA, Alonso A, Lee ME, Campbell P, Ondzeano C. 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology* **20**:1251-1261.

Laurance WF, Balmford A. 2013. Land use: a global map for road building. *Nature* **495**:308-309.

Liaw A, Wiener M. 2012. Classification and regression by random forest. *R News* **2**:18-22.

Lindsted SL, Miller BJ, Buskirk SW. 1986. Home range, time and body size in mammals. *Ecology* **67**:413-418.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB da, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecological Archives* **96**:3109-3109.

Núñez-Regueiro MM, Branch L, Fletcher Jr RJ, Marás GA, Derlindati E, Tálamo A. 2015. Spatial patterns of mammal occurrence in forest strips surrounded by agricultural crops of the Chaco region, Argentina. *Biological Conservation* **187**:19-26.

Ofstad EG, Herfindal I, Solberg EJ, Sæther BE. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society B* **283**.

Orlowski G. 2008. Roadside hedgerows and trees as factors increasing road mortality of birds: Implications for management of roadside vegetation in rural landscapes. *Landscape and Urban Planning* **86**:153-158.

Paglia AP, et al. 2012. Annotated Checklist of Brazilian Mammals 2nd Edition. *Occasional Papers in Conservation Biology* **6**:1-76. Penone C, Davidson AD, Shoemaker KT, Marco MD, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC. Imputation of missing data in life-history traits dataset: which approach performs the best? *Models in Ecology and Evolution* **5**:961-970.

Piacentini, et al. 2015. Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee. *Revista Brasileira de Ornitologia* **23**:91-298.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* **142**:1141-1153.

Ruiz-Capillas P, Mata C, Malo JE. 2012. Road verges are refuges for small mammal populations in extensively managed Mediterranean landscapes. *Biological Conservation* **158**:223-229.

Rytwinski T, Fahrig L. 2011. Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications* **21**:589-600.

Rytwinski T, Fahrig L. 2012. Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation* **147**:87-98.

Saeki M, Macdonald DW. 2004. The effects of traffic on the raccoon dog (*Nyctereutes procyonides viverrinus*) and other mammals in Japan. *Biological Conservation* **118**:559-571.

Santos RAL, Santos SM, Santos-Reis M, Figueiredo AP de, Bager A, Aguiar LMS, Ascensão F. 2016. Carcass persistence and detectability: reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLoS ONE* **11**:11.

Santos SM, Carvalho F, Mira A. 2011. How Long Do the Dead Survive on the Road? Carcass Persistence Probability and Implications for Road-Kill Monitoring Surveys. *PLoS ONE* **6**:9.

Santos SM, Lourenço R, Mira A, Beja P. 2013. Relative effects of road risk, habitat suitability, and connectivity on wildlife roadkills: the case of tawny owls (*Strix aluco*). *PLoS ONE* **8**:11.

Santos SM, Mira A, Salgueiro PA, Costa P, Medinas D, Beja P. 2016. Avian trait-mediated vulnerability to road traffic collisions. *Biological Conservation* **200**:122-130.

Slater FM. 2002. An assessment of wildlife road casualities - the potential discrepancy between numbers counted and numbers killed. *Web Ecology* **3**:33-42.

Souza JC, Cunha VP, Markwith SH. 2014. Spatiotemporal variation in human-wildlife conflicts along highway BR-262 in the Brazilian Pantanal. *Wetlands Ecology Management* **23**:227-239.

Stekhoven DJ, Bühlmann P. MissForest-non-parametric missing value imputation for mixed-type data. *Bioinformatics* **28**:112-118.

Teixeira FZ, Coelho AVP, Esperandio IB, Kindel A. 2013. Vertebrate road mortality estimates: Effects of sampling methods and carcass removal. *Biological Conservation* **157**:317-323.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecological Archives* **95**:2027-2027.

Supporting Information

A table containing the location of studies considered (Appendi S1), the details on the values used and how survey frequency was calculated (Appendix S2) and a list of the 10% most affected and threatened species (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

TABLE

Table 1. Species' traits explored as predictors of road mortality rates in Brazilian birds and mammals. Table includes trait name, definition, possible categories for birds and mammals, and data source.

Trait	Definition	Data source
Diet breadth	Number of dietary categories eaten by a species. Possible categories for birds: Invertebrate, Vertebrate, Fruit, Nectar, Seed, other plant material. For mammals: Vertebrate, Invertebrate, Fruit, Flowers/nectar/pollen, Leaves/branches/bark, Seeds, Grass/roots/tubers, other plant material.	Bird data: Elton Traits (Wilman et al. 2014). Mammal data: PanTHERIA (Jones et al. 2009).
Feeding behavior	Scavenger feeding behavior (at least 10% of its diet consists of dead animals). Possible categories for birds and mammals: Scavenger or Non-scavenger.	Elton Traits (Wilman et al. 2014).
Foraging substratum	Main substratum in which the species forages. Possible categories for birds: Aquatic/semi-aquatic, Terrestrial/understory, Arboreal/aerial. For mammals: Aquatic/semi-aquatic, Terrestrial/semifossorial/fossorial/scansorial, Arboreal/volant	Elton Traits ^a (Wilman et al. 2014). Annotated Checklist of BrazilianMammals ^b (Paglia et al. 2012).
Habitat breadth	Number of habitat categories a species is able to use. Possible categories for birds and mammals: Forest, Savanna, Shrubland, Grassland, Wetland, Marine neritic, Marine intertidal, Marine coastal/supratidal, Artificial terrestrial, Artificial aquatic.	First hierarchy level of IUCN Habitats Classification Scheme (Version 3.1).
Trophic level	Trophic level occupied by the species. Possible categories for birds and mammals: Herbivore, Omnivore, Carnivore.	Elton Traits (Wilman et al. 2014). PanTHERIA ^b (Jones et al. 2009).
Activity cycle	The main period a species is active. Possible categories for birds: Nocturnal, Non-nocturnal. For mammals: Nocturnal, Other º, Diurnal.	Elton Traits ^a (Wilman et al. 2014). PanTHERIA ^b (Jones et al. 2009).

Anthropogenic threaten factors	Presence or absence of direct anthropogenic threats faced by the species (Hunting & collecting terrestrial animals; Logging & wood harvesting). Possible categories for mammals: Presence or absence.	IUCN Threats Classification Schemes, category 5.1 (Version 3.2).
Body mass	The body mass of an adult individual. Category for birds and mammals: Weight (g).	Elton Traits (Wilman et al. 2014). Annotated Checklist of Brazilian Mammals ^b (Paglia et al. 2012). PanTHERIA ^b (Jones et al. 2009).
Home range	Home range size. Category for mammals: Area (km²).	PanTHERIA ^b (Jones et al. 2009).
Lifespan	The maximum age of an individual. Category for birds and mammals: Number of days.	Amniote database (Myhrvold et al. 2015). PanTHERIA ^b (Jones et al. 2009).
Maturity age	Age at which the species reaches sexual maturity. Category for birds and mammals: Number of days.	Amniote database (Myhrvold et al. 2015). PanTHERIA ^b (Jones et al. 2009).
Sociality	Whether a species spends most of its life in a group (social) or not (solitary). Possible categories for mammals: Social or Solitary.	PanTHERIA ^b (Jones et al. 2009).

^a only for birds; ^b only for mammals; ^c nocturnal/crepuscular, crepuscular, cathemeral, diurnal/crepuscular.



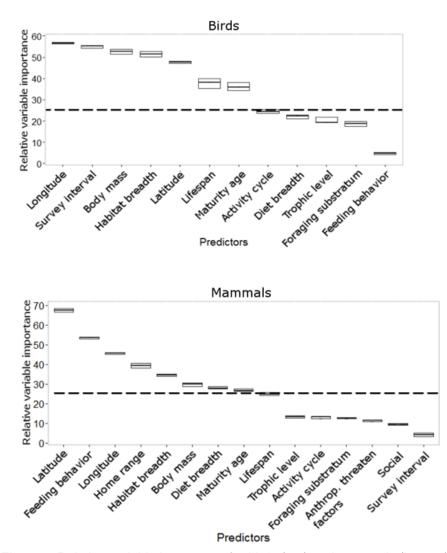
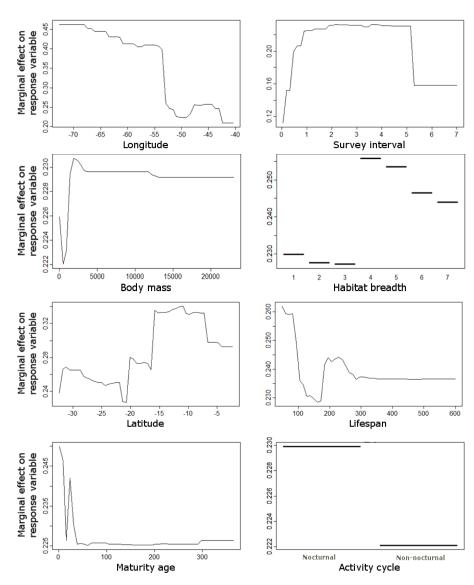
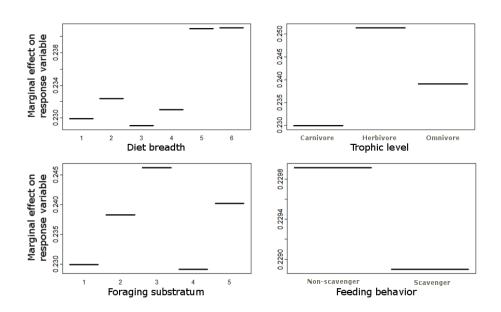


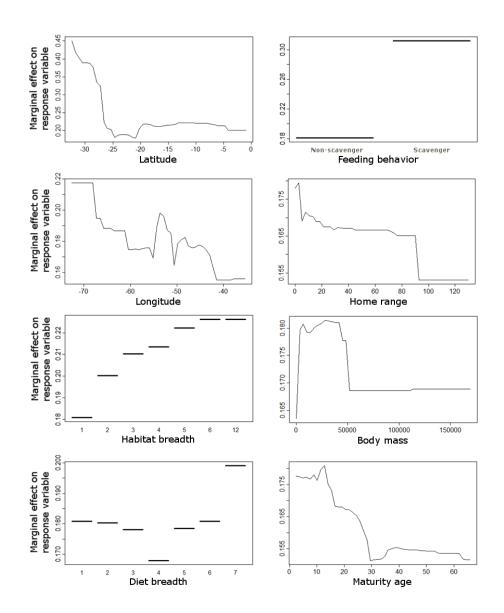
Figure 1. Relative variable importance for birds (top) and mammals (bottom). Each box plot presents the variation in results after running the model with each of the ten imputed datasets. Traits with a contribution higher than 25% are represented above the traced line. Despite only some traits needing imputation, the variation is a result of the way random forest works bootstrapping data and testing only a few variables at each node, producing slightly different outcomes each time.



Birds



Mammals



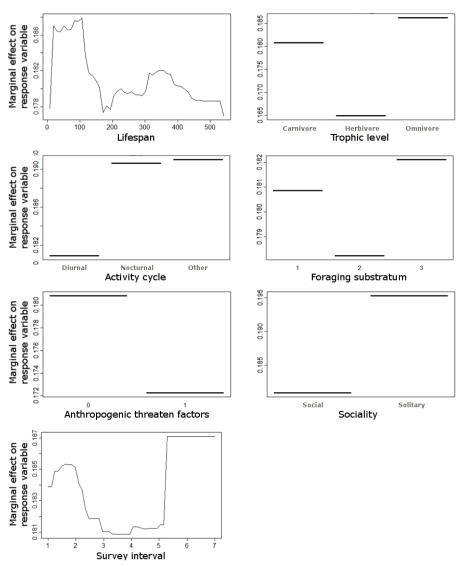


Figure 2. Partial dependence plots for birds and mammals showing the effect of a variable on the risk of mortality (higher values on the y-axis indicate higher risk). These plots show only one of the ten tested datasets. Differences between datasets outputs are minimal.

Appendix S1

Studies location in Brazil

Figure 1 below shows the approximate location of all 43 road surveys considered in our study.

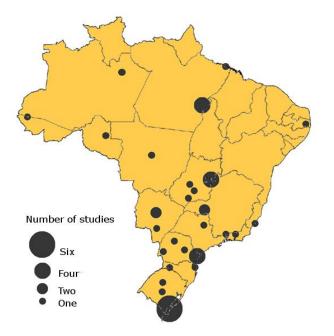


Figure 1 Approximate road survey location in Brazil.

Appendix S2

Correction rates applied on observed road-kill rates

The correction was based on Santos et al. (2011) (Fig. 1). We adapted the intervals and groups to suit our needs in terms of observed survey intervals and species. For example, Santos et al. (2011) considered intervals of one, two and seven days, whereas we also observed intervals of shorter than one day, or between two and seven days. Therefore, we selected the closest interval possible, in a conservative approach. For example, for an interval of 3.5 days we considered the correction applied to the interval of seven days, rather than for the two days. Road-kills tend to be underestimated (Santos et al. 2016), thus being conservative should provide results closer to the actual mortality rates.

Below (Table S1) we show all the intervals observed and how we applied the correction rates. The values provided by Santos et al. (2011) are for carcass persistence, therefore, we subtracted the values from one, in order to obtain the percentage of non-detected road-kills. The final corrected road-kill estimate is defined by multiplying the observed road-kill rate by 1+(x), in which x is the percentage of non-detected road-kills. For example, large mammals have a carcass persistence of 0.543 in a seven-day survey interval (Fig. 1). Therefore, the corrected road-kill rate is 1+(1-0.543) = 1.457. Intervals shorter than one day (ranging from twice a day to 16 times a day) were not corrected. Finally, we adapted the carnivores group by Santos et al. (2011) to reflect all large mammals. Body mass was given priority when defining groups, if inconsistencies were found (e.g. a bird of prey with 130 g was assigned to the "Small birds" groups, instead of "Birds of prey" group).

Table S1: Correction rates applied for observed road-kill rates. The correction consists of estimating the percentage of nondetected species for each taxon by subtracting from one the correspondent persistence estimate obtained by Santos et al. 2011. The result is then added to one to obtain the value by which the observed road-kill rate must be multiplied.

	Observed survey frequency							
	>7/week	7/week	5/week	4/week	3/week	2.5/week	2/week	1/week
				Survey	interval			
	>1	1	1.4	1.75	2.33	3	3.5	7
		s	urvey interva	al considere	d from Sante	os et al. (2011)		
	0	1	1	2	2	2	7	7
Taxonomic group*								
Small birds (8-200 g)	0	1.634	1.634	1.797	1.797	1.797	1.968	1.968
Large birds (200-1200 g, excluding birds of prey)	0	1.283	1.283	1.391	1.391	1.391	1.717	1.717
Birds of prey (175-1100 g)	0	1.255	1.255	1.327	1.327	1.327	1.555	1.555
Small mammals (11-300 g)	0	1.611	1.611	1.759	1.759	1.759	1.97	1.97
Large mammals (1100-2300 g)	0	1.196	1.196	1.294	1.294	1.294	1.294	1.457
Bats (6-23 g)	0	1.854	1.854	1.963	1.963	2	2	2

*Weight classes correspond to the ones used by Santos et al. (2011).

Table 1. Summary of results for persistence estimates for each taxonomic group and the "all taxa" data set (N: sample size; Median (95% CI): median persistence probabilities and corresponding 95% confidence intervals obtained with a Kaplan-Meier estimator; MPT: maximum persistence time recorded (in days); S(t = 1), S(t = 2), S(t = 7): estimate of persistence probability for 1-day, 2-day and 7-day intervals obtained with a Kaplan-Meier estimator).

Taxonomic group	N	Median (95% CI)	MPT (days)	S(t = 1)	S(t=2)	S(t = 7)
Toads	409	1 (1-1)	12	0.267	0.100	0.010
Salamanders	833	1 (1-1)	15	0.455	0.228	0.016
Lizards	107	1 (1-1)	4	0.056	0.019	0.000
Snakes	146	1 (1-1)	14	0.397	0.212	0.034
Freshwater turtles	22	3 (2-5)	51	0.818	0.591	0.182
Small birds	1990	1 (1-1)	63	0.366	0.203	0.032
Large birds	46	4 (2-6)	51	0.717	0.609	0.283
Birds of prey	110	6 (4-9)	94	0.745	0.673	0.445
Bats	82	1 (1-1)	5	0.146	0.037	0.000
Small mammals	270	1 (1-1)	16	0.389	0.241	0.030
Lagomorphs	208	2 (1-2)	25	0.505	0.351	0.077
Hedgehogs	106	4.5 (3-7)	106	0.774	0.632	0.377
Carnivores	92	9 (5-19)	158	0.804	0.706	0.543
GLOBAL	4447	1 (1-1)	144	0.407	0.241	0.063

Figure 1. Carcass persistence table elaborate by Santos et al. (2011).

Literature cited

Santos SM, Carvalho F, Mira A. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE* **6**:9.

Santos RAL, Santos SM, Santos-Reis M, Figueiredo AP de, Bager A, Aguiar LMS, Ascensão F. 2016. Carcass persistence and detectability: reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLoS ONE* **11**:11.

Appendix S3

Tables with the top 10% species predicted to be most affected by our models and their conservation status.

Birds

Species	Average predicted road-kill rates	IUCN status
Coturnicops notatus	0.138	Least concern
Chrysomus icterocephalus	0.132	Least concern
Pteroglossus azara	0.088	Least concern
Patagioenas cayennensis	0.078	Least concern
Embernagra platensis	0.063	Least concern
Embernagra longicauda	0.056	Least concern
Ortalis guttata	0.055	Least concern
Colinus cristatus	0.054	Least concern
Dendroplex picus	0.054	Least concern
Eubucco tucinkae	0.053	Least concern
Crex crex	0.051	Least concern
Corythopis delalandi	0.051	Least concern
Spiza americana	0.050	Least concern
Amazona amazonica	0.049	Least concern
Corythopis torquatus	0.049	Least concern
Ortalis canicollis	0.049	Least concern
Laterallus leucopyrrhus	0.048	Least concern
Phlegopsis nigromaculata	0.048	Least concern
Malacoptila semicincta	0.048	Least concern
Geranoaetus melanoleucus	0.047	Least concern
Crax blumenbachii	0.047	Endangered
Gymnopithys rufigula	0.044	Least concern
Pseudoseisura cristata	0.044	Least concern

Table 1. Bird species predicted to be most affect and their conservation status.

Tinamus tao	0.043
Gymnopithys leucaspis	0.043
Automolus melanopezus	0.043
Turdus albicollis	0.042
Pyriglena leuconota	0.042
Icterus nigrogularis	0.042
Sclerurus albigularis	0.042
Columbina cyanopis	0.042
Automolus infuscatus	0.041
Neothraupis fasciata	0.041
Setophaga striata	0.040
Gubernatrix cristata	0.040
Conothraupis mesoleuca	0.040
Porzana flaviventer	0.040
Furnarius leucopus	0.040
Pluvialis dominica	0.040
Chloephaga picta	0.040
Crax alector	0.040
Willisornis poecilinotus	0.039
Taraba major	0.039
Sporophila intermedia	0.038
Columbina squammata	0.038
Progne elegans	0.038
Saltator coerulescens	0.038
Sporophila luctuosa	0.038
Turdus iliacus	0.037
Cyanocorax heilprini	0.037
Nothura boraquira	0.037
Liosceles thoracicus	0.037
Catamenia homochroa	0.037
Hylopezus nattereri	0.036
Pyriglena atra	0.036
Cyphorhinus arada	0.036
Myrmornis torquata	0.036
Glaucidium minutissimum	0.036

Vulnerable Least concern Least concern Least concern Least concern Least concern Least concern Critically endangered Least concern Near threatened Least concern Vulnerable Least concern Endangered Least concern Least concern Least concern

Rhegmatorhina gymnops	0.036
Bucco tamatia	0.036
Microcerculus bambla	0.036
Syndactyla roraimae	0.036
Pithys albifrons	0.036
Conopophaga aurita	0.036
Synallaxis kollari	0.036
Synallaxis rutilans	0.036
Oneillornis salvini	0.036
Pachysylvia hypoxantha	0.036
Pachysylvia muscicapina	0.036
Panyptila cayannensis	0.036
Paroaria cervicalis	0.036
Paroaria xinguensis	0.036
Pauxi mitu	0.036
Pauxi tomentosa	0.036
Pauxi tuberosa	0.036
Percnostola minor	0.036
Percnostola subcristata	0.036
Phaethornis aethopygus	0.036
Phaethornis maranhaoensis	0.036
Phaethornis margarettae	0.036
Pheugopedius coraya	0.036
Pheugopedius genibarbis	0.036
Phlegopsis borbae	0.036
Piculus capistratus	0.036
Piculus laemostictus	0.036
Piculus paraensis	0.036
Piculus polyzonus	0.036
Picumnus buffonii	0.036
Picumnus pernambucensis	0.036
Picumnus undulatus	0.036
Pipraeidea bonariensis	0.036
Podicephorus major	0.036
Polioptila attenboroughi	0.036
-	

Vulnerable Least concern Least concern Least concern Least concern Least concern Critically endangered Least concern Least concern

Polioptila facilis	0.036
Polioptila paraensis	0.036
Porphyriops melanops	0.036
Procacicus solitarius	0.036
Psophia dextralis	0.036
Psophia interjecta	0.036
Psophia napensis	0.036
Psophia obscura	0.036
Psophia ochroptera	0.036
Pteroglossus beauharnaisii	0.036
Pteroglossus flavirostris	0.036
Pteroglossus mariae	0.036
Pygochelidon melanoleuca	0.036
Pyriglena pernambucensis	0.036
Pyrrhura anerythra	0.036
Pyrrhura coerulescens	0.036
Ramphocaenus sticturus	0.036
Rhopias gularis	0.036
Rhopospina fruticeti	0.036
Saltatricula atricollis	0.036
Schiffornis amazonum	0.036
Schiffornis olivacea	0.036
Sciaphylax hemimelaena	0.036
Sciaphylax pallens	0.036
Sclerurus cearensis	0.036
Sclerurus macconnelli	0.036
Scytalopus gonzagai	0.036
Scytalopus petrophilus	0.036
Serpophaga griseicapilla	0.036
Setophaga pitiayumi	0.036
Sirystes albocinereus	0.036
Sirystes subcanescens	0.036
Spinus magellanicus	0.036
Spinus yarrellii	0.036
Sporophila angolensis	0.036

Least concern Least concern Least concern Least concern Endangered Least concern Least concern Critically endangered Least concern Vulnerable Least concern Endangered Least concern Least concern

Sporophila beltoni	0.036	Least concern
Sporophila crassirostris	0.036	Least concern
Sporophila maximiliani	0.036	Vulnerable
Sporophila pileata	0.036	Least concern
Suiriri affinis	0.036	Least concern
Synallaxis cinerea	0.036	Least concern
Synallaxis hellmayri	0.036	Near threatened
Synallaxis simoni	0.036	Least concern
Syndactyla ucayalae	0.036	Near threatened
Tachycineta leucopyga	0.036	Least concern
Tangara argentea	0.036	Least concern
Tangara brasiliensis	0.036	Least concern
Tangara cyanomelas	0.036	Least concern
Tangara episcopus	0.036	Least concern
Tangara ornata	0.036	Least concern
Tangara palmarum	0.036	Least concern
Tangara sayaca	0.036	Least concern
Thamnophilus capistratus	0.036	Least concern
Thamnophilus melanothorax	0.036	Least concern
Tolmomyias sucunduri	0.036	Least concern
Trogon ramonianus	0.036	Least concern
Tunchiornis ochraceiceps	0.036	Least concern
Turdus sanchezorum	0.036	Least concern
Tyranniscus burmeisteri	0.036	Least concern
Urubitinga coronata	0.036	Endangered
Vireo chivi	0.036	Least concern
Vireo sclateri	0.036	Least concern
Willisornis vidua	0.036	Least concern
Xiphocolaptes carajaensis	0.036	Least concern
Xiphorhynchus atlanticus	0.036	Least concern
Xiphorhynchus beauperthuysii	0.036	Least concern
Xiphorhynchus chunchotambo	0.036	Least concern
Xiphorhynchus guttatoides	0.036	Least concern
Zimmerius chicomendesi	0.036	Least concern

Mammals

Species	Average predicted road-kill rate	IUCN Status
Pithecia irrorata	0.069	Data deficient
Pithecia pithecia	0.066	Least concern
Choloepus hoffmanni	0.065	Least concern
Pithecia albicans	0.065	Vulnerable
Cavia magna	0.064	Least concern
Cavia fulgida	0.064	Least concern
Pithecia monachus	0.063	Data deficient
Necromys lasiurus	0.060	Least concern
Vampyressa pusilla	0.050	Data deficient
Molossus rufus	0.046	Least concern
Alouatta belzebul	0.044	Vulnerable
Phaenomys ferrugineus	0.042	Least concern
Mico saterei	0.042	Least concern
Ateles chamek	0.041	Least concern
Calomys tener	0.038	Least concern
Choeroniscus godmani	0.037	Least concern
Saimiri vanzolinii	0.037	Vulnerable
Macrophyllum macrophyllum	0.037	Least concern
Gyldenstolpia fronto	0.037	Least concern
Gyldenstolpia planaltensis	0.037	Least concern
Holochilus brasiliensis	0.037	Least concern
Callicebus cinerascens	0.037	Least concern
Carollia benkeithi	0.037	Least concern
Cynomops planirostris	0.037	Least concern
Eptesicus furinalis	0.037	Least concern
Histiotus alienus	0.037	Least concern
Mico rondoni	0.037	Vulnerable
Sapajus cay	0.036	Least concern
Artibeus fimbriatus	0.036	Least concern
Dasyprocta azarae	0.036	Data deficient
Dasyprocta croconota	0.036	Least concern

Table 2. Mammals species predicted to be most affected andtheir status.

Marmosa demerarae	0.034	Least concern
Marmosa lepida	0.033	Least concern
Oxymycterus judex	0.033	Least concern
Phyllomys dasythrix	0.033	Least concern
Delomys sublineatus	0.033	Least concern
Molossus pretiosus	0.032	Least concern
Phyllostomus elongatus	0.032	Least concern
Myotis albescens	0.032	Least concern
Didelphis imperfecta	0.031	Least concern
Hylaeamys perenensis	0.031	Least concern
Rhipidomys emiliae	0.030	Least concern
Mico humeralifer	0.030	Data deficient
Alouatta discolor	0.030	Vulnerable
Dermanura anderseni	0.030	Least concern
Phyllomys sulinus	0.030	Data deficient
Thylamys karimii	0.030	Vulnerable
Thyroptera devivoi	0.030	Data deficient
Natalus macrourus	0.029	Least concern
Nyctinomops laticaudatus	0.029	Least concern
Saguinus fuscus	0.029	Least concern
Tadarida brasiliensis	0.029	Least concern
Dermanura cinerea	0.029	Least concern
Neacomys paracou	0.029	Least concern
Microsciurus flaviventer	0.029	Data deficient
Platyrrhinus infuscus	0.029	Least concern
Platyrrhinus recifinus	0.029	Least concern