Species' traits as predictors of avoidance towards roads and traffic

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Title: Species' traits as predictors of avoidance towards roads and traffic

Authors: Daniela Duffett[a,†], Marcello D'Amico[b,c,†], Margarita Mulero-Pázmány[d], Manuela González-Suárez[a,*]

Affiliations:

[a] Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading, Reading, RG6 6AS, UK

[b] THEOECO, CIBIO-InBIO, University of Porto, Vairão, 4485-661, Portugal

[c] School of Agriculture, CEABN-InBIO, University of Lisbon, Lisbon, 1349-017, Portugal

[d] School of Biological and Environmental Sciences. Liverpool John Moores University, UK

* Corresponding author: manuela.gonzalez@reading.ac.uk

[†] These authors contributed equally

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Abstract

Road-networks and their associated motorized traffic pose a threat to biodiversity and ecosystems, with different groups of species exhibiting different avoidance responses. The often species-specific nature of these behavioural responses to roads and traffic suggest that morphological, ecological, life-history and behavioural traits could be useful in explaining and predicting these responses. Trait-based predictive models have been used to assess extinction risk, land use impacts, and road mortality. Here we present the first, to our knowledge, test of their potential to address animal road avoidance. We studied the fleeing responses and spatial distribution in relation to roads of diverse ungulate species across three South African protected areas. Our results show that smaller, solitary species with non-grazing food habits are more likely to flee in response to presence of a vehicle. None of the tested traits showed a clear relationship based on biological hypotheses with initial distance to roads and tolerance distance to vehicles (used to describe behavioural avoidance towards roads and vehicles, respectively). However, we found significant effects that supported proposed methodological hypotheses. Our results show the potential to use traits as indicators of vehicle and traffic avoidance. Obtaining behavioural avoidance data in the field for many species and areas can be time consuming, but here we show it may be possible to use available trait data to generally predict species responses. This could be useful for initial species risk assessments.

Keywords: African ungulates, ecotourism, flight response, road avoidance, road ecology, traits-based model.

1. Introduction

The rapid and global expansion of road infrastructures and associated motorized traffic pose a great threat to biodiversity and ecosystems worldwide (Laurance *et al*., 2014; Ibisch *et al*., 2016), even within protected areas (Garriga *et al*., 2012; Monz *et al*., 2016). Roads and traffic affect wildlife by causing mortality due to collisions with vehicles (Coelho *et al.,* 2008; D'Amico *et al*., 2015; González-Suárez *et al*., 2018) and fragmenting and destroying habitat (Forman, 2000; Eigenbrod *et al*., 2008). The latter include direct loss due to road construction, as well as indirect losses via traffic emissions (e.g. noise, light, chemical pollution) deteriorating habitat quality within road-effect zones (Forman and Deblinger, 2000; Laurance *et al*., 2014). The combined action of increased mortality by roadkill and avoidance behaviours towards road-effect zones can produce barrier effects, which can lead to population fragmentation, genetic isolation and even local extinction (Grilo *et al*., 2012; Ceia-Hasse *et al*., 2018).

Distinct groups of species often exhibit different avoidance responses within road-effect zones, including: road avoidance (which includes road-surface avoidance and habitat-gap avoidance), traffic-emissions avoidance, and vehicle avoidance (Jaeger *et al*., 2005; D'Amico *et al*., 2016). Road-surface avoidance is common among small-sized species, such as rodents, that avoid the hostile conditions of the road surface (e.g. materials, temperature; McGregor *et al*., 2008; Brehme *et al*., 2013). Canopy birds and arboreal mammals usually exhibit habitat-gap avoidance caused by both natural and artificial gaps in the vegetation (Laurance *et al*., 2004; Chen and Koprowski, 2016). Traffic-emissions avoidance is probably the most common behavioural response to roads and traffic, with different species responding to different types of emissions. For example, nocturnal mammals tend to avoid street lights (Francis *et al*., 2015), many songbirds avoid traffic-related noise (including experimental phantom roads; McClure *et al*., 2013) and some ungulates preferentially graze away from linear infrastructures due to road dust (Ndibalema *et al*., 2008). Finally, vehicle avoidance mostly affects species that approach roads but still react to oncoming vehicles, a reaction observed in several scavenger species (Rytwinski and Fahrig, 2012).

The species-specific nature of behavioural responses to roads and traffic suggests that some morphological, ecological, life-history and behavioural traits could be useful to explain and predict these responses. Although previous studies have postulated that species' traits should produce, in turn, species-specific variations in animal abundance related to roads and traffic (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2011, 2012, 2013; Francis, 2015), no previous research, to our knowledge, has directly investigated the relationship between species' traits and behavioural responses to roads and traffic, and the potential of applying trait-based model to assess avoidance responses to roads and traffic/vehicles. Past studies have considered how species' traits influence roadkill probability (Ford and Fahrig, 2007; Barthelmess and Brooks, 2010; Cook and Blumstein, 2013; D'Amico *et al.*, 2015; Santos *et al.*, 2016), but only recently the full potential for using trait-based models in Road Ecology has started to be considered, and for now has only been explored for estimates of road-associated mortality (González-Suárez *et al*., 2018).

Our study addresses this knowledge gap by exploring the value of diverse species' traits to understand ungulate behavioural responses to roads and traffic. We considered several species' traits reflecting different biological hypotheses (Table 1) based on the general assumption that roads and vehicles can be perceived as a danger, similar to predators, by ungulates (Frid and Dill, 2002; Lima et al., 2015). We hypothesize an effect of morphology on avoidance responses, because smaller species have been found to be more cautious towards potential predators than larger species (Berger and Cunningham, 1988). Research has shown that ungulates such as pronghorns *Antilocapra americana* in North America (Gavin and Komers, 2006) and Tibetan antelopes *Pantholops hodgsonii* in Asia (Lian et al., 2011) can respond to vehicles as if these were predators. Species with relatively larger brains have greater learning and cognitive capacity (Shultz and Dunbar, 2006), thus, we propose they may be able to realize that vehicles are not actual predators (within protected areas) and show no or limited avoidance responses. Foraging habits have been shown to affect anti-predatory responses; the spatial distribution of browsing ungulates, but not of grazing species, has been shown to change in response to predators (Valeix *et al*., 2009), thus, we predict browsing species will avoid roads and vehicles more often. Longevity may also be important because long-lived species have greater learning capacities (Street *et al*., 2017) and their longer lifespan can allow them to learn by experience that vehicles are not predators. The trade-off between investment in reproduction and survival (Promislow and Harvey, 1990) proposes that slow-breeding species will invest more in self-maintenance and thus, should be more cautious towards potential predators (or roads and vehicles) than fast-breeding species. Finally, solitary species have been shown to be more wary of potential predators than gregarious species (Hunter and Skinner, 1998), thus we predict solitary animals will show higher avoidance. As alternative hypotheses, we considered methodological effects, mostly associated to detectability, that could also result in association between species' traits and behavioural responses (all biological and methodological hypotheses are summarized in Table 1).

To test these hypotheses, we analysed data from multiple ungulate species collected along the heterogeneous road-networks of three African protected areas (Fig. 1). We selected this system because African ungulates are relatively easy to detect from the road (Mulero-Pázmány *et al.*, 2016; González-Suárez *et al.*, 2017), and are important components of African ecosystems due to their roles as prey, ecosystem engineers and, in some cases, keystone species (e.g., Waldram *et al*., 2008; Pringle *et al*., 2007; Coverdale *et al*., 2016). Using this study system as a case study, we test the value of predictive trait-based models for avoidance behaviours towards roads and traffic. This approach can contribute to identify susceptible species and potentially generate risk assessments.

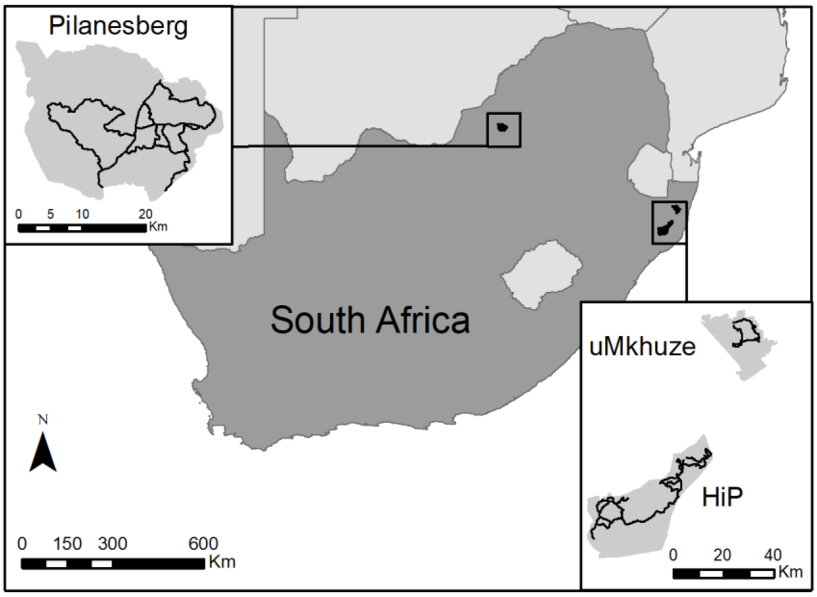

Figure 1. Map of the three studied protected areas in South Africa. Insets show the park boundaries and sampled transects.

2. Methods

2.1. Study area

Behavioural data were collected in three South African protected areas: Hluhluwe-iMfolozi Park (from here on, HiP; 28.2198° S, 31.9519° E), Pilanesberg National Park (25.2449° S, 27.0891° E), and uMkhuze Game Reserve (27.6519° S, 32.2435° E. Fig. 1). All these protected areas allow regulated human activities based on wildlife-watching tourism and have road-networks that include paved and unpaved road surfaces and varying traffic volumes (from virtually no vehicles to high-traffic intensity). The areas host diverse ungulate communities including abundant impala *Aepyceros melampus*, small steenbok *Raphicerus campestris* and large and iconic species such as African bush elephant *Loxodonta africana* and white rhinoceros *Ceratotherium simum* (Table 2 includes all observed species).

2.2. Data collection

Data were collected on African ungulate species in October 2016 along 66 transects consisting of both unpaved and paved roads, totalling 722 km surveyed (HiP: 36 transects, 401 km of road sampled; Pilanesberg: 26 transects, 274 km; uMkhuze: 4 transects, 47 km; Fig. 1). Each transect was sampled twice (except in uMkhuze where transects were surveyed once), driving in opposite directions and at different times of the day: once at either sunrise (06:00-07:00 h, local time) or sunset (17:00-18:00 h, local time) and another time at central hours of the day, to capture variability in daily activity patterns. Observations were gathered from a 4x4 vehicle driving at <30 km/h.

For each transect, two observers searched for individuals of any ungulate species located <320 m from each side of the road (estimated range of detection; Mulero-Pázmány *et al.*, 2016; González-Suárez *et al.*, 2017), whilst a third observer noted the number of vehicles circulating in the opposite direction. The number of incoming vehicles over the duration of the transect sampling was used to estimate *traffic intensity*. When an individual was sighted, the vehicle was stopped in the closest possible location while remaining on the road. The position of the vehicle was recorded using a GPS (Garmin GSPMAP 62, KS, USA) and the side of the road where the individual was located noted. If more than one individual of the same species was sighted together, the one closest to the road was selected as the focal individual and the minimum group size was estimated (the group size is a minimum because some individuals could be out of sight). When possible, sex of the focal individual and group composition (mixed sex and presence of young) were recorded.

For each sighting we recorded the distance from the road to the focal individual using an Opticron Tracker 670 rangefinder and noted if the individual exhibited a *flight response*, escape motion in reaction to a stimulus possibly indicative of danger (Stankowich, 2008). We recorded two distances: 1) *initial distance* - minimum perpendicular distance from the road to the initial location of the focal individual, 2) *tolerance distance* - minimum perpendicular distance to the road at which the focal individual was stationary in the presence of a stopped vehicle (following Mulero-Pázmány et al., 2016). Both distances were measured directly when possible or using reference points if the individual had moved. *Initial* and *tolerance distances* were identical if the individual did not move between the time it was first observed and the time our vehicle stopped. *Tolerance distance* could not be estimated sometimes because the focal individual did not stop moving while being observed or moved out of sight. It is important to note that recorded *tolerance distances* may not correspond to the minimum at which individuals can tolerate vehicles or to the commonly used flight-initiation distance FID (Frid and Dill, 2002). In these study areas it was not possible to leave the road to approach individuals until they fled as required to estimate FID.

Georeferenced locations were matched to *habitat ecozones* obtained from Park authorities. Original habitat types were reclassified into simplified categories for analyses (Supplementary materials, Table A1). Spatial analyses were done in ArcGIS 10.4 with *Cape Zone 36S Deprecated* projection (EPSG: 22236). Trait data for all species observed during the field study were obtained from published sources (Table 1).

2.3. Data analysis

We used generalized linear mixed effects models (GLMM) to evaluate if traits predicted *initial distance*, *tolerance distance* and *flight response*. We fitted separate models for each of the trait groups we considered (Table 1). All models included control predictors related to each observation: *road surface* (unpaved or paved), *traffic intensity*, and *standardized group size*. When modelling *flight responses, initial distance* was also included as a predictor. Observed minimum group size was standardized within species to facilitate comparison. For each observation, we subtracted the mean observed for the species and divided by the standard deviation. Therefore, positive *standardized group sizes* represent groups larger than the average observed group size for that species.

To avoid confounding allometric effects of *body mass* when testing *brain mass*, *longevity*, *sexual maturity age*, *gestation length*, and *litters per year* we used standardized residuals from log-log phylogenetic least squares models in which each of these traits was predicted by body mass (all variables were $\log_{10}$ transformed). We used the function pgls from the caper package (Orme *et al.*, 2013), using the updated mammalian supertree (Fritz *et al.*, 2009) to describe phylogenetic relationships.

Finally, to account for confounding factors associated to particular habitats, transects and the non-independence of trait data from related species, all GLMMs included *habitat ecozones*, a nested effect of *park*, *observation date*, and *transect ID*, and a taxonomic correction with *genus* nested within *family*. Distances were first transformed ($\log_{10}[x+1]$) and then modelled using the function lmer in the package lme4 (Bates *et al.*, 2015) with a Gaussian family. *Flight response* was modelled using the function glmer from the package lme4 using a binomial family (logit link). We evaluated predictor importance estimating 95% confidence intervals using bootstrapped sampling (using the function confint.merMod, with 2000 simulations and method=”boot” from the package lme4). We calculated Variance

Inflation Factors (VIF) for all models to detect collinearity issues. All analyses were completed in R version 3.3.2 (R Core Team, 2016).

All data and R scripts of completed analyses are available in the public repository Figshare (https://doi.org/10.6084/m9.figshare.12117564.v1).

3. Results

We recorded 513 sightings representing 18 species of African ungulates (Table 2). *Tolerance distance* was estimated for 448 of those sightings representing 17 species (no *tolerance distance* estimates were available for black rhino *Diceros bicornis*). In 20.7% (N=106) of those sightings we detected a *flight response*. Across all three parks we had a mean of 7.14 observations/10 km (SD = 4.36) with more observations in unpaved roads (mean ± SE = 7.53 ± 4.72 observations/10 km) than in paved roads (6.35 ± 3.49). The overall mean *traffic intensity* was 0.14 vehicles per minute (SD = 0.18), with more traffic in paved (0.26 ± 0.24 vehicles per minute) than in unpaved roads (0.08 ± 0.08). *Traffic intensity* varied by park, with higher levels in Pilanesberg (0.19 ± 0.23) and HiP (0.12 ± 0.13) than in uMkhuze (0.03 ± 0.04).

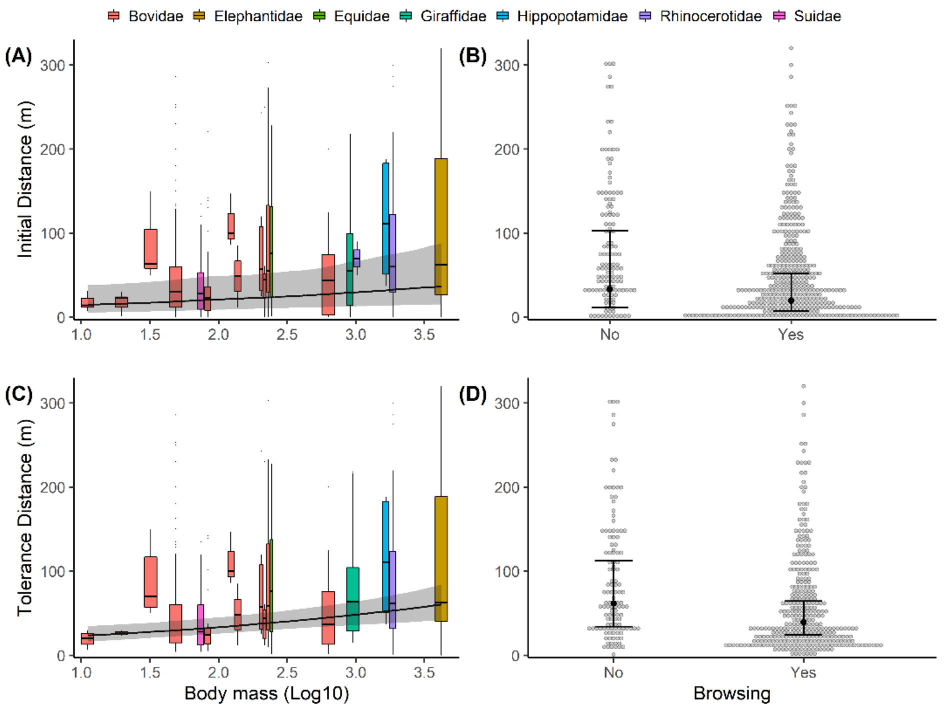

Figure 2. Observed (boxplots and dotplots) and predicted (line and error bars) *initial* (panels A and B) and *tolerance distances* (C and D) for ungulate species with different *body mass* values and different *browsing* foraging habits. In panels A and C boxplots represents distances observed for individual species with colours indicating the taxonomic family.

Predicted values were obtained using bootstrapped predictions from fitted models (Table 3) for a dataset representing the entire range of observed *body mass* values (for A and C), and a dataset representing each category of *browsing* behaviour (for B and D). In both datasets all other predictors set to observed mean value (predictions were made for the average population, without considering random factor values). The shaded areas (in A and C) and error bars (B and D) represent the 95% confidence interval of the bootstrapped predictions.

The traits *body mass* and *foraging habits* were identified as predictors of both *initial* and *tolerance distances*. In particular, small-sized, browsing ungulates were generally found closer to roads (both for *initial* and *tolerance distances*; Fig. 2, Table 3). These results align with our methodological hypotheses, which also predict no effect for a narrower observation area within which we hypothesize detectability would be unaffected by these traits (Table 1). When we fitted models considering only observations in the first 100 m from each side of the road for *initial distance* (data for 18 species and 392 records) and for *tolerance distance* (17 species and 337 records) we found no effect of *body mass* on either distance variable (while the effects of *traffic intensity* and *standardised group size* remained the same; Supplementary materials, Table A2). Browsing species still had shorter *initial* and *tolerance distances* within 100 m of roads, which may reflect a different biological mechanism affecting browsing behaviour near roads. *Longevity* and reproductive traits (i.e. *sexual maturity age*, *gestation length*, and *litters per year*) were not identified as relevant predictors of *initial* or *tolerance distance*.

Figure 3. Observed (circles) and predicted (lines and error bars) *flight responses* for ungulate species with different *body mass* (A), *grazing* food habits (B), and *social structure* (C). Observed values for panel A are represented grouping responses for each species, with circle size proportional to the number of observations. Colours indicate the taxonomic family. Predicted values were obtained for each plot using bootstrapped predictions for datasets

representing the entire range of *body mass* values for A, all *grazing* categories for B, and all *social structure* categories for C. All other predictors set to observed mean value (predictions were made for the average population, without considering random factor values). The shaded area (A) and error bars (B and C) represent the 95% confidence interval of the bootstrapped predictions.

Body mass, *social aggregation* and *foraging habits* were identified as predictors of *flight responses* (Fig. 3). Species with smaller *body mass*, solitary behaviour and non-grazing habits were more likely to flee (controlling for the significant effect of their *initial distance* to the road; Table 3). *Longevity* and reproductive traits (i.e. *sexual maturity age*, *gestation length*, and *litters per year*) were not identified as relevant predictors of *flight responses*.

Among the tested control predictors, we found a consistent effect of *traffic intensity* for both *initial* and *tolerance distance*, with ungulates located further from roads with more traffic, but no effect of *road surface* (Table 3). The *standardised group size* was also always important to explain *initial distance*, with relatively larger groups for each species often found closer to roads initially. This could reflect increased detectability when more individuals are together (larger relative group sizes). *Initial distance* was a strong predictor of *flight responses*, with ungulates located closer to roads being more likely to flee (Table 3). Collinearity among predictors was not a concern in our analyses with VIF values <2 in all fitted models.

4. Discussion

Our study is the first, to our knowledge, to test the value of species' trait models to explain and predict avoidance responses towards roads and traffic, offering a new approach to understand the mechanisms underlying the effects of infrastructures on wildlife. In particular, our results show the potential to use species traits as (biological) predictors of *flight responses*. We found that larger, gregarious species with grazing foraging habits are less likely to flee from vehicles.

Smaller species, such as duikers, are more susceptible to predation risk than larger species, such as rhinoceros; and thus, are expected to use anti-predatory responses, like flight responses, more often than larger species (Berger and Cunningham, 1988; Périquet *et al.*, 2012). Indeed, our analyses show *flight responses* can be explained by species' *body mass*. Differences in risk perception may explain why we found *grazing* habits were associated with fewer *flight responses* (Valeix et al. 2009). Grazing often occurs in open habitats (Pérez-Barbería et al., 2001), where anti-predator vigilance is easier to perform compared to environments with dense vegetation within which browsing is more common and predation alertness may be higher (Caro et al., 2004). Anecdotally, we found limited *flight responses* (7 out of 65) in white rhinoceros *Ceratotherium simum*, which predominantly graze, while both observed black rhinoceros *Diceros bicornis*, which are browsers, flew in response to the vehicle. Finally, our results support the biological prediction that solitary species would display more frequent *flight responses* than gregarious species or those in family groups. Species living in groups can perform cooperative vigilance, that generally reduces individual vigilance time, but could increase the cost of false responses as the whole group, not just one individual, moves. This may lead to more accurate anti-predatory behaviours in gregarious species as they have adapted or learned to react only to real threats. *Flight responses* may also be rarer in groups due to a dilution effect: the individual risk of attack is lower in larger groups, but the costs of fleeing do not change (individuals still need to stop their activity, e.g., foraging, to flee); therefore, unique individual may be less likely to flee when in a larger group (Hunter and Skinner, 1998; Creel et al., 2014; Moll et al., 2016).

While our findings support biologically relevant links between species' traits and flight responses, analyses of *initial* and *tolerance distance* only supported methodological hypotheses associated with detectability. Results suggest smaller animals were closer to roads, but this relationship likely reflected lower detectability of smaller individuals at greater distances from roads (Pollock and Kendall, 1987) as no difference was detected within a 100-meter range of the road. Previous studies have reported road avoidance in different ungulate species, with animals preferring areas further from roads (Mulero-Pázmány et al 2016; D'Amico et al 2016). An intriguing hypothesis derived from our results is that the road-avoidance zone is similar among species, reflecting a common boundary that is not affected by anti-predatory responses but instead may be driven by other factors (food availability, pollution effects, etc). In addition, we found browsing species closer to roads even within a 100-meter range of the road for both *initial* and *tolerance distance*. Vegetation changes, including greater local diversity, can occur near roads potentially attracting browsers to their proximity (Rea, 2003). Road avoidance by competitors or predators could also increase attractiveness of areas near roads for some species (Berger, 2007). Future studies are needed to determine if vegetation changes and/or species interactions are indeed affecting the use of areas near roads by browsing species.

While not the main focus of our study, our analyses also included some confounding variables that offer interesting insights. We found a consistent role of traffic but not of pavement surface in *initial* and *tolerance distances*. The impact of traffic on ungulate spatial distribution has been shown in previous studies (Leblond *et al*., 2013; D'Amico *et al*., 2016; Mulero-Pázmány *et al.*, 2016). However, because unpaved roads often have lower traffic than paved roads (Jaeger *et al*., 2005), previous studies could not disentangle the role of those factors. Our study was conducted in different protected areas with varying numbers of visitors which allowed us to consider both aspects jointly in our analyses without collinearity issues. The results suggest road avoidance in the studied species is influenced by traffic but not by the presence of pavement. To our knowledge this is the first time this distinction has been made, with potential implications for the management of traffic and roads in protected areas. Moreover, while flight responses were not directly affected by traffic intensity (or road surface), they were affected by *initial distance*, which in turn was affected by traffic, suggesting a potential indirect effect.

Overall, our study shows the potential to use trait-based models to assess road impacts, in particular, vehicle avoidance leading to flight responses. We found that several species' traits (i.e. body mass, social aggregation and foraging habits) that can potentially be used as predictors for flight responses by African ungulates. Predictive trait-based models that characterize wildlife responses to human impacts, such as roads and traffic, can be valuable tools for conservation. These models can assess risks across species and/or areas, and identify generalized risk factors that may offer insight into mitigation strategies of value for diverse species (i.e., focused on those common risk factors). In addition, predictive models can also be used to generate risk assessments for unstudied species which can be helpful for conservation and road planning. For example, we can identify areas with many susceptible species and thus, where development of new roads or additional traffic could be particularly detrimental (González-Suárez et al 2018). Future studies will be needed to establish the general value of trait-based predictive models for other regions and species. To generate those models, behavioural data from multiple sites would be very valuable. Efforts to compile larger datasets of other road impacts, such as roadkill, have already started (see González-Suárez *et al*., 2018). We need to expand those efforts to start collecting and compiling information on behavioural impacts to fully understand how the rapidly expanding global road-network affects wildlife, and offer tools and assessment that can aid road planning and management within protected areas and beyond.

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Table 1. Definition, hypothesis, predictions, and data sources of the species' traits tested as predictors of ungulate responses to roads and traffic.

Group	Variable definition	Hypotheses and predictions	Source
Morphology	***Body mass***: Average adult body mass in kilograms.	***Biological*: Smaller species will avoid roads/vehicles and exhibit more flight responses than larger species, because they have higher predation risk and thus, are more aware of potential predators. ***Methodological*:** Smaller species will be better detected close to roads/vehicles, due to detectability decreasing differently for different-sized individuals according to distance. Closer to roads (e.g., <100 m) detectability effects based on size should be minimized and distance to road should not vary with body mass.	Animaldiversity.org, 2018; Estes, 1991; Jones *et al*., 2009; Stuart and Stuart, 2015; Gonzalez-Voyer *et al*., 2016; Shultz and Dunbar, 2006
	Brain mass: Average adult brain mass in grams.*	***Biological*:** Small-brain species will avoid roads/vehicles and exhibit more flight responses than large-brain species, because they lack the cognitive capacities to learn that road/vehicles are not as threatening as actual predators. ***Methodological*:** None.	
Lifespan	***Longevity:*** Average lifespan in years, when available in the wild, and when not in captivity.	***Biological*:** Short-lived species will avoid roads/vehicles and exhibit more flight responses than long-lived species, because they have a shorter experience with roads and vehicles and cannot learn they are not as threatening as	Animaldiversity.org, 2018; Jones *et al*., 2009; Stuart and Stuart, 2015

		actual predators. ***Methodological*: None.**	
Reproduction	***Gestation length:*** Average length of gestation in years. ***Litters per year:*** Average number of litters per year. ***Sexual maturity age:*** Sex specific and combined average age of sexual maturity in years.	***Biological*:** Slow-reproducing species will avoid roads/vehicles and exhibit more flight responses than fast-reproducing species, due to higher investment in self-maintenance. ***Methodological*:** None.	Animaldiversity.org, 2018; Estes, 1991; Jones *et al*., 2009; Tacutu *et al*., 2018.
Foraging	***Foraging habits*** classified as grazing (binary descriptor of whether a species grazes to feed), browsing (binary descriptor of whether a species browses to feed), or other habits (binary descriptor of whether a species consumes items other than grass and leaves).	***Biological*:** Browsing species will avoid roads/vehicles and exhibit more flight responses than grazing species, because they have higher predation risk and thus, are more aware of potential predators. ***Methodological*:** Browsing species will be more detected close to roads/vehicles than far from them, due to detectability decreasing in their preferred habitat (i.e. dense vegetation). Note: closer to roads (e.g., <100 m) detectability effects should be minimized and distance to road should not vary with foraging habits.	Estes, 1991; Stuart and Stuart, 2015
Sociality	***Social aggregation*** classified as: solitary, gregarious, or	***Biological*:** Solitary species will avoid roads/vehicles and exhibit more flight responses than gregarious species,	Animaldiversity.org, 2018; Estes, 1991; Stuart and Stuart,

family groups.	because the lack of cooperative vigilance increases predation risk. ***Methodological:*** Solitary species will be more detected close to roads/vehicles than far from them, due to detectability decreasing according to distance. Note: closer to roads (e.g., <100 m) detectability effects should be minimized and distance to road should not vary with sociality aggregation.	2015

528 * For *Brain Mass* of *Phacochoerus africanus* we use data from a closely related species *Phacochoerus aethiopicus*.

Table 2. Number of sightings of each detected species (total and within each protected area).

Species	**HiP**	**uMkhuze**	**Pilanesberg**	**Total**
Impala (*Aepyceros melampus*)	74	16	54	144
White Rhino (*Ceratotherium simum*)	55	0	10	65
Blue Wildebeest (*Connochaetes taurinus*)	9	1	47	57
Plains Zebra (*Equus quagga*)	26	0	30	56
Warthog (*Phacochoerus africanus*)	37	0	10	47
Giraffe (*Giraffa camelopardalis*)	17	2	16	35
Nyala (*Tragelaphus angasii*)	24	11	0	35
African Buffalo (*Syncerus caffer*)	14	0	0	14
African Bush Elephant (*Loxodonta africana*)	5	0	7	12
Greater Kudu (*Tragelaphus strepsiceros*)	4	1	7	12
Springbok (*Antidorcas marsupialis*)	0	0	7	7
Steenbok (*Raphicerus campestris*)	0	0	6	6
Waterbuck (*Kobus ellipsiprymnus*)	1	0	5	6
Common Hippo (*Hippopotamus amphibius*)	0	0	5	5
Grey Duiker (*Sylvicapra grimmia*)	3	2	0	5
Tsessebe (*Damaliscus lunatus*)	0	0	3	3
African Black Rhino (*Diceros bicornis*)	1	0	1	2
Hartebeest (*Alcelaphus buselaphus*)	0	0	2	2
Total	270	34	211	513

Table 3. Coefficient estimates for models testing the effect of different traits in observed distances and *flight responses*. We report the best estimate (β) with their 95% confidence intervals, and the number of observations (N). All models included *road surface*, *traffic intensity*, and *standardized group size* as control predictors; the model for *flight response* also included *initial distance* as a control predictor. For several traits we used standardized residuals from a phylogenetic least squares models in which the log$_{10}$-transformed trait was predicted by log$_{10}$(*body mass*) with taxonomic order as a covariate to avoid the potential confounding effect of size. Predictors with 95%CI (bootstrapped estimates) non-overlapping with zero are marked in bold. We did not record tolerance distance for black rhino *Diceros bicornis*.

Models	***Initial distance*** **(N=513, 18 species)**		***Tolerance distance*** **(N=448, 17 species)**		***Flight response*** **(N=513, 18 species)**	
	β	95% CI	β	95% CI	β	95% CI
Lifespan						
Intercept	1.549	1.083 – 1.764	1.648	1.524 – 1.770	-1.998	-3.058 – -1.202
Road surface (unpaved)	-0.042	-0.166 – 0.140	0.034	-0.084 – 0.146	-0.198	-0.992 – 0.620
Traffic intensity	**0.112**	**0.038 – 0.196**	**0.091**	**0.033 – 0.148**	-0.338	-1.027 – 0.082
Standardized group size	**-0.058**	**-0.109 – -0.009**	-0.016	-0.054 – 0.020	-0.067	-0.372 – 0.211
Initial distance (log$_{10}$)	–	–	–	–	**-1.344**	**-1.742 – -1.046**
Longevity (residuals)	0.042	0.003 – 0.149	0.022	-0.044 – 0.085	0.246	-0.306 – 0.760
Morphology						
Intercept	1.397	1.050 – 1.748	1.615	1.507 – 1.726	-1.954	-2.728 – -1.430
Road surface (unpaved)	0.000	-0.169 – 0.161	0.048	-0.069 – 0.159	-0.060	-0.787 – 0.715
Traffic intensity	**0.121**	**0.041 – 0.202**	**0.096**	**0.036 – 0.154**	-0.304	-0.950 – 0.098

Standardized group size	**-0.058**	**-0.109 – -0.004**	-0.016	-0.055 – 0.021	-0.077	-0.405 – 0.193
Initial distance (log$_{10}$)	–	–	–	–	**-1.283**	**-1.638 – -1.024**
Body mass (log$_{10}$)	**0.090**	**0.029 – 0.221**	**0.095**	**0.036 – 0.154**	**-0.600**	**-0.973 – -0.303**
Brain mass (residuals)	0.025	-0.039 – 0.154	0.012	-0.042 – 0.063	-0.223	-0.611 – 0.132
Reproductive speed						
Intercept	1.437	1.076 – 1.805	1.650	1.526 – 1.776	-2.005	-3.099 – -1.197
Road surface (unpaved)	-0.011	-0.183 – 0.148	0.038	-0.074 – 0.149	-0.189	-0.947 – 0.599
Traffic intensity	**0.118**	**0.040 – 0.198**	**0.092**	**0.035 – 0.147**	-0.321	-1.070 – 0.086
Standardized group size	**-0.057**	**-0.109 – -0.004**	-0.016	-0.052 – 0.022	-0.066	-0.395 – 0.214
Initial distance (log$_{10}$)	–	–	–	–	**-1.344**	**-1.732 – -1.043**
Sexual maturity age (residuals)	-0.069	-0.101 – 0.094	-0.056	-0.119 – 0.011	0.317	-0.259 – 0.928
Gestation length (residuals)	-0.009	-0.178 – 0.098	0.011	-0.072 – 0.090	-0.219	-0.954 – 0.560
Litters per year (residuals)	-0.061	-0.121 – 0.096	-0.041	-0.111 – 0.031	-0.307	-0.947 – 0.396
Foraging						
Intercept	1.612	1.152 – 2.088	1.923	1.651 – 2.196	0.398	-2.228 – 3.082
Road surface (unpaved)	-0.021	-0.182 – 0.144	0.034	-0.084 – 0.146	-0.177	-1.035 – 0.692
Traffic intensity	**0.116**	**0.034 – 0.198**	**0.092**	**0.034 – 0.148**	-0.326	-1.116 – 0.143
Standardized group size	**-0.057**	**-0.112 – -0.005**	**-0.017**	-0.053 – 0.020	-0.079	-0.425 – 0.232
Initial distance (log$_{10}$)	–	–	–	–	**-1.348**	**-1.762 – -1.057**
Grazing	-0.006	-0.298 – 0.281	-0.139	-0.362 – 0.089	**-2.317**	**-4.626 – -0.482**
Browsing	**-0.228**	**-0.445 – -0.004**	**-0.190**	**-0.355 – -0.028**	-0.957	-2.840 – 1.090

Other foods	-0.064	-0.317 – 0.191	-0.090	-0.277 – 0.096	1.085	-0.786 – 2.945
Social structure						
Intercept	1.394	1.024 – 1.826	1.376	1.005 – 1.739	0.342	-1.429 – 2.591
Road surface (unpaved)	-0.037	-0.194 – 0.122	0.036	-0.073 – 0.150	-0.170	-0.977 – 0.705
Traffic intensity	**0.109**	**0.033 – 0.185**	**0.089**	**0.036 – 0.146**	-0.308	-1.093 – 0.128
Standardized group size	**-0.058**	**-0.108 – -0.004**	-0.016	-0.052 – 0.021	-0.071	-0.434 – 0.217
Initial distance (log$_{10}$)	–	–	–	–	**-1.335**	**-1.733 – -1.049**
Social: gregarious	0.177	-0.252 – 0.555	0.295	-0.070 – 0.656	**-2.741**	**-5.154 – -0.873**
Social: family groups	0.131	-0.327 – 0.546	0.250	-0.141 – 0.638	**-2.443**	**-5.314 – -0.419**