Species' traits as predictors of avoidance towards roads and traffic

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

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

4   González-Suárez[a,*]

5

6   **Affiliations:**

7   [a] Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading,

8   Reading, RG6 6AS, UK

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

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

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

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

13   [†] These authors contributed equally

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16

17   **Abstract**

18   Road-networks and their associated motorized traffic pose a threat to biodiversity and

19   ecosystems, with different groups of species exhibiting different avoidance responses. The

20   often species-specific nature of these behavioural responses to roads and traffic suggest that

21   morphological, ecological, life-history and behavioural traits could be useful in explaining

22   and predicting these responses. Trait-based predictive models have been used to assess

23   extinction risk, land use impacts, and road mortality. Here we present the first, to our

24   knowledge, test of their potential to address animal road avoidance. We studied the fleeing

25   responses and spatial distribution in relation to roads of diverse ungulate species across three

26   South African protected areas. Our results show that smaller, solitary species with non-

27   grazing food habits are more likely to flee in response to presence of a vehicle. None of the

28   tested traits showed a clear relationship based on biological hypotheses with initial distance to

29   roads and tolerance distance to vehicles (used to describe behavioural avoidance towards

30   roads and vehicles, respectively). However, we found significant effects that supported

31   proposed methodological hypotheses. Our results show the potential to use traits as indicators

32   of vehicle and traffic avoidance. Obtaining behavioural avoidance data in the field for many

33   species and areas can be time consuming, but here we show it may be possible to use

34   available trait data to generally predict species responses. This could be useful for initial

35   species risk assessments.

36

37

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

3

73 species' traits and behavioural responses to roads and traffic, and the potential of applying

74 trait-based model to assess avoidance responses to roads and traffic/vehicles. Past studies

75 have considered how species' traits influence roadkill probability (Ford and Fahrig, 2007;

76 Barthelmess and Brooks, 2010; Cook and Blumstein, 2013; D'Amico *et al.*, 2015; Santos *et*

77 *al.*, 2016), but only recently the full potential for using trait-based models in Road Ecology

78 has started to be considered, and for now has only been explored for estimates of road-

79 associated mortality (González-Suárez *et al*., 2018).

80   Our study addresses this knowledge gap by exploring the value of diverse species' traits

81 to understand ungulate behavioural responses to roads and traffic. We considered several

82 species' traits reflecting different biological hypotheses (Table 1) based on the general

83 assumption that roads and vehicles can be perceived as a danger, similar to predators, by

84 ungulates (Frid and Dill, 2002; Lima et al., 2015). We hypothesize an effect of morphology

85 on avoidance responses, because smaller species have been found to be more cautious

86 towards potential predators than larger species (Berger and Cunningham, 1988). Research has

87 shown that ungulates such as pronghorns *Antilocapra americana* in North America (Gavin

88 and Komers, 2006) and Tibetan antelopes *Pantholops hodgsonii* in Asia (Lian et al., 2011)

89 can respond to vehicles as if these were predators. Species with relatively larger brains have

90 greater learning and cognitive capacity (Shultz and Dunbar, 2006), thus, we propose they may

91 be able to realize that vehicles are not actual predators (within protected areas) and show no

92 or limited avoidance responses. Foraging habits have been shown to affect anti-predatory

93 responses; the spatial distribution of browsing ungulates, but not of grazing species, has been

94 shown to change in response to predators (Valeix *et al*., 2009), thus, we predict browsing

95 species will avoid roads and vehicles more often. Longevity may also be important because

96 long-lived species have greater learning capacities (Street *et al*., 2017) and their longer

97 lifespan can allow them to learn by experience that vehicles are not predators. The trade-off

98 between investment in reproduction and survival (Promislow and Harvey, 1990) proposes that

99 slow-breeding species will invest more in self-maintenance and thus, should be more cautious

100 towards potential predators (or roads and vehicles) than fast-breeding species. Finally, solitary

101 species have been shown to be more wary of potential predators than gregarious species

102 (Hunter and Skinner, 1998), thus we predict solitary animals will show higher avoidance. As

103 alternative hypotheses, we considered methodological effects, mostly associated to

104 detectability, that could also result in association between species' traits and behavioural

105 responses (all biological and methodological hypotheses are summarized in Table 1).

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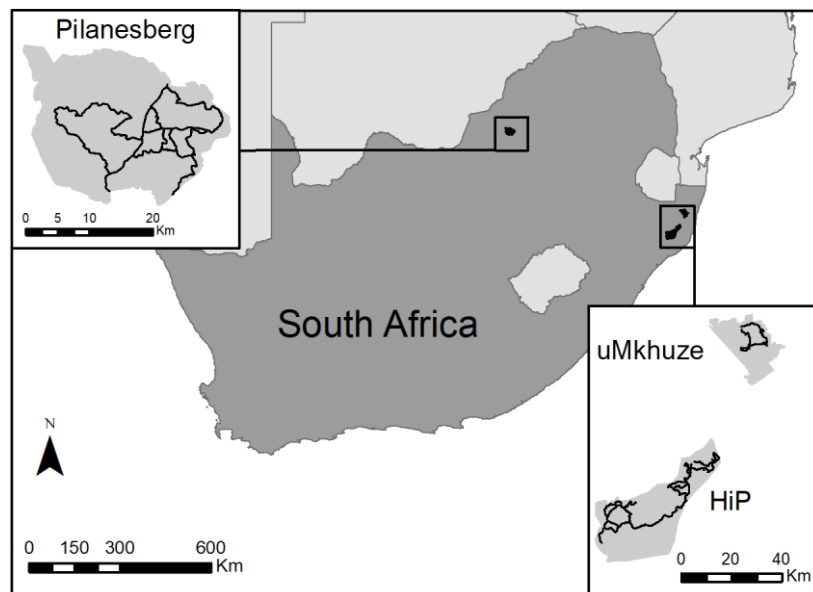114 susceptible species and potentially generate risk assessments.

115

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

118

2.   Methods

2.1.   Study area

121   Behavioural data were collected in three South African protected areas: Hluhluwe-
122 iMfolozi Park (from here on, HiP; 28.2198° S, 31.9519° E), Pilanesberg National Park
123 (25.2449° S, 27.0891° E), and uMkhuze Game Reserve (27.6519° S, 32.2435° E. Fig. 1). All
124 these protected areas allow regulated human activities based on wildlife-watching tourism and
125 have road-networks that include paved and unpaved road surfaces and varying traffic volumes
126 (from virtually no vehicles to high-traffic intensity). The areas host diverse ungulate
127 communities including abundant impala *Aepyceros melampus*, small steenbok *Raphicerus*
128 *campestris* and large and iconic species such as African bush elephant *Loxodonta africana*
129 and white rhinoceros *Ceratotherium simum* (Table 2 includes all observed species).

5

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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

164   at which individuals can tolerate vehicles or to the commonly used flight-initiation distance

165   FID (Frid and Dill, 2002). In these study areas it was not possible to leave the road to

166   approach individuals until they fled as required to estimate FID.

167   Georeferenced locations were matched to *habitat ecozones* obtained from Park

168   authorities. Original habitat types were reclassified into simplified categories for analyses

169   (Supplementary materials, Table A1). Spatial analyses were done in ArcGIS 10.4 with *Cape*

170   *Zone 36S Deprecated* projection (EPSG: 22236). Trait data for all species observed during the

171   field study were obtained from published sources (Table 1).

172

173   *2.3.   Data analysis*

174   We used generalized linear mixed effects models (GLMM) to evaluate if traits predicted

175   *initial distance*, *tolerance distance* and *flight response*. We fitted separate models for each of

176   the trait groups we considered (Table 1). All models included control predictors related to

177   each observation: *road surface* (unpaved or paved), *traffic intensity*, and *standardized group*

178   *size*. When modelling *flight responses, initial distance* was also included as a predictor.

179   Observed minimum group size was standardized within species to facilitate comparison. For

180   each observation, we subtracted the mean observed for the species and divided by the

181   standard deviation. Therefore, positive *standardized group sizes* represent groups larger than

182   the average observed group size for that species.

183   To avoid confounding allometric effects of *body mass* when testing *brain mass*,

184   *longevity*, *sexual maturity age*, *gestation length*, and *litters per year* we used standardized

185   residuals from log-log phylogenetic least squares models in which each of these traits was

186   predicted by body mass (all variables were $\log_{10}$ transformed). We used the function pgls

187   from the caper package (Orme *et al.*, 2013), using the updated mammalian supertree (Fritz *et*

188   *al.*, 2009) to describe phylogenetic relationships.

189   Finally, to account for confounding factors associated to particular habitats, transects

190   and the non-independence of trait data from related species, all GLMMs included *habitat*

191   *ecozones,* a nested effect of *park*, *observation date*, and *transect ID*, and a taxonomic

192   correction with *genus* nested within *family*. Distances were first transformed ($\log_{10}[x+1]$) and

193   then modelled using the function lmer in the package lme4 (Bates *et al.*, 2015) with a

194   Gaussian family. *Flight response* was modelled using the function glmer from the package

195   lme4 using a binomial family (logit link). We evaluated predictor importance estimating 95%

196   confidence intervals using bootstrapped sampling (using the function confint.merMod, with

197   2000 simulations and method="boot" from the package lme4). We calculated Variance

198 Inflation Factors (VIF) for all models to detect collinearity issues. All analyses were
199 completed in R version 3.3.2 (R Core Team, 2016).
200   All data and R scripts of completed analyses are available in the public repository
201 Figshare (https://doi.org/10.6084/m9.figshare.12117564.v1).
202

203 **3.   Results**

204 We recorded 513 sightings representing 18 species of African ungulates (Table 2). *Tolerance*
205 *distance* was estimated for 448 of those sightings representing 17 species (no *tolerance*
206 *distance* estimates were available for black rhino *Diceros bicornis*). In 20.7% (N=106) of
207 those sightings we detected a *flight response*. Across all three parks we had a mean of 7.14
208 observations/10 km (SD = 4.36) with more observations in unpaved roads (mean ± SE = 7.53
209 ± 4.72 observations/10 km) than in paved roads (6.35 ± 3.49). The overall mean *traffic*
210 *intensity* was 0.14 vehicles per minute (SD = 0.18), with more traffic in paved (0.26 ± 0.24
211 vehicles per minute) than in unpaved roads (0.08 ± 0.08). *Traffic intensity* varied by park,
212 with higher levels in Pilanesberg (0.19 ± 0.23) and HiP (0.12 ± 0.13) than in uMkhuze (0.03 ±
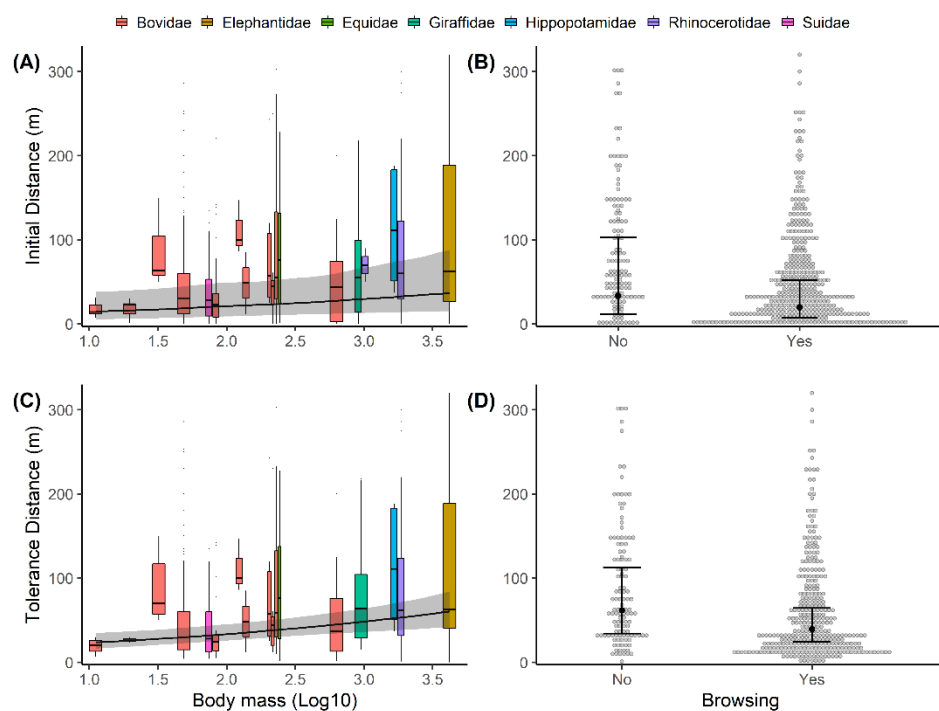213 0.04).

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

219   Predicted values were obtained using bootstrapped predictions from fitted models (Table 3)

220   for a dataset representing the entire range of observed *body mass* values (for A and C), and a

221   dataset representing each category of *browsing* behaviour (for B and D). In both datasets all

222   other predictors set to observed mean value (predictions were made for the average

223   population, without considering random factor values). The shaded areas (in A and C) and

224   error bars (B and D) represent the 95% confidence interval of the bootstrapped predictions.

225

226   The traits *body mass* and *foraging habits* were identified as predictors of both *initial* and

227   *tolerance distances*. In particular, small-sized, browsing ungulates were generally found

228   closer to roads (both for *initial* and *tolerance distances*; Fig. 2, Table 3). These results align

229   with our methodological hypotheses, which also predict no effect for a narrower observation

230   area within which we hypothesize detectability would be unaffected by these traits (Table 1).

231   When we fitted models considering only observations in the first 100 m from each side of the

232   road for *initial distance* (data for 18 species and 392 records) and for *tolerance distance* (17

233   species and 337 records) we found no effect of *body mass* on either distance variable (while

234   the effects of *traffic intensity* and *standardised group size* remained the same; Supplementary

235   materials, Table A2). Browsing species still had shorter *initial* and *tolerance distances* within

236   100 m of roads, which may reflect a different biological mechanism affecting browsing

237   behaviour near roads. *Longevity* and reproductive traits (i.e. *sexual maturity age*, *gestation*

238   *length*, and *litters per year*) were not identified as relevant predictors of *initial* or *tolerance*

239   *distance*.

240

241
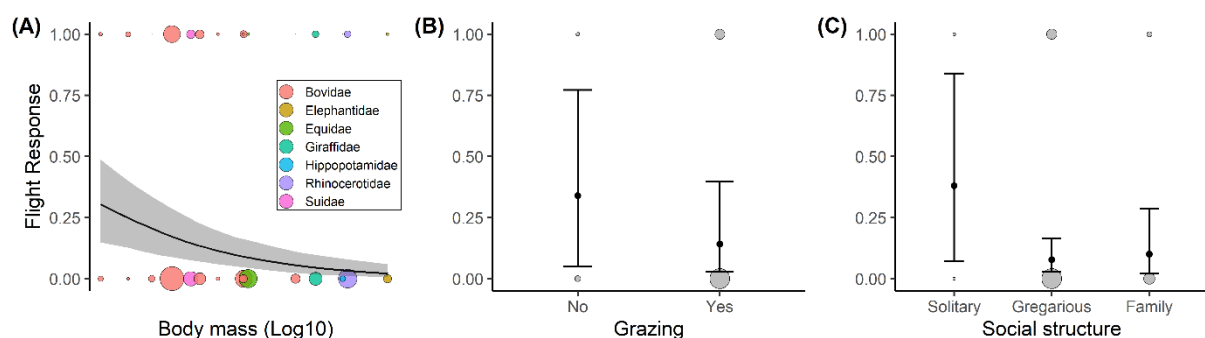
242   **Figure 3**. Observed (circles) and predicted (lines and error bars) *flight responses* for ungulate

243   species with different *body mass* (A), *grazing* food habits (B), and *social structure* (C).

244   Observed values for panel A are represented grouping responses for each species, with circle

245   size proportional to the number of observations. Colours indicate the taxonomic family.

246   Predicted values were obtained for each plot using bootstrapped predictions for datasets

247 representing the entire range of *body mass* values for A, all *grazing* categories for B, and all
248 *social structure* categories for C. All other predictors set to observed mean value (predictions
249 were made for the average population, without considering random factor values). The shaded
250 area (A) and error bars (B and C) represent the 95% confidence interval of the bootstrapped
251 predictions.
252
253   *Body mass*, *social aggregation* and *foraging habits* were identified as predictors of
254 *flight responses* (Fig. 3). Species with smaller *body mass*, solitary behaviour and non-grazing
255 habits were more likely to flee (controlling for the significant effect of their *initial distance* to
256 the road; Table 3). *Longevity* and reproductive traits (i.e. *sexual maturity age*, *gestation*
257 *length*, and *litters per year*) were not identified as relevant predictors of *flight responses*.
258   Among the tested control predictors, we found a consistent effect of *traffic intensity* for
259 both *initial* and *tolerance distance*, with ungulates located further from roads with more traffic,
260 but no effect of *road surface* (Table 3). The *standardised group size* was also always important
261 to explain *initial distance*, with relatively larger groups for each species often found closer to
262 roads initially. This could reflect increased detectability when more individuals are together
263 (larger relative group sizes). *Initial distance* was a strong predictor of *flight responses*, with
264 ungulates located closer to roads being more likely to flee (Table 3). Collinearity among
265 predictors was not a concern in our analyses with VIF values <2 in all fitted models.
266
267 **4.   Discussion**
268   Our study is the first, to our knowledge, to test the value of species' trait models to
269 explain and predict avoidance responses towards roads and traffic, offering a new approach to
270 understand the mechanisms underlying the effects of infrastructures on wildlife. In particular,
271 our results show the potential to use species traits as (biological) predictors of *flight*
272 *responses*. We found that larger, gregarious species with grazing foraging habits are less
273 likely to flee from vehicles.
274   Smaller species, such as duikers, are more susceptible to predation risk than larger
275 species, such as rhinoceros; and thus, are expected to use anti-predatory responses, like flight
276 responses, more often than larger species (Berger and Cunningham, 1988; Périquet *et al*.,
277 2012). Indeed, our analyses show *flight responses* can be explained by species' *body mass*.
278 Differences in risk perception may explain why we found *grazing* habits were associated with
279 fewer *flight responses* (Valeix et al. 2009). Grazing often occurs in open habitats (Pérez-
280 Barbería et al., 2001), where anti-predator vigilance is easier to perform compared to

10

281   environments with dense vegetation within which browsing is more common and predation

282   alertness may be higher (Caro et al., 2004). Anecdotally, we found limited *flight responses* (7

283   out of 65) in white rhinoceros *Ceratotherium simum*, which predominantly graze, while both

284   observed black rhinoceros *Diceros bicornis*, which are browsers, flew in response to the

285   vehicle. Finally, our results support the biological prediction that solitary species would

286   display more frequent *flight responses* than gregarious species or those in family groups.

287   Species living in groups can perform cooperative vigilance, that generally reduces individual

288   vigilance time, but could increase the cost of false responses as the whole group, not just one

289   individual, moves. This may lead to more accurate anti-predatory behaviours in gregarious

290   species as they have adapted or learned to react only to real threats. *Flight responses* may also

291   be rarer in groups due to a dilution effect: the individual risk of attack is lower in larger

292   groups, but the costs of fleeing do not change (individuals still need to stop their activity, e.g.,

293   foraging, to flee); therefore, unique individual may be less likely to flee when in a larger

294   group (Hunter and Skinner, 1998; Creel et al., 2014; Moll et al., 2016).

295   While our findings support biologically relevant links between species' traits and

296   flight responses, analyses of *initial* and *tolerance distance* only supported methodological

297   hypotheses associated with detectability. Results suggest smaller animals were closer to

298   roads, but this relationship likely reflected lower detectability of smaller individuals at greater

299   distances from roads (Pollock and Kendall, 1987) as no difference was detected within a 100-

300   meter range of the road. Previous studies have reported road avoidance in different ungulate

301   species, with animals preferring areas further from roads (Mulero-Pázmány et al 2016;

302   D'Amico et al 2016). An intriguing hypothesis derived from our results is that the road-

303   avoidance zone is similar among species, reflecting a common boundary that is not affected

304   by anti-predatory responses but instead may be driven by other factors (food availability,

305   pollution effects, etc). In addition, we found browsing species closer to roads even within a

306   100-meter range of the road for both *initial* and *tolerance distance*. Vegetation changes,

307   including greater local diversity, can occur near roads potentially attracting browsers to their

308   proximity (Rea, 2003). Road avoidance by competitors or predators could also increase

309   attractiveness of areas near roads for some species (Berger, 2007). Future studies are needed

310   to determine if vegetation changes and/or species interactions are indeed affecting the use of

311   areas near roads by browsing species.

312   While not the main focus of our study, our analyses also included some confounding

313   variables that offer interesting insights. We found a consistent role of traffic but not of

314   pavement surface in *initial* and *tolerance distances*. The impact of traffic on ungulate spatial

315   distribution has been shown in previous studies (Leblond *et al.*, 2013; D'Amico *et al.*, 2016;

316   Mulero-Pázmány *et al.*, 2016). However, because unpaved roads often have lower traffic than

317   paved roads (Jaeger *et al.*, 2005), previous studies could not disentangle the role of those

318   factors. Our study was conducted in different protected areas with varying numbers of visitors

319   which allowed us to consider both aspects jointly in our analyses without collinearity issues.

320   The results suggest road avoidance in the studied species is influenced by traffic but not by

321   the presence of pavement. To our knowledge this is the first time this distinction has been

322   made, with potential implications for the management of traffic and roads in protected areas.

323   Moreover, while flight responses were not directly affected by traffic intensity (or road

324   surface), they were affected by *initial distance*, which in turn was affected by traffic,

325   suggesting a potential indirect effect.

326   Overall, our study shows the potential to use trait-based models to assess road impacts,

327   in particular, vehicle avoidance leading to flight responses. We found that several species' traits

328   (i.e. body mass, social aggregation and foraging habits) that can potentially be used as

329   predictors for flight responses by African ungulates. Predictive trait-based models that

330   characterize wildlife responses to human impacts, such as roads and traffic, can be valuable

331   tools for conservation. These models can assess risks across species and/or areas, and identify

332   generalized risk factors that may offer insight into mitigation strategies of value for diverse

333   species (i.e., focused on those common risk factors). In addition, predictive models can also be

334   used to generate risk assessments for unstudied species which can be helpful for conservation

335   and road planning. For example, we can identify areas with many susceptible species and thus,

336   where development of new roads or additional traffic could be particularly detrimental

337   (González-Suárez et al 2018). Future studies will be needed to establish the general value of

338   trait-based predictive models for other regions and species. To generate those models,

339   behavioural data from multiple sites would be very valuable. Efforts to compile larger datasets

340   of other road impacts, such as roadkill, have already started (see González-Suárez *et al.*, 2018).

341   We need to expand those efforts to start collecting and compiling information on behavioural

342   impacts to fully understand how the rapidly expanding global road-network affects wildlife,

343   and offer tools and assessment that can aid road planning and management within protected

344   areas and beyond.

345

353

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527   **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. | 2015 |
| | **_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. | |

528   * For _Brain Mass_ of _Phacochoerus africanus_ we use data from a closely related species _Phacochoerus aethiopicus_.

529 **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

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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**

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