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

2

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

14

15 **Declarations of interest:** none.

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

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).

4

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.
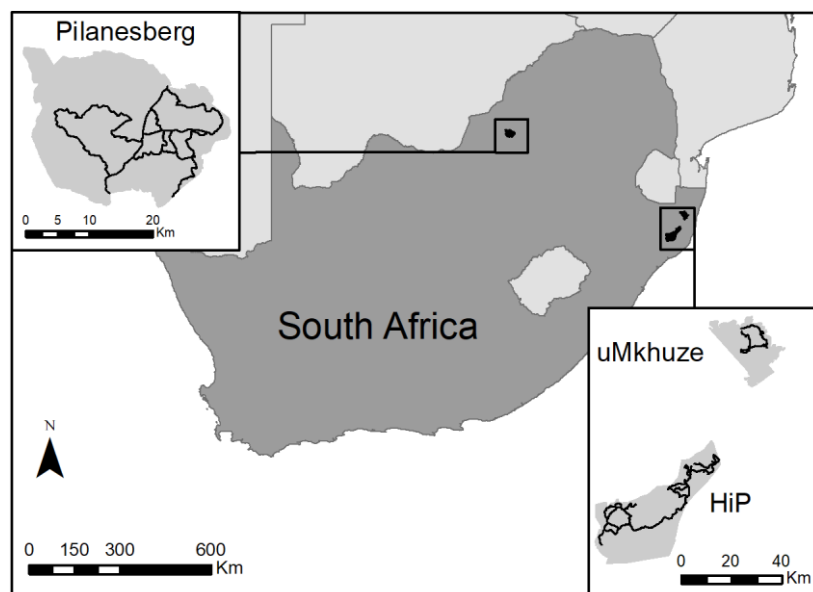
116   **Figure 1.** Map of the three studied protected areas in South Africa. Insets show the park

117   boundaries and sampled transects.

118

119   **2.   Methods**

120   *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

130

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

6

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

7

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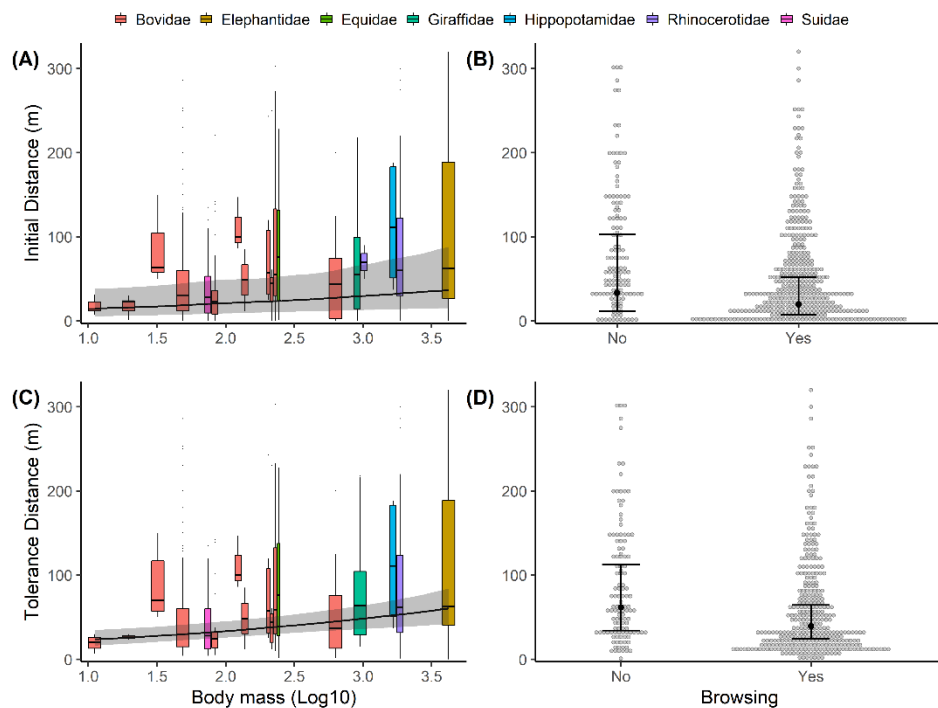
Figure 2. Observed (boxplots and dotplots) and predicted (line and error bars) *initial* (panels A and B) and *tolerance distances* (C and D) for ungulate species with different *body mass* values and different *browsing* foraging habits. In panels A and C boxplots represents distances observed for individual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

8

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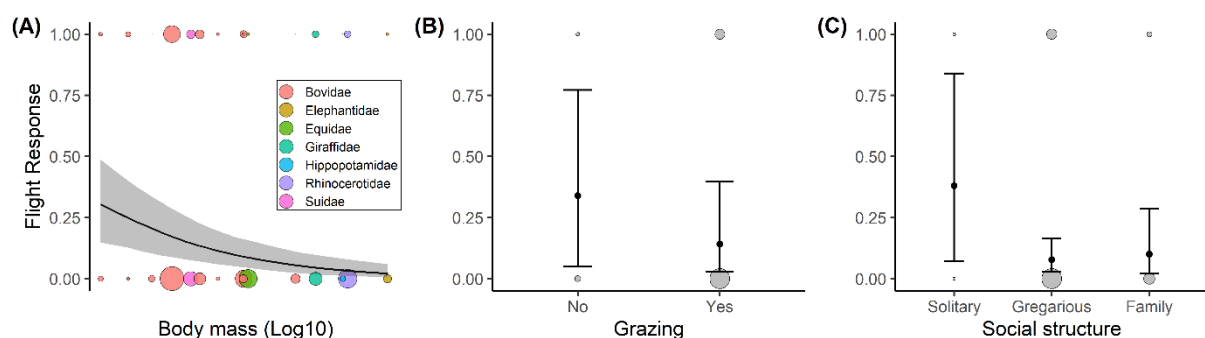
242   **Figure 3**. Observed (circles) and predicted (lines and error bars) *flight responses* for ungulate

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

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

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

11

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

354   **6.   References**

355   Animaldiversity.org (2018). *ADW: Home*. [online] Available at:

356   https://animaldiversity.org/.

357   Barthelmess, E. L. and Brooks, M. S. (2010). The influence of body-size and diet on

358   road-kill trends in mammals. *Biodiversity and Conservation*, 19(6), 1611-1629.

359   Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015). Fitting Linear Mixed-Effects

360   Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. Available at: https://CRAN.R-

361   project.org/package=lme4.

362   Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in

363   protected areas. *Biology Letters*, 3, 620-623.

364   Berger, J. and Cunningham, C. (1988). Size-related effects on search times in North

365   American grassland female ungulates. *Ecology*, 69, 177-183.

366   Brehme, C., Tracey, J., Mcclenaghan, L. and Fisher, R. (2013). Permeability of Roads

367   to Movement of Scrubland Lizards and Small Mammals. *Conservation Biology*, 27(4), 710-

368   720.

369   Caro, T. M., C. M. Graham, C. J. Stoner & J. K. Vargas (2004) Adaptive significance

370   of antipredator behaviour in artiodactyls. *Animal Behaviour*, 67, 205-228.

371   Ceia-Hasse, A., Navarro, L. M., Borda-de-Água, L. and Pereira, H. M. (2018).

372   Population persistence in landscapes fragmented by roads: disentangling isolation, mortality,

373   and the effect of dispersal. *Ecological Modelling*, 375, 45-53.

374   Chen, H. L. and Koprowski, J. L. (2016). Barrier effects of roads on an endangered

375   forest obligate: influences of traffic, road edges, and gaps. *Biological Conservation*, 199, 33-

376   40.

377   Coelho, I. P., Kindel, A. and Coelho, A. V. P. (2008). Roadkills of vertebrate species

378   on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *European*

379   *Journal of Wildlife Research*, 54(4), 689-699.

380   Cook, T. C. and Blumstein, D. T. (2013). The omnivore's dilemma: diet explains

381   variation in vulnerability to vehicle collision mortality. *Biological Conservation*, 167, 310-315.

382   Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A.,

383   Goheen, J. R., Palmer, T. M. and Pringle, R. M. (2016). Elephants in the understory: opposing

384   direct and indirect effects of consumption and ecosystem engineering by megaherbivores.

385   *Ecology*, 97, 3219-3230.

386   Creel, S., Schuette, P. and Christianson, D. (2014). Effects of predation risk on group

387   size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*,

388   25, 773-784.

389   D'Amico, M., Román, J., de los Reyes, L. and Revilla, E. (2015). Vertebrate road-kill

390   patterns in Mediterranean habitats: who, when and where. *Biological Conservation*, 191, 234-

391   242.

392   D'Amico, M., Périquet, S., Román, J. and Revilla, E. (2016). Road avoidance responses

393   determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied*

394   *Ecology*, 53(1), 181-190.

395   Eigenbrod, F., Hecnar, S. J. and Fahrig, L. (2008). Accessible habitat: an improved

396   measure of the effects of habitat loss and roads on wildlife populations. *Landscape Ecology*,

397   23(2), 159-168.

398   Estes, R. (1991). *The Behavior Guide to African Mammals: Including Hoofed*

399   *Mammals, Carnivores, Primates*. University of California Press.

400   Fahrig, L. and Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical

401   review and synthesis. *Ecology and Society*, 14(1), 21.

402   Ford, A. T. and Fahrig, L. (2007). Diet and body size of North American mammal road

403   mortalities. *Transportation Research Part D: Transport and Environment*, 12(7), 498-505.

404   Forman, R. T. T. (2000). Estimate of the area affected ecologically by the road system

405   in the United States. *Conservation Biology*, 14(1), 31-35.

406   Forman, R. and Deblinger, R. (2000). The Ecological Road-Effect Zone of a

407   Massachusetts (U.S.A.) Suburban Highway. *Conservation Biology*, 14(1), 36-46.

408   Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic

409   noise. *Global Change Biology*, 21(5), 1809-1820.

410   Francis, M. J., Spooner, P. G. and Matthews, A. (2015). The influence of urban

411   encroachment on squirrel gliders (*Petaurus norfolcensis*): effects of road density, light and

412   noise pollution. *Wildlife Research*, 42(4), 324-333.

413   Frid, A. and Dill, L. (2002). Human-caused disturbance stimuli as a form of predation

414   risk. *Conservation Ecology*, 6,Fritz, S. A., Bininda-Emonds, O. R. P. and Purvis, A. (2009).

415   Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the

416   tropics. *Ecology Letters*, 12, 538-549.

417   Garriga, N., Santos, X., Montori, A., Richter-Boix, A., Franch, M. and Llorente, G.
418   (2012). Are protected areas truly protected? The impact of road traffic on vertebrate fauna.
419   *Biodiversity and Conservation*, 21(11), 2761-2774.

420   Gavin, S. D. and Komers, P. E. (2006). Do pronghorn (*Antilocapra americana*) perceive
421   roads as a predation risk? *Canadian Journal of Zoology*, 84, 1775-1780.

422   González-Suárez, M., D'Amico, M. and Mulero-Pázmány, M. (2017). Advancing road
423   ecology in Africa with robust analyses and cautious inferences: a response to Jackson *et al.*
424   (2017). *Journal of Zoology*, 302(4), 224-227.

425   González-Suárez, M., Zanchetta Ferreira, F. and Grilo, C. (2018). Spatial and species-
426   level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*,
427   27(9), 1093-1105.

428   Gonzalez-Voyer, A; González-Suárez, M; Vilà, C; Revilla, E (2016) Large brain size
429   indirectly increases vulnerability to extinction in mammals. *Evolution* 70: 1364–1375

430   Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M.,
431   Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M. and Revilla, E. (2012). Individual spatial
432   responses towards roads: implications for mortality risk. *PLoS ONE*, 7(9), p.e43811.

433   Hunter, L. T. B. and Skinner, J. D. (1998). Vigilance behaviour in African ungulates:
434   the role of predation pressure. *Behaviour*, 135, 195-211.

435   Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L.,
436   DellaSala, D. A., Vale, M. M., Hobson, P. R. and Selva, N. (2016). A global map of roadless
437   areas and their conservation status. *Science*, 354(6318), 1423-1427.

438   Jachowski, D. S., Slotow, R. and Millspaugh, J. J. (2012). Physiological stress and
439   refuge behavior by African elephants. *PLoS ONE*, 7(2), e31818.

440   Jaeger, J., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N.,
441   Frank, K., Gruber, B. and von Toschanowitz, K. (2005). Predicting when animal populations
442   are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling*,
443   185(2-4), 329-348.

444   Jones, K., Bielby, J., Cardillo, M., Fritz, S., O'Dell, J., Orme, C., Safi, K., Sechrest, W.,
445   Boakes, E., Carbone, C., Connolly, C., Cutts, M., Foster, J., Grenyer, R., Habib, M., Plaster,
446   C., Price, S., Rigby, E., Rist, J., Teacher, A., Bininda-Emonds, O., Gittleman, J., Mace, G. and
447   Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography
448   of extant and recently extinct mammals. *Ecology*, 90(9), 2648-2648.

449   Laurance, S. G. W., Stouffer, P. C. and Laurance, W. F. (2004). Effects of road clearings
450   on movement patterns of understory rainforest birds in central Amazonia. *Conservation*

Biology, 18(4), 1099-1109.

Laurance, W., Clements, G., Sloan, S., O'Connell, C., Mueller, N., Goosem, M., Venter, O., Edwards, D., Phalan, B., Balmford, A., van Der Ree, R. and Arrea, I. (2014). A global strategy for road building. *Nature*, 513(7517), 229–232.

Leblond, M., Dussault, C. and Ouellet, J. P (2013). Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology*, 289, 32-40.

Lian, X., Zhang, T., Cao, Y., Su, J. and Thirgood, S. (2011). Road proximity and traffic flow perceived as potential predation risks: evidence from the Tibetan antelope in the Kekexili National Nature Reserve, China. *Wildlife Research*, 38, 141-146.

Lima, S. L., B. F. Blackwell, T. L. DeVault & E. Fernández-Juricic (2015). Animal reactions to oncoming vehicles: a conceptual review. *Biological Reviews*, 90, 60-76.

McClure, C., Ware, H., Carlisle, J., Kaltenecker, G. and Barber, J. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences*, 280(1773), 2290-2290.

McGregor, R., Bender, D. and Fahrig, L. (2008). Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology*, 45(1), 117-123.

Moll, R. J., Killion, A. K., Montgomery, R. A., Tambling, C. J. and Hayward, M. W. (2016). Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, 97, 1123-1134.

Monz, C., D'Antonio, A., Lawson, S., Barber, J. and Newman, P. (2016). The ecological implications of visitor transportation in parks and protected areas: examples from research in US National Parks. *Journal of Transport Geography*, 51, 27-35.

Mulero-Pázmány, M., D'Amico, M. and González-Suárez, M. (2016). Ungulate behavioral responses to the heterogeneous road-network of a touristic protected area in Africa. *Journal of Zoology*, 298(4), 233-240.

Ndibalema, V. G., Mduma, S., Stokke, S. and Røskaft, E. (2008). Relationship between road dust and ungulate density in Serengeti National Park, Tanzania. *African Journal of Ecology*, 46(4), 547-555.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. and Pearse, W. (2013). caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5.2. https://CRAN.R-project.org/package=caper.

Pérez-Barbería, F. J., I. J. Gordon & C. Nores (2001) Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research,* 3, 221-230.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays,

485 O., Fortin, D., Madzikanda, H. and Fritz, H. (2012). Influence of immediate predation risk by
486 lions on the vigilance of prey of different body size. *Behavioral Ecology*, 23, 970-976.

487 Pollock, K. H. and Kendall, W. L. (1987). Visibility bias in aerial surveys: a review of
488 estimation procedures. *Journal of Wildlife Management*, 51, 502-510.

489 Pringle, R. M., Young, T. P., Rubenstein, D. I. and McCauley, D. J. (2007). Herbivore-
490 initiated interaction cascades and their modulation by productivity in an African savanna.
491 *Proceedings of the National Academy of Sciences*, 104, 193-197.

492 Promislow, D.E. and Harvey, P.H. (1990). Living fast and dying young: A comparative
493 analysis of life-history variation among mammals. *Journal of Zoology*, 220(3), 417-437.

494 R Core Team (2016). *R: A Language and Environment for Statistical Computing*.
495 Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-
496 project.org.

497 Rea, R. V. (2003). Modifying roadside vegetation management practices to reduce
498 vehicular collisions with moose *Alces alces*. *Wildlife Biology,* 9**,** 81-91.

499 Rytwinski, T. and Fahrig, L. (2011). Reproductive rate and body size predict road
500 impacts on mammal abundance. *Ecological Applications*, 21(2), 589-600.

501 Rytwinski, T. and Fahrig, L. (2012). Do species life history traits explain population
502 responses to roads? A meta-analysis. *Biological Conservation*, 147(1), 87-98.

503 Rytwinski, T. and Fahrig, L. (2013). Why are some animal populations unaffected or
504 positively affected by roads? *Oecologia*, 173(3), 1143-1156.

505 Santos, S. M., Mira, A., Salgueiro, P. A., Costa, P., Medinas, D. and Beja, P. (2016).
506 Avian trait-mediated vulnerability to road traffic collisions. *Biological Conservation*, 200, 122-
507 130.

508 Shultz, S. and Dunbar, R. I. M. (2006). Both social and ecological factors predict
509 ungulate brain size. *Proceedings of the Royal Society B: Biological Sciences*, 273, 207-215.

510 Stankowich, T. (2008). Ungulate flight responses to human disturbance: a review and
511 meta-analysis. *Biological Conservation*, 141(9), 2159-2173.

512 Street, S.E., Navarrete, A.F., Reader, A.M. and Laland, K.N. (2017). Coevolution of
513 cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of*
514 *the National Academy of Sciences*, 114, 7908-7914.

515 Stuart, C. and Stuart, M. (2015). *Stuarts' Field Guide to mammals of southern Africa*.
516 Cape Town: Penguin Random House South Africa.

517 Tacutu, R., Thornton, D., Johnson, E., Budovsky, A., Barardo, D., Craig, T., Diana, E.,
518 Lehmann, G., Toren, D., Wang, J., Fraifeld, V. E. and de Magalhaes, J. P. (2018). Human

519   Ageing Genomic Resources: new and updated databases. *Nucleic Acids Research*, 46(D1),
520   D1083-D1090.
521   Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F.,
522   Fritz, H. and Macdonald, D.W. (2009). Behavioral adjustments of African herbivores to
523   predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23-30.
524   Waldram, M. S., Bond, W. J. and Stock, W. D. (2008). Ecological engineering by a
525   mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*, 11, 101-112.
526

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

530

531

Table 3. Coefficient estimates for models testing the effect of different traits in observed distances and *flight responses*. We report the best

533   estimate (β) with their 95% confidence intervals, and the number of observations (N). All models included *road surface*, *traffic intensity*, and

534   *standardized group size* as control predictors; the model for *flight response* also included *initial distance* as a control predictor. For several traits

535   we used standardized residuals from a phylogenetic least squares models in which the $\log_{10}$-transformed trait was predicted by $\log_{10}$(*body mass*)

536   with taxonomic order as a covariate to avoid the potential confounding effect of size. Predictors with 95%CI (bootstrapped estimates) non-

537   overlapping with zero are marked in bold. We did not record tolerance distance for black rhino *Diceros bicornis*.

538

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**

539