Advancing road ecology in Africa with robust analyses and cautious inferences: a response to Jackson et al. (2017)

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Title: Advancing road ecology in Africa with robust analyses and cautious inferences. A response to Jackson et al. (2017)

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Jackson et al. (2017) have written an extensive commentary on our published study of ungulate behavioural responses to roads and traffic in South Africa (Mulero-Pázmány et al. 2016). We welcome the opportunity to engage in discussion regarding road ecology in Africa and how to best assess impacts and interpret findings. We all agree that understanding anthropogenic impacts, including those of roads and traffic, on wildlife and protected areas is important and that speculative inferences should be avoided. However, we find Jackson et al.'s criticism largely unsubstantiated and affected by statistical misconceptions and errors. We comment on the key points made by Jackson et al. (2017) below.

Tolerance distance is a useful variable in areas with previous disturbances

In Mulero-Pázmány et al. (2016) we described *tolerance distance* as "*the perpendicular distance to the road of focal individuals engaged in stationary behavior (not involving prolonged directional movements, not fleeing or traveling)*". We argued this distance is a particularly useful variable in environments where disturbance is frequent and in which habituation may have occurred. In particular, we proposed *tolerance distance* as a more robust descriptor than the more commonly used *flight initiation distance* when previous, and non-controllable, disturbances are possible. Because our study site, Kruger National Park, is a very busy area with considerable amounts of traffic, we expected previous disturbances from other vehicles would be likely during our sampling, and importantly could be potentially variable across areas which we wished to compare (paved and unpaved roads with varying traffic). We also reasoned *tolerance distance* has the advantage of capturing information on the local spatial distribution from individuals that do not flee, and thus is useful for studying species with low flight response rates for which estimating *flight initiation distance* requires large sampling efforts and could cause considerable disturbance (estimating *flight initiation distance* requires eliciting a flight response and thus, disturbing the animal). Based on these arguments, we still believe that *tolerance distance* is a useful variable to evaluate road responses.

Jackson et al. (2017) apparently disagree with these arguments and claim our use of *tolerance distance* to evaluate behavioural responses is unsuitable based on their perceptions of what is "*ecologically relevant*" (although no new evidence or references to the literature are used to support this perception). Jackson et al. write "*To us, it seems unreasonable to assume that observations of impalas as far as 215 m away from the road represented the distance at which an individual tolerated vehicles*". However, the literature shows ungulates respond to vehicles at distances >215 m (Horejsi 1981, Blackwell and Seamans 2009, Marino and Johnson 2012). In fact, two of the authors in the commentary, Jackson and Røskaft, have themselves evaluated road impacts on impala in other regions of Africa using data from animals located from 0-300 meters from the road (Lunde et al. 2016). Presumably, in that study these authors thought it was ecologically relevant to evaluate road-related impacts at the same distances they criticize in our study. Regardless of what we may assume to be relevant ecologically, in response to comments about detectability (see below) we show that limiting our observations to the first 85 m from the road (a cut-off suggested by Jackson et al., thus, presumably "*ecologically relevant*") does not change our conclusions.

Additionally, Jackson et al. (2017) criticize our regression analyses to explain *tolerance distances* and propose instead to predict *tolerance distance* in a linear model with *initial distance* as an offset term. Using an offset in a linear regression is mathematically equivalent to using as the response variable the difference between the predictor and the offset (in our case the difference between *tolerance* and *initial distance*, which we may call *distance moved*). Therefore, Jackson et al.'s analyses used *distance moved* (in relation to the road) as the response variable, effectively addressing a different question to what they intended. Because in most of the observations individuals did not move (*initial* and *tolerance distance* are the same) we are not surprised there are no significant predictors in this model, although Jackson et al. unconventionally interpret as "*marginally higher along paved roads*" an effect with a reported P=0.168. In conclusion, contrary to their statements, Jackson et al.'s new analyses do not challenge our findings in any way, but rather explore a different question.

Flight response is an valuable variable, but inferences with small sample sizes should be made with caution

Jackson et al. (2017) consider the key variable to evaluate responses to roads and traffic should be *flight response* and present several new analyses of our data. Unfortunately, many of these new analyses suffer from pseudoreplication (observations from the same day and road transect are incorrectly treated as independent observations) and thus, these results are difficult to interpret. In addition, given the limited number of *flight responses* recorded, we think our data are not particularly well-suited to address all these new questions. Generally, we believe that exploring multiple variables reflecting different behavioural and spatial aspects is more powerful than limiting ourselves to a single descriptor. This is especially true in areas and species with low *flight response* rates for which inferences solely focused on *flight responses* could be limited and possible misleading. Furthermore, while we agree *flight responses* should be considered (as we did) we remain unconvinced by the idea of imposing thresholds as suggested by Jackson et al.: "*a lack of a flight response by impala far away from a road cannot be considered as no flight response*".

While exploring our dataset Jackson et al. (2017) detected some incongruences for flight responses that reflect an oversight on our part. We failed to include our comments and notes in the published dataset and apologize for any confusion this omission may have caused. A revised dataset including these comments and notes is now available on Figshare (https://doi.org/10.6084/m9.figshare.3180679.v3). While translating these notes from the original in Spanish (our common language), we additionally realized that our definition of *flight response* in Mulero-Pázmány et al. (2016) failed to describe events which we had classified as *flight responses*, including reactions to other passing vehicles that occurred while we were stopped, but after having estimated tolerance distance (approximately within 30 seconds of stopping our vehicle), and reactions that occurred as we departed. These additional reactions account for the nine observations identified by Jackson et al. (2017) in which *initial* and *tolerance distances* are the same. Using the definition of *flight responses* as stated in the original study (Mulero-Pázmány et al. 2016), we would recognize only 14 *flight responses*, further supporting our conclusion that there may be habituation (*flight responses* are relatively rare). Considering only these 14 *flight responses* we find results consistent with those reported by Mulero-Pázmány et al. (2016): reactions were more common in unpaved roads (11 cases out of 64) than in paved roads (3 cases out of 54), and more likely to occur among individuals closer to the road (mean *initial distance* for individuals that reacted 10.23 m, median 7 m, range 0-31 m; for individuals which did not react in the strict sense, mean *initial distance* 49.2 m, median 33.5 m, range 0-215 m; regression coefficient b=-2.32, SE=0.644, P<0.001; controlling for *herd size*: b = -0.44, SE = 0.361, P = 0.23).

Jackson et al. (2017) also state that "*values for the initial and tolerance distances differed for an additional five records in the supporting information. By definition, this implies that a flight response occurred*". As stated in the original study (Mulero-Pázmány et al. 2016) "*we did not consider an individual had fled if it did not move or moved parallel or toward the road*", thus, not all individuals in which *initial* and *tolerance distances* differ are "*by definition*" fleeing. In fact, we find puzzling that Jackson et al. would suggest a *flight response* should have been recorded in the case in which *initial distance* was greater than *tolerance*, that is, a case in which the animal actually approached the vehicle. Three other cases reflect situations in which the animal was crossing the road when sighted or was moving largely in parallel to the road which we do not consider *flight responses*. A final case reflects an error by which an *initial distance* was entered as 0 m when it should have been 12 m (observation recorded at 08:32 on 30/04/2014). Correcting this typo does not affect our results qualitatively, but reinforces the evidence for avoidance of the close proximity (<10m) of paved roads by reducing the number of observations from 6 to 5 (Fig. 2 in Mulero-Pázmány et al. 2016). The revised dataset available in Figshare (https://doi.org/10.6084/m9.figshare.3180679.v3) includes all comments and a correction of this error.

Clarifications about herd size and singletons

Jackson et al. (2017) find our definition of what constitutes a group unclear and express surprise regarding the number of single individuals, singletons, in our dataset. To clarify, we considered that individuals were in groups if found in close proximity (~15 meters) to other conspecifics. As we stated in Mulero-Pázmány et al. (2016), some members of a group may not have been visible, and therefore *herd size* is indicative rather than a true estimate. The high number of singletons may be explained because our sampling period coincided with the beginning of the rutting season, when it is more likely to find adult males alone (39 of the 56 singleton observations were males; Estes 2012).

Jackson et al. also explore some additional effects of *herd size*, but use Mann-Whitney tests which are affected by pseudoreplication, because observations from a given road and date cannot be considered as independent from each other, as we explained in the original study (Mulero-Pázmány et al. 2016). Importantly, we would like to point out that the new results are generally consistent with those reported in Mulero-Pázmány et al. (2016), and note that the effects of *herd size* were reported for all analyses.

Accounting for variation in detectability

Jackson et al. (2017) correctly point out that detectability is important, and we made efforts to address this issue in the original study. We agree that detectability likely varies across landscapes, and we used a proxy based on general habitat types to account for this variation. While this may not be viewed as ideal, Jackson et al. provide no evidence to back their claims that our approach is inadequate. Instead, they argue that detectability is likely different across paved and unpaved roads, and present descriptive statistics to suggest that observations at distances beyond 85 meters from the road may not be reliable. While we are not sure that their assumptions about paved roads always having better detectability are correct, we repeated our regression models for the subset of observations within 85 meters of the road (n=99), their suggested cut-off point. We controlled for *herd size* and used the appropriate random effects structure (same model reported in the original study). These results support our previous findings: *tolerance distances* were 10.1 m greater on paved roads compared to unpaved roads (F = 4.16, P = 0.05; *herd size* coefficient b=-0.13, SE=0.036, P<0.001; model $R^2_m = 0.15$, $R^2_c = 0.28$) and increased with *traffic intensity* (regression coefficient b=0.33, SE=0.119, P=0.02; *herd size* coefficient b=-0.13, SE=0.036, P<0.001; model $R^2_m = 0.17$, $R^2_c = 0.32$).

Road surface and traffic intensity are a correlated, recurrent problem in road ecology

As explained by Mulero-Pázmány et al. (2016), the problem of separating type of road from traffic intensity is not just a matter of statistical design, but of a reality in which paved roads have more traffic than unpaved roads. This is not unique to Kruger National Park, but rather a recurrent issue in the field of road ecology (Forman et al. 2003, D'Amico et al. 2016). When two variables are highly correlated (like type of substrate and traffic in our case), considering both in a single model can lead to collinearity issues which affect coefficient estimates (Zuur et al. 2010). In fact, the interaction model suggested by Jackson et al. results in Variance Inflation Factors >5, which affect coefficient estimates and their significance (Zuur et al. 2010). As stated in our original study (Mulero-Pázmány et al. 2016), we agree with Jackson et al. that additional data from quiet paved roads and busy unpaved surfaces would be useful to disentangle this issue. Unfortunately, using an interaction term with our data is not appropriate.

Discussion and the precautionary principle

Jackson et al. (2017) criticise our paper based on conceptual and methodological issues. We find that their arguments suffer from subjectivity and flawed analyses, and thus, offer few robust arguments to counter our findings. Jackson et al.’s attention to alternative questions regarding *herd size* and *flight responses* may be interesting, but testing new ideas does not invalidate our study or its conclusions. In fact, we appear to largely agree on the key points from our study: *flight responses* are limited, suggesting that habituation may occur, and impala generally avoid close encounters with vehicles, which means animals stay further away from busy, paved roads. We do disagree with Jackson et al. on the behavioural and ecological implications of these findings and on how those are to be communicated to the public and managers.

Jackson et al. (2017) claim that our results demonstrate habituation (“*As acknowledged by the authors, Kruger National Park’s impala population is habituated to the park’s steady flow of vehicles*”). We present habituation as a possible explanation to some of our results (i.e., few *flight responses*), but also report effects like avoidance of close proximity to paved roads. In general, habituation is not a black-or-white response, some individuals in a population may respond while others do not (for example due to differences in personality), and even one individual may respond to some levels of traffic or a road type but not others (within-individual variation). Additional studies are necessary to clearly determine the degree of habituation in Kruger National Park, but in the meantime, following a precautionary approach, we would advise against assuming that impala are fully habituated and are not affected by roads or traffic, as proposed by Jackson et al.

Similarly, we find that precaution may be necessary before assuming avoidance of the nearest 10 meters to paved roads is irrelevant (as stated by Jackson et al. (2017), “*At a landscape scale, distances of < 10 m are unlikely to have significant ecological or biological effects on impala distribution*.”). If we apply this buffer zone to the 850 km of paved roads within Kruger National Park, the potentially affected area is in fact quite large. Evaluating the population- and community-level as well as ecological consequences of this finding was beyond the scope of our paper;

however, we think that future work exploring these issues is necessary before we can conclude that visitor enjoyment or wildlife are unaffected.

Finally, Jackson et al. (2017) also comment on the media attention received by our paper. While we did not participate in the mentioned media piece (Goldman 2016), we find that Dr. Goldman reported our findings generally well, capturing the uncertainty of our results ("*could impact*"). We agree with Jackson et al. that speculative inferences should be avoided, but failing to follow their own advice these authors end their commentary with statements like impala "*are habituated to roads and only avoid direct and close approaches by vehicles by fleeing at a mean distance of 10 m from unpaved or paved roads, irrespective of traffic intensity*" which are not supported by evidence.

Overall, we are pleased to see the interest and ongoing discussion regarding how roads and traffic impact wildlife, particularly in Africa. We believe that this debate should be based on data and careful analyses, and therefore we look forward to seeing more road ecology studies conducted in Southern Africa, and continuing this debate to clarify how wildlife is affected. In the meantime, we recommend following the precautionary principle "*Where there is a threat of significant reduction or loss of biological diversity, lack of full scientific certainty should not be used as a reason for postponing measures to avoid or minimize such a threat*" (United Nations 1992).

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