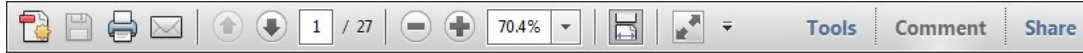
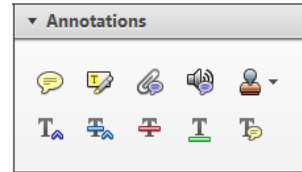


Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. [Replace \(Ins\)](#) Tool – for replacing text.

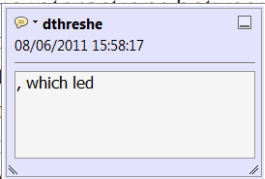


Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

standard framework for the analysis of microeconomic activity. Nevertheless, it also led to the development of a number of strategic approaches. The number of competitors in an industry is that the structure of the industry is a main component. At the industry level, are externalities important? (Mankiw henceforth) we open the 'black b



2. [Strikethrough \(Del\)](#) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by market structure. Blanchard ~~and Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply shocks in the classical framework assuming monopolistic competition are an exogenous number of firms

3. [Add note to text](#) Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups consistent with the VAR evidence

sation by Markov processes. The number of competitors and the impact on the structure of the sector is that the structure of the sector



4. [Add sticky note](#) Tool – for making notes at specific points in the text.

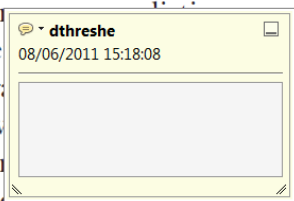


Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

and supply shocks. Most of the time, the number of competitors and the impact on the structure of the sector is that the structure of the sector



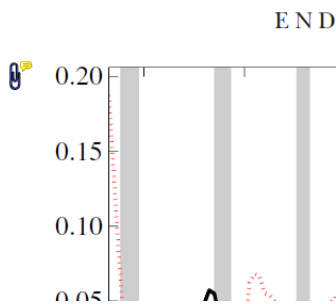
5. **Attach File** Tool – for inserting large amounts of text or replacement figures.



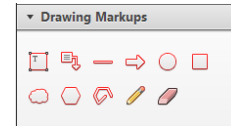
Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it

- Click on the **Attach File** icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

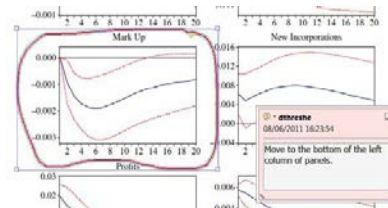


6. **Drawing Markups** Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks. Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



Ungulate behavioral responses to the heterogeneous road-network of a touristic protected area in Africa

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Keywords

African ungulates; anti-predator behavior; protected areas; impala *Aepyceros melampus*; road avoidance; traffic intensity; road network..

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Introduction

The worldwide development of road-networks and associated motorized traffic can greatly impact natural populations (Laurance *et al.*, 2014), a fact that has attracted the attention of conservation biologists leading to the rise of a discipline called road ecology (Trombulak & Frissell, 2000). The presence of roads can alter natural habitats and threat biodiversity through noise, light and chemical pollution, habitat destruction, disruption of communities, and facilitation of biological invasions (Forman & Alexander, 1998; D'Amico *et al.*, 2013). The most widely acknowledged road impacts for wildlife are vehicle-collision mortality and barrier effects (Conover *et al.*, 1995; Gagnon *et al.*, 2007) which are both consequence of an individual's choice to cross or avoid a road (Jaeger *et al.*, 2005; Grilo *et al.*, 2012). Specifically, barrier effects include the behavioral responses toward the road structure itself (road avoidance), the associated emissions (traffic avoidance), and/or

Abstract

Understanding how wildlife responds to road and traffic is essential for effective conservation. Yet, not many studies have evaluated how roads influence wildlife in protected areas, particularly within the large iconic African National Parks where tourism is mainly based on sightings from motorized vehicles with the consequent development and intense use of roads. To reduce this knowledge gap, we studied the behavioral response and local spatial distribution of impala *Aepyceros melampus* along the heterogeneous (with variation in road surface type and traffic intensity) road-network of Kruger National Park (KNP, South Africa). We surveyed different types of roads (paved and unpaved) recording the occurrence of flight responses among sighted impala and describing their local spatial distribution (in relation to the roads). We observed relatively few flight responses (19.5% of 118 observations), suggesting impalas could be partly habituated to vehicles in KNP. In addition, impala local distribution is apparently unaffected by unpaved roads, yet animals seem to avoid the close proximity of paved roads. Overall, our results suggest a negative, albeit small, effect of traffic intensity, and of presence of pavement on roads on the behavior of impala at KNP. Future studies would be necessary to understand how roads influence other species, but our results show that even within a protected area that has been well-visited for a long time, wildlife can still be affected by roads and traffic. This result has ecological (e.g., changes in spatial distribution of fauna) and management implications (e.g., challenges of facilitating wildlife sightings while minimizing disturbance) for protected areas where touristic activities are largely based on driving.

the immediate disturbances (vehicle avoidance; D'Amico *et al.*, in press; Jaeger *et al.*, 2005). These behavioral responses can change animal movement patterns (Cole, Pope & Anthony, 1997), fragmenting large and connected populations into small isolated ones (Vos & Chardon, 1998), and eventually compromising their persistence (Carr & Fahrig, 2001). Despite these potential effects, relative tolerance to motorized traffic has been observed in roads with frequent traffic, especially within protected areas (Wilmers *et al.*, 2003). This sort of habituation can be beneficial in the case of touristic areas by improving visibility of wildlife for visitors. However, habituation can present risks for both human and animals by increasing human-wildlife interactions which can lead to greater risk of wildlife attacks (Hubbard & Nielsen, 2009), road-associated mortality of protected species (Knapp, 2004), and increasing poaching risks near roads (Papaioannou & Kati, 2007).

Although there is a growing body of literature on barrier effect and road tolerance (Fahrig & Rytwinski, 2009), there are still

1 significant gaps in our understanding of how heterogeneous
 2 road-networks (i.e., those with variation in road substrates and
 3 associated traffic intensity) can affect wildlife. Heterogeneous
 4 road-networks are frequently found within rural and natural land-
 5 scapes where wildlife is often more abundant and road impacts
 6 can be more severe (Forman & Alexander, 1998; D'Amico
 7 *et al.*, in press). Few studies of road ecology have been con-
 8 ducted along road-networks in protected areas, even though in
 9 many protected areas human activities are centered on wildlife
 10 sightings from motorized vehicles, with the associated develop-
 11 ment of road-networks and traffic. Understanding road effects in
 12 these areas is critical for effective wildlife conservation, human
 13 safety, and tourism-related economy (Hubbard & Nielsen, 2009;
 14 Malo, Acebes & Traba, 2011).

15 This study aims to improve our understanding of the behav-
 16 ioral responses of ungulates to a heterogeneous road-network
 17 in an African protected area. Previous works of road effects in
 18 Africa have mainly focused on rainforest habitats (e.g., Laur-
 19 ance *et al.*, 2006) with few studies in more open areas (but
 20 see Newmark *et al.*, 1996; Ndibalema *et al.*, 2007) despite the
 21 fact that many emblematic African parks are largely open habi-
 22 tats. To address this gap, we conducted a study in Kruger
 23 National Park (KNP hereinafter), which is one of the main
 24 touristic attractions of South Africa. In particular, we studied
 25 the prevalence of flight responses and the local spatial distribu-
 26 tion of impalas *Aepyceros melampus* in relation to different
 27 types of roads with different traffic intensities, accounting also
 28 for other potentially important factors (i.e., herd size in Stanko-
 29 wicz, 2008; Périquet *et al.*, 2010; Malo *et al.*, 2011). We par-
 30 ticularly focused on impala because it is an abundant species
 31 (estimated current KNP population is 132 300–176 400 indi-
 32 viduals; KNP Scientific Services, 2015). Although not a con-
 33 servation target (listed as 'least concern' by the IUCN; IUCN
 34 SSC Antelope Specialist Group, 2008), it plays an important
 35 ecological role in the African savannah (Pienaar, 1969; Hay-
 36 ward & Kerley, 2008). Overall, our study aims to improve our
 37 understanding of how wildlife responds to roads and traffic.
 38 This knowledge can contribute to more effective conservation
 39 strategies, as well as improved management of touristic activi-
 40 ties within protected areas, particularly those in which motor-
 41 ized tourism is prevalent.

42 Methods

43 Study area

44 Kruger National Park (22°15'S–25°32'S; 30°50'E–32°02'E) is
 45 one of the largest reserves in Africa (nearly 20 000 km²) and
 46 part of the Great Limpopo Transfrontier Park. It has a subtropi-
 47 cal climate with hot-humid summers (October–April) and
 48 warm-dry winters (May–September) and encompasses diverse,
 49 mostly open habitat ecozones (Gertenbach, 1983). The first
 50 vehicle entered KNP in 1927 and currently there are *c.*
 51 2300 km of roads (850 of which are paved), which are used
 52 by over 1.5 million motorized visitors per year ([http://](http://www.sanparks.org/parks/kruger/all.php)
 53 www.sanparks.org/parks/kruger/all.php). Our study was con-
 54 ducted in the central part of KNP, between the Letaba and
 55 Skukuza camps (Fig. 1).
 56
 57
 58

Data collection and variables definition

Impala behavior was studied during April–May 2014 along 12
 transects (average length of 18 km) located on six paved and
 six unpaved roads (Fig. 1). Observations were gathered from a
 high-clearance 4 × 4 vehicle driving at <30 km h⁻¹ between
 08:00 and 17:00 h. While sampling a transect, two observers
 searched for impala individuals or herds located <300 m from
 each side of the road (our range of detection). A third observer
 noted the number of vehicles circulating in the opposite direc-
 tion. The number of counted vehicles over the duration of the
 sampling was used to estimate the number of vehicles per min-
 ute as a measurement of *traffic intensity* on the surveyed road.
 When herds were sighted, we selected a focal individual (the
 individual located closest to the road when the herd was first
 sighted), and estimated *herd size* (minimum group size because
 some individuals in large herds could have been out of sight).
 For each sighting, we recorded the position of our vehicle
 using a GPS (Garmin GSPMAP 62, KS, USA).

We evaluated impala behavior on each sighting using two
 response variables: (1) *flight response* and (2) *tolerance dis-*
tance. We recorded the occurrence of a *flight response* (binary
 variable) when the focal individual moved rapidly away from
 the road as a reaction to our approaching vehicle (i.e., vehicle
 avoidance). We did not consider an individual had fled if it
 did not move or moved parallel or toward the road. *Tolerance*
distances were defined as the perpendicular distance to the
 road (directness estimate *sensu* Bulova, 1994) of focal individ-

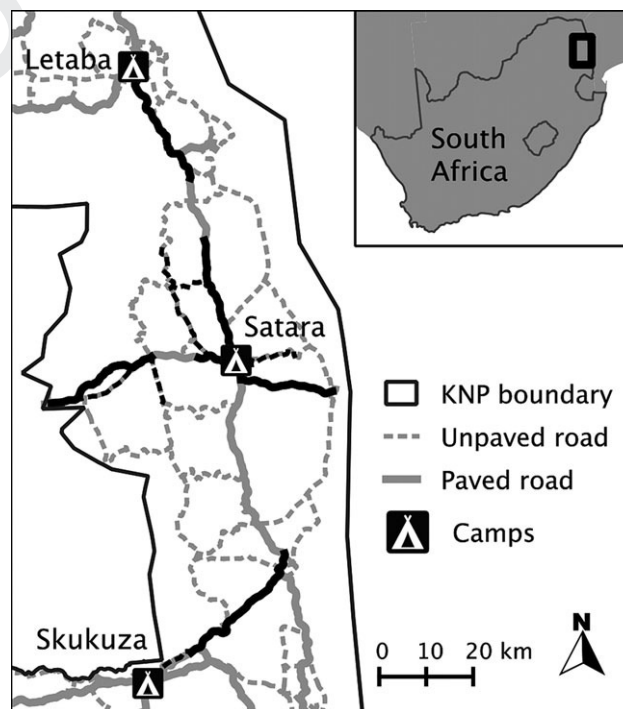


Figure 1 Study area, central Kruger National Park. Surveyed transects indicated by black lines (solid lines for paved roads, dashed lines for unpaved roads).

1 uals engaged in stationary behavior (not involving prolonged
2 directional movements, not fleeing or traveling). Distances
3 were estimated using a Leica Rangemaster 1200 CRF-M rangefinder by approaching the focal individual as close as possible while staying on the road. Observed *tolerance distances* may exceed the minimum at which individuals could tolerate vehicles, because we could not continue to approach individuals until they flee. Animals that ‘tolerated’ vehicles could have still perceived the vehicle and possibly experienced stress. If the focal animal had a stationary behavior when we approached, we directly estimated its *tolerance distance*. If it was traveling when first sighted or fled during our approach, we waited until its behavior became stationary to estimate the *tolerance distance*. If the individual moved out of sight, no *tolerance distance* was recorded. Additionally, for focal animals that were stationary upon first sight but subsequently travelled or fled during our approach, we also estimated the *initial distance* (perpendicular distance to the road from the location at which the individual was first sighted) using reference points. For focal animals that did not move, the *initial* and *tolerance distances* were the same.

Because detectability of impala and behavioral responses may differ between habitat types, we identified the *ecozone* for each sighting based on a simplified version of the KNP landscapes (originally described by Gertenbach, 1983) which includes five different categories (Supporting Information Table S1). *Ecozones* were assigned to georeferenced sighting locations using the *ecozone* GIS layer available from Sanparks (2014) with ArcGIS 9.4.

31 Data analysis

32 We evaluated the effects of road type and traffic on both recorded responses (*flight response* and *tolerance distance*) fitting generalized linear mixed models (GLMMs). *Flight responses* (present or absent) were modeled with GLMMs fitted with a binomial family (logit link). *Tolerance distances* were transformed ($\log_{10}[x + 1]$) and modeled with LMM (Gaussian family, identity link). Models were fitted with the functions *glmer* and *lmer* from the *lme4* package (version 1.1-7) in R 3.1.1 (R Core Team 2014). Models included as predictors either *road surface* (categorical factor with two levels: paved or unpaved) or *traffic intensity* (estimated as the observed number of incoming vehicles per min.), with *herd size* as a covariate (standardized by subtracting the mean and dividing by the standard deviation). Because *road surface* and *traffic intensity* are correlated, we could not fit a model including both variables as predictors to assess their potentially differential roles. To control for potential differences in detectability of impala and response patterns across roads, days, and vegetation zones, fitted models included the *transect identifier* (nested within *date*) and the *ecozone* as random effects. We evaluated model residuals to determine if model assumptions were met. Autocorrelation plots (function *acf*), and variograms (function *variog* of the library *geoR* in R, Ribeiro & Diggle, 2001) were used to detect evidence of temporal or spatial autocorrelation in model residuals. We calculated 95% confidence intervals of predicted values, using

bootstrap percentiles based on 5000 replicates (using the function *confint* in R). Here *P*-values were estimated with likelihood ratio tests. The model fit was described using R_c^2 representing the variation explained by both fixed and random factors; and R_m^2 represents the variation explained by the fixed factors only (Nakagawa and Schielzeth 2013). These R^2 values were estimated using the function *r.squared* GLMM from the package *MuMIn* (Barton 2013) in R.

4 Finally, we evaluated how the observed local spatial distribution (distance to the road) from each road surface differed from the expected in a hypothetical no-road situation. As we could not drive off-road to observe impala spatial distribution away from roads, we compared the observed distribution of *initial distances* in paved and unpaved roads versus the expected distribution under a null model. The null model assumes impalas are randomly distributed in relation to roads (i.e., roads do not affect local spatial distribution) and are detected with a probability that decreases with distance, following a negative exponential distribution curve, which is a commonly used detectability function (Thomas *et al.*, 2002). The rate parameter of the exponential curve was defined as the reciprocal of the observed global mean *initial distance* (rate = 0.023), thus assuming a common function for all roads. We then used the function *rexp* in R to define expected *initial distances* for 10 000 random samples of 54 and 61 observations (reflecting the available data from paved and unpaved roads, respectively). Using these random samples, we estimated the probability that observed distance distributions could have occurred if the null model (a hypothetical no-road situation) was true.

33 Results

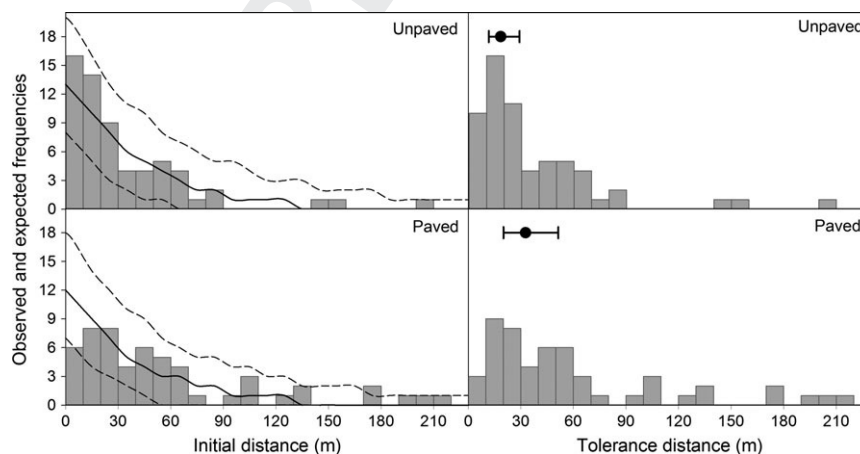
34 We observed impala on 54 occasions driving a total of 141 km along paved roads (an average of 3.8 impala observations/10 km), and on 64 occasions along 81 km of unpaved roads (7.7 observations/10 km. Full dataset available as Supporting Information Table S1). Impalas were found in herds with a mean size of 8.6 individuals ($SD = 14.49$) although observations of solitary individuals were common (42.6% in paved roads and 51.6% in unpaved roads). Based on our estimate of *traffic intensity*, paved roads had more traffic (mean = 0.60 vehicles min^{-1} , $SD = 0.349$), with on average six times more vehicles per minute than unpaved roads (mean = 0.10, $SD = 0.077$).

35 We detected relatively few *flight responses* (23 out of 118 observations) with more responses in unpaved roads (15 out of 64) compared to paved roads (8 out of 54). However, we found no evidence of a significant effect of *road surface* on the probability of *flight response* ($n = 117$; $F = 1.04$, $P = 0.32$; controlling for *herd size*: regression coefficient $\beta = -0.65$, $SE = 0.446$, $P = 0.064$. $R_m^2 \approx R_c^2 = 0.12$). Similarly, we found no effect of *traffic intensity* on the probability of *flight response* ($n = 117$; $\beta = -1.12$, $SE = 0.820$, $P = 0.150$; *herd size* $\beta = -0.66$, $SE = 0.448$, $P = 0.064$. $R_m^2 \approx R_c^2 = 0.15$). Instead, individuals that fled were significantly closer to the road (mean 30.5 m, range 0–154) than those that did not respond (mean 35.0 m, range 0–215). *Initial*

1 *distance* $\beta = -1.12$, $SE = 0.455$, $P = 0.012$; *herd size*
 2 $\beta = -0.68$, $SE = 0.437$, $P = 0.047$, $R_m^2 = 0.18$ and $R_c^2 = 0.19$;
 3 $n = 114$). Among the individuals that showed *flight response*,
 4 12 fled out of sight and the remaining 11 moved an average
 5 of 12 m (range: 3–23 m).

6 We estimated *tolerance distances* on 114 occasions (52
 7 observations from paved roads and 62 from unpaved roads,
 8 Supporting Information Table S1). *Tolerance distances* were
 9 an estimated 14.7 m greater on paved roads compared to
 10 unpaved roads ($F = 9.20$, $P = 0.008$, Fig. 2), with larger herds
 11 generally closer to the road (regression coefficient $\beta = -0.08$,
 12 $SE = 0.039$, $P = 0.037$. Model $R_m^2 = 0.10$ and $R_c^2 = 0.23$). Fitting
 13 an interaction term between *herd size* and *road surface*
 14 did not improve the model fit (interaction term $F = 0.03$,
 15 $P = 0.854$), suggesting the effect of *herd size* was similar in
 16 both paved and unpaved roads. *Tolerance distances* also
 17 increased with *traffic intensity* ($\beta = 0.42$, $SE = 0.132$,
 18 $P = 0.007$) controlling for the influence of *herd size*
 19 ($\beta = -0.09$, $SE = 0.038$, $P = 0.029$. Model $R_m^2 = 0.12$,
 20 $R_c^2 = 0.29$, Fig. 3). Evaluation of model residuals indicated that
 21 model assumptions were met with no evidence of temporal or
 22 spatial autocorrelation.

23 Finally, we compared the observed impala local spatial distribution
 24 with a null model that assumed roads did not influence
 25 distribution locally. Observed *initial distances* in unpaved
 26 roads did not depart from the expected under the null model:
 27 observed frequencies were within the 95% confidence intervals
 28 of the distribution of expected frequencies (Fig. 2). However,
 29 observed distances in paved roads deviated from the expected
 30 with an unlikely low number of sightings within the first 10
 31 meters (Fig. 2). If the null model were true, the probability of
 32 having only six sightings at this distance would be <0.06 , sug-
 33 gesting that impalas may be avoiding the areas closest to
 34 paved roads.



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53 **Figure 2** Observed *initial distances* (grey bars left panels) and *tolerance distances* (grey bars right panels) of impala *Aepyceros melampus* in
 54 unpaved and paved roads at Kruger National Park. The back lines on the left panels indicate the expected median (solid line) and 95%
 55 confidence intervals (dashed lines) frequencies under a null model that assumes impala are randomly distributed in relationship to the road and
 56 detectability decreases following a negative exponential curve. On the right panel the black symbols with error bars are the mean and 95% CI
 57 *tolerance distances* predicted by a linear mixed effects regression model that included *herd size* as a covariate and *transect identifier*, *date* and
 58 *ecozone* as random effects to control for potential differences in detectability across areas.

Discussion

Our study is the first assessment of ungulate behavioral responses toward roads and traffic at Kruger National Park, an emblematic touristic park in Africa, offering insights into the

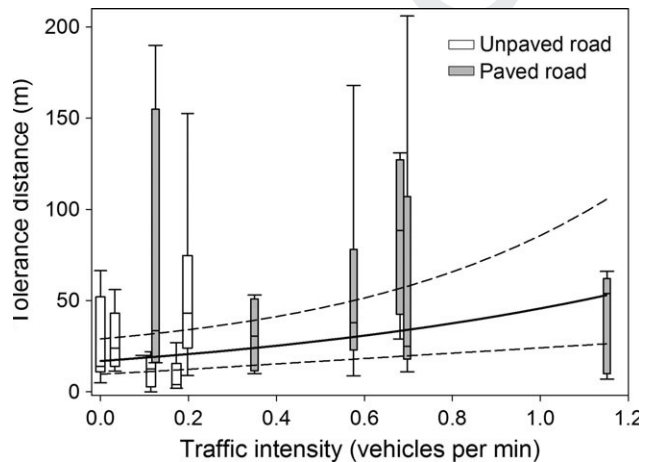


Figure 3 Observed (boxes) and predicted (lines) *tolerance distances* of impala *Aepyceros melampus* in response to estimated *traffic intensity* in Kruger National Park. Boxes indicate the 25, 50, and 75% quantiles of observed distances (whiskers are 10 and 90% quantiles). Gray bars represent paved roads, white bars unpaved roads. The solid line is the predicted relationship from a mixed effects regression model, including *herd size* as a covariate and *transect identifier*, *date*, and *ecozone* as random effects to control for potential differences in detectability across areas. Dashed lines represent the 95% confidence intervals of the predicted relationship.

1 complexity of wildlife responses to heterogeneous road-net-
2 works within protected areas. In particular, we found evidence
3 that impalas change their local spatial distribution near paved
4 and well-traveled roads. Nevertheless, our results also suggest
5 habituation may exist, given the limited flight responses
6 observed (19.5%) and the relatively short average distance at
7 which impalas fled from the vehicle (30.5 m) compared to dis-
8 tances registered for other ungulates (e.g., 132 m in Papouchis,
9 Singer & Sloan, 2001). Habituation would not be unexpected
10 in KNP, given that cars have been regularly present for >
11 50 years, and impalas and other ungulate species have been
12 shown to exhibit habituation in other protected areas (Setsaas
13 *et al.*, 2007; Stankowich, 2008; Malo *et al.*, 2011). However,
14 it is important to note that individuals may experience stress
15 even if flight responses are not observed; thus even apparently
16 habituated animals may be affected by human disturbances
17 (Herrero *et al.*, 2005).

18 Our results show that the local spatial distribution of impala
19 is largely unaffected by unpaved roads although animals
20 apparently avoid close proximity (first 10 m) to paved roads.
21 This distance is relatively short compared to edge effects
22 reported for other ungulate species that range from 50 to
23 2800 m (Alves & Bager, 2013), but could reflect a traffic-
24 induced landscape of fear which should be further studied
25 (Laundré, Hernández & Altendorf, 2001; Ciuti *et al.*, 2012).
26 As mentioned above, impala at KNP may exhibit partial habit-
27 uation to vehicles, which could reduce the avoidance of linear
28 infrastructures. Studies of impala in other areas have reported
29 both no evidence of road/traffic avoidance (Newmark *et al.*,
30 1996) and a tendency to avoid major roads (Mtui, 2014).
31 Differences in response may be explained by different method-
32 ologies or because different habitat features, histories of expo-
33 sure to roads and traffic patterns modulate impala responses
34 differently.

35 Avoidance of paved roads may be directly associated with
36 the presence of pavement (i.e., road avoidance) or with higher
37 traffic intensity. Based on our traffic estimates, paved roads at
38 KNP have approximately six times more cars per minute than
39 unpaved roads (see also Ferreira & Harmse, 1999). Unfortu-
40 nately, in our study, we could not disentangle the effect of
41 road surface from associated traffic as both are highly corre-
42 lated, a pattern often reported in studies of road ecology (Jae-
43 ger *et al.*, 2005; D'Amico *et al.*, 2015). Avoidance associated
44 with road surfaces has been found in small-sized species such
45 as amphibians and rodents (Merriam *et al.*, 1989; McGregor,
46 Bender & Fahrig, 2008), but it has not been reported for ungu-
47 lates. On the other hand, sensitivity to traffic has been sug-
48 gested for impalas based on observed changes in stress
49 hormones (Lunde, 2013) and it has been detected in other
50 ungulates (Creel *et al.*, 2002; Stankowich, 2008; St. Clair &
51 Forrest, 2009). Future work would be necessary to differentiate
52 the role of road surface versus traffic on impala responses and
53 to assess how these effects vary along time (Meisingset *et al.*,
54 2013 detected that reed deer road avoidance is lower at night
55 than during daylight).

56 Flight initiation distance (FID hereinafter, Stankowich, 2008)
57 is the most commonly used indicator in disturbance studies,
58 but it has been criticized (Dumont *et al.*, 2012) because esti-

mates can be affected by recent disturbances (i.e., a previous
vehicle) and/or by missed responses if the animal detects the
observer early. These confounding factors become especially
relevant to comparisons in which the probability of earlier dis-
turbances varies among the compared categories (e.g., recent
disturbances are more likely in roads with more traffic).
Although it is difficult to control for these effects, we propose
here the use of *tolerance distance* because it reflects the dis-
tance at which a focal individual remains stationary after being
exposed to a vehicle. We presume *tolerance distance* varies
less than FID after an immediate previous disturbance, and
therefore is more suitable to compare scenarios with different
levels of disturbance. This indicator also presents the advan-
tage of capturing information on the local spatial distribution
from individuals that do not flee, and thus is more convenient
for studying species with low flight response rates for which
estimating FID would require very high sampling efforts and
potentially result in greater disturbance.

Overall, this study shows that paved roads and traffic can
modify the behavior and local spatial distribution of impala at
KNP. However, our approach presented some limitations. First,
we gathered all data driving on public roads; thus, we could
not control the presence of other vehicles or study impala
responses driving off-road. Second, by not being able to gather
data on foot or using other approaches, we could not disen-
tangle the influence of our own vehicle from that of road surface
or overall traffic on impala responses. The use of alternative
methodologies to determine local spatial distribution, for exam-
ple, indirect cues (i.e., pellets surveys, bio-logging; Negrões
et al., 2011), or Unmanned Aircraft Systems (Mulero-Pázmány
et al., 2014) could help reduce observer interference. Despite
these limitations, and even though KNP has been a protected
area with regular presence of vehicles for a long time, we
observed an effect of traffic and paved roads on impala, which
raises a word of caution about possible ecological and manage-
ment implications that may be relevant to other species or
areas.

Managers of touristic protected areas have the difficult mis-
sion of keeping a sustainable balance between protecting biodi-
versity, satisfying visitors, and optimizing the profitability of
the park. In this study, we found that although impala may be
partly habituated, high traffic intensity and pavement could
lead to barrier effects. For instance, we recorded twice as
many impala observations per driven km in unpaved roads
compared to paved roads, and impala were sighted further
from paved roads, which are those most often used by tourists
(Ferreira & Harmse, 1999). This potential difference in
detectability and/or abundance could be relevant to tourism
management, as visitors want to see many animals and prefer
close-up experiences (Scholtz, Kruger & Saayman, 2013). At
the same time, a certain degree of road/traffic avoidance may
be beneficial if road-associated mortality is reduced. Many
studies suggest ways to mitigate barrier effect, for example,
through temporary and permanent traffic closures, or by limit-
ing the number of visitors (Forman, 2006; Jaarsma *et al.*,
2013). KNP authorities implemented several of these measures
in the past (Ferreira & Harmse, 1999), and these actions may
have contributed to the habituation suggested in this study. As

impalas are a key prey for many predators (Hayward & Kerley, 2008), impala responses could influence predator distribution and behavior. In turn, predator changes may influence other ungulates, which could also be directly affected by roads and traffic. Future work would be necessary to explicitly evaluate impacts on the overall KNP community, but our study offers a first evaluation of how a model ungulate species is influenced by a widely used heterogeneous road-network in an African protected area.

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Road ecology is a rising discipline, but there is a gap of knowledge concerning the traffic impact on wildlife within the large iconic African National Parks, where tourism is based on sightings from vehicles. We studied behavioral response and spatial distribution of impala *Aepyceros melampus* along the heterogeneous road-network (with variation in road surface and traffic) of Kruger National Park (South Africa). We surveyed: (1) flight responses among sighted impala; (2) impala spatial distribution in relation to paved and unpaved roads. We observed few flight responses (19.5% of 118 observations), suggesting habituation to vehicles. Nevertheless, impala tend to avoid the proximity of paved roads. Our results suggest a negative, albeit small, effect of traffic on the behavior of impala. This result has ecological and management implications for protected areas where touristic activities are largely based on driving.

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