We thank the recommender and all reviewers for their support and their insightful comments, that helped us increase the manuscript quality. Please find our answers to their remarks in the present document.

Round #1

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by Gloriana Chaverri, 2020-08-20 16:07

Dear Charlotte and co-authors,

We have already received comments (see below) on your preprint titled "Influence of local landscape and time of year on bat-road collision risks". Overall, the reviewers seem enthusiastic about your work, as am I, but point to a few issues that hopefully you can address before I decide to recommend the preprint. As you will notice, in addition to the comments by Brock Fenton and Mark Brigham, two of Mark's students kindly helped in the evaluation process and I am sure you will find their suggestions useful.

Comment 1

I also have a few comments of my own. First, I agree with Mark in that there is some speculation in the discussion that should be avoided. Some examples where I see speculation in the discussion: lines 487-491, 514, 519-520, 524-526, 535-537.

Reply to comment 1

We agree that there was speculation in some parts of the discussion. We simplified, removed or provided relevant references when needed:

> l.518-522:
> In addition, for the LRE guild, results show that vehicle avoidance was higher at simple parallel tree rows compared to double parallel tree rows. ~~It should be noted that we recorded a particularly high social activity of N. leisleri in most double parallel tree rows of hollow plane trees that provide roost for this species. If bats are less aware of the danger of vehicles when engaging in social activity, or if social activity is a proxy for the presence of maternity roosts with naïve juveniles, it could explain the fact that bats were less cautious in avoiding vehicles in double parallel tree rows.~~ <u>It seems difficult to provide a straight-forward explanation here, but the higher social activity of *N. leisleri* that we recorded at double parallel tree rows could be linked to less vehicle avoidance.</u>
>
> l. 547-553:
> Nonetheless, *P. kuhlii/nathusii* avoided more the zone at collision risk when traffic increased, possibly because they recognise the danger associated to vehicles, <u>although a specific data set would</u>

be required to test this hypothesis. Moreover, *P. pipistrellus* flew more often parallel and over the external sides of the road with increasing traffic. These results show that bats spatially avoid the vicinity of vehicles, completing the observations of Zurcher et al. (2010). The latter did not distinguish between species, but found that 60% of approaching individuals reversed their course in the presence of a vehicle. ~~In addition, it was shown that flying insect abundance decreases with increasing traffic (Martin et al., 2018). Reduced foraging opportunities might discourage bats from foraging over the road, concomitantly with a spatial avoidance of vehicles.~~

l.557-561:
It could be that because SRE fly lower and are more at risk when crossing (Roemer et al., 2017), they are more reluctant to approach vehicles. In addition, since the foraging abilities of SRE seem to be more impaired by light and noise than MRE (Siemers and Schaub, 2011, Stone et al., 2012, Azam et al., 2018), MRE might use roads as foraging grounds and take more risks than SRE.

l.572-573:
This result could also be explained by increased foraging opportunities ~~if insects are more attracted to the warm asphalt during colder times~~ on roads during colder times, as this was observed in swallows (Evans et al., 2003).

l.681-686:
Rhinolophus species are assumed to be very susceptible to road collisions because they fly very close to ground level (Fensome and Mathews, 2016; Jones and Rayner, 1989; Roemer et al., 2017). However Rhinolophus species, because of their very high sonar frequencies (Kingston et al., 2000), are very difficult to detect and to record, and this is why we could not study their flight behaviour with our method. Acoustic flight path tracking with only two microphones would allow a study of Rhinolophus collision risks, although with simpler metrics (Claireau et al., 2018). ~~One could speculate on Rhinolophus collision risks on roads from the SRE guild. However, since these bats have very particular foraging strategies (Denzinger et al., 2018), they could demonstrate quite different responses from other SRE.~~
→ Moved to the section "Limits of the study and perspectives"

Comment 2

Second, I am also having some difficulty with a few of your response variables and their contribution to your main question: what factors increase collision risks in bats? At the moment the only variable I think really would help you answer your question is the number of bat passes at risk of collision per night. At the moment you are including in your model 1) number of bat passes per night, which does not directly measure risk. You also include the 2) proportion of bat flights at vehicle height, yet this will not provide you with a total risk estimate. For example, in site A say you only detect two passes in a given night and both are at vehicle height, but in site B you detect 100 passes and 50 are at vehicle height; with these data you will find that 100% of passes are at risk at site A and only 50% at site B, when clearly more animals are at risk in site B. This will have major implications if and when proposing strategies to reduce vehicle collisions with bats.

Reply to comment 2

The article seems indeed to lack clarity on this point. The number of bat passes at risk of collision per night is definitely one of the keys to understand collisions, as the recommender suggests. We could have simply modelled this response, but to find out **why** collisions occur precisely, we needed to decompose it into conditional events:

*Bat density * percentage of bats flying at vehicle height * percentage of bats present simultaneously with a vehicle.*

Our hypotheses were that some explicative variables would only influence bat density, while other explicative variables would only influence bat behaviour. It is important to understand how each of them contributes to the total collision risk. To do so, we multiplied each of the conditional events to obtain the number of bat passes at risk of collision per night (see figures A2 and A3). As we found out, density is the conditional event that influences the most collision risks. This very important finding allows us to say in the discussion that surveys using simple passive recorders (the most popular method presently) can be sufficient in some contexts to provide a good estimate of collision risks at roads, but not in all contexts. Specifically, with an increasing traffic rate, the density of SRE decreased while the overall collision risk increased because the bat-vehicle co-occurrence rate increased.

Furthermore, as it is nicely described in Zimmermann Teixeira et al. (2017): "When road-kill hotspots do not indicate the best sites for road-kill mitigation", on sites that suffered a reduction in population size due to road mortality, the number of road kills (and conversely the number of individuals at risk of collision, used in our study as a proxy for roadkills) is not sufficient to select the best sites to implement mitigations. In some cases, it is of paramount importance to also have access to information on the current local population density at the road location, and thus on the proportion of impacted individuals (i.e. per-capita mortality).

We thus edited the introduction to help readers understand our demonstration, stressed this point in the discussion and added a section in the abstract to make it clearer:

l.17-27:
(Abstract)
Roads impact bat populations through habitat loss and collisions. High quality habitats particularly increase bat mortalities at roads, yet many questions remain concerning how local landscape features may influence bat behaviour and lead to high collision risks. ~~Moreover, no study provides an understanding of the extent to which mortalities result from bat density on one hand and from bat flight behaviour on the other hand, which is required when designing risk mitigation measures~~.
Moreover, when comparing the potential danger of different road sections, the most popular method today is the use of simple bat detectors to assess the local densities of current populations at road sites. Yet, it is not known to which extent bat behaviour influences collisions (i.e. bats flying at vehicle height or on the side or above, bats avoiding vehicles or not). Behaviour is very rarely taken into account in practice, and this might lead to hazardous site selections for mitigation. Our goals were thus (i) to estimate how local landscape characteristics affect each of the conditional events leading to collisions (i.e. bat presence, flight in the zone at collision risk and bat-vehicle co-occurrence), and (ii) to determine which of the conditional events most contributed to collisions risks.

l.110-125:
(Introduction)
Road collision risks in a species depend on (1) its local density, (2) the proportion of time spent in the zone at collision risk and (3) the simultaneous presence of bats and vehicles in the zone at

collision risk (Jaeger et al., 2005; Zimmermann Teixeira et al., 2017). It is therefore necessary to take each of these variables into account when investigating road collisions. Indeed, when comparing two different road locations within different landscape features, a higher bat acoustic activity (used as a proxy of bat density) does not necessarily lead to a higher proportion of flights at risk of collision for all species (see Abbott et al., 2012). In addition, even if more individuals are at risk of collision (or if mortality is higher) at one site compared to another, this does not necessarily mean that this site should be selected for mitigation. Indeed, local populations can be dramatically reduced due to road mortality year after year, and a measure of per capita mortality risk is essential to correctly identify dangerous locations and avoid wrong recommendations for the siting of mitigation measures (Zimmermann Teixeira et al., 2017). Per capita mortality is also a very useful tool to prioritise conservation actions in function of the susceptibility of species to anthropogenic impacts. For instance, bats of the *Nyctalus* genus are particularly susceptible to wind turbine collisions because a high proportion of the individuals are victims of collisions (Roemer et al., 2017); to spare their populations, wind energy planning should therefore avoid areas where these species are extant.

l.126-130:

(Introduction)

Our study aimed at (1) assessing the effects of the characteristics of the local landscape on bat activity and movement behaviour and consequently on road collision risks, ~~and~~ (2) disentangling the roles of density and movement behaviour in collision risks, (3) determining how the orientation of linear vegetation affected the orientation of bat trajectories, to provide guidance for mitigation measures and (4) providing a proxy for species susceptibility to road collisions independently of their population sizes.

l.137-147:

(Introduction)

Concerning the response variables, we expected bat density to be the main factor influencing collision risks in some contexts (for example at tree rows along streams, which are rich in insects), but we expected the proportion of individuals flying in the zone at collision risks to be the main factor in other contexts (especially in forested areas, possibly constraining bats to fly over the road). Concerning explicative variables, we expected (1) a higher bat density at good quality habitats (i.e. tree rows near streams and tall trees) and at roads with a lower traffic rate, (2) a higher proportion of individuals in the zone at collision risk when vegetation grows closer to the road and in habitats with dense vegetation at each side of the road compared to habitats without trees, (3) a correlation between the orientation of bat trajectories and the orientation of linear vegetation, (4) a larger proportion of individuals flying in the zone at collision risk for short-range echolocators than for mid-range echolocators and long-range echolocators, reflecting the vertical niches of those species (Roemer et al., 2019).

Comment 3

The other response variable, 3) vehicle avoidance, is very confusing in my opinion and assumes that bats are actively avoiding vehicles, which you are not providing strong evidence for.

Reply to comment 3

We agree that the name of this response variable is debatable. This conditional event provides the last step to fulfil a stepwise assessment of the risk of collision, by evaluating how the environment may influence the time lag between bats and vehicles (a proxy for bat avoidance of vehicles). We changed the name of this response variable to 'bat-vehicle co-occurrence'. We thus made name changes all the way through the manuscript (introduction, material and methods, results and discussion). The following figures and tables had to be changed since vehicle avoidance (0=no, 1=yes) is the inverse of bat-vehicle co-occurrence (0=no, 1=yes): Figure 4, Figure 6, Table 4, Figure A2. The R scripts were also modified accordingly (https://github.com/Charlotte-Roemer/bat-road-collision-risks).

We also clarified the definition of this response variable in material and methods:

> l.324-328:
>
> If the time lag was lower than 10 s, we considered that there was a bat-vehicle co-occurrence (1~~0~~). If the time lag was higher than 10 s, we considered that a bat was present during the absence of a vehicle (0~~1~~). ~~In fact, it might be argued that very long time lags between a vehicle pass and a bat pass cannot be considered as true vehicle avoidance, but rather coincidental bat absence on the road in the simultaneous absence of a vehicle. However, a~~A relatively higher proportion of long time lags between such bat passes and vehicle passes could be interpreted as a higher probability that bats avoid vehicles, thus we used this metric as a proxy for vehicle avoidance.

Comment 4

So to recapitulate, my suggestion is that a much more straightforward and clean model would only need to include bat passes at collision risk per night as your response variable.

Reply to comment 4

We kindly refer the recommender to our answer to comment 2, where we explained that the understanding of bat-vehicle collision risks necessitates the modelling of three conditional events. Even though this makes the analysis more complex, we think that it is necessary to understand the mechanisms of bat-vehicle collisions.

Comment 5

I see no need to include trajectory orientation since your variable measuring collision risk already takes into account the fact that bats are entering the zone of risk (above the road and at vehicle height). Finally, I would like to congratulate you on this wonderful work and all the effort undertaken to provide such detailed information on this very important topic.

Gloriana Chaverri

Reply to comment 5

Trajectory orientation is not used for calculating the total number of bat passes at risk of collision per night, but it is very informative for the design of mitigation measures such as hop-overs, and we think that it is worth to keep it this study. As this point lacked an explanation in the manuscript, we changed it accordingly:

l.126-130:

Our study aimed at (1) assessing the effects of the characteristics of the local landscape on bat activity and movement behaviour and consequently on road collision risks ~~and~~ (2) disentangling the roles of density and movement behaviour in collision risks, (3) determining how the orientation of linear vegetation affected the orientation of bat trajectories, to provide guidance for mitigation measures and (4) providing a proxy for species susceptibility to road collisions independently of their population sizes.

Reviews

Reviewed by Brock Fenton, 2020-07-21 20:40

Comment 1

This is an interesting and timely topic ... but there are some missing elements. The first missing element is a clear statement of the hypothesis underlying the work, and, associated with this, specific predictions that can be tested with the data. This approach would help the reader better appreciate the importance of the paper.

Reply to comment 1

Founding hypotheses of our work were indeed lacking and we edited the manuscript to include them at the end of our introduction. For those for which it was not the case before, we also mentioned whether those hypotheses were verified in the discussion:

l.137-147:

(Introduction)

Concerning the response variables, we expected bat density to be the main factor influencing collision risks in some contexts (for example at tree rows along streams, which are rich in insects), but we expected the proportion of individuals flying in the zone at collision risks to be the main factor in other contexts (especially in forested areas, possibly forcing bats to fly over the road). Concerning explicative variables, we expected (1) a higher bat density at good quality habitats (i.e. tree rows near streams and tall trees) and at roads with a lower traffic rate, (2) a higher proportion of individuals in the zone at collision risk when vegetation grows closer to the road and in habitats with dense vegetation at each side of the road compared to habitats without trees, (3) a correlation between the orientation of bat trajectories and the orientation of linear vegetation, (4) a larger proportion of individuals flying in the zone at collision risk for short-range echolocators than for mid-range echolocators and long-range echolocators, reflecting the vertical niches of those species (Roemer et al., 2019).

(Discussion)

l.500-501:

Our results demonstrate heterogeneity in the influence of explanative variables on the four response variables, depending on species.

l.509-513:

Interestingly, landscape type did not produce similar effects on bat density and on bat flight behaviour. Indeed, in the case of *P. pipistrellus* for instance, bat density was the highest in perpendicular tree rows formed by small streams. However, local landscapes eliciting the highest proportion of flights at risk of collision for this species were forests. This type of landscape was in fact a very high factor of presence at risk for most species and guilds, as we expected.

l.533-537:

As said in material and methods, distance to tree foliage was correlated to tree height in our study. In all species except *Plecotus sp*., density was negatively affected by an increasing distance to tree foliage, when selected. Conversely, taller trees led to a higher density of *M. myotis/blythii* and of the LRE guild. Our hypothesis according to which taller trees would be associated with a higher density was thus only verified for one species.

l.540-542:

In our study, the proportion of flights in the zone at collision risk was rarely influenced by tree height or distance to trees; nonetheless, increasing distance to trees was associated with higher proportions of flights at risk for *E. serotinus*, contrary to our expectation.

l.591-593:

This calculus placed MRE as the most susceptible bat guild to road collisions. This finding did not match our expectations since the lowest flyers were always thought to be the most susceptible to road collisions (Voigt and Kingston, 2016).

l.609-613:

However, while increasing traffic density was associated with a decrease in SRE density, it was associated with an increase in the overall collision risk (the product of quantitative models). This demonstrates, as we expected, that the measure of the number of bat passes can be a good proxy of bat collision risks in certain contexts, but that it is necessary to also measure bat behaviour to assess collision risks with certainty in all contexts.

Comment 2

More disturbing is the absence of any data about bat mortality during the study. Were any road-killed bats found? Did the authors look for road-killed bats?

It is possible that a skillfully constructed hypothesis and predictions would circumvent the lack of data on mortality, but I am not sure how. I realize that the absence of road-killed bats would not conclusively show no mortality, as bats are small and might not last long on the road.

Reply to comment 2

It is true that acoustic flight path tracking has not been used until recently to study anthropogenic collisions. Nonetheless, this method has been used in the field since 1966 and has since then shown its efficacy to acquire a large amount of precise information on bat movements (Koblitz, 2018). Acoustic flight path tracking was first used to study train collisions in Roemer et al. (2016) and road collisions by Claireau et al. (2019). In Roemer et al. (2017) we demonstrated that measures of bat flight height using a simple microphone array of two microphones were a good estimator of species collision risks at wind turbines. This result was based on the correlation between the proportion of bat flights in the zone at collision risk (above 25-30 m high, in the area swept with wind turbine blades) and an index of species susceptibility to wind turbines (calculated from mortality surveys).

The field worker nevertheless did look for bat carcasses at least once per study site, most often twice (on two different days), and more rarely up to four times (on four different days). Searches were done on sections 50 m in length along the road on each side of the study point. Because it was not the purpose of our study, searches were randomly conducted during the day (from 9 am to 9 pm), which has an influence on the finding success since small carcasses are rapidly scavenged. Only 2 carcasses were found overall. One juvenile female of *Rhinolophus hipposideros* was found on the 12th of August 2016 at study site n°11 (dense oak forest on both sides) and one adult *Pipistrellus pipistrellus* was found on the 7th of June 2016 on study site n°55 (“no vegetation”: some vines and croplands). Thus to attain our goal, we would have needed to perform carcass searches on many more days than what we have done with acoustics to obtain comparable results. Assessment of collision risks based on carcasses would not have been possible at the species level, and grouping different species would hinder our analysis greatly.

We propose to add a section in the discussion to provide more context on the pros and cons of both methods (underlined sentences in the box below):

l.500:
~~Moreover, contrary to the classic method of collecting bat carcasses, the results of AFPT are not biased by predation or observer efficiency, and AFPT may be applied to study roads after as well as before they are in service, if necessary.~~

l.599-628:
~~*Consistency (or discrepancy) between bat collision risk and measures of activity*~~
<u>*Advantages of conditional probabilities taking into account bat behaviour to assess road collision risks*</u>

All quantitative models succeeding the density model were interpreted as conditional probabilities that an individual is at risk of collision, and their predicted probabilities were multiplied to obtain the overall bat collision risk if a variable was selected in several of them. The product of all quantitative models showed that *H. savii* was more at risk of collision in forests and forests edges (and to a lesser extend at roads without trees), while *P. pipistrellus* was more at risk of collision at perpendicular tree rows. These products match the patterns of bat density in function of landscape type. The product of quantitative models also showed that the yearly patterns of collision risks matched the ones of bat density. Collision risks are more numerous in summer or autumn according to species, and explain the mortality patterns found in Fensome and Mathews (2016).
However, while increasing traffic density was associated with a decrease in SRE density, it was associated with an increase in the overall collision risk (the product of quantitative models). This demonstrates that the measure of the number of bat passes can be a good proxy of bat collision risks in certain contexts, but that it is necessary to also measure bat behaviour to assess collision risks with certainty in all contexts.

In addition, contrary to the classic method of collecting bat carcasses, the results of acoustic flight path tracking are not biased by predation or observer efficiency, and acoustic flight path tracking may be applied to study roads after as well as before they are in service, if necessary. It is also well known that bat carcasses are quite difficult to find (Slater, 2002; Santos et al., 2011) while acoustic flight path tracking provides a large amount of precise information on bat movements. Yet, out of curiosity, during field work, we looked for bat carcasses at least once per study site, most often twice (on two different days), and more rarely up to four times (on four different days). Searches were done along the road on sections 50 m in length, on each side of the study point. Because it was not the purpose of our study, searches were randomly done during the day (from 9 am to 9 pm), which has an influence on the finding success since small carcasses are rapidly scavenged (Slater, 2002). Nevertheless, only 2 carcasses were found overall (unpublished data). One juvenile female of *Rhinolophus hipposideros* was found on the 12th of August 2016 at study site #11 (dense oak forest on both sides) and one adult *Pipistrellus pipistrellus* was found on the 7th of June 2016 on study site #55 ("no vegetation": some vines and croplands). These results underline the need of using acoustic recordings to collect enough data per species to attain the aims of our study.

Comment 3

Another important issue could be the number of known bat roosts in the study area. But hindsight is a wonderful tool.

Reply to comment 3

We only have the almost complete knowledge of the presence of roosts for *M. schreibersii* and *M. capaccinii*. All other species might roost more or less closely to study sites, but it is impossible to assess it. However, we consider that the number of study sites (10 to 12 per landscape type) is sufficient to circumvent any bias linked to the proximity of roosts.

Comment 4

How would the findings of this paper alter conservation actions designed to protect bats?

I like the idea of the study but without evidence in the form of road-killed bats, I find it difficult to fully appreciate the work.

Brock Fenton

Reply to comment 4

It might be indeed interesting to comment on existing mitigation measures based on our results. We added a few sentences about this point in the Discussion (underlined sentences in the box below):

> l.630-633:
> Our first group of recommendations applies to habitat selection during road planning to avoid situations with enhanced collision risks. As has been recommended in previous studies (Medinas et al., 2013; Fensome and Mathews, 2016), 'quality habitats' – depending on species ecology – should generally be avoided to ensure that roads will avoid habitats with high bat density.
>
> l.662-672:
> Finally, our results allow us to provide insight on a low-cost mitigation measure that has been popularly proposed to reduce collisions at secondary roads: hop-overs. They consist in planting tall trees at each side of a road to help bats increase their flight height and cross safely (Limpens et al. 2005). Screens can be added at each side of the road to prevent bats from crossing at low height. Christensen et al. (2016) already found that this measure could be ineffective to help many species crossing roads safely, as many individuals will just fly around screens to cross. Based on our results, we expect that planting tall trees next to roads will create new foraging grounds, increase bat density and encourage individuals to fly in the zone at collision risk if trees are planted very close to the road, as it is often recommended (Voigt and Kinston, 2016). We thus expect more collision risks with hop-overs than without, and their use without other measures such as speed reduction should be prohibited until their efficacy is proven.

Reviewed by Mark Brigham, 2020-08-18 21:04

Overall. I think the premise of this work is very thoughtful and useful. While I am no expert about the analysis undertaken, it largely makes sense to me and I think the 3-D analysis is highly thoughtful. It's a shame that bats all react differently to vegetation, traffic volume etc. and there is no general outcome that applies even to most species. But that is what the science says and so be it.

Comment 1

Writing. I think the manuscript would benefit greatly from a thorough edit by a native English speaker. There are multiple instances of tense-subject and verb-subject disagreement. There are also numerous instances of awkward sentence construction that reflect French rather than English grammar. In some instances, this makes it difficult to ascertain the meaning of sentences so it is more than just a bit of a nuisance. I recognize that it must be inordinately difficult to write in a language other than one's native tongue and it is totally unfair that English is the language of science, but it is what it is.

Another thing that would help re writing would be to reduce the use of acronyms which makes reading harder. Not sure they are all really necessary (e.g., TOAD).

Reply to comment 1

We thank the reviewer for showing so much understanding for the task of writing in English for a non-native speaker! We asked a native English speaker to correct the grammar, so that the manuscript should be much easier to read now.

We removed the use of the following acronyms and wrote words in full letters:

- simple parallel tree rows (SPT)
- double parallel tree rows (DPT)
- perpendicular tree rows (PT)
- forests (F)
- forest edges (FE)
- no vegetation taller than 1.5 m (NV)
- acoustic flight path tracking (AFPT)

However we would like to keep the TOAD, SRE, MRE and LRE acronyms since they are commonly used in other studies and are quite convenient.

Comment 2

Sample sizes. The number of nights of sampling is reported differently in the manuscript. The Abstract says 2 nights whereas in the body of the text of the Methods it is reported as 2-5 nights.

Reply to comment 2

We agree that there were discrepancies in how we reported sampling between the abstract and the methods. We completed both sentences:

> l.28-30:
> In this study, we recorded bat activity and characterised flight behaviour with three variables: position at risk of collision, vehicle avoidance, and flight path orientation, using acoustic flight path tracking at 66 study sites in the Mediterranean region for two <u>to five</u> full nights.
>
> l.157-159:
> Bat behaviour was recorded at 66 sites (Figure 1, supplementary table 1) at national or departmental roads, <u>for a minimum of two nights per site, but recordings could continue up to five nights per site (mean = 2.6 nights +/- SD 0.9) depending on the schedule of the field worker and on battery strength.</u>

Comment 3

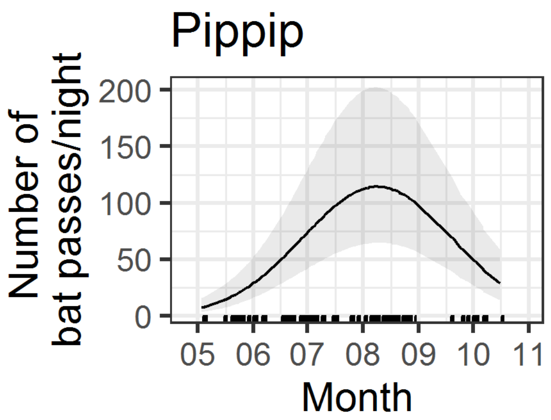
We are not told when the sampling happened and thus how there is the ability to assess the seasonal differences that are reported.

Reply to comment 3

Indeed, we forgot to mention the precise timing of sampling. We completed this part accordingly:

l.160: Sampling took place between the beginning of May and mid-October, depending on study site.

We modelled response variables in function of the time of the year using a Generalised Linear Mixed Model, therefore it was not necessary to sample each night each study site. Since our sampling design was balanced for each of the explanatory variables (which were taken into account in the models), we could infer the general effect of seasonality on the response variables. To have a more precise idea of the sampling effort, we refer the reviewer to the results for the density of any species in figure A2 and consider the ticks on the x axis, which represent the sampled nights:



The meaning of the tick was not mentioned in the figure's legend. We added it.

Comment 4

Further you say that sampling was done on "straight portions" of roads. Define what a straight portion is more precisely. Rather than defining sampling as occurring during optimal weather conditions, tell us what the min and/or max temperatures, maximum wind speed and maximum amount of precipitation were. Likewise for distance between microphones; give us the absolute max and min rather than the variation.

Reply to comment 4

We thank the reviewer for indicating where we lacked precision. We completed the manuscript according to his suggestions:

l. 189-191: All sites were situated in lowlands, on two-lane asphalt roads wide of 4 to 8 m, on straight portions (at least 200 m without curvature on each side of the sampling point), where vehicles were allowed to drive up to 90 km/h.

l. 196-201: Monitoring was performed exclusively during nights with optimal weather conditions for bat activity (temperature: mean = 20.6 +/- 6.5 °C, min = 8 °C, max = 34.9 °C; wind speed: mean = 7.5 +/- 8

km/h, min = 0 km/h, max = 31 km/h; cumulated rain per night: mean = 0.2 +/- 1.3 mm, min = 0 mm, max = 11 mm). However, the percentage of visible moon (mean = 49.2 +/- 35.8 %, min = 1 %, max = 99 %) was not a criterion we could control because of the time constrained field work schedule.

l.217-218:
Depending on the study site, minimum distance between microphones was ~~8.1 (+/- SD 1.6) m~~ 5.1 m and maximum distance was ~~16.8 (+/- SD 2.7) m~~ 22.6 m.

Comment 5

Actual collisions. In my view it needs to be made much more explicitly clear in the Introduction that vehicle-bat collisions are indeed common. This is buried amongst many citations to non-bat animals. While I think making the rationale of broad interest is beneficial, deer are not bats. It was my impression based on many years of driving at night, that bats flying over top of roads are very uncommon. I think that in aIl the night driving I have done I have only ever hit one and it was unhurt (An unusual technique for catching bats. Bat Research News 1996 37:115). However, the authors cite a number of papers that I was unaware of which show that my impression was wrong. I do think many others would share my impression. I think it is well known that bat flight is affected by roads and this may cloud the impression of many. I would disagree that it has not been emphasized that bats follow roads; I think this is reasonably well-established in the literature.

Reply to comment 5

Indeed, we did not explicitly cite studies that showed that vehicle-bat collisions are common, or that they are threatening populations. We edited the manuscript accordingly:

l.82-91:
For these reasons, even moderate increases in mortality rates may represent a serious threat to their survival. As a result, all European bats are now under strict protection (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, 1992).

Bat mortality at roads was investigated in numerous studies (Fensome and Mathews, 2016), and can locally threaten bat populations. For instance, an annual highway mortality of 5% was estimated for a colony of *Myotis sodalis* in the United States of America (Russell et al. 2009). Brinkmann et al. (2012) stated that a road mortality of 3 to 7 adult females in a colony of 100 female *M. myotis* or *Rhinolophus hipposideros* could lead to a negative population growth. A good understanding of the mechanisms leading to collisions between road vehicles and bats is therefore necessary to efficiently mitigate them (Fensome and Mathews, 2016).

There are mentions in the literature suggesting that bats may follow roads, especially small roads (Voigt and Kingston, 2016). However, mitigation measures are mostly proposed to help bats crossing roads, and not to reduce the attractiveness of roads for bats. Moreover, we are not aware of any study that quantifies bat crossings compared to bats following the road. These reasons might explain why experts exclusively propose mitigation measures at locations expected to elicit a lot of bat crossings. We propose to modify the paragraph to clarify our meaning:

l.523-531:

Contrary to our expectations, landscape types were not selected to explain the orientation of flight trajectories. Our results show that even in the presence of a perpendicular tree row or in the absence of trees, bats fly most of the time parallel to the road axis. This supports the fact, not often enough emphasised in collision risk assessments, that bats use roads as corridors, because road verges may offer foraging opportunities by attracting more insects than adjacent habitats (Medinas et al., 2019; Villemey et al., 2018), and because of the verge effect when trees are present (Brigham et al., 1997; Kalcounis-Rueppell et al., 2013; Verboom and Spoelstra, 1999). According to our results, it should be considered that on secondary roads, bats following the road axis may be as common as bats crossing roads, and that mitigation measures should deal with these two types of movements.

Comment 6

3-D positioning. This analysis is most interesting and I found it really impressive how you did this. I think you were appropriately conservative in assigning a position to the bats. I thank you for providing access to the R script. The precise definition of safe vs. unsafe was very clear. Well done. I like that you actually calculate an estimate of how many recorded passes actually put a bat into an unsafe position and thus estimate the actual number of potential collisions. While it obviously would be an overestimate, it gives some information about how many bats really could be killed by vehicles. However, this outcome does not get emphasized enough in the Discussion. I know it is impossible except at a species-specific level but some direct indication of what proportion of passes puts bats at risk would be useful.

Reply to comment 6

We thank the reviewer for this very interesting suggestion. We did this calculus for the three bat guilds and added the following sections in the introduction, material and methods, results and the discussion:

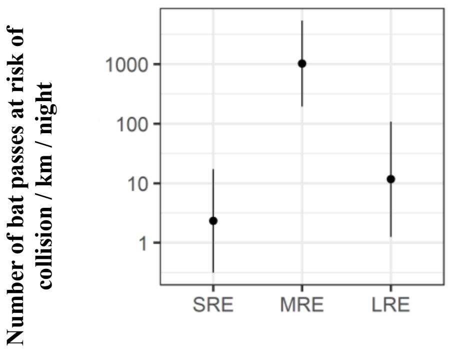
l.116-130:
(Introduction)
In addition, even if more individuals are at risk of collision (or if mortality is higher) at one site compared to another, this does not necessarily mean that this site should be selected for mitigation. Indeed, local populations can be dramatically reduced due to road mortality year after year, and a measure of per capita mortality risk is essential to correctly identify dangerous locations and avoid wrong recommendations for the siting of mitigation measures (Zimmermann Teixeira et al., 2017). Per capita mortality is also a very useful tool to prioritise conservation actions in function of the susceptibility of species to anthropogenic impacts. For instance, bats of the *Nyctalus* genus are particularly susceptible to wind turbine collisions because a high proportion of the individuals are victims of collisions (Roemer et al., 2017); to spare their populations, wind energy planning should therefore avoid areas where these species are extant.

Our study aimed at (1) assessing the effects of the characteristics of the local landscape on bat activity and movement behaviour and consequently on road collision risks, and (2) disentangling the roles of density and movement behaviour in collision risks, (3) determining how the orientation of linear vegetation affected the orientation of bat trajectories, to provide guidance for mitigation measures and (4) providing a proxy for species susceptibility to road collisions independently of their population sizes.

l.350-353:
(Material and Methods)
Since our results apply for road sections 20 m in length, we multiplied the expected mean number of bat passes at collision risk by 50 to obtain a mean number of bat passes at risk of collision per

kilometre and per night. To compare bat guild susceptibility to road collisions, we multiplied E2×E3; this result is an index of susceptibility to road collisions that is independent of local population densities and independent of the context (landscape type).

l.457-462:
(Results)
We found a mean number of bat passes at risk of collision per kilometer and per night of 2.3 for SRE, 1024.9 for MRE and 11.7 for LRE (figure 7).
The index of susceptibility to road collisions, which is independent of species population densities, placed MRE as the most susceptible guild (figure 8).



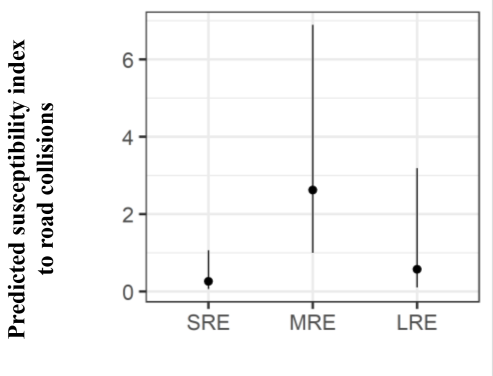


Figure 7: Predicted number of bat passes at risk of collision per night and per kilometre for each bat guild (logarithmic scale). 95% confidence intervals are shown. SRE: short-range echolocators. MRE: mid-range echolocators. LRE: Long-range echolocators.

Figure 8: Predicted susceptibility index to road collisions for each bat guild. 95% confidence intervals are shown. SRE: short-range echolocators. MRE: mid-range echolocators. LRE: Long-range echolocators.

l.585-598:
(Discussion)
(*Species differences*)
~~MRE seem to be generally more at risk of collision with vehicles than other species because they showed a higher proportion of bat-vehicle co-occurrence than SRE and because they had a higher proportion of trajectories in the zone at collision risk than SRE or LRE.~~

We found a mean number of bat passes at risk of collision per kilometre and per night of 2.3 for SRE, 1024.9 for MRE and 11.7 for LRE. We stress that these figures are necessarily an overestimate since we could not measure more precisely bat avoidance of vehicles when they were in the zone at collision risk at less than 10 s from a vehicle pass. In addition, readers have to bear in mind that these figures are not a proxy for the bat guild susceptibility to road collisions. For this, it is necessary to consider the proportion of individuals in the zone at collision risk multiplied by the co-occurrence of bats and vehicles. This calculus placed MRE as the most susceptible bat guild to road collisions. This finding did not match our expectations since the lowest flyers were always thought to be the most susceptible to road collisions (Voigt and Kingston, 2016). Fensome and Mathews (2016) found that low-flying species are more susceptible to collisions, however, it is important to mention that they included both SRE and MRE in this category. Our results show that MRE are more susceptible than SRE to road collisions because MRE fly more often in the zone at collision risk and are also more often present in this zone simultaneously to a vehicle pass. This classification, added to species conservation status, can be used to prioritise conservation actions at roads.

Comment 7

Outcomes. I find it interesting that the factors you assessed affect different species in really different ways so there appears to be no one thing that can be done to reduce the risk to bats.

Line 514 – not sure it is appropriate to assume that some bats "recognize the danger triggered by vehicles" (this is also an instance where the writing needs to be clearer – I think you mean to say "recognize the risk posed by vehicles"). To test this would take a specific data set.

Reply to comment 7

We agree that this sentence should be more carefully written. We propose to reformulate accordingly:

l.547-549:
Nonetheless, *P. kuhlii/nathusii* avoided the zone at collision risk more when traffic increased, possibly because they recognise the danger associated with vehicles, although a specific data set would be required to test this hypothesis.

Comment 8

Line 521 – if higher traffic volume is trivial, why talk about it?

Reply to comment 8

We wanted to leave out any unnecessary speculation for this result and this is why we still had to provide a short explanation.

Comment 9

Overall in the Discussion I think there is too much speculation – e.g., warm asphalt effects, Rhinolophus issues. Stick to the main outcomes and add a real estimate of likelihood of collision. Do you really think that forests around roads should be cleared to reduce risk to bats? It appears to me that this would really only help some.

Reply to comment 9

According to the reviewer's suggestion, we tried to remove some parts where there was too much speculation, or justify them with references. See also our answer to comment 1 of Gloriana Chaverri.

l.572-573:
This result could also be explained by increasing foraging opportunities ~~if insects are more attracted to the warm asphalt during colder times~~ on roads during colder times, as this was observed in swallows (Evans et al., 2003).

l.681-686:
Rhinolophus species are assumed to be very susceptible to road collisions because they fly very close to ground level (Fensome and Mathews, 2016; Jones and Rayner, 1989; Roemer et al., 2017). However Rhinolophus species, because of their very high sonar frequencies (Kingston et al., 2000), are very difficult to detect and to record, and this is why we could not study their flight behaviour with our method. Acoustic flight path tracking with only two microphones would allow a study of Rhinolophus collision risks, although with simpler metrics (Claireau et al., 2018). ~~One could speculate on Rhinolophus collision risks on roads from the SRE guild. However, since these bats have very particular foraging strategies (Denzinger et al., 2018), they could demonstrate quite different responses from other SRE.~~
→ Moved to the section "Limits of the study and perspectives"

l.518-522:
In addition, for the LRE guild, results show that vehicle avoidance was higher at simple parallel tree rows compared to double parallel tree rows. ~~It should be noted that we recorded a particularly high social activity of N. leisleri in most double parallel tree rows of hollow plane trees that provide roost for this species. If bats are less aware of the danger of vehicles when engaging in social activity, or if social activity is a proxy for the presence of maternity roosts with naïve juveniles, it could explain the fact that bats were less cautious in avoiding vehicles in double parallel tree rows.~~ It seems difficult to provide a straight-forward explanation here, but the higher social activity of *N. leisleri* that we recorded at double parallel tree rows could be linked to less vehicle avoidance.

l. 547-553:
Nonetheless, *P. kuhlii/nathusii* avoided more the zone at collision risk when traffic increased, possibly because they recognise the danger associated with vehicles, although a specific data set would be required to test this hypothesis. Moreover, *P. pipistrellus* flew more often parallel and over the external sides of the road with increasing traffic. These results show that bats spatially avoid the vicinity of vehicles, completing the observations of Zurcher et al. (2010). The latter did not distinguish between species, but found that 60% of approaching individuals reversed their course in the presence of a vehicle. ~~In addition, it was shown that flying insect abundance decreases with increasing traffic (Martin et al., 2018). Reduced foraging opportunities might discourage bats from foraging over the road, concomitantly with a spatial avoidance of vehicles.~~

l.557-561:
It could be that because SRE fly lower and are more at risk when crossing (Roemer et al., 2017), they are more reluctant to approach vehicles. In addition, since the foraging abilities of SRE seem to be more impaired by light and noise than MRE (Siemers and Schaub, 2011, Stone et al., 2012, Azam et al., 2018), MRE might use roads as foraging grounds and take more risks than SRE.

It is true that we were not specific enough while discussing the management of vegetation as a means to reduce collisions. Because distance to foliage (correlated with tree height, and probably with primary productivity) led to a decrease in bat density for species from all three guilds, we are convinced that reducing foraging opportunities at roads by clearing roadside vegetation can be a relevant measure to reduce road collisions for most bat species. Hard edges explained the proportion of bats in the zone at collision risk mainly for mid-range echolocators and we were not specific enough on this point. We edited the paragraph accordingly:

> l.644-661:
> Our second recommendation applies to the management of roadside vegetation during construction work and during the operational phase, to reduce collision risks. A gap of five meters between the road edge and tree foliage significantly decreased the activity levels of several species across the three different guilds. Our appreciation of study sites suggests that this effect could be due to higher primary productivity when vegetation is higher and closer to the road. If less primary biomass is available to insects, foraging opportunities for bats decrease, and so does their density (Threlfall et al., 2012). It is however controversial to recommend cutting trees at road sides, because this decision will engender habitat loss in numerous taxa, especially in large-scale impacted areas such as linear transport infrastructures. Opening habitat at road edges also creates suitable foraging grounds for birds of prey for instance (Morelli et al., 2014), and will increase their collision probability. It is possible to make these open verges less attractive by converting them to gravel surface (Kociolek et al., 2015), but this will eliminate plant habitats. In our results, hard edges also led to higher rates of MRE in the zone at collision risk. Another possibility for the management of vegetation is thus to only cut a certain number of trees and clear shrub layers periodically (a frequent practice in French Mediterranean forests to prevent fires) to reduce primary production and to allow bats to navigate between trees rather than above the asphalt. The local management will thus depend on the biodiversity stakes of the area. In areas of high stakes, reducing vehicle speed limit could be an efficient solution, but this was not tested on bats to our knowledge.

Comment 10

Tables and Figures. I am not sure that the inset to Figure 1 is really necessary. All of the sampling sites are in the same biogeographic region – so just say that.

Reply to comment 10

We removed the inset, that was indeed not really necessary.

Comment 11

Tables 2-4 are very busy. I don’t have any good suggestions about how to make them better but there is a lot to take in.

Mark Brigham

Reply to comment 11

We do have the same impression, but we think that the information provided is still necessary.

I also had two of my students undertake independent reviews of the MS. Those reviews follow.

Student 1.

Overall, this study was well-conducted and contained interesting and valid data, particularly the three-dimensional call modeling. However, the main issue lies in a lack of clarity and cohesion in the writing. With this in mind, I suggest Roemer et al. make the following changes to their manuscript:

Comment 1

• Provide further justification for the study other than "no study provides an understanding" of the topic thus far (line 19).

Reply to comment 1

We changed this sentence according to the reviewer's suggestion:

> l.20-27:
> Moreover, when comparing the potential danger of different road sections, the most popular method today is the use of simple bat detectors to assess the local densities of current populations at road sites. Yet, it is not known to which extent bat behaviour influences collisions (i.e. bats flying at vehicle height or on the side or above, bats avoiding vehicles or not). Behaviour is very rarely taken into account in practice, and this might lead to hazardous site selections for mitigation. Our goals were thus (i) to estimate how local landscape characteristics affect each of the conditional events leading to collisions (i.e. bat presence, flight in the zone at collision risk and bat-vehicle co-occurrence), and (ii) to determine which of the conditional events most contributed to collisions risks.

Comment 2

• Include examples of the "many questions [that] remain concerning how local landscape features may influence bat behaviour" (line 18).

Reply to comment 2

We changed this sentence according to the reviewer's suggestion:

> l.17-20:
> High quality habitats particularly increase bat mortalities at roads, yet many questions remain concerning how local landscape features may influence bat behaviour and lead to high collision risks (e.g. influence of distance to trees, or of vegetation density).

Comment 3

• Address the discrepancy in the number of nights per site (line 128) and why visible moon percentage was not considered a criterion (line 165).

Reply to comment 3

We changed these sentences according to the reviewer's suggestion:

l.157-159:
Bat behaviour was recorded at 66 sites (Figure 1, supplementary table 1) at national or departmental roads, for a minimum of two nights per site, but recordings could continue up to five nights per site (mean = 2.6 nights +/- SD 0.9) depending on the schedule of the field worker and on battery strength.

l. 196-201:
Monitoring was performed exclusively during nights with optimal weather conditions for bat activity (temperature: mean = 20.6 +/- 6.5 °C, min = 8 °C, max = 34.9 °C; wind speed: mean = 7.5 +/- 8 km/h, min = 0 km/h, max = 31 km/h; cumulated rain per night: mean = 0.2 +/- 1.3 mm, min = 0 mm, max = 11 mm). However, the percentage of visible moon (mean = 49.2 +/- 35.8 %, min = 1 %, max = 99 %) was not a criterion we could control because of the time constrained field work schedule.

Comment 4

• Provide evidence to support the claim that "driver avoidance of collision is probably less important for smaller animals" (line 65).

Reply to comment 4

We removed this sentence since we have no evidence to support it, and since it is not really needed for the introduction.

Comment 5

• Define "tree essences" and how they differ (line 475).

Reply to comment 5

We changed "tree essence" for "tree species" for more clarity.

Comment 6

• Address issues of clarity and brevity in the writing. Certain phrases fail to translate well into English and result in disjointed sentences, such as "P. kuhlii/nathusii avoided more the zone at collision risk when traffic increased…" (lines 513-514) and "probably because bats have no choice but crossing the road closely in time to vehicle passes when traffic is high" (lines 522-523). Other issues with word order include "zone at collision risk" (lines 32-33) as opposed to "collision risk zone". In addition, there are several instances of verbose writing that would benefit from re-wording, such as "our study aimed at 1) assessing the effects of the characteristics of the local landscape on bat activity and movement behaviour and consequently on road collision risks" (lines 109-110).

• Verify that verb tenses are being used consistently, such as "local landscapes eliciting the highest proportion of flights at collision risk for this species were forests" (line 478).

• Proofread for typos prior to submission, such as missing conjunctions (line 47) and "a lesser extent" instead of "a lesser extend" (line 566).

Reply to comment 6

We asked a native English speaker to correct the grammar, so that the manuscript should be much easier to read now.

Student 2.

I want to begin by saying I am no expert on this topic and am just beginning my career in the field of scientific research but I hope my comments can help.

In my opinion, you collected an extensive amount of good data that indicates differences in the collision risks of bats based on a variety of variables. However, the quality of the study is undermined by lack of clarity and so much information that understanding and following the manuscript proved rather difficult.

Comment 1

In the abstract it is stated that sites were sampled for two full nights; in the methods it is indicated that sites were sampled for two to five nights; and ultimately the effect of seasonality on bat collision risks was investigated. The sampling schedule needs to be clarified and explained so readers can understand exactly how often and for how long sites were sampled. For example, if sites were sampled for only “two full nights”, how can seasonality be considered in the study? My guess is that you sampled sites for two to five nights with the total amount of time over those nights amounting to two full nights?

Reply to comment 1

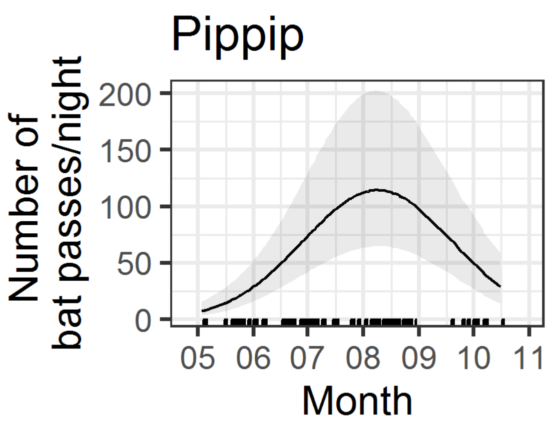
We agree that there were discrepancies in how we reported sampling between the abstract and the methods. We also should have provided more information about the timing of sampling. We completed these sentences according to the reviewer’s suggestion:

> l.28-30:
> In this study, we recorded bat activity and characterised flight behaviour with three variables: position at risk of collision, vehicle avoidance, and flight path orientation, using acoustic flight path tracking at 66 study sites in the Mediterranean region for two <u>to five</u> full nights.

> l.157-160:
> Bat behaviour was recorded at 66 sites (Figure 1, supplementary table 1) at national or departmental roads, <u>for a minimum of two nights per site, but recordings could continue up to five nights per site</u>

(mean = 2.6 nights +/- SD 0.9) depending on the schedule of the field worker and on battery strength. Sampling took place between the beginning of May and mid-October, depending on the study site.

In fact, when modelling a response variable in function of the time of the year using a Generalised Linear Mixed Model, it is not necessary to sample each night each study site. Since our sampling design was balanced for each of the explanatory variables (which were taken into account in the models), we could infer the general effect of seasonality on the response variables. To have a more precise idea of the sampling effort, please refer to the results for the density of any species in figure A2 and consider the ticks on the x axis, which represent the sampled nights:



Comment 2

I envy your efforts, the amount of data you collected, and the number of variables you considered; however, ultimately I think including this large a breadth of information all in one manuscript was not beneficial. There are simply too many variables and so much information covered that I had great difficulty following and understanding what the take home message was meant to be. Perhaps focusing on the local tree height and distance from the road and how they may influence the flight position of bats over roads would clear up the writing and improve the focus. I think a lot of really interesting information is lost amongst the large amount of text and I hope you consider revisiting the results section in particular to see if there is a clearer way of conveying your findings.

Reply to comment 2

We understand that this study is uncommonly complex in the number of models and variables tested. We could have simply modelled number of bat passes at risk of collision per night, but to find out why collisions occur precisely, we needed to decompose it into conditional events:

*Bat density * percentage of bats flying at vehicle height * percentage of bats present simultaneously with a vehicle.*

Our hypotheses were that some explicative variables would only influence bat density, while other explicative variables would only influence bat behaviour. It is important to understand how they contribute to the total collision risk. To do so, we multiplied each of the conditional events to obtain the number of bat passes at risk of collision per night (see figures A2 and A3). As we found out, density is the conditional event that most influences collision risks. This very important finding allows us to say in the discussion that surveys using simple passive recorders (the most popular method presently) can be sufficient in some contexts to provide a good estimate of collision risks at roads, but not in all contexts. We modified the following parts of the manuscript to make our approach clearer:

l.20-27:
(Abstract)
Roads impact bat populations through habitat loss and collisions. High quality habitats particularly increase bat mortalities at roads, yet many questions remain concerning how local landscape features may influence bat behaviour and lead to high collision risks. ~~Moreover, no study provides an understanding of the extent to which mortalities result from bat density on one hand and from bat flight behaviour on the other hand, which is required when designing risk mitigation measures~~. Moreover, when comparing the potential danger of different road sections, the most popular method today is the use of simple bat detectors to assess the local densities of current populations at road sites. Yet, it is not known to which extent bat behaviour influences collisions (i.e. bats flying at vehicle height or on the side or above, bats avoiding vehicles or not). Behaviour is very rarely taken into account in practice, and this might lead to hazardous site selections for mitigation. Our goals were thus (i) to estimate how local landscape characteristics affect each of the conditional events leading to collisions (i.e. bat presence, flight in the zone at collision risk and bat-vehicle co-occurrence), and (ii) to determine which of the conditional events most contributed to collisions risks.

l.110-125:
(Introduction)
Road collision risks in a species depend on (1) its local density, (2) the proportion of time spent in the zone at collision risk and (3) the simultaneous presence of bats and vehicles in the zone at collision risk (Jaeger et al., 2005; Zimmermann Teixeira et al., 2017). It is therefore necessary to take each of these variables into account when investigating road collisions. Indeed, when comparing two different road locations within different landscape features, a higher bat acoustic activity (used as a proxy of bat density) does not necessarily lead to a higher proportion of flights at risk of collision for all species (see Abbott et al., 2012). In addition, even if more individuals are at risk of collision (or if mortality is higher) at one site compared to another, this does not necessarily mean that this site should be selected for mitigation. Indeed, local populations can be dramatically reduced due to road mortality year after year, and a measure of per capita mortality risk is essential to correctly identify dangerous locations and avoid wrong recommendations for the siting of mitigation measures (Zimmermann Teixeira et al., 2017). Per capita mortality is also a very useful tool to prioritise conservation actions in function of the susceptibility of species to anthropogenic impacts. For instance, bats of the Nyctalus genus are particularly susceptible to wind turbine collisions because a high proportion of the individuals are victims of collisions (Roemer et al., 2017); to spare their populations, wind energy planning should therefore avoid areas where these species are extant.

Comment 3

There are a few occurrences of typos and poor grammar and I unfortunately cannot send a marked-up version of the manuscript because I could not edit the document but I do encourage a review of the manuscript to look at the sentence and grammar structure.

I applaud you for revealing the potential conflict of interest of Charlotte Roemer and Thierry Disca. I believe that is really respectable and good on you.

Reply to comment 3

We asked a native English speaker to correct the grammar, so the manuscript should be much easier to read now.

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