Road ecology: toward a predictive model of wildlife-vehicle collisions

Annaëlle Bénard

THESE de DOCTORAT DE
L'UNIVERSITE CLAUDE BERNARD LYON 1

Ecole Doctorale N° 341
ÉVOLUTION, ÉCOSYSTÈMES, MICROBIOLOGIE ET MODÉLISATION (E2M2)

Discipline : Écologie

Soutenue publiquement le 01/12/2023, par :
Annaëlle BÉNARD

Road ecology: toward a predictive model of wildlife-vehicle collisions

---

Devant le jury composé de :

GONZÁLEZ-SUÁREZ Manuela, Associate Professor, University of Reading	Rapportrice
JULLIARD Romain, DR CNRS, CESCO UMR 7204	Rapporteur
RODRIGUES Ana, DR CNRS, CEFE UMR 5175	Rapportrice
DESOUHANT Emmanuel, PU, Université Lyon 1	Président du jury
LOISON Anne, DR CNRS, LECA UMR 5553	Examinatrice
LENGAGNE Thierry, CR CNRS, LEHNA UMR 5023	Directeur de thèse
BONENFANT Christophe, CR CNRS, LBBE UMR 5558	Co-directeur de thèse

Table of Contents

REMERCIEMENTS

Après 3 années passées sur les routes d'Auvergne-Rhône-Alpes, à traquer le moindre animal écrasé, à grimper dans les arbres pour y poser des pièges photos, à transporter des chevreuils morts à travers le campus, je suis enfin en mesure de pouvoir me poser et faire le point. Ces années ont été formatrices, riches en rencontres, en science, et en découvertes.

Je remercie tout d'abord les rapporteurs qui a accepté de relire ce manuscrit : Drs. Julliard, González-Suárez et Rodrigues, mais aussi mes examinateurs, Drs. Desouhant et Loison. À l'heure où j'écris ces mots, nous ne nous sommes pas encore rencontrés, mais je tiens à vous remercier de l'intérêt que vous m'avez témoigné lorsque je vous ai contactés. J'espère que vous vous apprécierez ce manuscrit, et que vos rêves ne seront pas hantés par des visions d'animaux écrasés sur les routes.

I would like to start by thanking the referees who agreed to review this manuscript: Drs. Julliard, González-Suárez and Rodrigues, but also my examiners, Drs. Desouhant and Loison. As I write these words, we haven't yet met, but I'd like to thank you for the interest you showed when I first contacted you. I hope you enjoy this manuscript, and that your future dreams aren't haunted by visions of animals crushed on roads.

Je remercie infiniment mes directeurs de thèse qui m'ont encadrée et épaulée tout au long de cette thèse.

Thierry, pour ton enthousiasme débordant, ton savoir-faire et ta bonne humeur, je te remercie de m'avoir soutenue comme tu l'as fait. Je suis toujours époustouflée par ta capacité à imaginer des expériences et méthodologies qui ont rendu ce travail possible, et par ta volonté de m'accompagner sur le terrain par des températures négatives pour traîner des buses mortes sur la chaussée pendant plusieurs heures.

Christophe, pour ta rigueur scientifique, ton encadrement qui m'a beaucoup fait évoluer en tant que jeune chercheuse, et pour m'avoir aidée à surmonter bien des épreuves. Je te dois également beaucoup pour avoir impulsé plusieurs collaborations scientifiques, bien que celles-ci ne figurent pas dans ce manuscrit. Merci également de m'avoir accompagnée à la gendarmerie, ce qui m'a permis de repartir non seulement avec un piège photo mais aussi un casier judiciaire vierge.

Un immense merci également à toutes les personnes qui se sont impliquées de près ou de loin dans ce projet : Julien Girard-Claudon, pour ta réactivité et ta maîtrise sans faille de la base de données, je regrette que l'on n'ai pu se rencontrer face à face que si tard. Maudit Covid :) !

À l'ensemble de la LPO de l'Ain, et notamment son directeur Francisque Bulliffon, ainsi que Alexandre Roux et Emilie Müller qui se sont personnellement impliqués dans ce projet. Également, je remercie les LPO des autres départements, dont les présidents Louis Granier et Patrick Balluet, qui ont rendu possible certaines de ces expériences. Enfin, je remercie chaleureusement la LPO Auvergne-Rhône-Alpes, et en particulier Marie-Paule De Thiersant (présidente) ainsi que Sébastien Teyssier (directeur), qui se sont impliqués et s'impliquent encore pour m'aider à valoriser cette base de données unique et prometteuse. Merci d'avoir cru et de croire encore en ce projet !

Bien que je ne puisse pas vous citer pour des raisons éthiques, je remercie du fond du coeur tous les bénévoles qui ont répondu présent pour participer aux expériences de cette thèse. Ce sont des personnes comme vous, prêtes à donner de leur temps, qui rendent les sciences participatives possibles. Vous avez été nombreux à répondre à l'appel, et à vous déplacer, parfois plusieurs fois par jour, pour effectuer les différentes missions. Vos efforts sont précieux, et j'espère que ce manuscrit leur rendra justice. Je me permet tout de même de citer C. Guyard et O. Chevreuil qui ont fourni un effort remarquable, valorisé dans le second chapitre de ce manuscrit. Je remercie en particulier Maurice Benmergui, qui m'a en plus aidée à recruter des volontaires, toujours dans la bonne humeur !

Pour continuer sur le sujet du bénévolat, je remercie tout particulièrement l'équipe du Tichodrome, centre de soins pour faune sauvage de l'Isère, qui a accepté de collaborer avec nous sur ce projet. Vous avez répondu à l'appel et vous êtes pliés à nos exigeances pour trier les espèces, malgré la charge de travail que cela vous a demandé. Aucune des expériences de ce projet n'aurait été possible sans vous, et je reverserai une partie de la cagnotte de ma thèse à votre refuge.

Je remercie le SR3A, et en particulier Emilie Genelot, pour le soutien financier, mais aussi technique que vous m'avez apporté. Cette convention de recherche aura été longue à finaliser, mais nous y sommes arrivés !

Bien sûr, que seraient les remerciements d'une thèse sans parler de mes collègues !
Caro, Loïc, Yann, Damien, FX, Nathalie, Adeline, Anne, Louise, l'ensemble de l'équipe E2C, pour votre bonne humeur, les conversations du midi, pour les boites de haribos qui apparaissent soudainement dans le bureau, pour les ballons, les croissants, les petits gâteaux, et le canapé ! Je remercie également Vanessa, qui a accepté de m'accompagner sur le terrain pour traîner des renards morts sur la route (vous remarquerez qu'il y a un thème dans ces remerciements). L'ensemble des membres du LEHNA, les doctorants, le secrétariat, et notamment Nadine qui a su d'un coup de téléphone régler ce sur quoi nous nous cassions les dents depuis des mois. J'ai également une pensée pour l'équipe pédagogique ainsi que Gisèle et Gaëlle qui m'ont épaulée lors de mes premiers pas en tant qu'enseignante.

Vous me voyez venir, je réserve une place toute particulière à vous, les andouilles du bureau. Julia et Chloé, j'espère que l'on aura l'occasion de continuer à cohabiter. Vous allez mener des thèses brillantes, et n'oubliez pas de vous amuser !
À Aude, que j'ai eu beaucoup de plaisir à rencontrer. Je te souhaite tout le meilleur pour la suite de ta vie professionnelle et personnelle, n'écoute que toi et trace ta route.
Julien, je regrette que tu n'aies pas commencé la thèse plus tôt car nous étions fais pour nous entendre. Ton enthousiasme est une bouée dans la tempête, contrebalancé seuleument par tes capacités de survie en milieu urbain. Je sais que nous ne perdrons pas contact, mais au cas où, fais attention aux trams.

Jessica et Ambre, je n'ai rien à écrire que vous ne sachiez pas déjà. Je n'aurais pas pu traverser ces trois années sans vous à mes côtés, et je nous imagine ridées et cheveux gris dans un bois quelque part à faire brûler des sortilèges. Je n'ai pas les mots pour décrire à quel point je suis heureuse que le hasard nous ai fait nous rencontrer (pour la deuxième fois pour Ambre, comme quoi des fois, il faut insister).

Merci à ma famille, Baptiste, ma mère, et mon père sans qui ma petite voiture n'aurait jamais fait le trajet jusqu'à Lyon sans me lâcher sur l'autoroute. Merci de m'avoir encouragée à suivre mes envies et mes rêves, et de m'avoir apporté tout ce qu'il faut pour réussir. J'ai une pensée particulière pour mon défunt grand-père, Michel Bénard, pour les souvenirs, pour la passion et l'émerveillement constant du monde qui nous entoure que tu as su transmettre à ton fils, ainsi qu'à moi. Mamie, si tu lis ces mots, ce manuscrit de thèse vous est dédié.

Je termine ces remerciements en mentionnant Anna, Inès, Cécile, Marie et Héloïse, Edern, Léna, et tous.tes les ami.e.s que j'ai pu rencontrer au cours de ma vie et au détour de mes études.
J'espère que vous ferez toujours partie de ma vie.

Ce projet n'aurait pas été possible sans l'appui scientifique et technique de la
This project would not have been possible without the scientific and technical support of the

Ligue de Protection des Oiseaux de la région Auvergne-Rhône-Alpes

Je remercie en particuller mon co-encadrant Julien GIRARD-CLAUDON pour le soutien apporté tout au long de cette thèse.
I would particularly like to thank my co-supervisor Julien GIRARD-CLAUDON for his unfailing support throughout this thesis.

Le contrat doctoral ministériel à l'origine de ce projet a été accordé par l'École Doctorale E2M2.
This doctoral contract, funded by the ministry, was granted by the doctoral school E2M2.

Les travaux présentés ici ont été en partie financés par le Syndicat de la Rivière d'Ain Aval et de ses Affluents
The work presented was partly funded by the Syndicat de la Rivière d'Ain Aval et de ses Affluents

Ainsi que par le Centre de ressources pour les sciences de l'évolution de l'Université Claude Bernard Lyon 1.
As well as the Centre de ressources pour les sciences de l'évolution of the Claude Bernard Lyon 1 University.

RÉSUMÉ

Les infrastructures linéaires de transport font peser de nombreuses pressions sur les écosystèmes. Selon le dernier rapport de l'IPBES, on peut attribuer le déclin actuel de la biodiversité à quatre grandes causes majeures : la destruction des habitats, leur dégradation par de la pollution d'origine humaine, l'arrivée d'espèces étrangères invasives dans les milieux, et l'exploitation directe des espèces animales et végétales. Or, lorsque l'on étudie une route, chacune de ces causes est représentée. Bien sûr, la construction d'une route empiète sur les habitats naturels des espèces sauvages, mais au-delà du goudron, la présence d'une route a de nombreux impacts sur un écosystème : pollution aux métaux lourds, hydrocarbures, gaz à effet de serre, mais également pollution sonore et lumineuse. Cette pollution peut conduire les populations à éviter les bords de routes, laissant parfois jusqu'à plusieurs kilomètres de zone tampon. Les habitats proches des routes sont alors des habitats dégradés, qui ne sont propices ni à la présence, ni à la reproduction des espèces. La qualité amoindrie des habitats, en particulier des bords de routes, est en revanche profitable à l'établissement et la propagation d'espèces invasives, généralement plus résilientes que les espèces natives. Les véhicules eux-mêmes peuvent participer à la dispersion de graines ou d'espèces animales, et les routes sont des couloirs de dispersion parfaits pour des espèces invasives qui ont besoin de surfaces sans obstacles pour se déplacer. Pour finir, les collisions entre faune sauvage et véhicules sont une source de mortalité représentant un prélèvement direct d'individus dans les populations sauvages. Cette mortalité, en s'ajoutant au reste des pressions générées par l'activité humaine, peut mettre en péril la survie de nombreuses espèces.

Il apparaît donc crucial de pouvoir quantifier les pertes occasionnées par les collisions, ainsi que de savoir les prédire dans le temps et dans l'espace. Grâce à ces informations, il est possible de mettre en place des mesures de réduction, telles que des ponts, passages couverts, ou bien la fermeture temporaire de certains axes. De plus, il y a un intérêt scientifique à comprendre le fonctionnement du phénomène des collisions : les réseaux routiers sont de très bons modèles d'étude pour mieux comprendre les relations entre les activités humaines et la biodiversité, et notamment comment les nouvelles pressions évolutives générées peuvent modifier les écosystèmes sur le long terme. La communauté scientifique étudie depuis longtemps le phénomène des collisions. Cependant, devant la difficulté de surveiller l'ensemble des infrastructures de manière régulière, nous ne pouvons donner que quelques estimations de la mortalité, qui se chiffrerait à plusieurs centaines de millions d'écrasements annuellement à l'échelle européenne. Depuis une décennie, de nombreux projets collaboratifs de surveillance des collisions font leur apparition dans le monde : les utilisateurs de la route sont mis à contribution pour reporter eux-mêmes les animaux écrasés rencontrés sur les routes. Malgré cet engouement, les données collaboratives

sont plus difficiles à exploiter que celles générées lors d'expériences scientifiques protocolées, et leur utilisation n'est pour le moment que marginale dans les publications scientifiques.

Cette thèse s'articule autour de trois grands axes. Tout d'abord, en partant du constat que la plupart des interactions identifiées entre les caractéristiques des paysages, la biologie des espèces, les facteurs temporels et la survenue de collisions, il apparaît que le déplacement des animaux est probablement le mécanisme sous-jacent le plus proéminent de la mortalité routière. Le premier axe de cette thèse (chapitre 1) propose un modèle mécaniste, c'est-à-dire basé sur une modélisation mathématique sans apport de données réelles, qui replace le mouvement des animaux et des véhicules au centre du système. Nous démontrons de manière formelle que certains prédicteurs pressentis, tels que le trafic routier ou le mode de déplacement des animaux, ont un réel lien de cause à effet avec les collisions. En revanche, d'autres prédicteurs, comme la vitesse des véhicules, n'impactent pas beaucoup les risques de collision. Pour finir, nous avons effectué une analyse de sensibilité du modèle, qui nous a permis d'identifier les paramètres clés pour lesquels de petites variations ont le pouvoir de réduire considérablement le nombre de morts sur les routes. Il ressort de cette analyse que toute la compréhension des collisions routières doit s'articuler autour de la question du déplacement des animaux, qui explique la majeure partie des variations dans les risques d'écrasement.

La seconde partie de cette thèse (chapitres 2, 3 et 4) se penche sur la question de la collecte des données de collision. Nous avons travaillé à partir d'un modèle conceptuel représentant les différentes étapes du signalement d'un animal écrasé dans un projet collaboratif : l'animal écrasé doit rester en place assez longtemps pour permettre le passage d'une personne qui participe au projet collaboratif, puis doit être détecté par cette personne, et enfin, doit être effectivement signalé. Le chapitre 2 se penche sur la question du temps de persistance des carcasses animales sur les routes, qui est un aspect crucial des projets de report collaboratifs aussi bien que des comptages protocolés plus traditionnels. Nous avons estimé, par intervalles de deux heures, le temps de disparition des petites carcasses d'amphibiens et de passereaux. Si le temps de disparition d'un passereau, estimé à environ 20 minutes, n'est pas modifié par la pluie ou par le trafic de la route, la disparition des amphibiens est largement dépendante du nombre de véhicules passant sur la route : la disparition moyenne peut survenir entre 1h et 18h après la collision. Au cours d'une seconde expérience, nous avons suivi la disparition d'un grand nombre d'oiseaux et de mammifères, au moyen de pièges photographiques qui se déclenchent au mouvement. Nous étudions en particulier les interactions entre la cause de la disparition et deux prédicteurs potentiels du temps de persistance : le poids de l'espèce et le volume de trafic. Les animaux disparaissaient de la route selon deux mécanismes principaux, soit l'écrasement répété par les pneus (plutôt lié aux petites espèces tuées sur des axes avec un fort trafic), soit le déplacement volontaire de l'animal par une personne (plutôt lié

aux gros animaux sur les petites routes). Il apparaît cependant que le temps de disparation n'est pas dépendant du poids de l'animal, ou du trafic, ce qui nous permet de tirer un seul et unique estimateur de la persistance pour ces espèces : suivant la collision, l'animal ne restera visible qu'en moyenne 10 heures. Un cas d'étude est également présenté à la fin de ce chapitre. Nous y expérimentons une nouvelle méthodologie pour étudier la disparition des animaux suite à la collision, en se reposant sur la participation de collaborateurs volontaires. Cette expérience permet de confirmer les résultats obtenus précédemment, et nous encourageons les scientifiques à développer ce type d'approche pour améliorer la précision des estimateurs de persistance, qui sont nécessaires pour développer ensuite des estimations de la mortalité routière.

Les chapitres 3 et 4 se penchent sur les sciences participatives et en particulier la base de données de collisions constituée via le portail Faune-Auvergne-Rhône-Alpes, qui compte près de 100 000 signalements d'animaux retrouvés morts sur les routes de la région. De part sa taille, cette base est l'une des plus importantes au niveau mondial. Nous étudions d'abord l'efficacité de détection des conducteurs, en comparant notamment la probabilité de détection d'un animal mort lorsque le conducteur est activement à la recherche de carcasses à celle d'un conducteur qui ne l'est pas. Nous démontrons que la détection d'un animal est conditionnelle à sa taille, son espèce, mais aussi que les conducteurs qui ne sont pas en recherche active détectent 34 fois moins de carcasses. Ces résultats ont de fortes implications pour les projets collaboratifs : en effet, dans ces projets, les contributeurs ne conduisent pas uniquement pour relever les écrasements, à la différence des comptages routiers menés par des chercheurs. Pour finir, nous proposons dans le chapitre 4 une méthodologie innovante pour calculer le taux de signalement des animaux repérés dans le projet Faune-Auvergne-Rhône-Alpes. À l'aide de fausses carcasses placées sur les routes, de questionnaires semi-dirigés, et d'un modèle mathématique basé sur une chaine de Markov, nous démontrons formellement et pour la première fois dans la littérature que l'effort de signalement dans les projets collaboratifs n'est pas égal au nombre d'animaux détectés. Ce résultat, obtenu ici dans la cadre du signalement collaboratif des collisions routières, s'étend probablement à l'ensemble des projets collaboratifs pour reporter la présence de tous types d'espèces animales. Cependant, s'agissant d'une expérience préliminaire, nous ne sommes pas en mesure de fournir des estimations très précises de ce taux de signalement : il pourrait se situer entre 5 % et 72 % pour Faune-Auvergne-Rhône-Alpes, avec une proportion moyenne estimée à 33 %. L'amélioration du traitement mathématique des données devrait permettre de fournir des résultats plus précis.

Le dernier axe de cette thèse se penche sur l'application directe des résultats obtenus pour transformer les signalements d'écrasements de la faune présents dans Faune-Auvergne-Rhône-Alpes en estimations de la mortalité réelle dans la région. À titre d'exemple, nous estimons le nombre de collisions pour certaines

espèces : la buse variable *Buteo buteo*, le renard roux *Vulpes vulpes*, l'écureuil roux *Sciurus vulgaris*, et enfin, les petits passereaux (mésanges, moineaux…). Grâce aux estimateurs obtenus précédemment, nous estimons que 800 000 passereaux sont morts sur les routes de la région en 2022, soit un taux de 10 collisions par km² et par an. Pour le renard, ce serait 6500 cas de collisions en 2022, soit 0,1 renard par km². Les populations d'écureuils auraient perdu 9000 individus sous les roues des voitures (0,13/km²/an) et les buses, 1600 individus (soit 0,02/km²/an). Cette mortalité, qui est entièrement d'origine humaine, vient s'additionner à la mortalité naturelle ainsi qu'aux autres pressions anthropiques qui pèsent sur les populations. Elle peut donc avoir des conséquences catastrophiques sur la survie à long terme des populations sauvages de la région.

Les travaux présentés sont innovants par biens des points : nous proposons de nouvelles méthodologies pour étudier les collisions, et pour mettre en valeur les base de données de signalements participatifs des collisions existantes. L'étude et la valorisation des projets de sciences participatives est un cercle vertueux, car la valorisation rigoureuse de ces données contribue à l'avancement de l'état des connaissances scientifiques, ce qui valorise le travail des contributeurs bénévoles et permet d'impulser de nouveaux projets touchant à d'autres domaines des sciences. Le cadre théorique apporté par le premier chapitre de cette thèse permet d'orienter les futurs efforts de recherche dans le domaine de l'écologie des routes. En effet, le modèle mécaniste que nous avons construit fournit une base de travail pour comprendre le phénomène des collisions, et donne des pistes concrètes pour modéliser de manière efficace les données de collisions telles que celles présentes sur le portail Faune-Auvergne-Rhône-Alpes. La synergie de ces deux approches, l'une basée sur la théorie et l'autre sur les données empiriques, est la piste la plus prometteuse pour arriver, à terme, à un modèle prédictif des risques de collision entre véhicules et faune sauvage.

SUMMARY

Linear transport infrastructures have substantial effects on ecosystems. According to the latest IPBES report, the current decline in biodiversity can be attributed to four major causes: habitat loss, their decline in quality, invasive alien species, and the direct exploitation of animals and plants. Roads represent each of these causes. This thesis focuses specifically on collisions between wildlife and vehicles, which is a direct source of mortality for wildlife. This mortality, in addition to other pressures generated by human activity, can jeopardize the survival of many species. It is therefore crucial to be able to quantify the losses caused by collisions, and predict them both in time and space. Beyond the pragmatic need to reduce these collisions through means such as wildlife crossing structures, there is scientific value in understanding how the wildlife-vehicle collision system works: road networks are excellent models for studying the relationship between human activities and biodiversity, and in particular how the new evolutionary pressures generated can modify ecosystems in the long term. Given the difficulty of monitoring all roads on a regular basis, there are few estimates available for the magnitude of this mortality which is nevertheless estimated at several hundred million deaths per year in Europe. Collision monitoring projects based on citizen science are gaining traction in many countries: road users are asked to contribute their own reports of animal carcasses encountered on roads. However, citizen science data is more difficult to exploit than data generated through standardized scientific surveys, and is currently under-exploited in scientific publications.

This thesis is structured around three main objectives. Chapter 1 presents a mechanistic model that places animal and vehicle movement at the center of the wildlife-vehicle collisions system. We formally demonstrate causal links between certain predictors, such as road traffic or animal movement, and collision risks. A sensitivity analysis shows that wildlife-vehicle collisions research should center around movement ecology paradigms, as animal trajectories explained the major part of the variations in collision risks. Chapters 2, 3 and 4 contain an in-depth analysis of the roadkill data collection process. Each of the steps involved in reporting roadkill is addressed: roadkill persistence on road, detection rates by drivers, and reporting rates of detected roadkill in the context of citizen sciences. Carcass persistence, crucial to both citizen science projects and standardized surveys, was estimated for amphibians, birds, and mammals. In, addition, we investigated the effects of rainfall, traffic volume and body mass on persistence. A case study is also included at the conclusion of this chapter, where we introduce a novel approach for conducting roadkill persistence studies using citizen science, and validate prior findings.

Chapters 3 and 4 look at citizen science through the Faune-Auvergne-Rhône-Alpes reporting project, which has currently accumulated over 100 000 reports. We first study the search efficiency of drivers in the context of opportunistic reporting of roadkill, and find it to be 34 times less than during standardized surveys, which has major implications for citizen science projects. Chapter 4 presents an innovative methodology for estimating the reporting rate of animals spotted on the road to Faune-Auvergne-Rhône-Alpes. Using roadkill decoys, semi-directed interviews, and a Markov chain model, we demonstrate formally and for the first time in the literature that the reporting effort in opportunistic monitoring projects is not equal to the number of animals detected. This result has major implications for all biodiversity monitoring projects based on citizen science. The final objective of this thesis was to provide direct applications of the results obtained, and convert Faune-Auvergne-Rhône-Alpes reports of wildlife mortality on roads into estimates of the number of collisions in the region for select species.

This manuscript contains new methodologies for studying wildlife-vehicle collisions and leveraging existing databases of collision reports. The rigorous use of citizen science data contributes to advancing scientific knowledge, which in turn recognizes the valuable work of volunteer contributors, and drives new projects in other scientific fields. The theoretical framework presented in the first chapter of this thesis provides guidance for future research efforts in the field of road ecology: the mechanistic model we have developed serves as a foundation for understanding the collision system and offers practical approaches for statistical modelling of collision data, such as citizen science data. The combination of these two approaches, one rooted in theory and the other relying on robust empirical data, holds great promise for ultimately developing a comprehensive predictive model of the risk of collision between vehicles and wildlife.

Introduction

“ IN PUSHING OTHER SPECIES TO EXTINCTION, HUMANITY IS BUSY SAWING OFF THE LIMB ON WHICH IT PERCHES.” Paul Ehrlich[1]

1. The importance of roads in ecology and conservation

As I write these words, the world is experiencing its hottest month ever at the global scale (Copernicus, 2023). Human activities have significantly impacted the Earth's ecosystem, limiting the ability of ecosystems to provide services that are essential to our survival (Lafortezza & Chen, 2016). One major consequence of humanity’s actions is the Holocene extinction, a mass extinction event projected to lead to the extinction of approximately one million species within the next decade (IPBES, 2019). The IPBES has identified the global factors contributing to the current loss of biodiversity: changes in land use, pollution of the air, water, and soil, invasions by non-native species, and the direct exploitation of wildlife. These factors are all notably embodied by the terrestrial transportation network, comprising both roads and railroads.

Our transportation systems have a significant impact on greenhouse gas emissions, accounting for 25% of overall emissions in Europe (European Environment Agency, 2019). However, it is important to recognize that roads themselves also have pervasive effects on the surrounding natural environment: they have numerous impacts on ecosystems, spanning from altering erosion patterns to directly influencing the behaviour of species (Spellerberg, 1998). In France, roads cover over 1 million kilometers, occupying 2% of the total area and are used in 72% of travels (Ministère de la Transition Écologique, 2020). Globally, the estimated length of roads, which currently stands at 21 million kilometers, is projected to increase by up to 23% in the next two decades (Meijer et al., 2018). With roads being so prevalent, and their significant influence on our ecosystems, it is not surprising that Harvard landscape ecologist Richard Forman referred to them as the “sleeping giants” of environmental sciences. The term “Road Ecology[2]” was therefore proposed to unify the previously disconnected understanding of the various ecological effects of roads into a cohesive framework (Forman & Alexander, 1998).

---

1 This quote appears in the Hall of Biodiversity of the American Museum of Natural History, NYC, USA.

2 Often attributed to Forman, the first mention of this term in the literature can be found in Walper *et al.* (1981) according to van der Ree *et al.* (2011)

Ecological effects of the road network

In the last *global assessment report on biodiversity and ecosystem services* (2019), the IPBES lists changes in land use, pollution, invasive alien species and direct exploitation of the natural resources as major drivers of the current decline in biodiversity. By demonstrating each of these drivers, the road network serves as an exemplary representation of anthropogenic change (Spellerberg, 1998). Naturally, a road's surface does not provide a hospitable habitat for species. Although the construction of a road leads to a seemingly small loss of square footage, a highway can still occupy up to 0.1km² per kilometer of road (Seiler, 2001). As a point of reference, the French road network covers a total of 10,300 km², and this network covers 81,000km² in the United States (Carr et al., 2002). However, it would be incorrect to assume that the loss and degradation of habitats is only limited to the physical presence of roads. For example, the presence of roads affects the patterns of soil erosion and thus modifies the geomorphic and hydrological settings of landscapes (Shi et al., 2008; Valentin et al., 2005). Unpaved roads in particular erode at a faster rate than the surrounding areas, and the eroded materials can directly enter water streams (Fu et al., 2010; Reid & Dunne, 1984), posing a threat to the persistence of wildlife by altering the physical and chemical properties of the water column (Ellis, 1936). Wind erosion of roads also leads to the release of dust into the atmosphere (Středová et al., 2021; Yulevitch et al., 2020), causing significant negative impacts on human health, climate, and ecosystems (Walker & Everett, 1987).

Furthermore, road traffic generates both acoustic and light pollution, significantly diminishing the overall quality of the surrounding habitats (Seiler, 2001). Road surfaces often contain residues of gasoline, oil, and heavy metals all stemming from engines, fuel consumption, brake pads and tires. These substances are then deposited on the sides of roads and can be transported to the surrounding habitat through water runoff (Deletic & Orr, 2005). Consequently, the physico-chemical properties of road-adjacent habitats are altered, usually exhibiting elevated levels of lead, cadmium, copper, zinc, and nickel, all of which originate from vehicular traffic (Timothy & Tagui Williams, 2019). Additionally, polluted road water runoff can enter nearby freshwater systems with devastating impacts on the organisms (Dugan & Arnott, 2023).

Multiple authors have explored the concept of “road-effect zones”, which refers to the area of the habitat that is directly ecologically impacted by the presence of a road (Forman & Alexander, 1998). Early research has shown that the density and reproductive success of bird populations can be negatively affected up to 3km on both sides of major roads, likely due to the noise and pollution generated by traffic (Forman et al., 2002; Reijnen et al., 1995). In general, the destruction and degradation of habitats contribute to a decrease in species richness, reproductive success, immunity, and genetic diversity in populations and communities of amphibians (Eigenbrod et al., 2009; Lesbarrères et al., 2003; Semlitsch

et al., 2007; Tennessen et al., 2014), large mammals (Newmark et al., 1996; Shanley & Pyare, 2011), birds (Crino et al., 2013; Kroeger et al., 2022) and reptiles (Boarman & Sazaki, 2006) in proximity to roads.

Roads are also perhaps the most compelling visual representation of landscape fragmentation (fig. 1). The fragmentation of landscapes has been identified as one of the most significant drivers of biodiversity loss and poses a significant threat to the survival of plant and animal communities alike (Aguilar et al., 2019; Kuipers et al., 2019). Roads fragment landscapes by creating barriers to movement and dispersal. This barrier effect can be attributed to the inhospitable nature of road surfaces, fencing, the volume of traffic leading to high levels of noise and disturbance, light and chemical pollution, as well as the direct mortality caused by animal-vehicle collisions (Jacobson et al., 2016; Jaeger et al., 2005; Lesbarrères & Fahrig, 2012). Consequently, the presence of roads has the potential to diminish the connectivity of landscapes, thus impeding gene flows between populations (Garcia-Gonzalez et al., 2012; Keller & Largiadèr, 2003; Riley et al., 2006; but see Prunier et al., 2014) and compromising their persistence (Couvet, 2002).

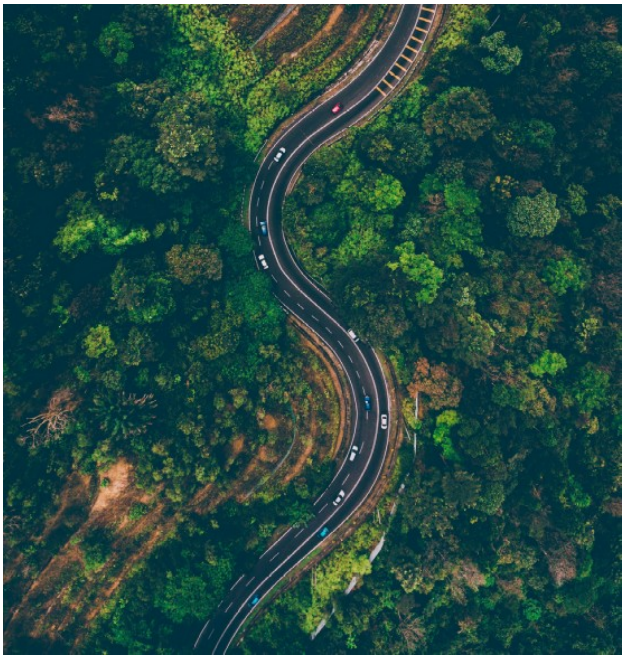


Fig. 1: Roads provide compelling visual representations of landscape fragmentation, which is recognized as one of the major contributors to the current decline in biodiversity.

Credit: Deva Darshan.

Paradoxically, while roads hinder the dispersal of many species, they can also facilitate the dispersal of others. The vegetation along road verges can support biodiversity (Rotholz & Mandelik, 2013), but these habitats are polluted by heavy metals and gasoline residue and tend to be particularly favorable to invasive and non-native species, which use roads as corridors for dispersal (Nunes et al., 2020; Padmanaba & Sheil, 2014). This dispersal is further enhanced by seeds hitching a ride on car tires and exteriors (Ansong & Pickering, 2013). This phenomenon is not exclusive to flora, as invasive animal species also use roads and road verges as dispersal corridors, taking advantage of the low or lack of vegetation to move freely (*e.g.*, cane toad *Rhinella marina*: Brown et al., 2006) or being transported by

vehicles (*e.g.*, ant *Lasius neglectus:* Gippet et al., 2015; Asian tiger mosquito *Aedes albopictus*: Miller & Loaiza, 2015).

Roads also have documented positive impacts, such as providing shelter for various species of small mammals and arthropods, leading to the formation of unique communities at the road level (Rotholz & Mandelik, 2013). Road surfaces can also serve as basking areas for reptiles (Meek, 2009), and as foraging grounds for carrion-feeders consuming roadkill (Schwartz et al., 2018). However, the occurrence of wildlife in close proximity to roads as well as behaviours that result in animals coming into contact with the road surface, such as basking and scavenging, have the potential to increase the risks of collisions between wildlife and vehicles (Coleman et al., 2008; González-Suárez et al., 2018; Meek, 2009; Slater et al., 2022).

2. A closer look at wildlife-vehicle collisions (WVC)

2.1. The toll of road traffic collisions with wildlife

Encountering animal carcasses resulting from collisions with vehicles is a universal experience among car drivers, but the ecological consequences of this anthropogenic source of mortality remain uncertain. Road mortality is established as a significant source of mortality for many terrestrial species (amphibians: Hels & Buchwald, 2001; Schmidt & Zumbach, 2008; mammals: Moore et al., 2020, Seiler 2004, reptiles: Selvan, 2012; birds: Loss et al., 2014; see Hill et al., 2019 for a comprehensive review). Current large-scale estimates for road mortality in birds and mammals stand at respectively 29 million and 192 million each year on European roads (Grilo et al., 2020), 8 million and 2 million in Brazil (González-Suárez et al., 2018). Loss et al. (2014) estimated between 89 and 340 million annual bird roadkill for the United States. In addition, an estimated 0.2 million reptiles and 1 million amphibians die in road traffic annually in Finland (Manneri, 2002). Although the magnitude of these estimates is substantial, their relevance to the long-term survival of populations requires to take into consideration the populations' sizes, which may not always be known at such large scales.

At smaller scales, studies using bio-logging to follow the movements of select individuals in a population can help provide figures regarding the relative impact of road mortality within wild populations. The proportion of the population lost to road mortality over the course of a study ranged from less than 1% in the Eurasian otter *Lutra lutra* (Balčiauskas, 2012) and least weasel *Mustela nivalis* (Sidorovich, 2020), to 1%-10% in the amphibians *Rana temporaria, Rana arvalis* and *Pelobates fuscus (*Hels & Buchwald, 2001), and the European polecat *Mustela putorius* (Sidorovich, 2020), red squirrel *Sciurus vulgaris* (Fey et al., 2016), European hedgehog *Erinaceus europaeus* (Bearman-Brown et al., 2020) and elk *Cervus canadensis* (DeVivo et al., 2011). In some studies, the estimated proportion of the population lost to road collisions even climbed over 10% of the study sample: coyotes *Canis latrans (*Stevenson et al., 2016), woodchucks *Marmota monax* (Lehrer et al., 2012), European hares *Lepus europaeus* (Cukor et al., 2018) and bobcats *Lynx rufus* (Serieys et al., 2021).

Yet, despite these sometimes alarming numbers, the implications of road mortality on the demography of populations are still in question. Recently published reviews highlight the current lack of knowledge surrounding the long-term effects of roadkill on wild species (Barrientos et al., 2021; Moore et al., 2023). Moreover, roadkill can be selective, with dispersing or less experienced individuals being often more vulnerable to collisions. For example, Burgstahler et al. (2023) found higher incidences of road mortality among female ground squirrels *Callospermophilus lateralis*, which may be attributed to their heightened activity levels during the summer season, and inexperienced juvenile Florida scrub jays *Aphelocoma coerulescens* were also more often killed by vehicles than adults in Mumme et al. (2000). In consequence, sex ratios and age structures found in roadkill may differ from the general population (Moore et al., 2023), with possible detrimental effects on the persistence of populations even when the overall road mortality rate is low (Baker et al., 2007; Burgstahler et al., 2023; Ryu & Kim, 2021).

2.2. Is roadkill inevitable?

When confronted with the ecological consequences of wildlife mortality caused by vehicle collisions, the next natural steps are to attempt to minimize this issue. There is an extensive literature dedicated to exploring and evaluating roadkill mitigation measures. Among the commonly employed approaches, we find non-disruptive and seemingly cost-effective methods such as wildlife warning reflectors and repellents (Gladfelter, 1984). Reflectors are designed to reflect the headlights of approaching vehicles, thus scaring animals away from the road. However, several studies have indicated that these reflectors are not associated to decreased roadkill rates (Benten et al., 2018; Brieger et al., 2022). Acoustic and olfactory repellents are sometimes placed in the vicinity of roads, but also demonstrate little effectiveness in mitigating road mortality (Bíl, Kušta, et al., 2020; Coulson et al., 2019; Grilo et al., 2010, but see Balčiauskas & Jasiulionis, 2012).

Traffic-calming refers to a collection of techniques primarily aimed at decreasing traffic speeds and volumes through strategies such as urban planning, strict speed limits, and the use of various devices such as chicanes, signage, and rumble strips. The implementation of traffic-calming measures has been suggested in the context of roadkill prevention (Jaarsma, 1997). Road signage for the presence of wildlife, occasionally augmented with flashing lights, may have limited effectiveness in altering driver behaviour and reducing roadkill incidents (Pojar et al., 1975; Seburn & McCurdy-Adams, 2019, but see Collinson et al., 2019). The other traffic-calming measures can however be effective in reducing roadkill (Farmer & Brooks, 2012; Hobday & Minstrell, 2008; Jones et al., 2014). However, these approaches are not well-suited for long-term and extensive mitigation measures, and are instead best for temporary or targeted mitigation in strategic locations and during roadkill peaks (Ascensão et al., 2022).

Finally, road crossing structures, often accompanied by road fencing, can help prevent animals from accessing roads while also preserving or restoring landscape connectivity (Glista et al., 2009). Crossing structures include overpasses and underpasses (fig. 2), and their efficiency is only achieved through careful planning as they must ensure successful use by wildlife (Denneboom et al., 2021; Mata et al., 2008; Testud et al., 2020; Woltz et al., 2008). These structures must be placed in strategical locations in order to efficiently mitigate roadkill and restore ecological continuities (Loraamm & Downs, 2016). When implemented correctly, the combination of fencing and crossing structures has proven to be highly effective in reducing roadkill by up to 83% (Rytwinski et al., 2016; Villalobos-Hoffman et al., 2022). However, it is important to note that these structures are associated with significant costs of construction

and maintenance, ranging from tens of thousands of euros to several millions[3] (Helldin, 2022; Sijtsma et al., 2020).

In recent years, the rise of self-driving cars has led to advancements in automatic collision avoidance systems that can be fitted on autonomous and semi-autonomous vehicles (Riaz & Niazi, 2016.). These systems, which detect and avoid obstacles present on road lanes, have been extended to the avoidance of collisions with wildlife (Gupta et al., 2021; Saad & Alsayyari, 2020; Saxena et al., 2021; Sharma & Shah, 2017). Although not yet widely implemented, such advances deserve to be mentioned in this section, as they may become more significant in the near future. However, these approaches primarily focus on ensuring public safety, and therefore put an emphasis on collisions with large wildlife species which can pose significant threats to human lives (Al-Zahrani et al., 2011), such as ungulates (Sharma & Shah, 2017). In addition, the 'avoidance' aspect of the systems, often left to the drivers as the systems only alerts of the presence of an animal, may not always be achievable, especially for vehicles moving at high speeds (Sharma & Shah, 2017).

Fig. 2: Example of wildlife crossing structures: the Varennes overpass on highway A89, Puy-de-Dôme, France (top) and an amphibian underpass on road D14 (bottom, located in Doubs, France).

Photo credits: ASF, FNTP.

Wildlife mortality resulting from collisions with vehicles is a pervasive source of mortality. To effectively address this potential threat to biodiversity, two key elements are essential. First, it is crucial to recognize and evaluate the impact of roadkill on populations, as this information should be integrated into species conservation planning efforts (Grilo et al., 2021). Generating awareness about the significance of this issue can also help secure adequate funding for research efforts and the implementation of appropriate mitigation measures. Secondly, as discussed previously, a comprehensive understanding of where and when roadkill incidents occur, as well as the vulnerability of each species, is vital for targeted and efficient interventions (Teixeira et al., 2017). Beyond the pragmatic focus on

3 Wildlife underpasses, *e.g.* to allow amphibian movement during breeding migrations, range from 30 000€ to over 600 000€ depending on the location (France 3 régions). The construction of wildlife overpasses on french highways can cost 3-10 million of euros (APRR, 2023), and a crossing structure is reportedly under development in California, United States with a projected budget of $90 million (20 minutes).

roadkill mitigation, there is value in the comprehension of the ecological significance of road mortality as an anthropogenic pressure in the larger context of global change. In particular, the relatively recent threat of vehicles has the potential to induce notable changes in evolutionary pressures, an aspect that currently lacks sufficient attention from the scientific community (Brady & Richardson, 2017).

3. Toward a predictive model of WVC occurrences

Predictive modelling in the field of ecology can be categorized into two approaches: statistical (or phenomenological) and mechanistic (Robertson et al., 2003), which are not necessarily mutually exclusive (*e.g.*, Louvrier et al., 2020). When studying a biological system, statistical models rely on describing samples of the observed outcomes to predict future outcomes of the system. In ecology, this process often takes the form of delineating correlative patterns between the sampled outcomes and a set of predictors (Freedman, 2009). On the other hand, mechanistic modelling does not rely on empirical observations of the system's outcomes, but instead employs mathematical models to simulate the underlying mechanisms at play within the system (Rastetter et al., 2003). The validity of a mechanistic model can be explored by comparing the predictions it yields to the actual outcomes of the system (*e.g.*, Nathan et al., 2001).

In other words, statistical models describe the outcomes of a system, and mechanistic models describe the system itself, each approach with its own merits and limits. Statistical models, for instance, often make assumptions about the potential predictors involved and the nature of the relationships with the sampled outcomes (*e.g.*, assuming linear relations). Moreover, the accuracy of a statistical model is closely tied to the quality of the data sample (Baguley, 2004). Mechanistic models, however, require a precise comprehension of the underlying processes operating within a system, which are frequently simplified to enable their description (Batty & Torrens, 2001). The representation of reality through models is inherently flawed as they solely provide an approximation rather than an exact depiction, as stated in the famous maxim "*all models are wrong, but some are useful*" (Box, 1979).

Mechanistic approaches to WVC prediction are not frequent, although mechanistic modelling is well-developed in other areas of ecology, such as species distribution modelling (Peterson et al., 2015). In contrast, statistical modelling, often in the form of linear regression models, has been extensively employed to explore roadkill datasets. They often utilize predictors such as landscape features, temporal

variables and species' life-history traits to identify high-risk species and predict potential hotspots and peaks of roadkill (*e.g.*, Chyn et al., 2021; Farmer & Brooks, 2012; Santos et al., 2018).

3.1. Identified factors influencing the distributions of collisions

Several key conclusions arise from the examination of the literature focused on modelling wildlife-vehicle collisions with statistical models: (1) collisions are not randomly distributed, but instead tend to occur in specific areas and at certain times, respectively known as collision hotspots and collision peaks, (2) the rates of collision vary between species, and (3) there are interactions among the spatial, temporal and biological predictors of roadkill. Comprehensive reviews and meta-analyses of the documented factors correlated to the observed distributions of WVC help provide a global overview of the state of the literature in this field (*e.g.*, Grilo et al., 2020; Gunson et al., 2011; Litvaitis & Tash, 2008; Pagany, 2020). As such, the following section is not intended to serve as a comprehensive review of all the predictors of roadkill that have been identified, but instead aims at introducing the reader to select examples including some widely accepted factors influencing collisions, and others that are still debated as repeated studies tend to yield conflicting outcomes.

Spatial factors

Land use and habitat features are frequently examined as potential indicators of hotspots for wildlife-vehicle collisions (Pagany, 2020). Research indicates that roads passing through forested habitats are often associated with higher occurrences of WVC (Gunson et al., 2011), although some studies found that the reverse was true (Grilo et al., 2015; Saint-Andrieux et al., 2020; Tatewaki & Koike, 2018). Similarly, grassland and other open areas are associated with both increased or decreased WVC risks (Pagany, 2020). Collisions with birds, amphibians, and reptiles are generally more likely to occur near open water bodies (Gunson et al., 2011). Roadside characteristics also influence WVC, with general increases in collisions when road verges are planted with vegetation (Pagany, 2020), although the opposite has also been evidenced (Hoermann et al., 2020; Skórka et al., 2015). On a larger scale, the diversity and connectivity of landscapes can also be linked to the occurrence of WVC in both positive and negative ways (Pagany, 2020).

The characteristics of the road itself can also indicate the probability of WVC. Collisions can increase (Barrientos & Bolonio, 2009; Seiler, 2005) or decrease with increasing speeds of traffic (Bashore et al., 1985; Murphy & Xia, 2016). The relation between road traffic volume and WVC risk has been theorized to be non-linear (fig. 3). In this conceptual model, the probability of collision first increases and then decreases (or stagnates) with increasing volumes of road traffic: the road becomes progressively less traversable when it gets more and more frequented by vehicles (*e.g.*, noise and disturbance generated by traffic), which may deter animals from crossing (Seiler, 2001). Although there is some empirical support for this model (Clarke et al., 1998; Oxley et al., 1974), some dispute its validity (Bright et al., 2015; Grilo et al., 2015).

Other road characteristics have received less attention in comparison, such as the width and number of lanes, the presence of embankments, fences, the use of de-icing salt, and the slope and sinuosity of the road. Although these have been linked to WVC occurrences, there are once again conflicting findings in this regard (Gunson et al., 2011; Pagany, 2020). Some authors have pointed out an “end of fence” effect, in which roadkill hotspots are artificially created by fences positioned along roads: while fenced sections contain little roadkill, both ends of the fence, which allow wildlife to cross roads again, coincide with increased collision numbers (Helldin & Petrovan, 2019; Huijser et al., 2016; Plante et al., 2019).

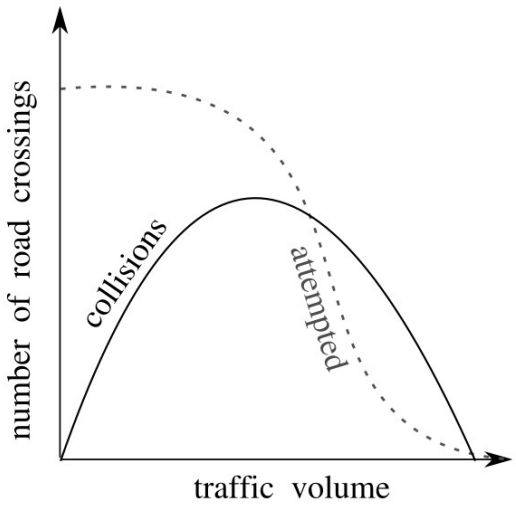


Fig. 3: Adapted from Seiler & Helldin (2006). Conceptual model: wildlife attempts at crossing roads decrease with the volume of traffic, because highly frequented roads generate noise and disturbance that deter animals from approaching. In result, there is a predicted non-linear relation between traffic volume and the number of WVC.

Temporal factors

Wildlife collisions vary throughout the year: mammal, bird and amphibian collisions are usually highest in the spring according to Pagany (2020), although Bullock et al. (2011) found higher rates of bird-vehicle collisions during the summer in Kalahari, South Africa, and Kreling et al. (2019) found the highest rates of large mammal collisions during the fall season in California, United States. In general, authors recognize that seasonal peaks in WVC could be explained by levels of activity or specific

behaviours of species, *e.g.*, breeding migrations in amphibians generating high WVC probabilities (Zhang et al., 2018), and deer rutting seasons coinciding with periods of high road mortality (Steiner et al., 2014). Collision risks also vary throughout the day, and depending on the day of the week (Steiner et al., 2014), which could be theorized as the result of changes in traffic volumes (Van Langevelde & Jaarsma, 2005), wildlife activity, and driver visibility (Pagany, 2020).

Finally, some studies have evidenced correlations between the phases of the moon and roadkill occurrences: deer-vehicle collisions peak during full moons (Colino-Rabanal et al., 2018; Steiner et al., 2021), while darker nights account for most of the mortality in the Iberian ribbed newt *Pleurodeles waltl* (Mestre et al., 2019). However, other authors detected no correlation between WVC and lunar phases across several mammalian species (Kreling et al., 2019), which hints once again at a complex relationship between this predictor and road mrotality. Recently, the COVID-19 pandemic and its associated lock-downs (*i.e.*, significant and sudden drops in traffic volumes) have granted a reprieve to wildlife (Driessen, 2021), although reductions in roadkill have not been observed for all species and locations (Asari, 2022; Pokorny et al., 2021) which may serve as evidence that road traffic volume alone cannot predict the occurrence of collisions.

Life-history traits

The correlation between abundance and roadkill has long been noted (D'Amico et al., 2015; George et al., 2011), although some species are found on road more (or less) often than expected based on their abundance (Quiles, 2018). Life-history traits can predict the probability of road mortality. Grilo et al. (2020) provided a handy meta-analysis of European species traits associated with higher WVC risks: they conclude that species characterized by high population density, small body mass and early maturity are the most often killed by traffic. Additional ecological traits have been shown to impact the relative risks of WVC, such as moving speeds and flying abilities (González-Suárez et al., 2018).

Some species-specific behaviours can increase the risk of roadkill, such as basking on roads in reptiles (Meek, 2009) or salt licking in cervids (Grosman et al., 2009). As vehicles constitute recently appeared threats in the evolutionary sense, some species may also be unable to detect them or exhibit maladaptive responses, such as freezing in front of oncoming cars (Lima et al., 2015). In contrast, some species may have the cognitive ability to actively avoid collisions: several bird species have been shown to adapt their flight initiation distance to the speed limit of the road (DeVault et al., 2014; Legagneux & Ducatez, 2013), and it has been suggested that black bears *Ursus americanus* can learn to avoid vehicles while crossing (Jaeger et al., 2005). Therefore, the cognitive and learning abilities of a species may help predict

their tendency to get killed on roads, and it has been suggested that individual personality traits may also induce differences in collision risks within a population (Lima et al., 2015).

These findings indicate that roads and the associated risk of mortality may lead to rapid adaptations through changes in behaviour, but they may also exert unique evolutionary pressures on species, thereby altering both wildlife and ecosystems in ways extending well beyond the mere loss of individuals to human transportation. For example, Brown & Bomberger Brown (2013) have found that the wing length of cliff swallow *Petrochelidon pyrrhonota* showed a general decrease over 30 years, while road-killed individuals consistently had longer wings than the population average. They proposed that the length of the wing may predict the ability to avoid an oncoming vehicle through a vertical take-off, such that the threat of roadkill selects for shorter wings. The evolutionary changes brought about by the road network have yet to received significant attention from the scientific community (Brady & Richardson, 2017).

Conclusion

This section offers a concise overview of the identified factors influencing WVC, and emphasizes the discrepancies in findings in the literature (fig 4). WVC hotspots can potentially be forecasted based on spatial predictors at both broad scales (such as land use patterns) and localized scales (such as fencing and roadside vegetation). Likewise, some temporal patterns in roadkill have been described, encompassing variations occurring within a day as well as seasonal differences. Finally, the risks of WVC are influenced by species and individual characteristics, and therefore extend beyond a mere reflection of species abundance.

All of these predictors appear intricately linked, which may explain why correlations identified in one study may not be repeatable in other contexts. For example, temporal predictors of roadkill often find likely explanations in changes in the species' abundance and behaviour, or in traffic volume. Similarly, patterns of land use, roadside vegetation or the use of de-icing salt most likely directly affect the presence of wildlife in proximity of the road, which in turn drives collision risks. Teixeira et al. (2013) revealed that the spatial distribution of roadkill hotspots was not coincidental across taxa, and temporal patterns of WVC also vary depending on the species (Raymond et al., 2021). As previously discussed, if statistical models highlight correlative patterns between WVC occurrences and its predictors, they are not best-suited for causal inference. Discerning the individual effects of the identified predictors can be difficult with statistical modelling, due to the potential high degree of correlation among them. For instance, there is a likely consistent correlation between certain road characteristics, such as width, number of lanes, traffic volume and speed limits. In addition, we can cite the well-described allometric relationship

between body mass and population density (Peters & Wassenberg, 1983; White et al., 2007), which may play a role in some of the identified patterns of correlation.

In conclusion, the use of observed distributions of roadkill is a commonly employed approach for identifying predictors of WVC, and although the predictors of roadkill identified in studies are pertinent within the specific scope of the investigation, scaling up to comprehensive predictive models of WVC is not straightforward due to the inherent complexity of the wildlife-vehicle collision system. Beyond the prediction of WVC, there is also a heuristic value in comprehending the causal relationships between anthropogenic pressures such as road mortality and various other factors.

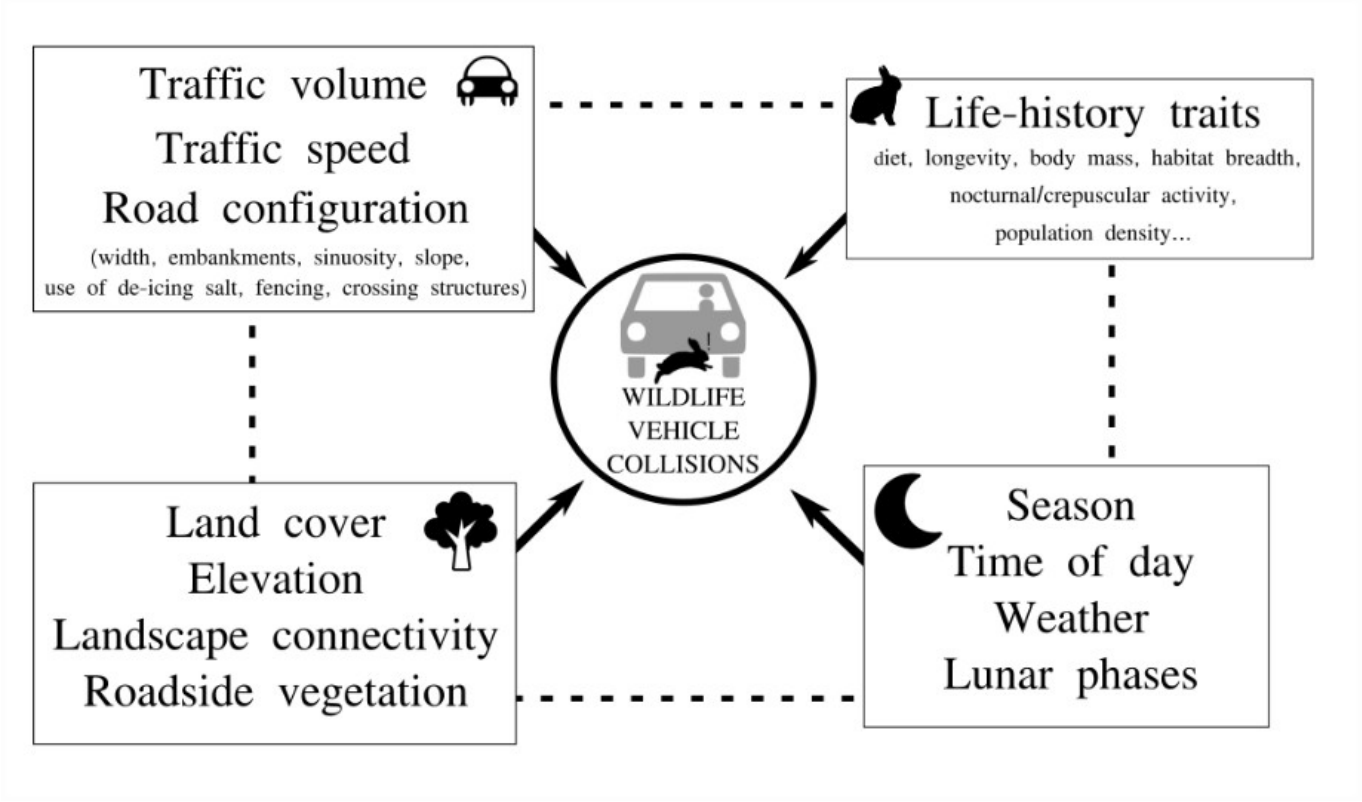


Fig. 4: Interdependencies of the currently identified wildlife-vehicle collision predictors (Pagany, 2020; Gunson et al., 2011; Grilo et al., 2020).

3.2. Challenges in WVC data collection

As described earlier, the observed outcomes of a system (in this case, wildlife-vehicle collisions) are central to statistical modelling approaches. Ideally, comprehensive models of WVC should incorporate large-scale dataset to obtain reliable predictions (Denny & Benedetti-Cecchi, 2012). However, while I have so far used *roadkill* and *collisions* interchangeably, it is important to recognize the distinction: roadkill is the observable consequence of an animal-vehicle collision. Ideally, we should rely upon the latter, as the ultimate goal is to understand and predict the mortality generated by road traffic on wild populations. For example, analyses such as fine-scale analysis of the temporal distribution of WVC are not possible with roadkill data, because there is no information available on the time of the collision, and instead only the time of discovery of the carcass is known. In practice however, *roadkill* is often the only accessible data to study WVC, while the collisions themselves are seldom witnessed

Roadkill is often gathered through periodic road surveys, generally performed by research teams, which makes data gathering costly and often limits its scale. Roadkill data can also be provided through opportunistic reporting by road maintenance crews (*e.g.,* Williams et al., 2019) or volunteers (*e.g.*, Swinnen et al., 2022). In contrast, collision data can be obtained from insurance companies or police reports (subsequent to insurance claims from drivers involved in WVC, *e.g.,* dos Santos et al., 2017). However, such data is difficult to assess as it may suffer from over or under-reporting (*e.g.,* insurance fraud, Inbar et al., 2002), and it will logically only represent the limited set of large-bodied species which cause damages to vehicles upon impact. Roadkill data differs from collision data because (1) not all carcasses persist on roads long enough to be detected during surveys, (2) not all carcasses present on the road are successfully detected and (3) in the case of opportunistic sampling by volunteers or maintenance crews, it is possible that not all detected carcasses will be reported. In addition, an unknown percentage of animals involved in collisions may not immediately perish on the road. Instead, they may ultimately succumb shortly after leaving the road, be ejected due to the force of the impact, or become trapped in the front grill of vehicles (Glista, 2008; fig. 5). Beyond mere underestimations of the road mortality due to

Fig. 5: Pheasant trapped in a front grill following a collision.

Photo credit: Julien Bouvet (2023)

overlooked animal carcasses, there is evidence that the persistence of carcasses on roads (Henry et al., 2021; Santos et al., 2016) and the rates of their detection (Collinson et al., 2014; Teixeira et al., 2013) are contingent upon biological and contextual factors. As a result, there likely are biases in roadkill datasets, with inevitable repercussions on the outcomes and predictions derived from statistical models.

In recent years, there has been growing attention ported to the biases present in roadkill datasets (Guinard et al., 2023; Santos et al., 2016; Teixeira et al., 2013). In general, improving the accuracy of roadkill carcasses requires more frequent road surveys (up to several times a day, Antworth et al., 2005) to counter the high rates of carcass disappearance from roads, as well as conducting surveys on foot or bike rather than from cars to improve the detection rates (Gerow et al., 2010). The sampling efforts required to detect all carcasses are however often incompatible with the human and financial resources available to research projects (Henry et al., 2021), which limits the scope and feasibility of these studies. In consequence, *post-hoc* corrections of the datasets (*e.g.,* accounting for the number of roadkill missed during surveys with estimations of the persistence of carcasses on roads and of the detection rates by observers) have been developed and applied as alternative solutions (González-Suárez et al., 2018; Grilo et al., 2020; Teixeira et al., 2013). Consequently, there is a growing need in WVC research for identifying, understanding and providing estimates of the biases in roadkill data collection, such as the persistence of carcasses on roads or the detection rates of carcasses by observers during surveys.

Even with the help of post-hoc corrections, the cost (both financial and in man-hours) of “professional” roadkill monitoring (*i.e.,* conducted by research teams with a rigorous sampling protocol) is nonetheless considerably high. Consequently, its implementation at extensive spatial or temporal scales is infrequent, thus reducing the relevance of the predictive models that can be produced (Denny & Benedetti-Cecchi, 2012). Similar limitations are present in biodiversity monitoring in general (Proença et al., 2017), which has in consequence led to the rise of citizen sciences as a valuable tool for collecting extensive ecological datasets (Deguines et al., 2012; J. L. Dickinson et al., 2010; Thel et al., 2021). In WVC research, citizen science datasets cover large temporal and spatial scales, usually by taking advantage of smartphone apps from which volunteers can report observed roadkill from anywhere at anytime (Vercayie & Herremans, 2015). In the last decade, several roadkill monitoring schemes using volunteer contributors have emerged around the globe, often covering entire countries at a time (South Africa: Périquet et al., 2018; UK: Petrovan et al., 2020; US: Shilling & Waetjen, 2015; Korea: Shin, Kim, Groffen, Woo, Song, & Borzée, 2022; Belgium: Swinnen et al., 2022; Taiwan: Yue et al., 2019), with some projects achieving upwards of 90 000 roadkill observations in over a decade (*e.g.,* Faune-Auvergne-Rhône-Alpes). Therefore, they represent a promising avenue for large-scale predictive modelling of WVC (Shilling & Waetjen, 2015).

However, in addition to the sources of biases presented above, citizen science projects also suffer from their opportunistic nature, meaning that sampling effort is likely to be unevenly distributed across time and space (Petrovan et al., 2020). In WVC research, some projects have attempted to standardize sampling effort by adding the possibility to report the presence and absence of roadkill during itineraries (*i.e.*, sampling along transects, Swinnen et al., 2022), but the vast majority of datasets mostly contain opportunistic reporting of roadkill. Furthermore, in addition to issues with carcass persistence and carcass detection rates, there is currently no research on the rates of the *willingness to report*[4] roadkill from contributors, or whether this reporting is selective toward more charismatic species. Indeed, it is important to consider that reports in unstructured citizen science biodiversity monitoring—including but not limited to roadkill reporting—may represent only a subset of the detected animals, that could potentially be influenced by observers' biases (Callaghan et al., 2021; Koch et al., 2022).

4 Throughout the course of this work, I will be using the term "roadkill reporting probability" to encompass the concept of willingness to report roadkill in citizen science projects. This is not to be confused with the term "reporting rate" which is sometimes used to signify the rate at which new roadkill is reported in a database.

3.3. Mechanistic approaches to WVC prediction

Although statistical methods are more commonly used for predicting wildlife-vehicle collisions, there are also authors who have employed mechanistic approaches. In a formal sense, the probability of a WVC can be described as the combination of three probabilities: the probability of coming across a road, of stepping onto the road surface, and the probability of being struck by a vehicle while on the road (fig. 6).

Fig. 6: Conceptual model of a wildlife-vehicle collision model. The probability of collision is the result of three consecutive steps: the probability to encounter a road, the decision to step on the road surface, and finally, the probability of a collision with a vehicle while on the road surface.

Some authors have developed mechanistic models of road traversability, *i.e.* the collision probability for an animal crossing the road (Hels & Buchwald, 2001; Jaarsma et al., 2006; Van Langevelde & Jaarsma, 2005). Assuming that the number of vehicles passing a given point, denoted X, follows a Poisson distribution (Breiman, 1963; Oliver, 1961), then the probability for an animal on the road to encounter at least one vehicle is given by $P(X \geq 1) = 1 - e^{-\lambda . \delta T}$, where λ is the volume of traffic of the road and δT is the time the animal spends on the road (defined as the time to cross the road perpendicularly, Van Langevelde & Jaarsma, 2005). This model has direct practical uses to predict the proportion of a population killed during road-crossing events, for example in conjunction with metapopulation models (*e.g.*, breeding migrations in amphibians, Hels & Buchwald, 2001). The significant advantage of this model lies in its ability to predict collision probabilities by considering only two variables: traffic, and the time required to cross the road. However, this approach is limited to the scale of a road and is therefore not designed for large-scale predictions, as it does not incorporate road encounter probabilities, and does not consider animal behaviours other than road crossing (*e.g.*, consumption of roadkill, basking on the asphalt, salt licking…). Furthermore, there may be a difference between encountering a vehicle while on the road surface, and getting hit by said vehicle.

The probability of crossing a road, especially at large scales, can be explored through the lens of landscape connectivity, or "the degree to which a landscape facilitates or impedes movement" (Taylor et al., 1993). Previous studies have found that well-connected landscapes tend to have higher occurrences of roadkill (Grilo et al., 2011; Kang et al., 2016; Santos et al., 2013). Landscape connectivity models, drawing for example from concepts in electrical circuits theory, can help identify the most likely locations where the paths of wildlife intersect with roads, and therefore the sections of roads that pose the greatest risk (Girardet et al., 2015; Swanson et al., 2008). This information is particularly valuable in cases where, for example, there is a need to strategically place wildlife crossing structures (Downs & Horner, 2012; Gurrutxaga et al., 2010), or other mitigation measures. However, it should be noted that these approaches do not consider the probability of animals colliding with vehicles while on the road, only the most likely crossing points based on the characteristics of the landscape. In addition, as previously discussed, some characteristics such as high road traffic volume can modify the traversability of roads for many species (Seiler, 2005). Connectivity metrics can be used as covariates in statistical models of roadkill, in addition to road characteristics that are often found to be associated with WVC (*e.g.*, road traffic volume, width or elevation, Girardet et al., 2015).

In summary, existing mechanistic models describe the probability of wildlife-road encounters, or the probability of wildlife-vehicle collisions during the time the animal is on the road surface. To the author's best understanding, there is currently no all-encompassing framework that combines both road encounter

and collision probabilities to mechanistically generate dependable estimates of road mortality within a given landscape. One avenue to successfully combine all the steps presented in figure 6 would be to put an emphasis on modelling the movement and trajectories of animals through the habitats, and on the road surface. There is some empirical support for the importance of animal (and vehicle) movement in understanding the WVC system, such as correlation patterns between roadkill and the presence of specific patches of habitats (in which animal may move differently, Saint-Andrieux et al., 2020), the level of activity of the animals (Steiner et al., 2014), their space-use behaviour (Meek, 2009) and their travel speed (González-Suárez et al., 2018), as well as the speed and density of road traffic (Pagany, 2020).

In movement ecology, the individual trajectories of animals can be described through stochastic equations of two or three-dimensional random walks, such as the Brownian motion (initially describing the motion of particles suspended in a liquid or gas), or correlated random walks (Fagan & Calabrese, 2014). Modelling individual trajectories and behaviour (*agent-based* modelling) can help explain patterns observed at larger scales (*e.g.,* the group behaviour of starling murmurations is modelled with individual trajectories, Reynolds, 1987, the same is true for groups' responses to predators, Viscido et al., 2001). Agent-based models focusing on individual movement and trajectories have also been applied in the context of wildlife management, to help understand the responses of animals to changing environments (McLane et al., 2011). In road ecology, agent-based approaches have been used to explore the costs and benefits of road fencing on population genetics and roadkill risk (Ascensão et al., 2013), and, more specifically, movement-oriented agent-based models have been applied to moose-vehicle collisions mitigation (Grosman et al., 2009) or to model the temporal dynamics of roadkill hotspots by introducing population depletion mechanisms (Teixeira et al., 2017). Although the animal trajectories are simulated, none of these example also considered vehicles as agents, *i.e.,* as entities with their own movement and trajectories. In consequence, collision risks were treated input parameters: animals stepping on the road had a pre-established probability of dying. To the author's best knowledge, no agent-based model has been developed to model the WVC system at large scales to explore the causal relations between spatial, temporal or biological factors and the risk of roadkill for an individual and a population.

4. The Faune-Auvergne-Rhône-Alpes roadkill dataset

The Faune-Auvergne-Rhône-Alpes (thereafter: Faune-AuRA) project is a citizen science initiative focused on biodiversity monitoring, involving both systematic and opportunistic monitoring of all terrestrial species in the Auvergne-Rhône-Alpes region (fig. 7). This regional database is integrated into the Faune-France national database. The monitoring project is overseen by the Ligue de Protection des Oiseaux (translation: *Bird Protection League*, thereafter: LPO).

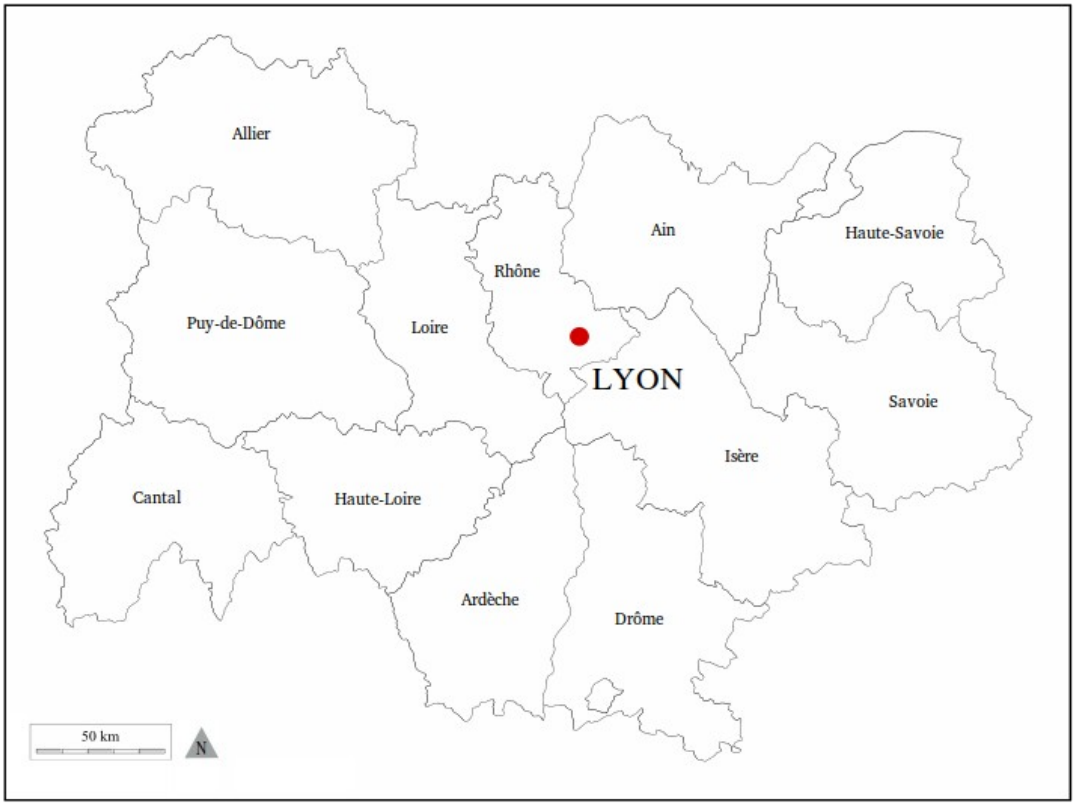


Fig. 7: Map of the Auvergne-Rhône-Alpes (AuRA) region, France and its 12 departments. It covers an area of about 70 000 km².

Since 2010, Faune-AuRA has integrated the possibility to report incidents of animal mortality on roads. As of July 27th, 2023, the roadkill dataset includes a total of 95,610 reports covering 589 species of reptiles, amphibians, mammals, birds, and insects (fig. 8). Reporting roadkill incidents can be done through a web interface or via the *Naturalist* mobile app, which is available for all Android devices. The roadkill reports include the following information: date, time, location, species, number of carcasses, photograph (optional) and contributor's comment (optional). The project currently involves 4059

contributors, among which many are LPO members. About 15% of the contributors are professionals (LPO technical staff, naturalists, forest and wildlife rangers, researchers…; LPO France, 2021). Despite the inherent value of a dataset of this scale for WVC research, it has never been cited in published work.

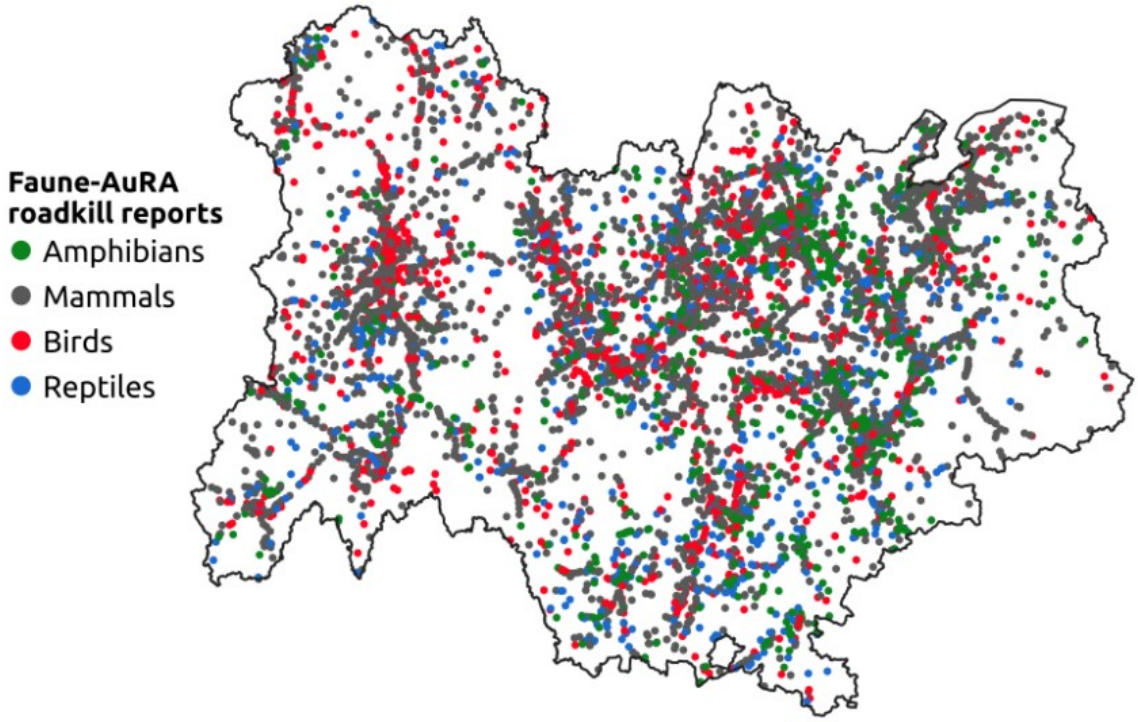


Fig. 8: The Faune-AuRA roadkill database for the year 2022. There are 7235 reports of roadkill, 20% of which are amphibians, 53% are mammals, 18% are birds and 9% are reptiles.

Overall, the most reported species in Faune-AuRA is the European hedgehog *Erinaceus europaeus* (>5000 reports), following by the European badger *Meles meles* (~3000 reports) and the red fox *Vulpes vulpes* (~2000 reports). The most reported bird is the common blackbird *Turdus merula* (~800 reports), the most reported reptile is the green whip snake *Hierophis viridiflavus* (~700 reports) and the most reported amphibian is the common toad *Bufo bufo* (~1600 reports).

In addition to producing roadkill maps and comparing the number of roadkill reports per species, we can detect temporal trends in Faune-AuRA. One striking example is the common toad road mortality, which is known to explode in spring during the annual breeding migration of the species (Hels & Buchwald, 2001). This pattern is present in the Faune-AuRA database (fig. 9). However, both the number of reports and the spatio-temporal patterns in this dataset may misrepresent the actual patterns of wildlife-vehicle collisions, as Faune-AuRA is an opportunistic reporting project which suffers from the numerous biases previously cited.

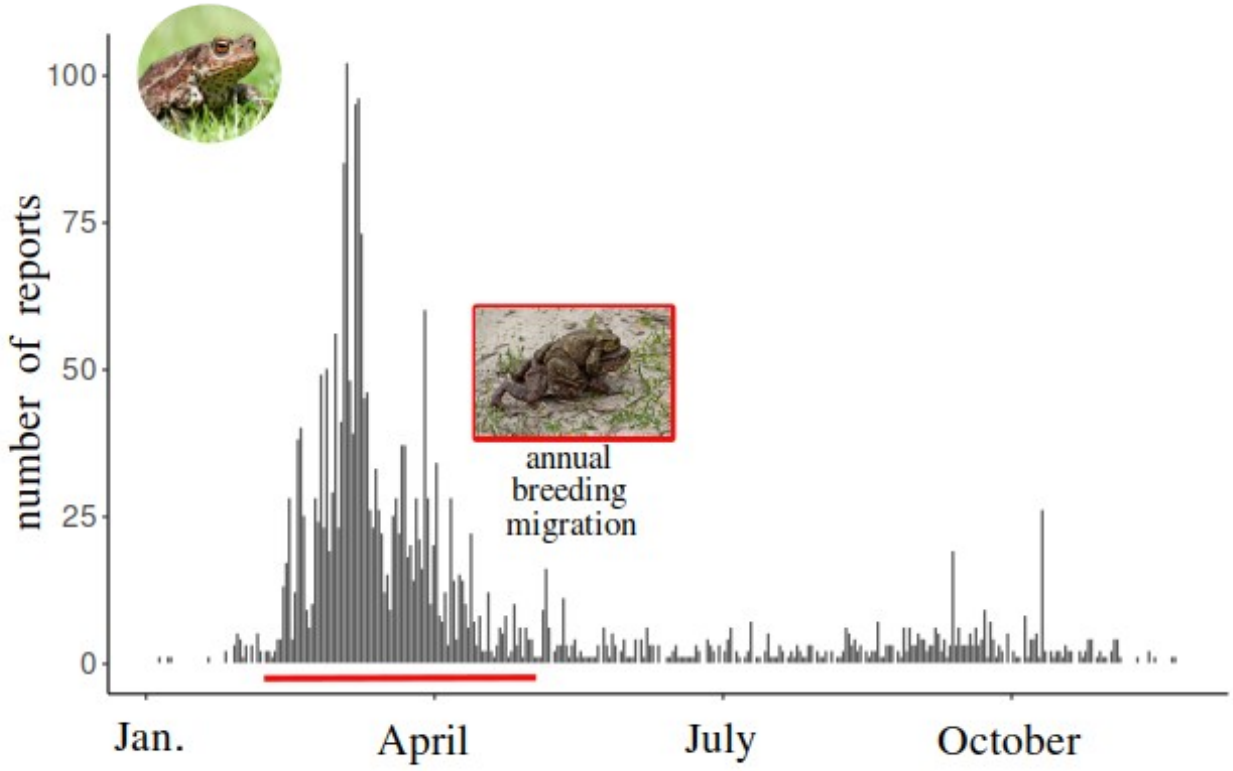


Fig. 9: Temporal trends in roadkill reporting of the common toad *Bufo bufo* to the Faune-AuRA citizen science project.

5. Objectives and hypotheses

The main objective of this project is to work toward comprehensive predictive models for wildlife-vehicle collisions at large scales, both spatially and temporally. We will explore both mechanistic and statistical approaches (fig. 10). This thesis is composed of 4 manuscripts, either submitted or in preparation, plus 2 case studies. Case studies detail preliminary experiments, conducted during the thesis project to explore new methodological approaches.

Objective 1:

The first chapter of this thesis will present a **mechanistic model of wildlife-vehicle collisions**. This model is an agent-based approach, **based on the individual trajectories of both animals and vehicles**, which aims at reuniting road encounter probabilities with vehicle collision probabilities in a unified framework. We aimed at providing a theoretical framework based on movement ecology that would encompass all aspects of road mortality risks.

We investigate the hypothesis that there is a **causal relationship** between predictors of WVC identified in empirical studies (such as road characteristics: traffic volume, speed, road sinuosity, and biological traits: animal speed, behaviour, and density) and wildlife-vehicle collisions. In addition, sensitivity analyses are used to identify the predictor(s) that have the biggest impact on collision numbers, a valuable insight for both the design of empirical studies and applied roadkill mitigation.

Objective 2:

The subsequent chapters will focus on the **data collection process** in WVC studies. Robust roadkill datasets are valuable in both mechanistic and statistical approaches, and we focus particularly on an existing dataset from **an opportunistic citizen science project (Faune-Auvergne-Rhône-Alpes)** that collects data at the scale of the Auvergne-Rhône-Alpes region, France.

We aim at:

1. Improving the understanding of **carcass persistence** on roads. The main hypotheses we will explore are that:

- Roadkill persistence time in the Auvergne-Rhône-Alpes region is comparable to previously published work in other parts of the world,

- Roadkill persistence is influenced by factors such as traffic volume, weather, and roadkill species,

- Roadkill removal from roads is the result of several mechanisms, that will interact with the predictors cited above.

2. Providing estimates of the **detection probability** of roadkill carcasses and exploring the influence of external factors on the detectability of roadkill. In particular, we postulate that:

- Detectability is dependent on the roadkill carcass body size,

- Detectability differs between standardized roadkill surveys and opportunistic ones.

3. Demonstrating that ***willingness to report*** is another source of bias in citizen science roadkill monitoring, and providing estimates of the reporting probabilities of the contributors from the Faune-AuRA project.

Objective 3:

We plan to **integrate the estimates** of the 3 existing biases (persistence, detection, report) in the Faune-AuRA project to produce **corrected datasets**. This will improve the understanding of the impact of road mortality across the Auvergne-Rhône-Alpes region, and open perspectives for the use of this database for (1) mechanistic model validation and (2) statistical modelling. We anticipate significant disparities between the current number of reports in the dataset and the estimates of road mortality our corrections will produce.

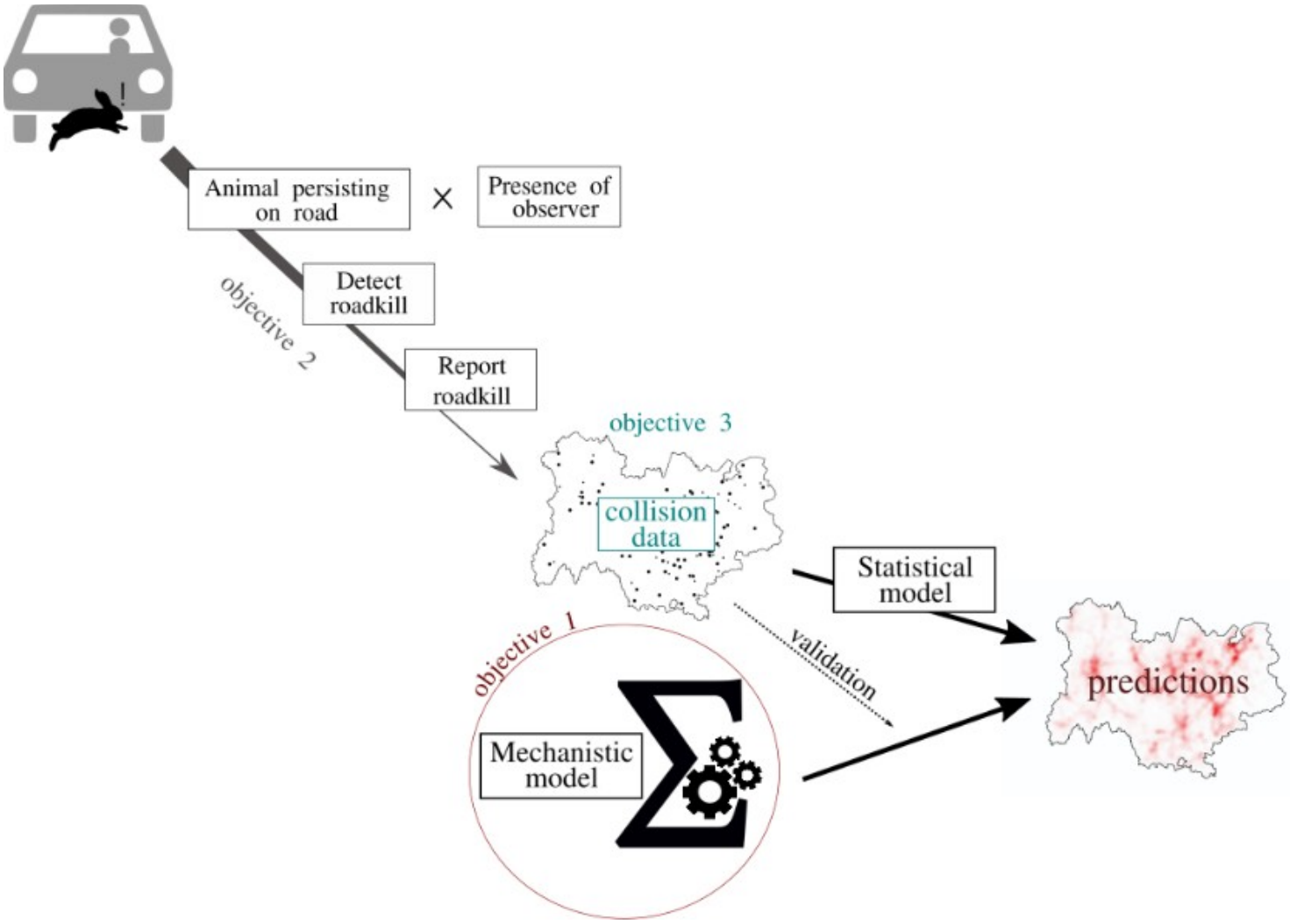
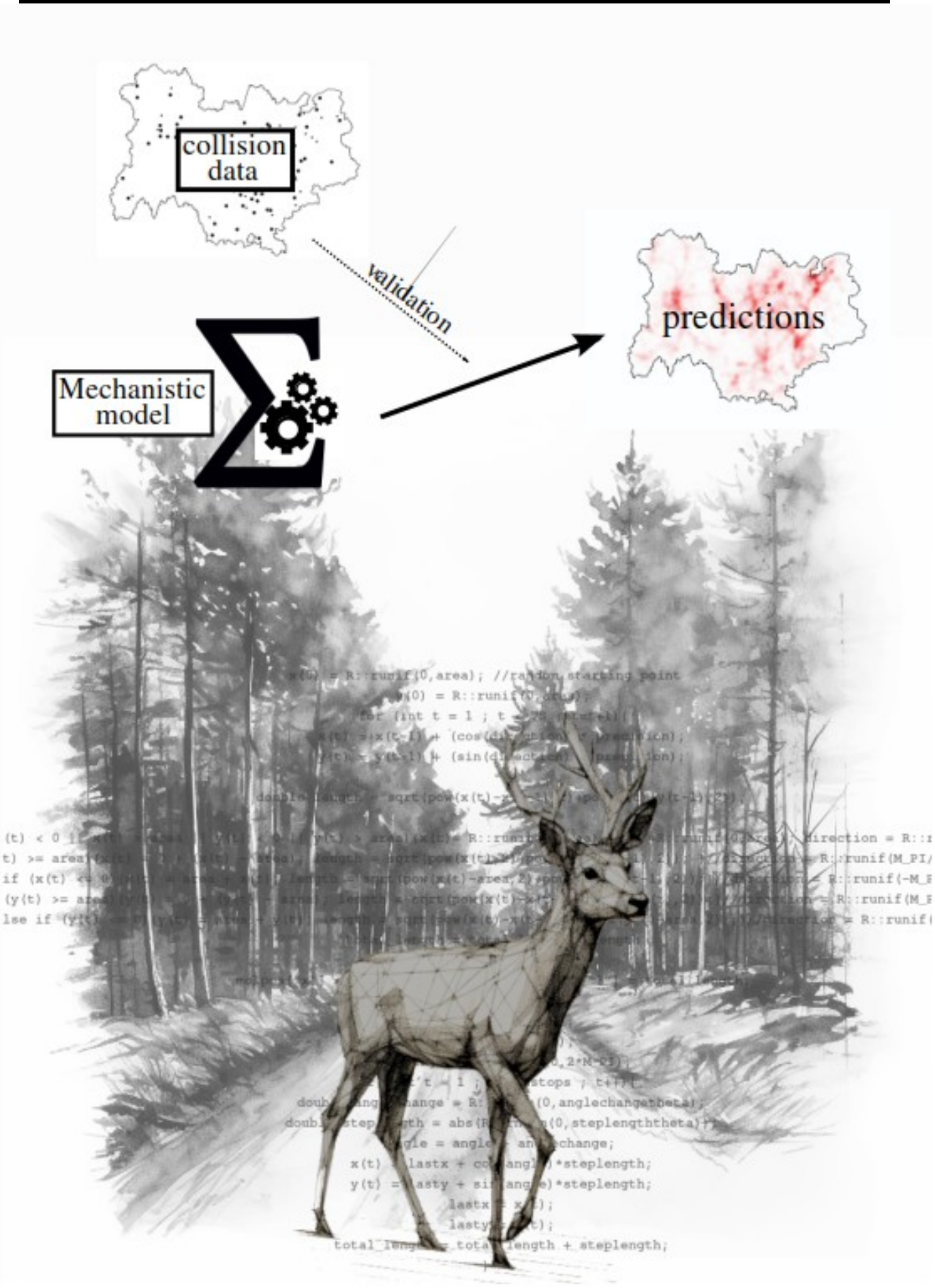


Fig. 10: Conceptual framework of wildlife-vehicle collisions (WVC) prediction. This project will focus on working toward a large-scale predictive model of WVC through (1) mechanistic modelling approaches and (2) the roadkill data collection process, and in particular the citizen science monitoring scheme Faune-AuRA as a source of roadkill data in the Auvergne-Rhône-Alpes region of France.

Chapter 1: Agent-based modelling of wildlife-vehicle collisions



A biologically realistic model to predict wildlife-vehicle collision risks (under review)

Annaëlle Bénard, Thierry Lengagne and Christophe Bonenfant

under review in *Ecological Modelling*

CONTEXT

In light of the ongoing biodiversity crisis, it is imperative to understand the mechanisms responsible for wildlife mortality on roads. However, there is currently no comprehensive theoretical framework addressing this issue. Numerous correlations have been identified between landscape characteristics, biological traits and collision risks, but it remains challenging to disentangle the relative effects of various risk factors in empirical studies.

OBJECTIVES

- Construct an agent-based stochastic model of wildlife-vehicle collisions that incorporates recent insights from movement ecology.

- Evaluate the causal relationships between animal and vehicle movement parameters, such as speed, abundance and traffic, road sinuosity, animal space-use, and the risks of collision.

- Determine the relative impacts of these parameters on collision risks with sensitivity analyses.

KEY RESULTS

- There are causal relationship between WVC risks and most parameters of animal and vehicle movements, which are contingent upon the space-use patterns of the individuals.

- Relationships between predictors and collision risks are often non-linear.

- Animal movement has a greater influence on collision risks than vehicle movement.

CONCLUSIONS

- Mechanistic modelling in the field of wildlife-vehicle collisions has the potential to offer valuable insights and should be explored further, especially modelling focused on movement: animal patterns of movement and activity levels appear as the primary explanatory factors for collision risks.

- Variability in road mortality risk among individuals with different movement patterns may generate selection pressures.

- Effective mitigation of wildlife-vehicle collisions should be species-specific, but also behaviour-specific.

Abstract

Road networks have major ecological impacts on living organisms consequent to habitat loss and fragmentation, chemical and acoustic pollution, and direct mortality when wildlife-vehicle collisions are involved (WVC). The many past empirical studies revealed biological traits shared by species most vulnerable to roadkill (*e.g.*, population density). Similarly, spatial locations of WVC hot-spots are associated to landscape features at large spatial scales, and to road characteristics at small spatial scale. We currently lack a comprehensive theoretical framework for WVC. Animal movement in relation to habitats is an essential driver of encounters with roads, but this remains largely ignored in studies, even when movement ecology provides the necessary tools to investigate the impact of animal movement on WVC. We built a general individual-based model incorporating recent knowledge in movement ecology (movement typology: roaming, migratory route crossing a road, active attraction and active repulsion of roads) to estimate WVC risks. We explored the relative effects of animal and vehicle movement parameters (speed, abundance, road sinuosity and animal movement pattern) on collision probability. We show that animal behaviour toward roads has major impacts on the number and risks of WVC, but also modulate the effects of other factors (animal traveling speed, species local abundance, road traffic volume) on WVC. Sensitivity analyses show that the movement and behaviour of the animal has more influence on WVC risks than any of the characteristics of roads and vehicles we tested. Our results suggest that (1) effective roadkill mitigation should be species-specific and could vary in efficiency depending on the target's movement pattern (mating and migratory seasons, foraging habits. . .) and (2) empirical studies of WVC should incorporate knowledge about the behavioural habits of the focal species in relation to roads.

1. Introduction

The last century has witnessed a continuous and tremendous urbanization of almost all ecosystems, with profound influences on living organisms (Corlett, 2015). A particularly important anthropogenic factor generating major ecosystem modification and disturbance is the increasing densification and encroachment of the earth-bound transportation systems, and particularly of the road network (Davenport & Davenport, 2006). The presence of roads modify the local and large-scale environment of species as a consequence of chemical and noise pollution, changes in vegetation diversity, habitat loss and fragmentation (see Forman & Alexander, 1998; Coffin, 2007, for reviews). Roads can also have profound effects on ecosystem functioning and the biology of living organisms (Holderegger & Di Giulio, 2010). For instance, road mortality is a key driver of biodiversity loss in amphibians (Hels & Buchwald, 2001), birds and mammals (Grilo et al., 2020) and has been shown to affect animal behaviours (Andrews & Gibbons, 2005; Legagneux & Ducatez, 2013). In the context of the ongoing biodiversity crisis (Ceballos & Ehrlich, 2002), knowledge about the mechanisms that lead to road mortality in wildlife is therefore critical.

For decades, empirical studies have been accumulating, reporting on collision hot-spots (Teixeira et al., 2013; Silveira Miranda et al., 2020), animal foraging habits near roadsides (Carvalho-Roel et al., 2019), or the seasonal variation in the number of reported cases (Medinas et al., 2021). We now have a clearer picture of what factors mainly account for collision risks (Table 1). Species with life history traits such as extended home ranges or slow travel speeds, and species occurring at high abundances are more often subjected to roadkill. Road characteristics (such as high traffic volume) and landscape features (*e.g.* habitats promoting high levels of animal activity and mobility) account for WVC hot-spots locations at small spatial scales, but collisions distribution can also be predicted for large spatial scales with variables such as road density, hunting bags (Saint-Andrieux et al., 2020) or landscape connectivity (Girardet et al., 2015). However, the relative effects of risk factors are difficult to disentangle. For example, as traffic mortality depletes local populations, roadkill numbers will decrease and simply counting collisions in high-risk areas could lead to an underestimation of the importance of animal abundance as a key determining factor of roadkill hot-spots (Teixeira et al., 2017). So far few attempts at a theoretical model for wildlife-vehicle collisions (WVC) have been made, and our current knowledge on the quantitative effects of traffic on encounter and mortality risks for wildlife remains essentially descriptive, with little predictive abilities.

The very first model dealing with collision probabilities at a large spatial scale is the ideal gas model, first coined by physicist J. C. Maxwell in the context of molecule collisions in a gas (Maxwell, 1860). The ideal gas model posits that encounter rate within a defined volume or plane is a function of molecule

speed, density and collision zone (Hutchinson & Waser, 2007). Despite its heuristic value in ecology, to estimate encounter rates between males and females of a given species for example, it has seldom been used to study WVC as the general application in this context is not straightforward. For example, in most wildlife-vehicle encounters the animal is likely to die and will no longer be at risk of collision again, which is not reflected in colliding molecules. Others proposed WVC-specific mechanistic models: Hels & Buchwald (2001) modelled the probability of death for an amphibian crossing a road (see Gibbs & Shriver, 2002; van Langevelde & Jaarsma, 2005, for an application to other species), allowing the integration of road mortality into population persistence models (Gibbs & Shriver, 2002).

A shortcoming shared by all current WVC models is the lack of consideration for animal movement and habitat use behaviour, often limiting when one aims at describing the complexity of animal movement in a heterogeneous landscape (Siniff & Jessen, 1969). For example, not only do animals cross roads, but they can roam along roadsides to forage hence putting them at much higher risk of being hit by a car (scavenging: Schwartz et al. 2018; Ratton et al. 2014, hunting: Gomes et al. 2009; D'Amico et al. 2013, salt licking: Fraser & Thomas 1982). More importantly, collision probabilities in a landscape are intrinsically linked to the number of encounters an animal has with roads, and peaks in activity such as mate searching, breeding, and juvenile dispersal have repeatedly been cited to explain seasonal patterns in WVC numbers (Steiner et al., 2014; Ryu & Kim, 2021; Raymond et al., 2021). Despite this, the influence of patterns of space use by animals on WVC has yet to be adequately addressed in mechanistic models.

Patterns of space use are described within the frameworks of movement ecology. Species distributions are generally divided into broad strategies comprising several patterns of space use that depend both on the biological traits of the species and the environment: sedentary populations that occupy a restricted geographical area (often referred to as home range or territory), migratory individuals who exhibit long-distance and often periodic displacements, and nomadic populations whose movements are neither confined to specific geographic areas nor predictable (Mueller & Fagan, 2008). These large-scale patterns emerge from movement at the individual level: for example, oriented movement, based on environmental cues or memory, is the basis for migratory routes and sedentary ranges (Mueller & Fagan, 2008; Van Moorter et al., 2009). The advances of the last decades in bio-logging (*e.g.,* animal-borne GPS collars, tags or transponders) have made it increasingly easy to acquire position data characterizing these individual trajectories for a growing number of species, therefore providing a solid empirical basis to develop mathematical models of animal movement. To our knowledge however, WVC studies seldom incorporate paradigms from movement ecology, although space use is the main driver of animal encounters with roads. Therefore, we argue that modelling wildlife-vehicle collisions from a movement

ecology perspective would improve our ability to understand the main factors driving WVC (Hels & Buchwald, 2001; van Langevelde & Jaarsma, 2005).

We here propose an individual-based model to simulate animal trajectories using biased and unbiased correlated random walks, as a mean of exploring the effects of road characteristics, species traits and patterns of space use on the number and probability of collisions between animals and vehicles. Our two main goals are i) to quantify the relative effects of several road characteristics (road sinuosity, vehicle speed and traffic volume) and species traits (animal speed, local abundance, movement patterns, foraging and dispersal behaviours) on WVC occurrences and ii) for a set of biologically realistic scenarios of animal movement, to identify what factors have the largest impact on wildlife-vehicle collision risks. Understanding which biological, human and environmental factors modulate the risks of wildlife-vehicle collisions is key to the selection and implementation of efficient mitigation policies such as fences, over or underpasses, and traffic signage that raises drivers' attention (Davenport & Davenport, 2006). Our model should help to build qualitative predictions either for inter-specific studies or WVC mitigation.

Table 1: An overview of the different factors correlated to the incidence of wildlife-vehicle collisions in the current literature.

IOLOGICAL FACTORS	**Animal Speed**	While crossing a road, slower-moving animals such as herpetofauna will be more impacted by roadkill. Hels & Buchwald 2001, Eigenbrod et al. 2009, Grilo & Bissonette 2010, Van Langevelde & Jaarsma 2005
	Habitat use	Highly mobile individuals cross roads more often. When mobility levels are season, age or sex-dependant, these biases are reflected in roadkill (more mobile individuals being killed more often). Steen & Smith 2006, Aresco 2005, Coelho et al. 2008, Newell 1999
	Road-related behaviours	Some species can be attracted to roads, including but not limited to: - Ungulates licking salt on or near roadsides (Rea et al. 2021) - Carrion feeders foraging on roadkill (Laurance et al. 2009, Mukherjee et al. 2013) - Birds using roadside perches (Grilo et al. 2011) - Reptiles using road surfaces to bask (Meek 2009) - Turtles laying eggs on road shoulders (Aresco 2005) - Amphibians breeding in road-adjacent water retention ponds (Smith & Dodd 2003, Hamer et al. 2012)
	Species local abundance	*"To some extent, road-kill statistics actually give a crude but useful index of wildlife occurrences in a region"* Seiler & Helldin 2006
	Car avoidance behaviours	Species-specific or individual reactions to oncoming vehicles dictate whether the animal will have a chance of avoiding a collision. Documented behaviours that increase roadkill probabilities include: - not detecting oncoming vehicles, - habituation and not perceiving moving vehicles as threats, - freezing in front of vehicles and following conspecifics on the road. Lima et al. 2015
ANTHROPOGENIC FACTORS	**Traffic volume**	Roadkill occurrences increase with traffic volume until a certain threshold where traffic-generated disturbances (movement, noise, chemical emissions) repel most of the wildlife Seiler 2005, van Langevelde et al. 2009
	Traffic speed	High-speed roads generate more roadkill Hobday & Minstrell 2008, Farmer & Brooks 2012
	Road characteristics	Roads on which WVC are more frequent include: - wider roads with multiple lanes (Bright et al. 2015), - raised roads and embankments promoting low-altitude flight in birds (Canal et al. 2019) - sinuous roads (Grilo et al. 2011, Zuberogoitia et al. 2014)
	Mitigation measures	- Warning signage is often ineffective in preventing collisions (Huijser et al. 2015) - Road-crossing structures (bridges, underpasses) can counter-intuitively correspond to roadkill hotspots when looking at species they are not suitable for, *e.g.* by lacking proper fencing for smaller vertebrates (D'Amico et al. 2015)
LANDSCAPE	**Roadside features**	"*The concentration of forage or cover plants, accumulation of salt, or close proximity of wetland may cause some animals to concentrate their activities near roadsides*" Livaitis & Tash 2008
	Landscape connectivity	Landscape connectivity, by influencing animal movement, is a predictor of roadkill spatial patterns: roads in high-connectivity landscapes are more dangerous. Grilo et al. 2011, Fabrizio et al. 2019, Girardet et al. 2015
	Adjacent habitats suitability	Roadkill occurrences in a species are higher in the presence of optimal habitats. At broad scales, habitat suitability models are used as predictors for spatial roadkill patterns. Balčiauskas et al. 2020, Wright et al. 2020

2. Material & Methods

Following previous work on simulations for the ideal gas model (Hutchinson & Waser, 2007), we constructed a discrete-time simulation of particles movement in which all trajectories were approximated by a series of straight-line steps of constant duration. Two classes of particles were considered: vehicles and animals, each with their own speed, movement patterns and density. We conducted preliminary testing of the model by replicating the conditions under which the ideal gas model applies, and subsequently ensured that simulation results matched the model's predictions. From there, we used biased and unbiased correlated random walk models to represent animal movement more realistically. Random walk parameter values were chosen to match real-life scenarios. The goal of the simulations was to keep track of the number of encounters between vehicles and animals per unit of time (fig. 1). We set a duration of 12 hours per simulation run, as a broad representation of the amount of time during which most diurnal and nocturnal terrestrial species are active (Refinetti, 1999). Two types of experiments were conducted: (1) to test the quantitative and qualitative effects of the different focal parameters (animal and vehicle speed, movement and densities) independently, we replicated the simulation for different values of the parameter under study, holding everything constant and (2) to evaluate the relative importance of each focal parameters on the number of WVC, we conducted one-at-a-time sensitivity analyses.

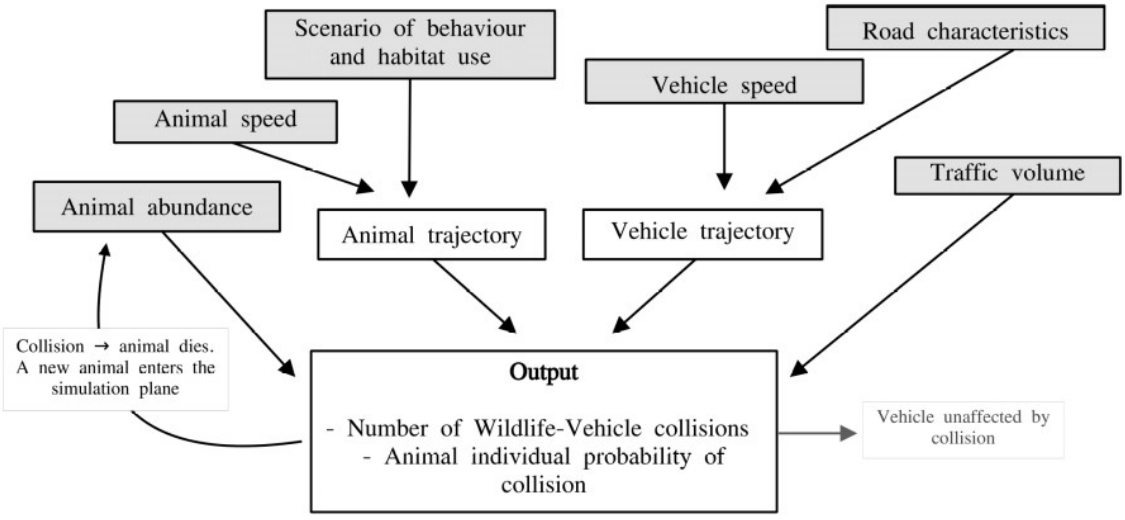


Fig. 1: **Conceptual diagram of the Wildlife-Vehicle Collision model** – We constructed a discrete time, agent based simulation of collisions between animals and vehicles. Using biased correlated random walks, we investigated the effects of individual and species-specific traits (behaviour, habitat use, animal speed, population densities) as well as road and vehicles characteristics (vehicle speed, volume of traffic, sinuosity of the road) on the number and probabilities of Wildlife-Vehicle Collisions during 12 hours simulation runs. A collision did not affect the vehicle, but the animal involved was killed and replaced by a new individual in order to keep animal density constant.

2.1 Basic simulation layout

We first assumed two separate entities, thereafter designated ’vehicles’ and ’animals’, moving on a 30x30km2 plane mapped by x and y axes. We treated the plane like a torus, meaning that an animal or a vehicle crossing the edge reappeared at the same location, but on the opposite edge of the plane (see fig. 2). The vehicle movement followed a road defined as $0 \leq x \leq 30$ and $y = \cos(\alpha.x)$, where α controlled road sinuosity. We computed an index of sinuosity for each simulated road as the ratio of the road’s length to 30 (i.e. the x axis’ length). A sinuosity index of 1 indicated a straight road, and the index increased as the road became more and more sinuous. The number of vehicles on the road at any given time followed a Poisson distribution (Breiman, 1963) and all vehicles moved at constant speed with no intra-class variability. For animal movement, we used biased correlated random walks (BCRW), a combination of correlated random walks where animals have a directional persistence and therefore avoid backtracking, and biased random walks where animals are attracted to one or several centers of attraction spatially defined on the simulation plane. BCRW are highly flexible models proven to fit animal trajectories at different spatial scales for a range of terrestrial species in heterogeneous landscapes (red deer (*Cervus elaphus*): Berthelot et al., 2020; caribou (*Rangifer tarandus*) and bears (*Ursus arctos and U. maritimus*): Auger-Methe et al., 2016; cactus bugs (*Chelinidea vittiger*): Schooley & Wiens, 2003).

Animals moved on the plane from time steps t = 0 to T according to a BCRW:

$$x_a(t) = x_a(t-1) + \cos(\theta_t) * d$$

$$y_a(t) = y_a(t-1) + \sin(\theta_t) * d$$

$$x_a(0) \sim U(0,30)$$

$$y_a(0) \sim U(0,30)$$

with step length d drawn from a zero-truncated normal distribution $N(\mu, .5)$, μ the mean animal speed and $U(0, 30)$ the uniform distribution between 0 and 30. We computed the direction of the walk $0 \leq \theta_t \leq 2\pi$ as the mean between the *correlated* direction $\theta_t^c \sim N(\theta_{t-1}^c, \sigma^2 = 5)$ with θ_0^c randomly drawn between 0 and 2π, and the *biased* direction θ^b, the direction of the nearest attraction center. It resulted that the direction of the walk was the outcome of two competing processes: the persistence, the animal’s internal propensity to walk without backtracking in a given direction θ_0^c, and the attraction toward the nearest attraction center. The relative importance of the attraction with respect to the persistence was defined by

the associated weight of attraction *w* (Duchesne et al., 2015). Accordingly, *w* controlled the strength with which animals are attracted to the attraction center: $w = 0$ produces unbiased correlated random walks (no attraction), and $w \rightarrow \infty$ tends towards biased random walks. In practice, for high values of *w* the animal made a beeline towards the nearest center of attraction because the attraction to the nearest center takes over the persistence of the correlated walk in orienting the walk. Once the animal reached the attraction center, it orbited around it, as a result of the persistence pulling away in its own direction while the attraction component brought the animal back towards the center. In consequence, high values of *w* would imply less spread-out orbiting behaviours, mimicking animals staying in close proximity of the attraction center (see fig. S1 in supplementary material).

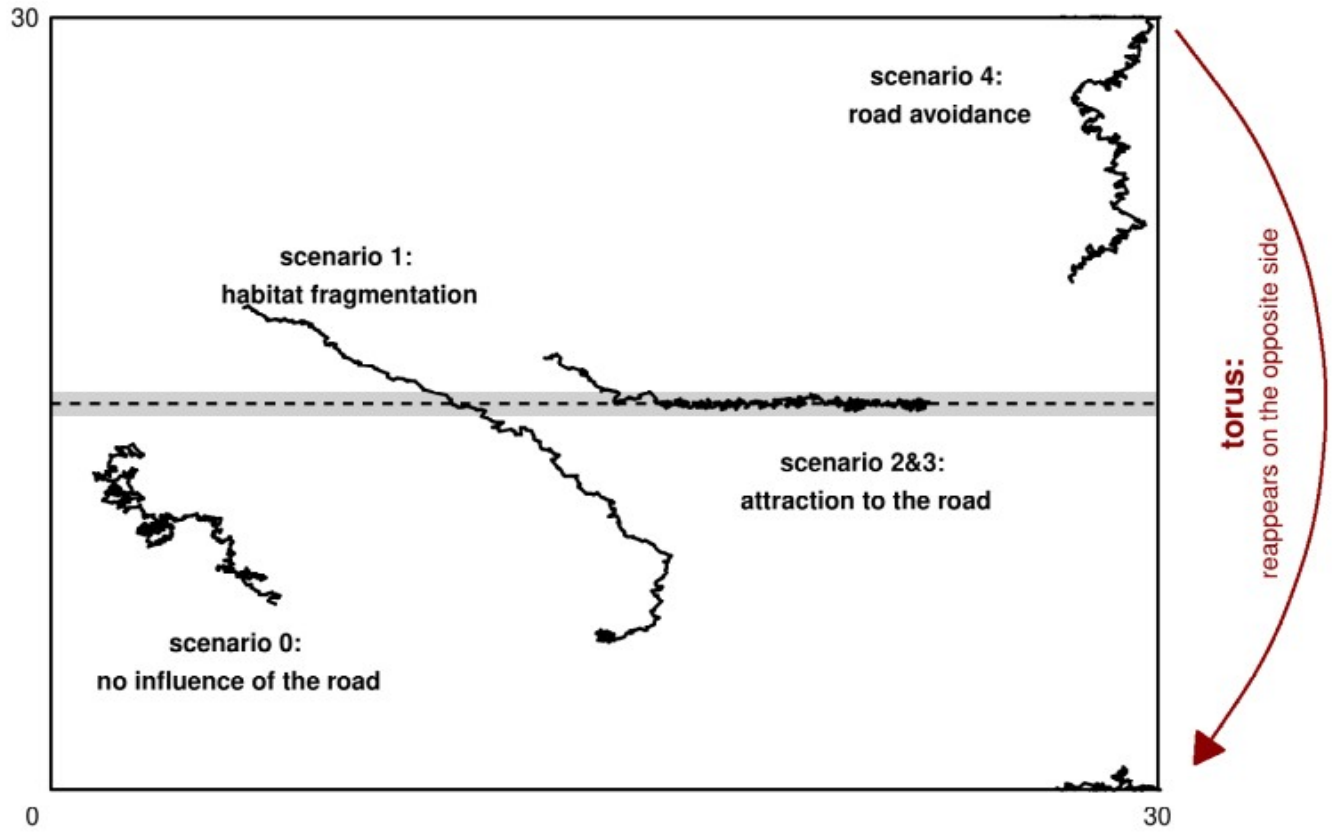


Fig. 2: Using biased correlated random walks, 5 scenarios of animal habitat use are implemented on the 30x30km² plane to study collisions between moving animals and vehicles. Animals and vehicles that reach one of the edges of the plane will continue their walk on the opposite edge. In other words, they move on a torus and can never leave the simulation plane.

We defined an animal-vehicle collision as a time-step during which the distance between an animal and a vehicle was less than 5 meters (Euclidean distance). If that condition was satisfied, the animal died and stopped moving, while the car continued to move along the road. For each collision, a new animal would enter the plane in order to keep the animal density constant. We did not implement any sort of behavioural reactions from the animals to an incoming vehicle, or from the driver in the presence of an animal on the road or roadside. Given its stochastic nature, the model was run N = 1000 times to produce a mean collision number and estimate an individual probability of collision. The simulation used R package Rcpp (Eddelbuettel & Balamuta, 2018).

2.2 Behavioural scenarios of animal movement and space use

We considered 5 different scenarios designed to mimic real-life animal behaviours described in the literature (fig. 2).

2.2.1 Scenario 0: no influence of the road

In scenario 0, the weight of attraction *w* was set at 0 resulting in animals performing (unbiased) correlated random walks (CRW). In CRW, successive steps directions are correlated, resulting in a directional bias: the animal walked forward and rarely backtracked. CRW have been used to describe the movement of several species (Mouse (*Apodemus sylvaticus*): Benhamou 1991, Reindeer (*Rangifer tarandus*): Marell, Ball & Hofgaard 2002, Red fox (*Vulpes vulpes*), Snowshoe hare (*Lepus americanus)*: Siniff & Jessen 1969). CRW imply that animals did not factor in the presence of a road or moving vehicles in their movement, which could be especially prevalent on smaller or unpaved roads (Brehme et al., 2013). This simple movement model also served as a null model, i.e. a scenario without attractive or repellent effects of road presence on animal movement.

2.2.2 Scenario 1: habitat fragmentation

All animals started the simulation run in the top-left corner of the simulation plane, always above the road, while the single attraction center (w=1.5) was randomly located below the road. The resulting BCRW simulated a migration of individuals between patches during which they had no choice but to cross the road. This scenario could match many migrating species such as amphibians converging towards open waters for reproduction (Hels & Buchwald, 2001; Sillero, 2008), large mammals migrating to their summer or winter ranges (Avgar et al., 2014) and crab species moving back to sea during breeding migrations (Ryu & Kim, 2020).

2.2.3 Scenarios 2 & 3: attraction to the road

Scenario 2 emerged from the frequently reported attraction to roads in many species: salt licking on roadsides by large mammalian herbivores (Fraser & Thomas, 1982), use of roads and roadsides for foraging or hunting (Diurnal raptors: Meunier et al., 2000; Passerines: D'Amico et al., 2013) or carnivores scavenging on carrions from animals hit by cars (Schwartz et al., 2018; Ratton et al., 2014). Arguably, this scenario could encompass the case of reptiles that bask on warm road surfaces (Meek, 2009). Attraction centers (w = 3) were placed every 300m on the road, such that animals converged towards the closest attraction center. Once an animal had reached an attraction center, it would orbit around until another attraction center in the vicinity became the new closest center, at which point the animal would leave its current attraction center to walk towards the new one. Little by little, an animal would visit several attraction centers during a simulation run, and would often walk on or in close proximity to the road while moving in-between attraction centers.

Scenario 3 is a slightly modified version of scenario 2, intended for animals with flying ability (birds, bats. . .) and using roads as corridors for long-range displacements, or for hunting because roads "drive" preys in the landscape (Kerth & Melber, 2009; Schwartz et al., 2018). Flying animals often make low-altitude flight to catch a prey or land on the road to feed (Grilo et al., 2014; see also the "leap and strike" hunting behaviour of owls: Norberg & Norberg, 1970; Southern, 1954). To this end, we added a third dimension z describing the altitude of the animals to their existing *(x,y)* position on the plane. The altitude was a function of the distance to the nearest attraction center: $z(t) = \exp(0.3 * ||d||) - 1$, $||d||$ the Euclidean distance between the animal and the closest attraction center. This distribution of altitudes entailed that animals got progressively closer to the ground as they approached the attraction center. In consequence, they were only susceptible to collision when within a radius of 5m around a center of attraction.

2.2.4 Scenario 4: road avoidance

The last scenario accommodated animal movement for road avoidance behaviours. Road avoidance has been reported in several species (Grizzly bear (*Ursus arctos*): Mace et al., 1996; Wild boar (*Sus scrofa)* and Red deer (*Cervus elaphus*): D'Amico et al., 2016), possibly resulting from chemical, noise pollution, or road surface avoidance (Andrews & Gibbons, 2005; Schaub et al., 2008; Jaeger et al., 2005). Building upon scenario 2, we only modified the attraction angle to be computed as $\theta^{\flat} + 180°$, meaning that the animal moved away from the center instead of towards it.

2.3 Qualitative and quantitative predictions of the model

For each of the scenarios described above, we derived qualitative and quantitative predictions for 6 parameters of interest, by running the simulation at different values of this parameter while holding everything else constant. The parameters of interest were: animal mean speed, vehicle speed, animal density, traffic volume, weight of attraction centers *w* (scenarios 1 through 4 only) and road sinuosity (Table 2).

Mean animal travel speed values covered the observed speed range of most terrestrial species (from slowest to fastest, migrating amphibians: Hels & Buchwald 2001, foraging badgers (*Meles meles*): San et al. 2007, migrating ungulates: Berger et al. 2006; Singh & Ericsson 2014). Considering that this range is wide, we extracted mean travel speed estimations for several species from the literature (Rowcliffe et al., 2016; Farley et al., 1993) and set our baseline at the mean value of 5 $km.h^{-1}$. Vehicle speed encompassed slow vehicles up to high-speed trains, and the baseline was set at the current speed limit on main roads in France (80 $km.h^{-1}$). Local animal densities, traffic volume ranges and baselines were mostly dictated by computational limitations, although the baseline of 250 $vehicles.hour^{-1}$ is representative of average sized roads in France (French Ministry of Ecological Transition, 2022).

The weight of attraction *w* in BCRW scenarios was a dimensionless unit ranging from 1 (attraction to centers is equal to the correlated direction of the walk, spread-out orbiting behaviour around attraction center) to 20 (when attraction was 20 times more important in walk orientation, animals walked in nearly straight paths toward the attraction center and stayed mostly in place once it was reached). Baseline values for *w* were scenario-dependent as $w = 5$ for scenario 1 ensured that over 90% of animals cross the road in less than 12 hours and $w = 3$ for scenarios 2 and 3 ensured that animals would effectively visit several attraction centers during the simulation run.

Finally, road sinuosity was investigated following observed sinuosities which are publicly available for the road network of Ireland (Transport Infrastructure Ireland, 2022). Two types of results were extracted from simulation runs: the mean number of collisions recorded over the course of a 12 hours run, and the individual probability of collision for animals. Considering that new individuals replaced dead animals, not all animals were present from the start of the simulation run and collision risk was not constant across all animals. Consequently, we estimated the individual probability of collision from a logistic regression (0: alive, 1: hit by a vehicle) as a function of the parameter under study, and where the time of arrival in the simulation was entered as an offset predictive variable (Agresti & Coull, 2002).

Table 2: The six parameters of interest, relating to animal and vehicle movement, and that appear to be pivotal factors driving collision numbers according to most studies (Table 1). While the effects of one parameter on collisions are being explored, all other parameters assume their baseline values. To produce quantitative and qualitative predictions, we explored for each parameter a range of values contained within biologically relevant intervals.

	Parameter of interest	Baseline value	Explored range
ANIMAL	Mean speed ($km.h^{-1}$)	5	0.1 – 30
	Density ($ind.km^{-2}$)	0.016	0.001 – 0.03
	w	5 *(scenario 1)* ; 3 *(scenarios 2-4)*	1 - 20
VEHICLE	Speed ($km.h^{-1}$)	80	30 – 300
	Traffic volume ($vehicle.h^{-1}$)	30	10 – 250
	Road sinuosity index	1 *(straight road)*	1 – 3.5

2.4 Sensitivity analyses of collision number

Sensitivity analyses were conducted on each scenario, following a one-at-a-time approach, meaning that we measured the variation in collision numbers while keeping all input factors fixed except the one that is being perturbed (Saltelli et al., 2019). In practice, we computed the mean number of collisions y for factor of interest x at a reference value x_1, and after 10% increase in value (denoted x_2). To explore possible non-linearity, we repeated this for several reference values x_1 within the relevant range of x (see section 2.3 for parameter ranges). We then defined the sensitivity measure as $OR_{x1} = y_{x2} / y_{x1}$, *i.e.*, the odd ratio of the collision probabilities that results from a 10% increase of parameter x at reference value x_1. For example, an OR_{x1} of 1 indicated no change in the odds of collisions between parameter values x_1 and x_1+10%, while ORx1 > 1 indicated greater odds of collision after a 10% increase in x_1. The overall strength of the influence of parameter x on the collision number in its relevant range was defined by how far the mean of the ratios (OR_{mean}) for all tested values of x deviated from 1 (*e.g.*, OR_{mean} = 1 indicated no overall influence of factor x on collision numbers).

3. Results

3.1 Qualitative and quantitative model predictions

Applying baseline values to all parameters of interest, mean values ranged from 0.16 to 17.2 animal-vehicle collisions over 12 hours (individual probabilities of collision for animals: 0.4% - 45.6%). As expected, the movement of animals had major effects on the probability for an animal to get hit by a car (fig. 3). With baseline parameter values, animals attracted to the road (scenarios 2 and 3) were hit more often than in any other scenario, with an increase in odds of collision for terrestrial animals (scenario 2) compared to flying animals such as birds and bats (scenario 3). Compared to the null model (scenario 0, roaming with no attraction/avoidance of the road), migrating animals crossing the road exactly once (scenario 1) were hit more often, while the odds of collisions for active road avoidance (scenario 4) were reduced. This ranking between scenarios was not always maintained for other values of the tested parameters.

Overall, parameters response functions had similar shapes whether the outcome was measured as the mean number of collisions or as the individual probability of collision, with the exception of animal density. Vehicle speed had no effect on collision numbers and probabilities in any of the scenarios (fig. 3b and 4b). Animal density was positively and linearly associated with collision numbers, which translated into a constant individual probability of collision no matter the local abundance in animals (fig. 3d and 4d). The influence of the remaining parameters (animal speed, weight of attraction, traffic volume and road sinuosity) was non-linear and/or scenario-dependent.

Traveling faster reduced collision numbers and probabilities for migrating animals (scenario 1) but had the opposite effect on roaming and road-avoiding animals (scenarios 0 and 4). In scenarios with road-attracted animals, collision occurrences increased with mean animal speed up to moderate speed values, after which the relation was reversed (fig. 3a, 4a). Higher volumes of traffic on the road increased collision numbers and probabilities although scenarios 0, 2, 3 and 4 present inflexion points after which the increase in collision occurrences slowed down, which was not observed within the explored range of traffic volume for scenario 1 (fig. 3c, 4c). Similarly, increasingly sinuous roads had moderate to low positive effects on collision number and probabilities in all but one scenario: scenario 3 yielded no apparent effect of road sinuosity (fig. 3f, 4f). Finally, increasing weights of attraction (or repulsion for scenario 4) led to more collisions (and higher individual probabilities) in scenarios 2 and 3 with inflexion points around w=5, but increasing w values were associated to less collisions and lower probabilities of WVC in scenarios 1 and 4 (fig. 3e, 4e)

3.2 Sensitivity analyses

For roaming animals (scenario 0), the most influential parameter was the animal density (OR_{mean}=1.091) followed by animal speed (OR_{mean}=1.032). In all other scenarios (scenarios 1, 2, 3 and 4), the weight of attraction *w* had the largest influenced (respectively OR_{mean}=0.888, 2.019, 1.155 and 0.843) followed by animal density (respect. OR_{mean}= 1.098, 1.095, 1.101 and 1.108). The least influential parameters was traffic volume for scenario 0 (OR_{mean}=0.996), vehicle speed for scenarios 1 and 3 (respect. OR_{mean}=1.01, 1.006) and road sinuosity for scenarios 2 and 4 (respect. OR_{mean}=0.998, 0.993). Using OR_{mean} is, however, a simplified view of the non-linear effect of parameters, as it was sometimes pulled in one direction by one or a few extreme OR values. For example, some parameters such as the weight of attraction/repulsion generally had a substantial influence on collision numbers at lower values (w = 1) while higher values had OR values closer to 1 (fig. 5).

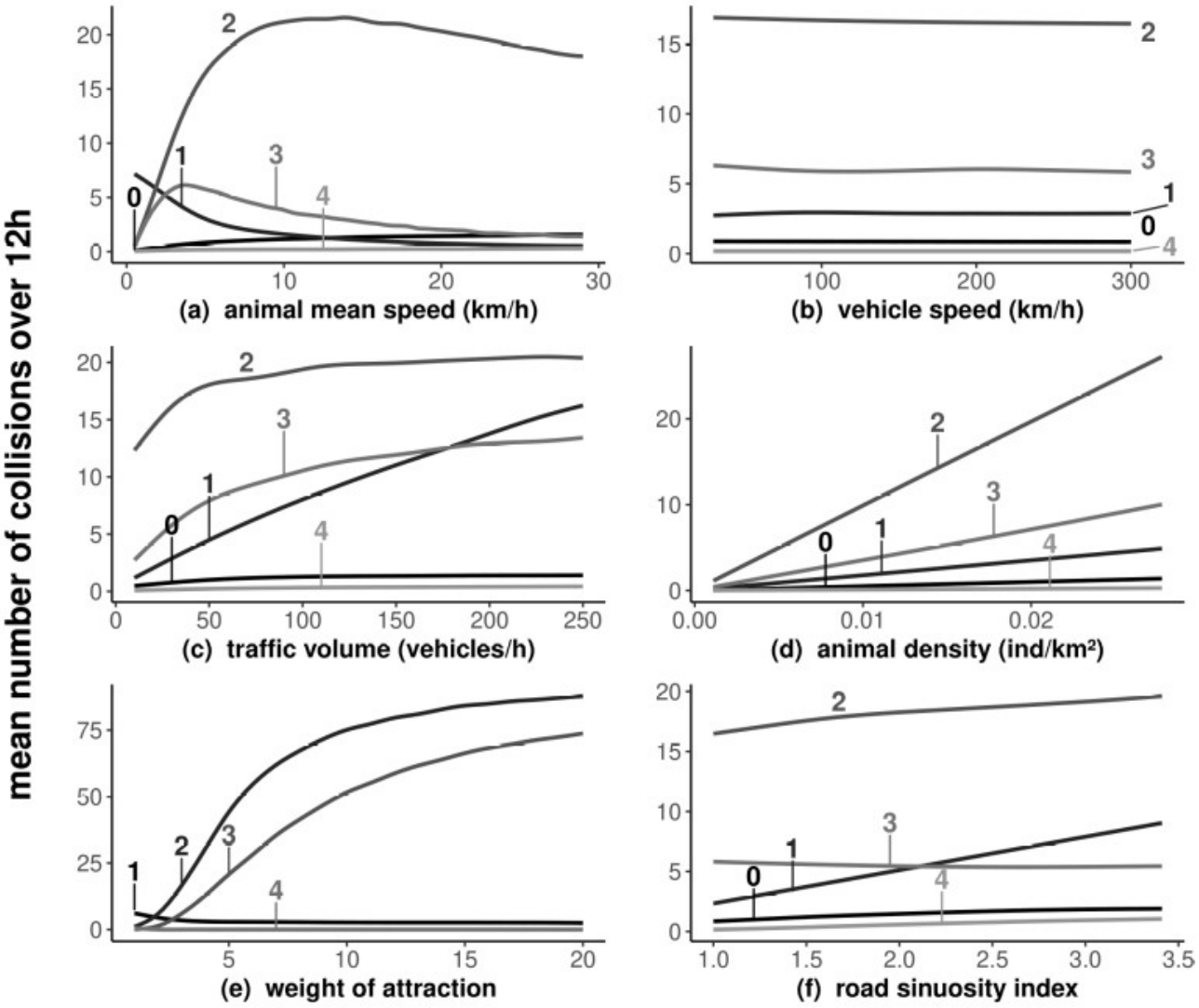


Fig. 3: **Mean number of collisions** - For each scenario, the total number of collisions occurring within a 12-hours simulation run (mean number over 1000 runs). The weight of attraction *w* has no meaning for (non biased) correlated random walks and is therefore not considered for scenario 0.

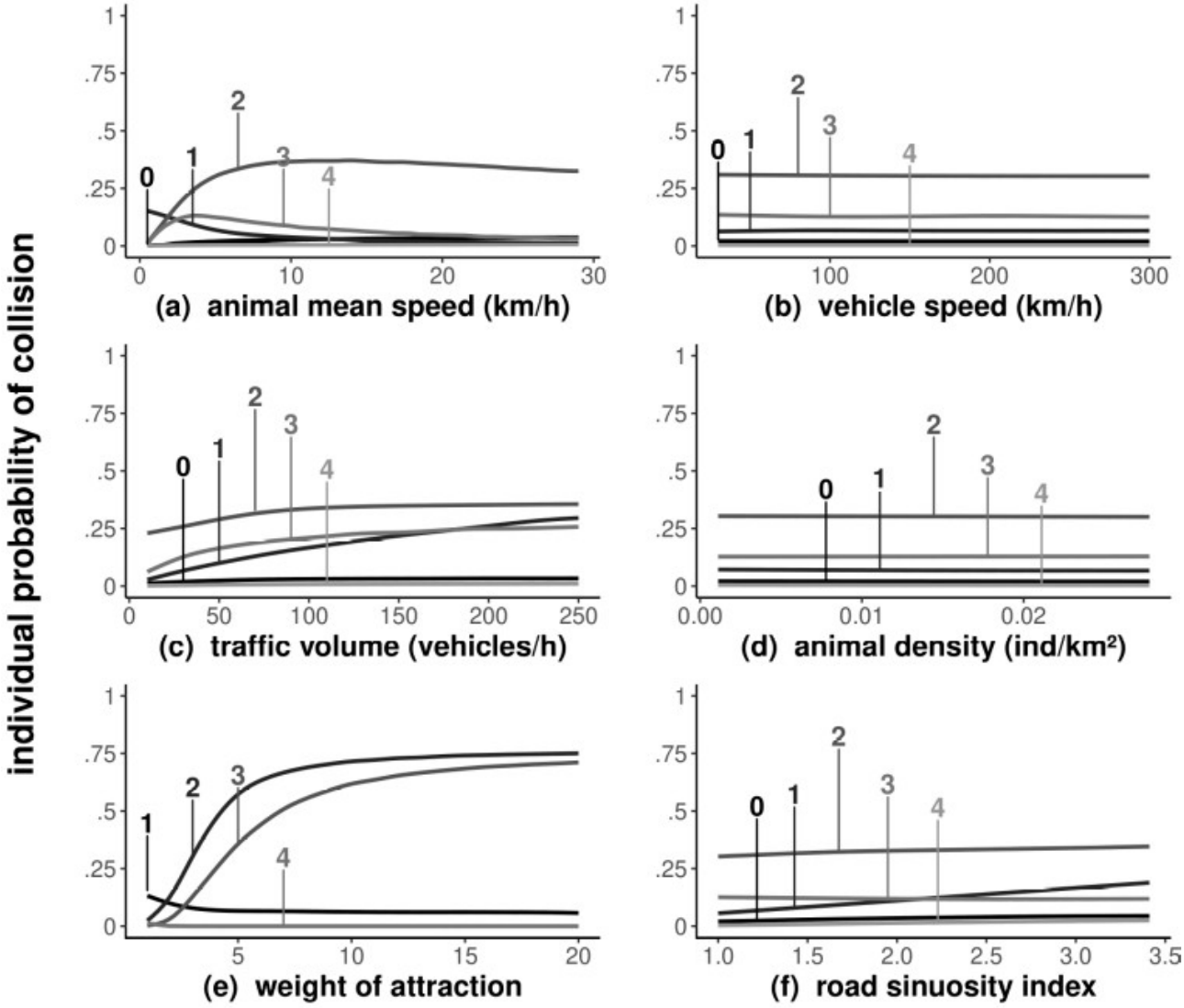


Fig. 4: **Individual probability of collision** - For each scenario, the individual probability of collision estimated from 6 separate logistic regressions in which the studied parameter was used as a response variable and the individual time of exposure to vehicles was used as an offset.

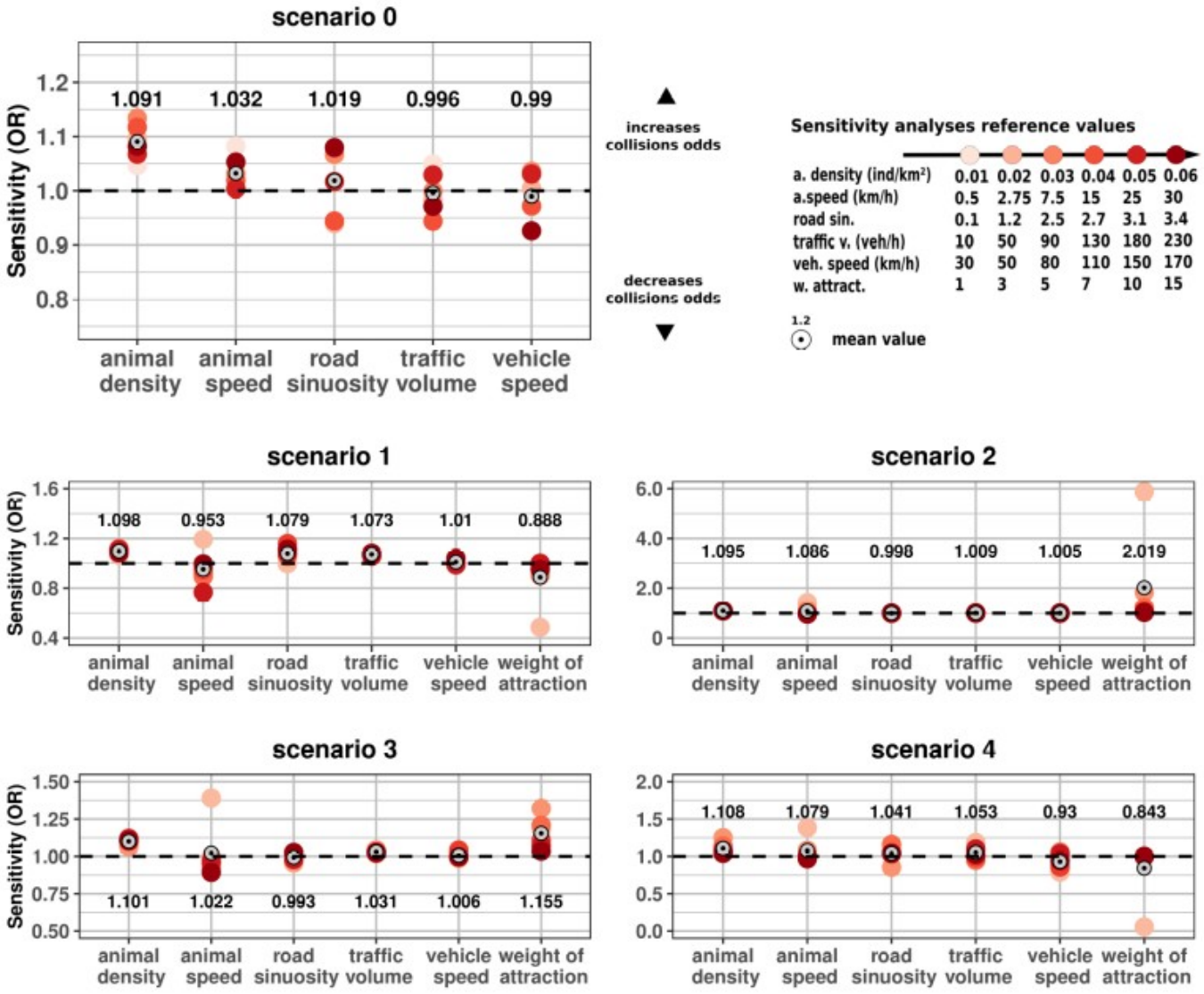


Fig. 5: **Sensitivity analyses** - We compute the odds ratios (OR) of the mean number of collisions for a 10% increase in a given parameter reference value. For example, the darkest circle (●) under ”traffic volume” is the ratio of the mean number of collisions with 230 + 10% = 253 vehicles/hour over the mean number of collisions with 230 vehicles/hour. An OR > 1 shows that an increase in traffic volume has increased the number of collisions (and conversely for OR < 1). The further from 1 the mean is, the more influential the parameter is on collision numbers.

4. Discussion

Road mortality of wildlife is a pervasive and widespread cause of biodiversity loss across the world that should be seriously considered in wildlife management and conservation programs. In spite of its ecological importance and relevance, we are still lacking a strong formalization of WVC to grasp what are its main biological, ecological and anthropogenic determinants. By combining earlier encounter models with the current knowledge about movement ecology, our work should help at formulating qualitative predictions for reducing the number of WVC or to predict what species should be at greater risks of being hit by a vehicle.

Our simulations show how collision numbers and probabilities differ markedly with the movement behaviour of animals, such as migration or ranging, or with its locomotion (terrestrial vs. flight). We suggest this contrast in mortality risk between individuals with different movement types could lead to selection forces on animal habitat use with regard to road avoidance or attraction. In practice, the knowledge about animal movement of species should be an essential part of WVC studies as it seems the most influential variable on WVC occurrence compared to any changes in vehicle speed or road sinuosity for instance.

4.1 Effects of animal movement on WVC risks

WVC broadly results from two competing mechanisms: the number of times an individual will cross or stay close to a road, and the time spent at risk of collision when on the road while crossing, foraging or basking. Both mechanisms are modulated by patterns of space use (in our simulation, the different scenarios of behaviour), and their modulations through the weight of attraction/repulsion w and the speed at which animals travel. Obviously, individuals actively avoiding roads (scenario 4) should be the least at risk of collision with a vehicle and, conversely, terrestrial individuals attracted to the road for foraging or basking (scenario 2) should be the most at risk. This is in line, for example, with Western green lizards (*Lacerta bilineata*) being road-killed in higher proportions than the other sympatric lizard species that do not bask on roads (Meek, 2009). Flying carrion feeders (mostly diurnal and nocturnal raptors) are less likely to be killed than their terrestrial counterparts, a difference that may be further widened by some species' cognition and ability to successfully evade oncoming vehicles, as is the case with corvids (Mukherjee et al., 2013; Lima et al., 2015). Nevertheless, we show here that other parameters of both animal and vehicle movement have the ability to modulate these conclusions. For example, slow moving

animals (less than 15km.h^{-1}) were more often hit when migrating (scenario 1) than roaming freely (scenario 0), but the reverse was true for faster animals (fig. 3a).

By mimicking the presence of attractive or repulsive areas for animals in the landscape, the attraction/repulsion weight (*w*) ultimately controls the time spent in the vicinity of the road, which is positively correlated to collision numbers and probabilities. The relationship between *w* and the time spent on the road is easily interpreted for scenarios of road attraction (scenarios 2 and 3, *w* is positively correlated to time on road surface) and avoidance (scenario 4, *w* value is negatively correlated to time on road surface). When animals travel from a departure point to an attraction center (scenario 1), the time spent crossing is negatively correlated to *w*: high *w* values means straight trajectories between departure and attraction center, and thus less time on the road.

Collision risks in animals roaming freely in a landscape (scenario 0, no *w* variable) are dictated by their speed: the faster the animal, the more it explores its environment during a simulation run and thus encounter roads more often, even though each crossing becomes concurrently less dangerous as fast animals cross the road in less time (see fig. S2 in supplementary material). For the same reason, when animals cross the road only once (scenario 1), we would also expect the animal travel speed to be a key variable in decreasing collision numbers. However, this was not reflected by Or_{mean} in the sensitivity analyses, the most likely explanation being that the mean sensitivity OR_{mean} for travel speed in scenario 1 is pulled up by the odds ratio for very low travel speeds (odds ratio OR0.5 comparing collisions at 0.5 and 0.55 km.h^{-1}) where more animals would cover the distance between their departure point and the road during the simulation when traveling at 0.55 km.h^{-1} (fig. 5). Nevertheless, these results demonstrate that the cumulative time spent on or near roads by animals, through repeated road encounters and/or a long time spent on the road at each encounter (modulated here by patterns of space use, animal speed and biased random walk parameter w), is the most influential parameter driving collisions probabilities for an animal, and has more importance than road characteristics such as traffic volume or speed limits.

These findings are consistent with studies exploring the relationship between landscape features and roadkill hot-spots: factors such as the presence of attractive habitats on roadsides as well as a high connectivity landscapes conducive to wide ranges of movement are often linked to high road mortality (Table 1, see also de Freitas et al. 2013; de Freitas et al. 2015). Similarly, the temporal distribution of roadkill is dictated by the level of activity, and periods of high mobility such as rut, mating or migrating seasons are especially risky for animals (Table 1). Larger home ranges and spread-out exploratory behaviours contribute to higher fitness for individuals by increasing foraging opportunities (Andersson, 1978), but the presence of roads (also applicable to aircrafts, ships or trains) in a landscape lead to costs

in the form of road mortality and selection pressure may lead to road avoidance (Meisingset et al., 2013; Jaeger et al., 2005; Husby & Husby, 2014).

4.2 Effect of animal density on WVC risks

The impact of spatial and temporal variations in animals density has been repeatedly reported as a significant driver of WVC (Joyce & Mahoney, 2001; Taylor et al., 2010; Saint-Andrieux et al., 2020). Some authors suggested that the number of carcasses on roads could serve as an index of animal abundance (Seiler & Helldin, 2006; George et al., 2011). We show that this relationship is linear but strongly modulated by animal movement (fig. 3): compared to animals with no attraction or avoidance towards roads, the slope of the relation between local density and roadkill number is 8 times greater for terrestrial animals attracted to roads and about 70 times smaller when there is road avoidance. When dealing with different species, or with large temporal or spatial scales in which animal movement might be modified by biological seasons and/or landscape features, WVC counts are meaningless, unless the average movement of animals is precisely known. Furthermore, all slopes deviates from isometry ($\beta < 1$), suggesting that the number of casualties on the roads underestimates high population abundances.

Animal density has an impact on collision numbers, but not on the probability of collision for the individual: WVC are coincidental and have no upper threshold for the number of roadkill, contrary to, for example, a predator looking to feed on a set number of prey. Because of this, there is no mechanism of dilution, or “safety in numbers”, in which we might expect a lower collision risk for the individual in a large group of conspecifics (Lehtonen & Jaatinen, 2016). We need to mention that changes in local density have documented effects on individual behaviour which were not explored in the model, and that will in turn affect movement (Kjellander et al., 2004; Dahle & Swenson, 2003; Sword, 2005).

4.3 Effects of traffic volume on WVC risks

A general consensus arises in the literature on the number of WVCs increases with road traffic (Fahrig et al., 1995; Rosen & Lowe, 1994; Inbar & Mayer, 1999; Joyce & Mahoney, 2001). This correlation is, however, much discussed with some authors proposing a linear relationship (Fahrig et al., 1995); and others a barrier effect (high-traffic roads having fewer WVCs than less frequented roads because animals avoid the noise and other disturbances they generate: Seiler & Helldin, 2006; Clevenger et al., 2002; van Langevelde et al., 2009). Others explained the lower-than-expected number of collisions reported on

some high-traffic roads by a depletion of local animal populations due to roadkill (Ascensao et al., 2019). Those arguments may be unnecessary given our results: the theoretical relationship between traffic and WVCs can be non-linear even in the absence of traffic-dependent road avoidance or source-sink dynamics, and roads with heavy traffic would not necessarily have higher collision rates than intermediate roads.

Whatever assumption we make on animal movement, the number and the individual probability of WVC grow asymptotically within the explored range of traffic (fig. 3 and 4). This observation agrees with the mechanistic model of WVCs by Hels & Buchwald (2001) that too predicts a logarithmic relationship between traffic volume and WVC occurrence. A noticeable difference between the two models is that while the probability of dying animals asymptotically approaches 1 for Hels & Buchwald's model, the asymptotic number and probability of WVC lie below a 100% in all our simulations. In one case no asymptote is visible (scenario 1), which possibly results from the limited range of traffic volume we considered due to computational limitations (major highways worldwide can see up to 15 000 vehicles per hour).

4.4 Effects of vehicle speed on WVC risks

In our model, the speed of the moving vehicles is unrelated to the number and individual risk of WVC over the simulated range of speed (0–300 km.h−1, see fig. 3 and 4). At first sight, a lack of effect of vehicle speed may appear at odds with the previous theoretical models suitable for WVC, but it is not: in the ideal gas model (Hutchinson & Waser, 2007), the equations for encounters feature the length of the path of the molecule (speed × time spent moving) rather than the speed itself. In our model, the distance travelled by a vehicle is constant: they move from one end of the road to the other, and a higher speed does not equate with a longer distance, therefore speed does not increase WVC risks. In contrast, on the subject of the animal's speed, when higher speed means longer travel distances (for scenarios 0 and 4; and scenarios 1, 2 and 3 are more complex as the movement is also directed), it leads to higher WVC occurrences and risks. In addition, the travelled distance by vehicles was increased by simulating more tortuous roads (high sinuosity index), and the number and probabilities of collision for animals increased as well (fig. 3), as expected under the ideal gas framework.

For flying carrion feeders (scenario 3) only, sinuosity is not or slightly negatively correlated to WVC numbers and individual probabilities. We do not have a satisfactory answer to this, but suggest that the Euclidean distance between two attraction centers placed on the road changes with road sinuosity and could impact (with our method of simulating flight) the altitude and therefore the collision risk, which is

why terrestrial animals (scenario 2) are not impacted. Road sinuosity can also be treated as a measure of the density of roads, i.e. the surface of road per unit of area, where sinuous roads equate to a higher density than straight roads. In that sense, we show that the density of roads is positively correlated to WVC number and risks.

Both vehicle speed and road sinuosity are among the least influential factors across all space use patterns: we would expect that fast-moving vehicles (*e.g.*, high speed trains)to be no more dangerous to wildlife than slow vehicles. Empirically, speed is regarded as a significant component of WVCs: the faster the vehicles, the more likely is a collision with an animal (Table 1, see also Farmer & Brooks 2012; Hobday & Minstrell 2008). This discrepancy can be explained: fast-moving vehicles equates to reduced reaction time for both animals and drivers (Lima et al., 2015) and vehicles moving at high speeds are most of the time traveling on multi-lane highways with heavy traffic. The reported association between WVCs and vehicle speed may therefore be confounded with unsuccessful collision avoidance, traffic density (that we find to be a strong driver of WVC) or road width (in relation to the time spent crossing the road).

4.5 Model limits

We find that the time spent on the road is the critical factor driving WVC number and probabilities independently of space use patterns, and consequently behaviours we did not implement but that modify the time the animal spends on the road surface (road avoidance, pausing on the road, speeding away from vehicles, evading oncoming vehicles, see Jacobson et al. 2016; Lima et al. 2015) are likely to be key components of WVC occurrences. For example, the implementation of a barrier effect (avoidance of roads proportional to road traffic volume) would have predictable effects on WVC occurrences: we know that the strength of avoidance is negatively correlated to the number and probabilities of WVC (fig. 3 and fig. 4, scenario 4), which indicates that traffic-dependent road avoidance in animals roaming, migrating or foraging on the road (respectively scenarios 0, 1, 2 and 3) will decrease the number and probabilities of collisions proportionally to the volume of traffic. This would lead to the relation between traffic volume and WVC numbers to be an inverted U-shaped curve where roads of intermediate traffic volume are more dangerous than high-traffic and low-traffic roads, as conceptualized by Seiler (2006) and Jacobson et al. (2016). We can predict selection pressure on these behaviours will be strong for populations living in the proximity of roads, as documented in the example of road-adjacent cliff swallow populations being selected for longer wings, allowing for better chances of escaping oncoming vehicles (Brown & Bomberger Brown, 2013).

The main focus of this work was the movement of the animals, and we reduced ”collisions” to the number of times an animal and a vehicle were located less than 5 meters away from each other. This will likely overestimate collision probabilities, especially for smaller-bodied species that can easily fit in-between car tires (Hels & Buchwald, 2001; van Langevelde & Jaarsma, 2005). This is a classical simplification from the ideal as model that we expect will not alter the general patterns we report but simply move all the curves down. Finally, we designed the simulation to have constant animal density, which does not allow for population depletion dynamics (justified by the limited temporal scale of 12 hours per simulation run). Based on our conclusions, the total number of roadkill would decrease linearly with population decline but have no impact on individual probabilities of collision (fig. 3 and fig. 4).

4.6 Practical implications

4.6.1 Investigating roadkill patterns using movement data

The theoretical framework developed here can direct future research on roadkill spatial and temporal patterns. We have shown that collision risks in a landscape for species are highly dependent on their movement characteristics: for example, WVC in species with a home range that are not attracted nor avoiding roads (described by scenario 0) should be best predicted by the speed of movement of the individuals (fig. 5, scenario 0). Faster travel speeds for the individuals should lead to increased collision risks with vehicles (fig. 3a). In section 3 of the supplementary material, we use the case of the European roe deer *Capreolus Capreolus*, whose movements fit the scenario 0 of our model (Saïd et al., 2009). Roe deer movement is season-dependant, with males having distinct peaks in activity during the mating season (March to August, Krop-Benesch et al. 2013). In figure S3a-b, we show the seasonal increases in male roe deer speed in adults and subadults from the GPS data of individuals tracked during in the Bavarian forest, Germany. Temporal collision patterns for this species are also known to peak during spring (Steiner et al., 2021; Mayer et al., 2021). We show roadkill reports from the citizen science database (Faune-Auvergne-Rhône-Alpes) over a period of 12 years (2010 to 2022) in figure S3c. As predicted, seasonal increases in roe deer speed correlate to increases in roadkill reports. Efforts should be made at connecting more often movement ecology to roadkill research to understand the inter-specific and spatio-temporal variations in WVC.

4.6.2 Roadkill mitigation

In this study, we demonstrate that animal movement characteristics are far more important than road characteristics in managing roadkill. More precisely, the time spent on the road by the animal is the main

contributing factor to WVC occurrences, and total roadkill numbers depend on animal density rather than traffic volume or speed. In practice, mitigation measure should therefore focus on keeping animals away from the road by prioritizing fencing, or over-passes and other crossing structures for wildlife over driver-targeted measures such as signage and reduced traffic flow. Crossing structures can also restore connectivity in landscapes where roads represent a significant barrier to movement (Grilo et al., 2011). For species that forage on roads surfaces, we suggest that reducing the attractiveness of the road by removing carrion, salt pools and limiting the presence of preys (such as rodents) on roadsides is the most efficient solution. For example, decommissioning roadside salt pools has been shown to reduce the time moose spend on the road and could in theory reduce moose-vehicle collisions by up to 49% (Rea et al., 2021; Grosman et al., 2009). Mitigation policies should also be species-specific (Teixeira et al., 2013; Saint-Andrieux et al., 2020). Characteristics such as large home ranges, wide diet and habitat breadths will belong to species with a particularly high-risk of WVC, as the animals that explored more of the simulation plane (scenario 0, high animal speed) were more often killed than those that stayed in smaller areas (González-Suárez et al., 2018; Grilo et al., 2020; Ford & Fahrig, 2007).

4.7 Conclusion

Empirical studies focusing on animal behaviour and movement in addition to other biological traits, road-side habitat type and road characteristics can give valuable insights as to why some species are more often killed on roads than others. We show here that animal behaviour in the presence of roads is a key component of roadkill occurrences, and that understanding space use patterns can give insights on the vulnerability of a species to roadkill. Although this model is not intended to provide quantitative predictions of roadkill for particular species, we show that future predictive models should incorporate components of movement ecology to properly address road mortality. Animal behaviours in the proximity of transport infrastructures could also be of interest in evolutionary studies, an aspect of road ecology that is lacking so far in the literature (Brady & Richardson, 2017).

Acknowledgments

This work was performed using the computing facilities of the CC LBBE/PRABI. We thank Simon Benhamou, Jean-Michel Gaillard and Marion Valeix for comments on previous drafts of this work.

Author Contributions

Annaëlle Bénard: coding work and analysis of the data generated, lead writing of the manuscript, equal contribution to the methodology. Thierry Lengagne and Christophe Bonenfant: equal contribution to the methodology, writing, reviewing and editing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Open research statement

Code is provided as private-for-peer review via the following link: https://gitlab.in2p3.fr/annaelle.benard/a-simulation-of-animal-vehicle-collisions.

Upon acceptance data will be publicly accessible. No data were collected for this study.

References

Agresti, A. & Coull, B.A. (2002) The analysis of contingency tables under inequality constraints. *Journal of Statistical Planning and Inference*, 107, 45–73.

Andersson, M. (1978) Optimal foraging area: size and allocation of search effort. *Theoretical population biology*, 13, 397–409.

Andrews, K.M. & Gibbons, J.W. (2005) How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia*, 2005, 772–782.

Ascensao, F., Kindel, A., Teixeira, F.Z., Barrientos, R., D'Amico, M., Borda-de Agua, L. & Pereira, H.M. (2019) Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation*, 19, e00661.

Auger-Methe, M., Derocher, A.E., DeMars, C.A., Plank, M.J., Codling, E.A. & Lewis, M.A. (2016) Evaluating random search strategies in three mammals from distinct feeding guilds. *Journal of Animal Ecology*, 85, 1411–1421.

Avgar, T., Street, G. & Fryxell, J. (2014) On the adaptive benefits of mammal migration. *Canadian Journal of Zoology*, 92, 481–490.

Benhamou, S. (1991) An analysis of movements of the wood mouse *Apodemus sylvaticus* in its home range. *Behavioural Processes.*

Berger, J., Cain, S.L. & Berger, K.M. (2006) Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters*, 2, 528–531.

Berthelot, G., Sa¨ıd, S. & Bansaye, V. (2020) How to use random walks for modeling the movement of wild animals. preprint, bioRxiv.

Brady, S.P. & Richardson, J.L. (2017) Road ecology: shifting gears toward evolutionary perspectives. *Frontiers in Ecology and the Environmen*t, 15, 91–98.

Brehme, C.S., Tracey, J.A., Mcclenaghan, L.R. & Fisher, R.N. (2013) Permeability of Roads to Movement of Scrubland Lizards and Small Mammals: Animal Movement and Road Permeability. *Conservation Biology*, 27, 710–720.

Breiman, L. (1963) The poisson tendency in traffic distribution. *The Annals of Mathematical Statistics*, 34, 308–311.

Brown, C.R. & Bomberger Brown, M. (2013) Where has all the road kill gone? *Current Biology*, 23, R233–R234.

Carvalho-Roel, C.F., Iannini-Custodio, A.E. & Marc¸al Junior, O. (2019) Do roadkill aggregations of wild and domestic mammals overlap? *Revista de Biologia Tropical*, 67, 47–60.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science*, 296, 904–907.

Clevenger, A.P., Chruszcz, B. & Gunson, K.E. (2002) Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation*, 109, 285–287.

Coffin, A.W. (2007) From roadkill to road ecology: a review of the ecological effects of roads. *Journal of transport Geography*, 15, 396–406.

Corlett, R.T. (2015) The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, 30, 36–41.

Dahle, B. & Swenson, J.E. (2003) Home ranges in adult scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, 260, 329–335.

D'Amico, M., Periquet, S., Roman, J. & Revilla, E. (2016) Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology*, 53, 181–190.

D'Amico, M., Rouco, C., Russell, J.C., Roman, J. & Revilla, E. (2013) Invaders on the Road: Synanthropic Bird Foraging Along Highways. *Oecologia Australis*, 17, 86–95.

Davenport, J. & Davenport, J. (2006) T*he Ecology of Transportation: Managing Mobility for the Environment*, volume 10. ISSN: 1566-0745.

de Freitas, S.R., Sousa, C.O. & Bueno, C. (2013) Effects of landscape characteristics on roadkill of mammals, birds and reptiles in a highway crossing the atlantic forest in southeastern brazil. *International Conference on Ecology and Transportation (ICOET 2013)*. Arizona.

de Freitas, S.R., de Oliveira, A.N., Ciocheti, G., Vieira, M.V. & da Silva Matos, D.M. (2015) How landscape patterns influence road-kill of three species of mammals in the brazilian savanna. *Oecologia Australis*, 18.

Duchesne, T., Fortin, D. & Rivest, L.P. (2015) Equivalence between Step Selection Functions and Biased Correlated Random Walks for Statistical Inference on Animal Movement. *ONE*, 10, e0122947.

Eddelbuettel, D. & Balamuta, J.J. (2018) Extending extitR with extitC++: A Brief Introduction to extitRcpp. *The American Statistician*, 72, 28–36.

Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D. & Wegner, J.F. (1995) Effect of road traffic on amphibian density. *Biological conservation*, 73, 177–182.

Farley, C.T., Glasheen, J. & McMahon, T.A. (1993) Running springs: speed and animal size. *Journal of experimental Biology*, 185, 71–86.

Farmer, R.G. & Brooks, R.J. (2012) Integrated risk factors for vertebrate roadkill in southern Ontario. *The Journal of Wildlife Management*, 76, 1215–1224.

Ford, A.T. & Fahrig, L. (2007) Diet and body size of North American mammal road mortalities. *Transportation Research Part D: Transport and Environment*, 12, 498–505.

Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207–231.

Fraser, D. & Thomas, E.R. (1982) Moose-Vehicle Accidents in Ontario : Relation to Highway Salt. *The Wildlife Society Bulletin*, 10, 261–265.

George, L., Macpherson, J.L., Balmforth, Z. & Bright, P.W. (2011) Using the dead to monitor the living: can road kill counts detect trends in mammal abundance? *Applied Ecology and Environmental Research*, 9, 27–41.

Gibbs, J.P. & Shriver, W.G. (2002) Estimating the Effects of Road Mortality on Turtle Populations. *Conservation Biology*, 16, 1647–1652.

Girardet, X., Conruyt-Rogeon, G. & Foltete, J.C. (2015) Does regional landscape connectivity influence the location of roe deer roadkill hotspots? *European Journal of Wildlife Research*, 61, 731–742.

Gomes, L., Grilo, C., Silva, C. & Mira, A. (2009) Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. *Ecological Research*, 24, 355–370.

Gonzalez-Suarez, M., Ferreira, F.Z. & Grilo, C. (2018) Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, 27, 1093–1105.

Grilo, C., Reto, D., Filipe, J., Ascensao, F. & Revilla, E. (2014) Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. *Animal Conservation*, 17, 555–564.

Grilo, C., Bissonette, J. & Cramer, P. (2011) *Mitigation measures to reduce impacts on biodiversity*, pp. 73–114.

Grilo, C., Koroleva, E., Andrasik, R., B´ıl, M. & Gonzalez-Suarez, M. (2020) Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, 18, 323–328.

Grosman, P.D., Jaeger, J.A., Biron, P.M., Dussault, C. & Ouellet, J.P. (2009) Reducing moose-vehicle collisions through salt pool removal and displacement: An agent-based modeling approach. *Ecology and Society*, 14.

Hels, T. & Buchwald, E. (2001) The effect of road kills on amphibian populations. *Biological Conservation*, 99, 331–340.

Hobday, A.J. & Minstrell, M.L. (2008) Distribution and abundance of roadkill on Tasmanian highways: Human management options. *Wildlife Research*, 35, 712–726.

Holderegger, R. & Di Giulio, M. (2010) The genetic effects of roads: a review of empirical evidence. *Basic and Applied Ecology*, 11, 522–531.

Husby, A. & Husby, M. (2014) Interspecific analysis of vehicle avoidance behavior in birds. *Behavioural Ecology*, 25, 504–508.

Hutchinson, J.M. & Waser, P.M. (2007) Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews*, 82, 335–359.

Inbar, M. & Mayer, R.T. (1999) Spatio-Temporal Trends in Armadillo Diurnal Activity and Road-Kills in Central Florida. *Wildlife Society Bulletin* (1973-2006), 27, 865–872.

Jacobson, S.L., Bliss-Ketchum, L.L., De Rivera, C.E. & Smith, W.P. (2016) A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, 7, 1–15.

Jaeger, J.A., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. & Von Toschanowitz, K.T. (2005) Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling*, 185, 329–348.

Joyce, T.L. & Mahoney, S.P. (2001) Spatial and Temporal Distributions of Moose-Vehicle Collisions in Newfoundland. *Wildlife Society Bulletin* (1973-2006), 29, 281–291.

Kerth, G. & Melber, M. (2009) Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, 142, 270–279.

Kjellander, P., Hewison, A., Liberg, O., Angibault, J.M., Bideau, E. & Cargnelutti, B. (2004) Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus L.*): a comparison of two long-term studies. *Oecologia*, 139, 478–485.

Krop-Benesch, A., Berger, A., Hofer, H. & Heurich, M. (2013) Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology*, 80, 69–81.

Legagneux, P. & Ducatez, S. (2013) European birds adjust their flight initiation distance to road speed limits. *Biology Letters*, 9, 20130417.

Lehtonen, J. & Jaatinen, K. (2016) Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, 70, 449–458.

Lima, S.L., Blackwell, B.F., DeVault, T.L. & Fern ´andez-Juricic, E. (2015) Animal reactions to oncoming vehicles: a conceptual review. *Biological reviews of the Cambridge Philosophical Society*, 90, 60–76.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J. & Zuuring, H. (1996) Relationships Among Grizzly Bears, Roads and Habitat in the Swan Mountains Montana. *Journal of Applied Ecology*, 33, 1395–1404. Publisher: [British Ecological Society, Wiley].

Maxwell, J.C. (1860) V. Illustrations of the dynamical theory of gases.—Part I. On the motions and collisions of perfectly elastic spheres. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, 19, 19–32.

Mayer, M., Coleman Nielsen, J., Elmeros, M. & Sunde, P. (2021) Understanding spatio-temporal patterns of deer-vehicle collisions to improve roadkill mitigation. *Journal of Environmental Management*, 295, 113148.

Medinas, D., Marques, J.T., Costa, P., Santos, S., Rebelo, H., Barbosa, A.M. & Mira, A. (2021) Spatiotemporal persistence of bat roadkill hotspots in response to dynamics of habitat suitability and activity patterns. *Journal of Environmental Management*, 277, 111412.

Meek, R. (2009) Patterns of reptile road-kills in the Vendée region of western France. *Herpetological Journal*, 19, 135–142.

Meisingset, E.L., Loe, L.E., Brekkum, Ø., Van Moorter, B. & Mysterud, A. (2013) Red deer habitat selection and movements in relation to roads. *Journal of Wildlife Management*, 77, 181–191.

Meunier, F.D., Verheyden, C. & Jouventin, P. (2000) Use of roadsides by diurnal raptors in agricultural landscapes. *Biological Conservation*, 92, 291–298.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos*, 117, 654–664.

Mukherjee, S., Ray-Mukherjee, J. & Sarabia, R. (2013) Behaviour of American Crows (*Corvus brachyrhynchos*) when encountering an oncoming vehicle. *The Canadian Field-Naturalist*, 127, 229–233.

Marell, A., Ball, J.P. & Hofgaard, A. (2002) Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology*, 80, 854–865.

Norberg, R. & Norberg, R.A. (1970) Hunting Technique of Tengmalm's Owl *Aegolius funereus (L.). Ornis Scandinavica*, 1, 51.

Ratton, P., Secco, H. & da Rosa, C.A. (2014) Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research*, 60, 543–546.

Raymond, S., Schwartz, A.L.W., Thomas, R.J., Chadwick, E. & Perkins, S.E. (2021) Temporal patterns of wildlife roadkill in the UK. *PLoS One*, 16, e0258083.

Rea, R.V., Scheideman, M.C., Hesse, G. & Mumma, M.A. (2021) The effectiveness of decommissioning roadside mineral licks on reducing moose (*Alces alces*) activity near highways: implications for moose–vehicle collisions. *Canadian Journal of Zoology*, 99, 1009–1019.

Refinetti, R. (1999) Relationship between the daily rhythms of locomotor activity and body temperature in eight mammalian species. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 277, R1493–R1500.

Rosen, P.C. & Lowe, C.H. (1994) Highway mortality of snakes in the sonoran desert of southern Arizona. *Biological Conservation*, 68, 143–148.

Rowcliffe, J.M., Jansen, P.A., Kays, R., Kranstauber, B. & Carbone, C. (2016) Wildlife speed cameras: measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, 2, 84–94.

Ryu, M. & Kim, J.G. (2020) Influence of roadkill during breeding migration on the sex ratio of land crab (*Sesarma haematoche*). *Journal of Ecology and Environment*, 44, 23.

Ryu, M. & Kim, J.G. (2021) Coastal road mortality of land crab during spawning migration. *Scientific Reports*, 11, 6702.

Said, S., Gaillard, J.M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D. & Roux, C. (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, 118, 1299–1306.

Saint-Andrieux, C., Calenge, C. & Bonenfant, C. (2020) Comparison of environmental, biological and anthropogenic causes of wildlife–vehicle collisions among three large herbivore species. *Population Ecology,* 62, 64–79.

Saltelli, A., Aleksankina, K., Becker, W., Fennell, P., Ferretti, F., Holst, N., Li, S. & Wu, Q. (2019) Why so many published sensitivity analyses are false: A systematic review of sensitivity analysis practices. *Environmental Modelling & Software*, 114, 29–39.

San, E.D.L., Ferrari, N. & Weber, J.M. (2007) Spatio-temporal ecology and density of badgers *Meles meles* in the swiss jura mountains. *European Journal of Wildlife Research*, 53, 265–275.

Schaub, A., Ostwald, J. & Siemers, B.M. (2008) Foraging bats avoid noise. *Journal of Experimental Biology*, 211, 3174–3180.

Schooley, R.L. & Wiens, J.A. (2003) Finding habitat patches and directional connectivity. *Oikos*,

102.

Schwartz, A.L., Williams, H.F., Chadwick, E., Thomas, R.J. & Perkins, S.E. (2018) Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, 4, 1–7.

Seiler, A. & Helldin, J.O. (2006) *Mortality in wildlife due to transportation.* pp. 165–189.

Sillero, N. (2008) Amphibian mortality levels on Spanish country roads: Descriptive and spatial analysis. *Amphibia Reptilia*, 29, 337–347.

Silveira Miranda, J.E., de Melo, F.R. & Keichi Umetsu, R. (2020) Are Roadkill Hotspots in the Cerrado Equal Among Groups of Vertebrates? *Environmental managemen*t, 65, 565–573.

Singh, N.J. & Ericsson, G. (2014) Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. *Biology letters*, 10, 20140379.

Siniff, D.B. & Jessen, C.R. (1969) *A Simulation Model of Animal Movement Patterns. Advances in Ecological Research, volume 6*, pp. 185–219. Academic Press, Cambridge, MA, USA.

Southern, H.N. (1954) Tawny Owls and Their Prey. *Ibis*, 96.

Steiner, W., Leisch, F. & Hackl ¨ander, K. (2014) A review on the temporal pattern of deer-vehicle accidents: Impact of seasonal, diurnal and lunar effects in cervids. *Accident Analysis and Prevention,* 66, 168–181.

Steiner, W., Scholl, E.M., Leisch, F. & Hacklander, K. (2021) Temporal patterns of roe deer traffic accidents: Effects of season, daytime and lunar phase. *PLoS One*, 16, e0249082.

Sword, G.A. (2005) Local population density and the activation of movement in migratory band-forming mormon crickets. *Animal Behaviour,* 69, 437–444.

Taylor, B.D., Goldingay, R.L., Taylor, B.D. & Goldingay, R.L. (2010) Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research,* 37, 320–331.

Teixeira, F.Z., Coelho, I.P., Esperandio, I.B., Rosa Oliveira, N., Porto Peter, F., Dornelles, S.S., Rosa Delazeri, N., Tavares, M., Borges Martins, M. & Kindel, A. (2013) Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis,* 17, 36–47.

Teixeira, F.Z., Kindel, A., Hartz, S.M., Mitchell, S. & Fahrig, L. (2017) When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, 54, 1544–1551.

van Langevelde, F. & Jaarsma, C.F. (2005) Using traffic flow theory to model traffic mortality in mammals. *Landscape ecology*, 19, 895–907.

van Langevelde, F., van Dooremalen, C. & Jaarsma, C.F. (2009) Traffic mortality and the role of minor roads. *Journal of Environmental Management*, 90, 660–667.

Van Moorter, B., Visscher, D., Benhamou, S., B ¨orger, L., Boyce, M.S. & Gaillard, J.M. (2009) Memory keeps you at home: A mechanistic model for home range emergence. *Oikos*, 118, 641–652.

Supplementary Material

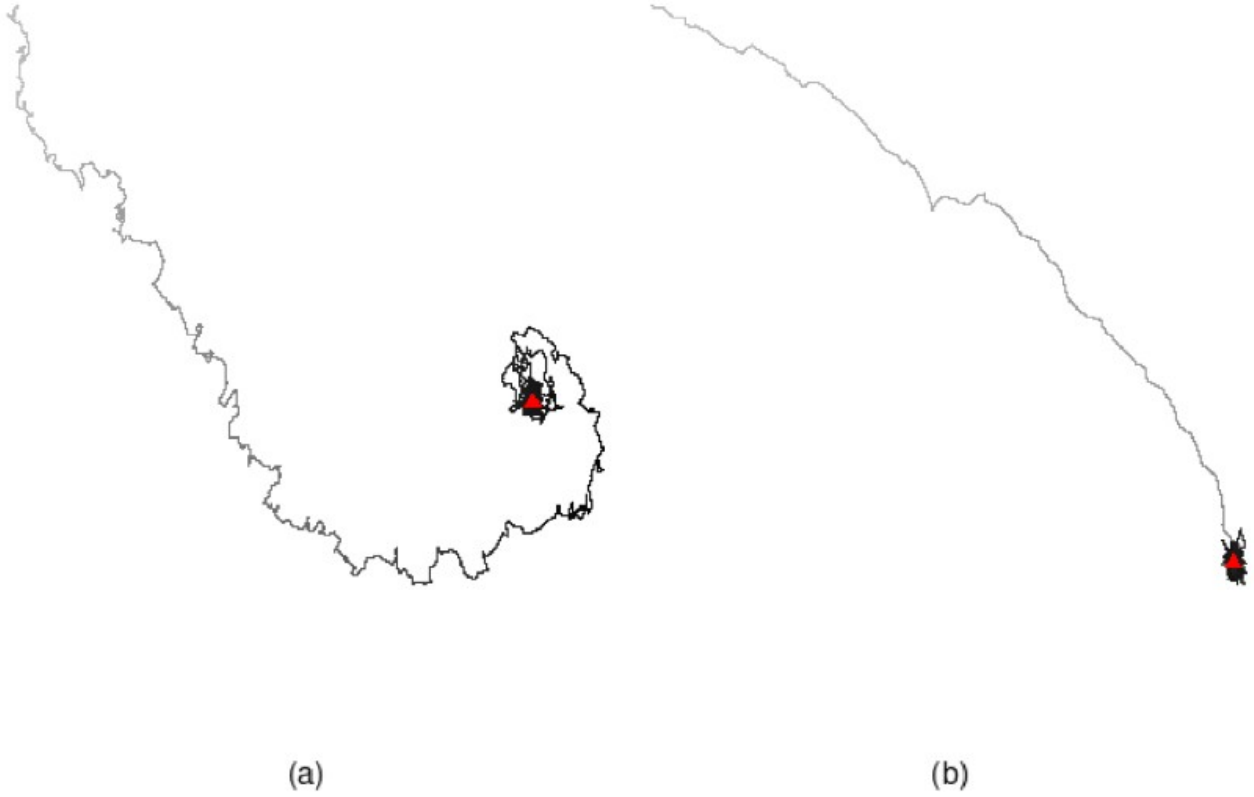


Fig. S1: The animals' movements are simulated using biased correlated random walks. The orientation of the walks is computed for each time step as a weighted mean between the persistence (correlated random walk) and the directional bias towards a center of attraction (▲). (a): the weight of attraction is w=3. (b): the weight of the attraction is w=20. The higher the weight w of the directional bias, the quicker the animal reaches the center. Once the attraction center is reached, the animal will orbit around it indefinitely.

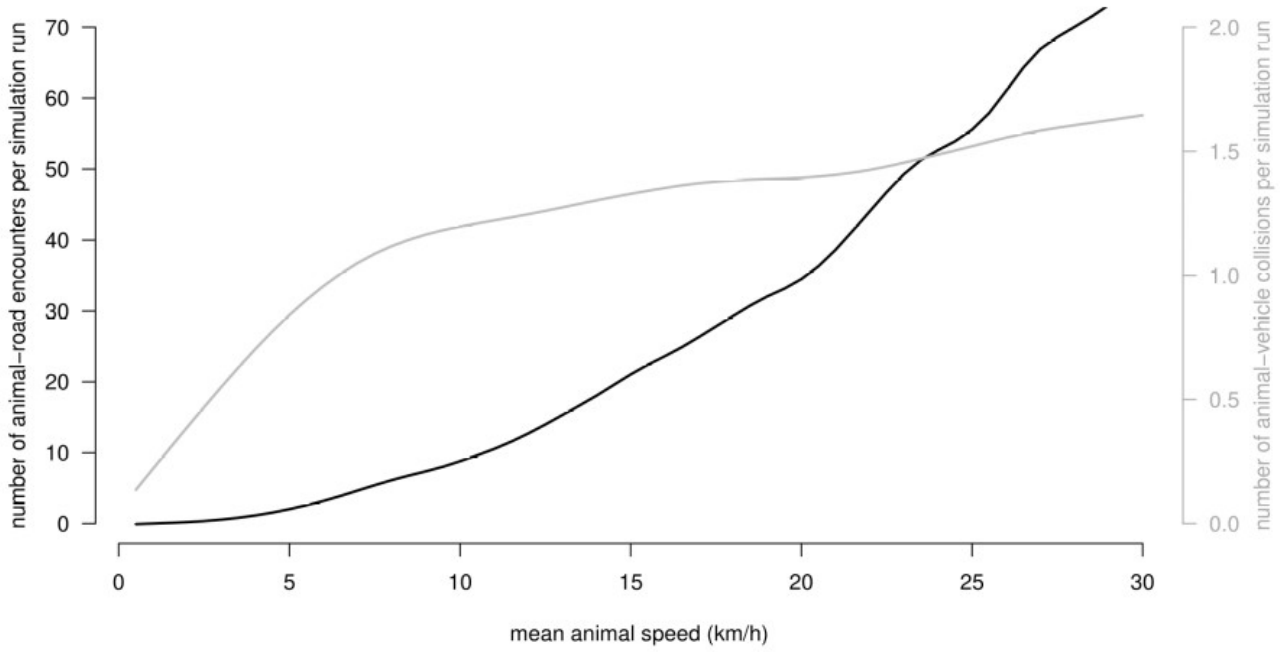


Fig. S2: For animals roaming freely (scenario 0), we retrieve from the WVC simulation both the mean number of animal-road encounters (black line) and the number of actual animal-vehicle collisions (grey line) per simulation run. The distance each animal travels during each run increases with animal speed, leading to more animals encountering the road more often. Simultaneously, faster animals decrease their probability of collision per road crossing as they cross the road in less time. As a result, the number of collisions does not increase with the same rate as the number of road encounters: increasing the mean animal speed produces more but less dangerous road encounters for animals.

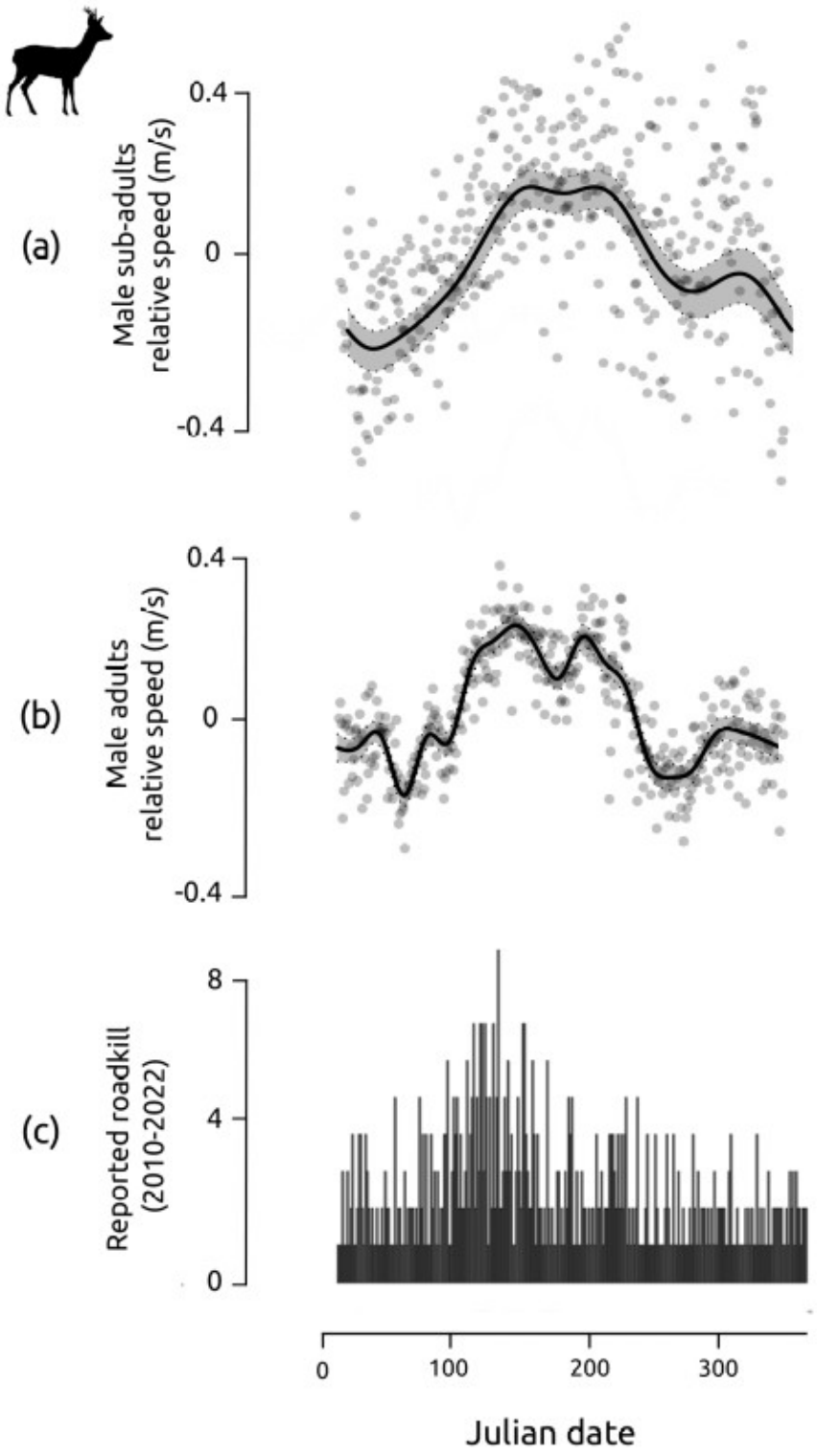
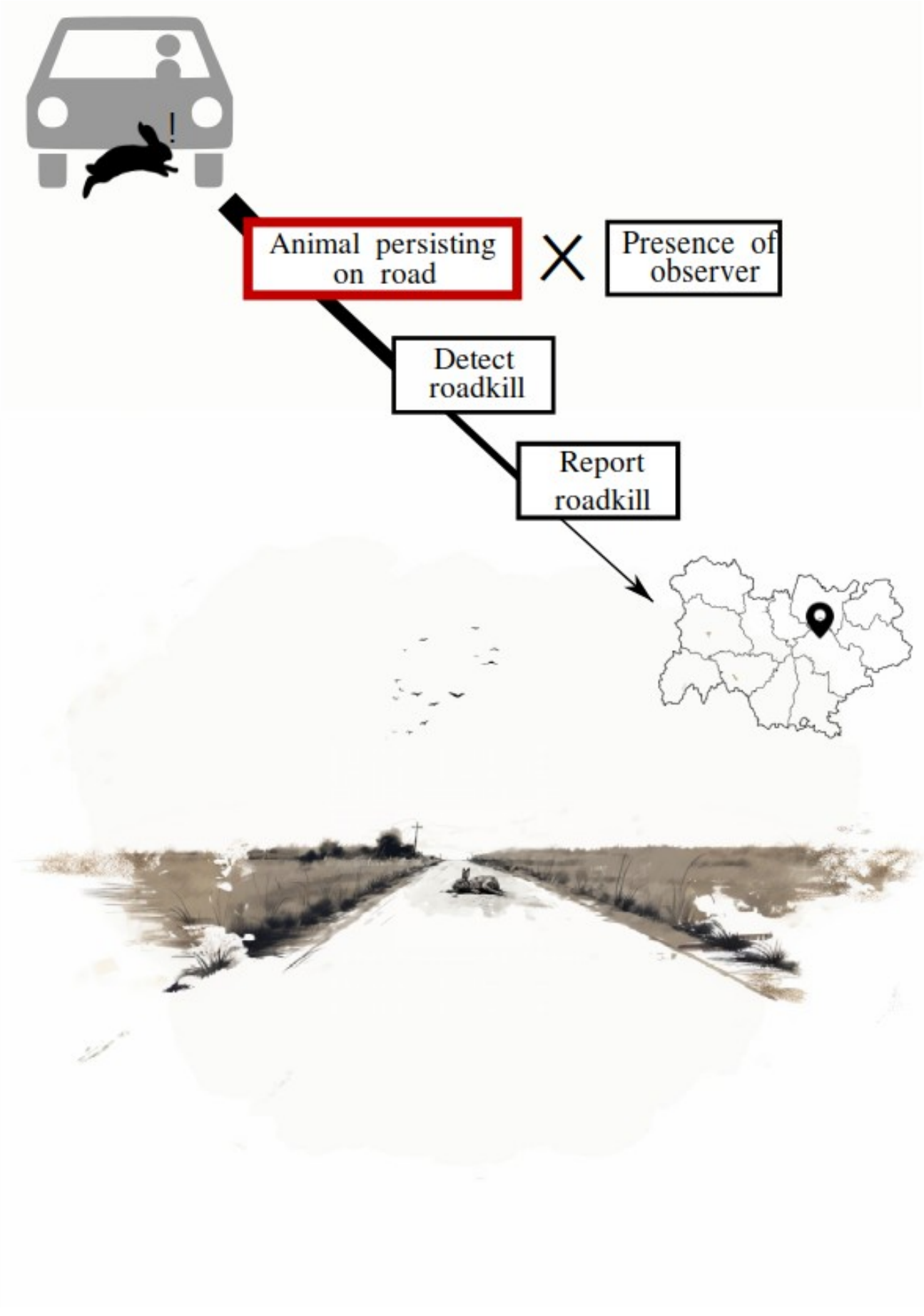


Fig. S3: Seasonal patterns in male individuals' speed (deviation to the mean, a,b) and reported roadkill (c) for the European roe deer *Capreolus capreolus*. We obtained 672 roadkill data from the citizen science database Faune-Auvergne-Rhône-Alpes (fauneauvergnerhonealpes.org), between 2010 and 2022 in the Auvergne-Rhône-Alpes region of France. The speed for male roe deer (adults and sub-adults) was measured on GPS-tracked individuals during in the Bavarian forest (Germany). Male roe deer have distinct peaks in speed and activity during the mating season (March to August). Increases in individual speed correlate to increases in the number of roe deer-vehicles collisions reported, as predicted by the wildlife-vehicle model (fig. 2&4, scenario 0).

Chapter 2: Roadkill persistence on the road



Influence of traffic and weather on small wildlife carcass persistence time on roads (under review)

Annaëlle Bénard, Thierry Lengagne and Christophe Bonenfant

Transportation Research Part D: Transport and Environment

DOI: 10.1016/j.trd.2023.104012

CONTEXT

The expansion of road networks is posing a threat to the survival of many terrestrial species due to the increasing number of wildlife-vehicle collisions. However, the roadkill datasets underestimate collision numbers, as the persistence of roadkill carcasses is often shorter than the frequency at which roads are monitored.

At present, estimates of persistence only have a temporal resolution of 24 hours, while also concluding that most roadkill is removed within a day. Unfortunately, more detailed persistence estimates at finer temporal scales are not available for most species.

OBJECTIVES

- Estimate the persistence of two types of small-bodied roadkill (amphibians and small passerines) with a temporal resolution of 2 hours.

- Evaluate the spatio-temporal structure of persistence times by testing roadkill persistence under varying conditions of traffic volume and in the presence and absence of rainfall.

- Integrate the persistence estimates into the Faune-AuRA roadkill dataset, allowing for more accurate estimates of the number of collisions in the Auvergne-Rhône-Alpes region.

KEY RESULTS

- Amphibian persistence was strongly influenced by road traffic, with median persistence ranging from 1 to 18 hours. Passerine persistence was independent of road traffic, and they persisted on average less than 2 hours.

- Rainfall had no significant effect on persistence times.

- We estimated that up to 700,000 small passerines fatalities occurred in 2022 in the Auvergne-Rhône-Alpes.

CONCLUSIONS

- Most amphibians and small passerines persist on roads for only a few hours, leading to a probable significant underestimation of their mortality in uncorrected roadkill datasets.

- Persistence of roadkill and its spatial structure are species-dependent. This structure suggests that uncorrected roadkill datasets also incorrectly estimate the influence of road traffic on collision rates.

- The magnitude of small passerine road mortality is much greater than previously suspected.

Abstract

The rapidly expanding road network threatens the persistence of many terrestrial species through mortality associated with wildlife-vehicle collisions. Roadkill monitoring under-estimate actual collision numbers, as the time during which roadkill carcasses remain visible on the road is often shorter than the frequency of road monitoring. By placing passerine and amphibian carcasses on stretches of roads we surveyed every 2 hours, we fine-tuned existing persistence estimates for these species. The time for half of the carcasses to disappear was less than 30 minutes for birds and 1-18 hours for amphibians depending on the volume of traffic, which is much shorter than previous estimates. We show the implications of these results by performing roadkill surveys on common toads 3 hours after the window of reproductive migration, showing roadkill is under-estimated by half, and by estimating from citizen science data that passerine collisions could be as high as 10 individuals/km²/year in France.

1. Introduction

Human activities and their role in the ongoing global biodiversity decline have been identified as the main cause of biodiversity loss over the past decades (Pollock et al., 2020). Of particular importance are linear transportation infrastructures such as roads (Forman et al., 2003) that threaten the viability of many wildlife populations (Moore et al., 2023), first and foremost of endangered species (Martin et al., 2018; Shepard et al., 2008; Taylor & Goldingay, 2009). The rapidly expanding road network concentrates all major threats of biodiversity at particular locations in space (Forman & Alexander, 1998; Rytwinski & Fahrig, 2015) jeopardizing the fitness of individuals. First, road surfaces hamper animal movement and gene flows through habitat fragmentation and destruction (Goosem, 2007; Lesbarrères & Fahrig, 2012; Prunier et al., 2014). Chemical pollutants accumulating on roads alter the composition of roadside vegetation communities, often favoring the expansion of invasive species (Lagerwerff & Specht, 2002; Nunes et al., 2020; Valladares et al., 2008). Traffic noise and light were shown to alter physiology and behaviour, lower the reproductive success, and deter the presence of multiple species up to several hundreds of meters away from the road (Lengagne, 2008; Parris & Schneider, 2009; Reijnen & Foppen, 1994; Troïanowski et al., 2017). Finally, of all these ecological effects, roadkill is perhaps the most critical driver of biodiversity loss in relation to roads: wildlife-vehicle collisions most likely affect all terrestrial species, but on a scale we have yet to fully understand (Grilo et al., 2020, 2021; Moore et al., 2023).

One reason for this lack of knowledge is the quantification of roadkill numbers that are likely heavily underestimated due to unknown persistence and imperfect detection of dead animals along roads. Past studies suggested that performing road surveys on foot or bike at low speed improves accuracy by increasing the detection rates of roadkill carcasses (Barrientos et al., 2018; Ogletree & Mead, 2020). Once killed, an animal can either be scavenged, mechanically disappear with the flow of vehicles, or be displaced by people. This persistence time of carcasses on the road dictates the amount of time carcasses are at risk of detection (Ratton et al., 2014). The direct consequence of a persistence time of carcasses shorter than the frequency of surveys is a severe underestimation of roadkill numbers. Surprisingly, few authors have focused on the importance of carcass persistence and its structuring factors in roadkill surveys (but see Ratton et al., 2014; Santos et al., 2011; Teixeira et al., 2013).

Most attempts at estimating the persistence time of carcasses focus on scavenging rates using chicks and other small-bodied animals as bait for carrion feeders, and find that these carcasses seldom persist more than a few days after being placed on the road (Antworth et al., 2005; Ratton et al., 2014; Santos & Ascensão, 2019; Schwartz et al., 2018). Santos et al. (2011) recorded persistence times for a wide range of species and have highlighted the roles of road traffic, species and seasons on carcass removal rates.

They found that carcasses disappeared quicker from smaller roads, possibly because low traffic volumes allow carrion-feeders easier access to roadkill (see also Ratton et al., 2014). Rain and high humidity also accelerated carcass disappearance. Humid conditions promote faster soft tissue decay (Brand et al., 2003), and Santos et al. (2011) suggested that in the case of roadkill, humidity promotes carcass dismemberment by vehicles. To our knowledge, there is no other published data on the relation between rain and roadkill persistence. The position of the carcass on the road also has been shown to influence persistence, with rodent carcasses on the lane disappearing faster than carcasses on the road shoulder (Santos & Ascensão, 2019).

The median persistence time (*i.e.*, the time at which 50% of the carcasses have disappeared) of small-bodied fauna including reptiles, amphibians, small birds (<200 g), bats and other small mammals (<300 g) is approximately 1 day (Santos & Ascensão, 2019; Santos et al., 2011). Considering that in these studies, the surveys were done every 24 hours, median persistence time for these species might in reality be even less than a day. Indeed, Stewart (1971) placed 50 house sparrow carcasses on the surface of a highway and found that none remained after 2 hours. Roadkill surveys, even when performed daily, may under-estimate the number of collisions for the smallest species. Given the distribution of body size among mobile and terrestrial vertebrates (Smith & Lyons, 2013), road mortality could likely be underappreciated for 60% of the extent species. Consequently, efficient mitigation and conservation measures for these species require accurate estimations of persistence time and its spatio-temporal variability (Teixeira et al., 2013).

Many small species of vertebrates are indeed of conservation concerns (Pereira et al., 2010). Roadkill data for small-bodied species such as rodents, small passerines or reptiles is scarce (but see Meek, 2009; Morelli et al., 2020; Ruiz-Capillas et al., 2015). Amphibian roadkill is better documented because massive roadkill occurs during the breeding season when amphibians leave their terrestrial habitat to gather in breeding ponds. It is the most endangered vertebrate group and has shown a significant decline in the last decades due to environmental disturbance (Wise, 2007). Mitigation measures were often used to reduce mortality during road crossings (Beebee, 2013; Helldin & Petrovan, 2019; Testud, 2020). Yet, for all small-bodied species including amphibians, we lack good quality data leading to robust estimations of persistence time, and consequently are left with unreliable estimates of roadkill occurrence.

To fill the gap in knowledge for small-bodied wildlife road mortality, we experimentally estimated the persistence time after a collision by placing carcasses on roads and monitoring their removal time and rate at a fine temporal resolution of 2 hours. We estimated persistence time on roads of different traffic volumes and under different weather conditions, predicting that persistence time would be shorter on

smaller roads and in high humidity conditions (Santos et al., 2011). As carcass position on the lane could affect persistence (Antworth et al., 2005; Santos & Ascensão, 2019), we randomized the placement of the animal. Santos et al. (2011) found significant differences in persistence between species of similar body sizes but different taxa, so we used both small amphibians and birds (< 20g) in an effort to generalize our results to other small-sized species. Lastly, using roadkill surveys we performed during the reproductive migration of the common toad *Bufo bufo* and citizen science data on small passerine road mortality, we estimated the proportion of missed carcasses, and therefore the number of amphibian roadkill during surveys as well as the number of small passerine roadkill in the Auvergne-Rhône-Alpes region France.

2. Material and Methods

2.1 Study location and sampling design

We measured persistence time between March and July 2022 for dry days, October and December 2022 for rainy days. We bought amphibian carcasses (*Pelophylax kl. esculentus)* from a licensed supplier (SONODIS) and procured small passerine carcasses (< 20g) from a wildlife rehabilitation center (Le Tichodrome, Isère, France). We stored all carcasses at -20°C and thawed them for 24h before the day of the experiment.

We selected 4 roads for passerine trials, and 7 roads for amphibians (speed limit: 80 $km.h^{-1}$). We chose experimental locations to cover a wide range of road traffic volumes (130 to 9 300 $veh.day^{-1}$). We retrieved the average traffic volume estimation over the last 3 years from local authorities for all roads but the smallest and less frequented ones (referred to as "*Petit Nice"* thereafter). We estimated missing traffic volume values by placing a camera-trap overlooking the road, and recording 1-minute videos every 5 minutes during 24 hours. We previously compared traffic estimations as provided by authorities and our method using camera traps, and found camera traps yielded very satisfactory results (camera-trap estimation: 11 220 $veh.day^{-1}$; official mean daily traffic estimation: 11 135 $veh.day^{-1}$).

On each road, we placed N=10 carcasses on the asphalt road surface. We chose the lane using a random number generator so that carcasses could be on road shoulders, in the center of the lane so they would fit in-between the tires of most vehicles, or directly in the path of the left or right vehicle tires (fig. 2). We surveyed the carcasses on foot every two hours to determine whether they had disappeared. We considered a complete removal of a carcass when the observer could no longer detect it when walking on the road. Before running the experiment, we conducted training to ensure the different observers agreed on what a 'removed' carcass was. For passerines, we replicated the experiment on a rain-free day when

the road surface was completely dry, and on a rainy day. For amphibians, we completed the experiments on the 8 locations during rain-free days, but replicates on rainy days were limited to 3 locations only corresponding to traffic volumes of 130, 4160 and 8 000 veh.day^{-1}.

2.2 Data analyses of persistence time

We obtained data in which the removal of the carcass from the road was only known to occur within an interval of two hours: for example, a carcass that was present on the first survey but had disappeared on the second had disappeared after a period of 2 to 4 hours on the road surface. The observations could be right-censored if the carcass was still present at the end of the experiment. As ignoring interval-censoring in survival data can lead to biases in survival estimates (Radke, 2003), we chose to model the persistence with interval-censored survival models, an extension of traditional survival models designed to analyze survival data in which the event of interest (here, disappearance from road) is only known to occur within a defined time interval (Anderson-Bergman, 2017). Interval censored models accommodate right-censored data points. We modeled the persistence of amphibians and small passerines in two separate models.

We used R package *icenReg* (Anderson-Bergman, 2017) for the R statistical software (R Core Team, 2021) which provides tools for implementing parametric interval-censored proportional hazards survival models. We selected the underlying parametric distributions of each model by visually comparing the available distributions to the corresponding Cox-PH model and selecting a distribution with no systematic deviation (Anderson-Bergman, 2017). Amphibian persistence was modeled using a gamma distribution, and passerine persistence using a log-normal distribution. We modeled the effects of road traffic volume (continuous variable), weather (2 modalities categorical variable: dry vs. rain) and position on the lane (2 modalities categorical variable: placed in the path of the tires or outside, see fig. 2) on the persistence of the carcasses. We included observer ID (A/B) to accommodate for systematic differences in measurement between the two observers when analyzing amphibian data, but not for passerines because it lined up with the weather variable (all dry days were conducted by observer A, and all rainy days by observer B). We entered road traffic volume on persistence as a linear covariable, and as a log-transformed variable to account for potential non-linear relationships with carcass persistence. We represented the predicted median persistence by each model (linear vs. log-transformed) and the median persistence times of each road using the Turnbull estimator. We selected the log-transformed model for amphibian persistence and the linear model for passerine persistence based on visual fit (fig. A1).

2.3 Estimation of roadkill numbers

Using our measurements of persistence times, we computed the number of road-killed amphibians and small passerines during road surveys. For amphibians, we performed two roadkill surveys on foot on separate evenings in March 2022, during the common toad reproductive migration at a known road-crossing location on road D1504. The time elapsed between the collision window and the survey was 3 hours, and the D1504 road a mean daily traffic volume estimated at 3379 veh.day^{-1}, which we adjusted to 1126 veh.day^{-1} considering the rule of thumb that only 25% of the traffic occurs between 7p.m. and 7a.m, the time of the survey, while the persistence experiments were conducted during the day (Van Langevelde & Jaarsma, 2005). Using the traffic volume and the time elapsed between collision window and road survey, we estimated from the survival model the proportion of carcasses having already disappeared from the road surface.

For passerines, roadkill count data was extracted for birds species < 20g from *Faune-Auvergne-Rhône-Alpes*, a citizen science database that compiles species presence as well as roadkill data submitted in real time by volunteers from the region Auvergne-Rhône-Alpes (thereafter: AuRA), France. We extracted the daily roadkill reports during the year 2022. Following Teixeira et al. (2013), the roadkill rate λ (collision.day^{-1}) can be estimated as $\lambda = \frac{N}{p.T_R}$ where N is the number of roadkill carcasses counted, p is the detection rate of the carcasses by the observer and the characteristic time T_R is the time needed to reduce the number of remaining carcasses on the road by $1 - \frac{1}{e^1} \sim 63\%$. We estimated T_R from the fitted survival model. We used it to estimate the daily number of collisions for 2022 in AuRA. We assumed detection rate $p = 1$ (all carcasses are detected) as we had no information about detection probabilities for small passerines. We explored the implications of imperfect carcass detection on passerine roadkill estimations in section 3 of the supplementary material.

To take into account the underlying distribution patterns of passerine species, we extracted the presence/absence data for each species in AuRA municipalities from Faune-AuRA, and for each municipality, computed the corresponding cumulative length of all roads accessible by car. We used this information to give estimates of the number of roadkill per kilometer of road in areas where the species was present.

3. Results

3.1 Carcasses persistence on the road

Half of the amphibians placed on the road disappeared within the first 5 hours on all roads except for the smallest (“*Petit Nice”* road, 130 veh.day^{-1}). We projected that at t=24h, 95% of the amphibians should disappear from all roads, except for *Petit Nice* (52% at t=24h). In the following, we report model estimates for all covariables by hazard ratio (standard error); z-value and p-value. In accordance with our predictions, roads with higher traffic led to shorter amphibian carcass persistence: an increase of 50% in daily traffic increases the probability of removal from the road by 1.23 (hazard ratio = 1.67 (0.09); z = 5.62; $p < 0.001$; fig. 1a). As predicted, we observed that probability of disappearance was 1.97 (0.23) times faster for amphibians placed in the path of car tires compared to road shoulder (z = 3.86; $p < 0.001$; fig. 2a). However, rain did not decrease or impact persistence (hazard ratio = 1.19 (0.3); z = 0.58; p = 0.56, fig. 1a). There were no differences in amphibian persistence between observers (hazard ratio = 0.94 (0.29); z = -0.19; p = 0.85).

Within the first 2 hours, 80% of the passerines were no longer visible on any of the roads. We modeled road traffic volume as a linear covariable of persistence (fig. A1). Our model predicted that virtually all passerine carcasses (97%) would disappear at time t = 24h. Contrary to all previous hypotheses, we found no differences in passerine persistence time depending on road traffic (hazard ratio = 1.0 (4.5e^{-5}); z= 0.94 ; p = 0.347; fig. 1b), carcass position on the lane (hazard ratio = 0.99 (0.27); z = -0.003; p = 0.996; fig. 2b) or weather (hazard ratio = 1.23 (0.26); z = 0.81; p = 0.420; fig. 1b).

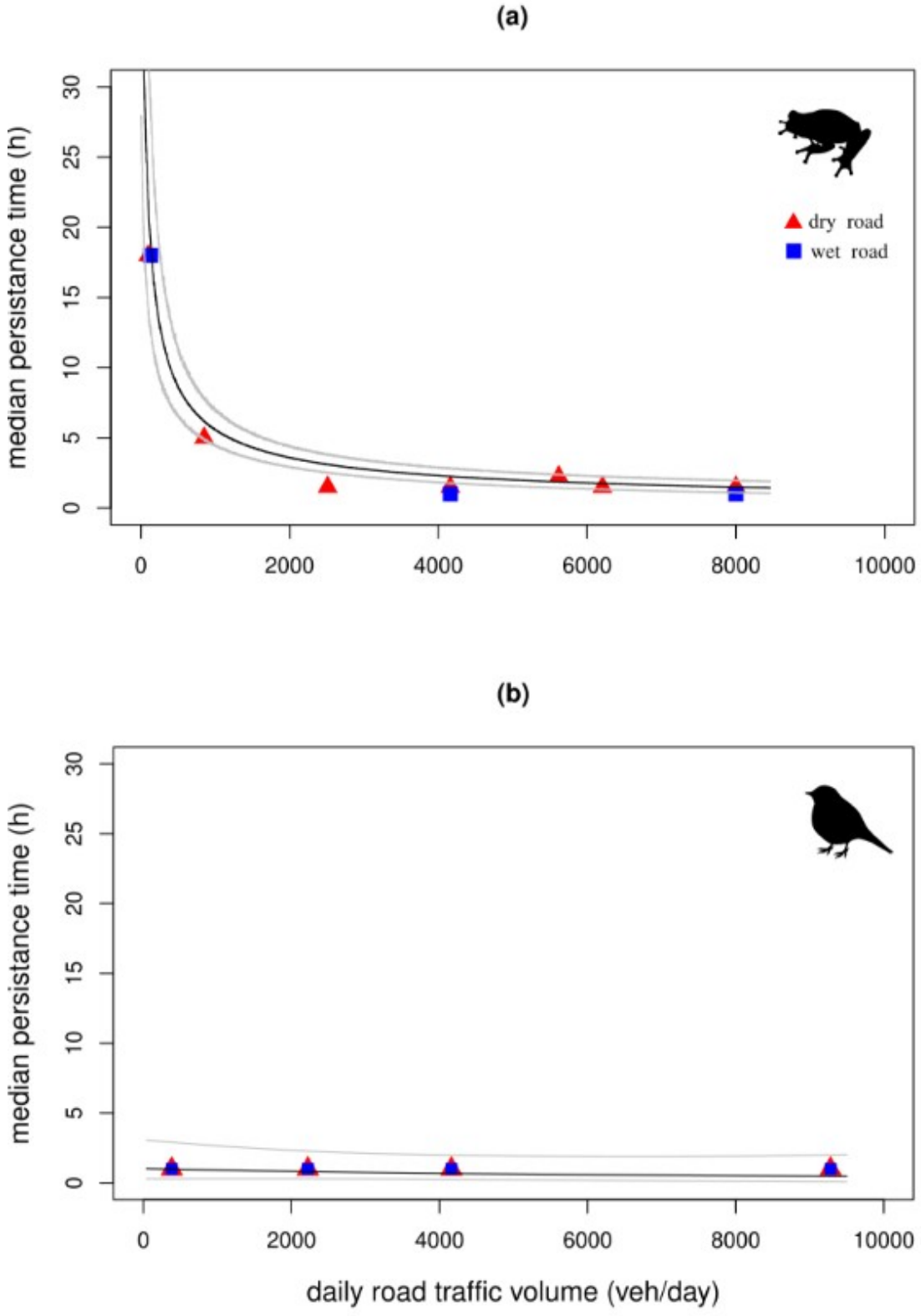


Fig. 1: **Carcass persistence on the road.** We performed roadkill persistence trials on 8 different roads for amphibians (a) and 4 roads for small passerines . At each location, 10 carcasses are placed on the road surface, and surveyed every two hours until complete disappearance. We represent the median persistence time (time for 50% of carcasses to disappear) of each road estimated during dry days without rainfall (▲) and rainy days (■). Predictions from the fitted parametric survival models are represented as black lines (grey lines as the 95% confidence interval).

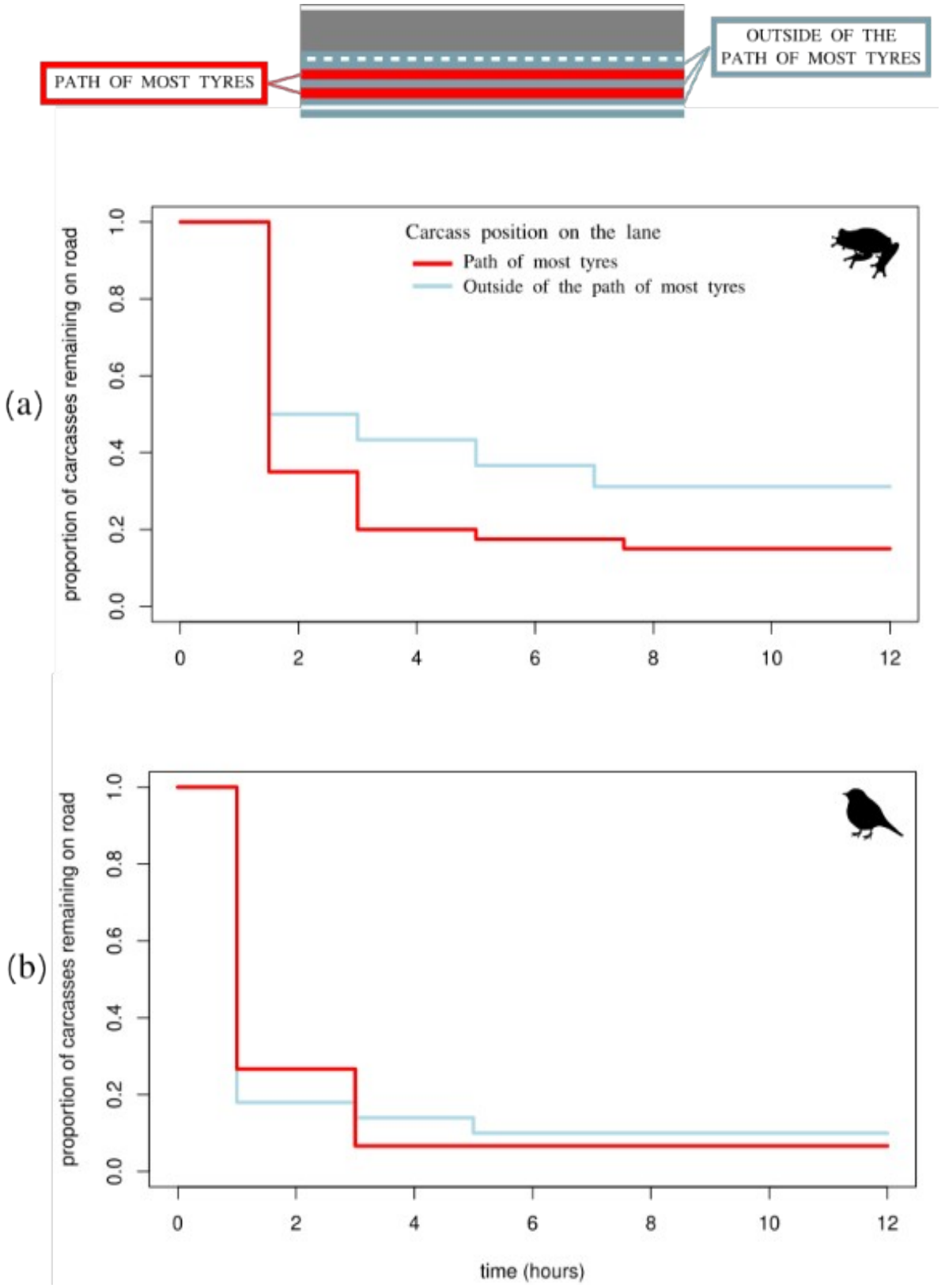


Fig. 2: **Kaplan-Meier curves of carcass persistence.** We randomly positioned carcasses of 90 frogs (a) and 80 carcasses from multiple species of small passerines (b) on the surface of different roads. We represent here the Kaplan-Meier survival curves of the first 12 hours of carcass persistence time across all roads. Carcasses were randomly positioned to be either in the path of the tires of most 4-wheeled vehicles (red), or outside of the path of the tires (blue). Parametric survival models showed that frog carcasses disappeared faster when placed in the path of vehicle tires while passerines had similar persistence on every position on the lane.

3.2 Practical implications for roadkill estimations

On March 15th and March 20th 2022, we counted respectively 12 and 30 common toad carcasses on road D1504. Using the fitted survival model of amphibian persistence described above, we predicted the proportion of missing carcasses on the road according to traffic volume. After 3 hours, we estimated that 49.6% (95% confidence interval: 39.4, 60.5) of the carcasses had already been removed from the road at the time of survey meaning that, assuming perfect detection of carcasses on the road, they were 17.9 (16.7, 19.1) toad casualties on March 15th and 44.8 (41.8, 48.1) on March 20th.

For passerines, 201 small passerines from 21 species were reported by contributors in 2022 (see Table 1 for a complete list). We estimate the characteristic time T_R at 0.0283 days (95% confidence interval: 0.009, 0.088). Accounting for carcass removal rates amounts to 7093 (2270, 22120) passerines road-killed in 2022 in the AuRA region (Table 1). The most commonly killed species on roads is the house sparrow *Passer domesticus* with 0.87 individuals killed per year every 100km, and the least common is the long-tailed tit *Aegithalos caudatus* with 0.019 individuals. These estimates assume that carcasses are always detected and reported by Faune-AuRA contributors. Straightforward estimates of roadkill numbers accounting for imperfect detection and report can be derived from these results: assuming that 1% of passerine carcasses present on the road are seen and reported, 0.87/0.01 = 87 house sparrows and 0.019/0.01 = 19 long-tailed tits are killed annually per 100km of road, and 709 300 (227 000, 2 212 000) passerines could have been killed on roads in the AuRA region in 2022 (fig. A2).

Table 1: We used roadkill reports for small passerine (< 20g) in the Auvergne-Rhône-Alpes (AuRA) region of France from the citizen science database Faune-AuRA in 2022. We corrected the reports for carcass removal rate from road (Teixeira et al., 2013) and then, using the presence data from Faune-AuRA to infer species distribution patterns, we give estimations of roadkill per 100 km of road in areas where the species is present. These estimations of roadkill rates account for the speed of carcass disappearance from the road, but not for the number of carcasses missed or not reported by the observers.

	Reported in Faune-AuRA (2022)	**Number of collisions after correcting for persistence (95% confidence interval)**	**Number of roadkill per 100km of road (95% confidence interval)**
Long-tailed tit *Aegithalos caudatus*	1	35.3 (11.3, 110.1)	0.019 (0.006, 0.06)
European goldfinch *Carduelis carduelis*	5	176.5 (56.5, 550.3)	0.081 (0.03, 0.25)
Eurasian blue tit *Cyanistes caeruleus*	2	70.6 (22.6, 220.1)	0.030 (0.01, 0.09)
Cirl bunting *Emberiza cirlus*	1	35.3 (11.3, 110.1)	0.025 (0.008, 0.08)
Yellowhammer *Emberiza citrinella*	2	70.6 (22.6, 220.1)	0.069 (0.022, 0.21)
European robin *Erithacus rubecula*	58	2046.9 (655.2, 6382.9)	0.84 (0.28, 2.63)
Common chaffinch *Fringilla coelebs*	16	564.6 (180.7, 1760.8)	0.23 (0.07, 0.7)
White wagtail *Motacilla alba*	6	211.8 (67.8, 660.3)	0.12 (0.03, 0.33)
Great tit *Parus major*	10	352.9 (112.9, 1100.5)	0.14 (0.05, 0.44)
House sparrow *Passer domesticus*	56	1976.3 (632.6, 6162.8)	0.87 (0.28, 2.7)
Black redstart *Phoenicurus ochruros*	11	388.2 (124.3, 1210.6)	0.18 (0.06, 0.56)
Common redstart *Phoenicurus phoenicurus*	3	105.9 (33.9, 330.2)	0.081 (0.03, 0.25)
Willow warbler *Phylloscopus trochilus*	1	35.3 (11.3, 110.1)	0.05 (0.02,0.15)
Whinchat *Saxicola rubetra*	1	35.3 (11.3, 110.1)	0.052 (0.02, 0.16)
European stonechat *Saxicola rubicola*	6	211.8 (67.8, 660.3)	0.13 (0.04, 0.42)
European serin *Serinus serinus*	1	35.3 (11.3, 110.1)	0.022 (0.007, 0.07)
Eurasian blackcap *Sylvia atricapilla*	12	423.5 (135.6, 1320.6)	0.18 (0.06, 0.56)
Garden warbler *Sylvia borin*	1	35.3 (11.3, 110.1)	0.057 (0.02, 0.18)
Common whitethroat *Sylvia communis*	1	35.3 (11.3, 110.1)	0.034 (0.01, 0.11)
Sardinian warbler *Sylvia melanocephala*	1	35.3 (11.3, 110.1)	0.14 (0.04, 0.44)
Eurasian wren *Troglodytes troglodytes*	3	105.9 (33.9, 330.2)	0.05 (0.02, 0.16)
TOTAL	**201**	**7093 (2270.6, 22120.2)**	**3.39 (1.08, 10.57)**

4. Discussion

4.1 Persistence on road and implications for road monitoring

Most small carcasses of amphibians and birds in this experiment were removed from the road surface in less than a day. We estimated the median persistence time (*i.e.*, the time needed for half of the carcasses to be removed from the road) of small passerines (< 20g) at t = 22 minutes using a parametric survival model, and this persistence was not affected by road traffic volume, position of the carcass on the road or rain. Common toad carcass persistence was similarly unaffected by rain but was largely dependent on the traffic volume of the road within the explored range (130 - 9000 veh.day^{-1}): the more vehicles, the less time the carcasses remained visible. On roads with 1000 vehicles per day or more, amphibian median persistence time is 5 hours or less. Amphibians placed directly in the path of the tires disappeared nearly twice as fast as the amphibians positioned elsewhere on the road surface.

Santos et al. (2011) found that 50% of small carcasses disappeared in one day for small-sized species (amphibians, reptiles and small birds). Our results agree with these previous observations, and the fine-tuning of previous estimations shows that the median persistence time is actually less than 24h for both amphibians and small birds. For passerines, 80% of carcasses had disappeared within 2 hours across all locations, and 94% after 12h. For amphibians, after 12h we found that over half of the carcasses had disappeared across all locations: 60% had disappeared from *Petit Nice,* a road with little vehicular traffic, and none remained on the major road *Caluire Saône*. Daily roadkill surveys have been previously recommended for accurate roadkill data for small-bodied species (Henry et al., 2021; Santos et al., 2015). Our results suggest instead that even daily road monitoring will largely underestimate the actual number of collisions of amphibians and small passerines with road vehicles. In fact, the short persistence of these species on the road indicates that roadkill surveys will always underestimate casualties unless we monitor roads continuously. Because this is an impossible task, authors should focus instead on implementing persistence corrections (see Teixeira et al., 2013) to their survey methodology. Body size is often cited as the biggest predictor of carcass persistence time on the road (Barrientos et al., 2018; Guinard et al., 2012; Henry et al., 2021). Nevertheless, we found substantial differences in the persistence time between amphibians and small passerines of similar sizes. Hence, the generalization of persistence times between small-bodied species is not possible, and our results are not suitable to assess the persistence of lizards, snakes, bats and other smalls mammals. We suggest instead that other experiments of persistence with fine-tuning should be conducted on these species to assess the proportion of missed carcasses by daily road surveys.

Scavenger activity is often cited as the main cause of carcasses disappearance in roadkill persistence studies (Antworth et al., 2005; Erritzoe et al., 2003; Slater, 2002). For instance, Schwartz et al. (2018) determined that fresh roadkill attracts corvids and foxes that could remove up to 62% of the carcasses within 2 hours. Smaller roads might be easier to access for carrion-feeders than highly-frequented ones, and roadkill persistence studies report that roadkill generally disappeared faster on smaller roads compared to more frequented ones (Santos et al., 2011; Slater, 2002).We found instead that amphibian persistence decreased with the volume of traffic, suggesting that this is not true for all taxa, or that scavenging is not the main mechanism of carcass removal in this case. It has been suggested that common toads are not attractive to carrion-feeders due to their though skin (Hels & Buchwald, 2001). Instead, mechanical fragmentation of tissues by cars appears to play a major role in amphibian carcass disappearance: the accumulation of repeated crushing of biological tissues by tires flattened most of the carcasses we placed on the road surface that became less and less visible at each observation. This mechanism is consistent with findings that traffic volume significantly decreases persistence time in amphibians (fig. 1a) and that carcasses directly in the path of the tires of most vehicles were removed 2 times faster compared to carcasses placed outside of it (fig. 2a).

Passerine carcasses disappeared at higher rates than amphibians (80% within the first 2 hours) and at the same speed across all tested locations and all positions on the lane. Ratton et al. (2014) and Antworth et al. (2005) found longer carcass persistence when using *Gallus domesticus* chick carcasses (resp. 66% removed within 12h and 40% within 2h). However, the chick carcasses weighted slightly more than the wild passerine species used here: reportedly around 30 grams in both studies, against 20g or less in this experiment. Domestic species are also known to have higher removal rates than wild species in open fields (Prosser et al., 2008). To our knowledge, the only other roadkill persistence experiment at a fine temporal resolution using passerines was conducted by Stewart (1971) with house sparrows *Passer domesticus*. Interestingly, he reported persistence estimates similar to our results (100% removal within the first two hours) on a highway but found very contrasted results on a smaller country road: all carcasses were still visible after 12 hours. On the contrary, and similarly to our findings, chick persistence did not vary between a frequented highway and a low traffic dirt road in Ratton et al. (2014). Small birds persistence on roads appear to be highly variable between species and locations.

Contrary to common toads, passerine persistence on roads showed no correlation to road traffic volume. It could be that the temporal resolution of 2-hours intervals is not fine enough to capture the variability in passerine removal rates from roads. During the experiments, and contrary to amphibians, bird carcasses often disappeared without a trace in-between surveys, which could instead suggest that the high removal rate is the result of scavenging activity (Antworth et al., 2005). We conducted a complementary

experiment with continuous observation of the carcasses during 2 hours (Supp. Mat. Section 3). We placed 12 passerine carcasses randomly on a highly-frequented portion of road (8000 veh.day^{-1}) in an urban setting with no unpaved shoulder where the speed limit was 50 km.h^{-1}. We found a higher persistence than previous estimates : 5 out of 12 (41%) were invisible by the end of the 2 hours, against an average across all roads of 80% in the main experiments. Carcasses disappeared at variable rates, with some becoming undetectable after the passage of 10 vehicles and other being still visible after 800 vehicles (median = 178 vehicles, fig. A3). All carcasses were crushed by vehicle's tires, including carcasses originally placed out of the path of the tires (center of the road, center of the lane in-between tires, roadside) that were either crushed by vehicles swerving on the lane to avoid obstacles such as parked cars or displaced by the turbulence following passing vehicles. Contrary to the common toad, we observed that passerine body shape and feathers could promote carcass mobility on the road surface. Passerines carcasses that are displaced by passing vehicles can also potentially end up in the vegetation of the road shoulder, masking them from view during surveys (AB personal observations).

Season and weather influence the speed of carcass disappearance in open fields where removal is usually the result of decomposition or scavenging, and the highest rates of removal are found during the summer months when temperatures are high (Costantini et al., 2017; Prosser et al., 2008; Sharanowski et al., 2008). Carcass persistence on roads was instead found to be lower during spring in France (Guinard et al., 2012), and high temperatures and humid conditions accelerated the disappearance of carcasses from roads in Portugal (Santos et al., 2011). We tested here the effect of rainfall on persistence time, and expected carcasses to disappear faster under the rain. We found instead similar persistence between dry and rainy days for both amphibians and passerines (fig. 1). Rain and humidity might not make a difference when a small-bodied fresh carcass is confronted to a tire, as opposed to bigger animals. Instead of weather, persistence on the road for small species could vary between seasons following scavenger activity (Guinard et al., 2012; Schwartz et al., 2018).

4.2 Impact of vehicular collisions in biodiversity loss

Collisions of wildlife with vehicles have long-been suspected of being a significant threat to the persistence of many amphibian populations (Glista et al., 2008; Puky, 2005) but estimating the biodiversity loss in terms of abundance remains a major challenge. In the case of common toads, because amphibian roadkill during the reproductive migration happens during a short time window, we were able to estimate the time since collision. When the speed of carcass removal from the road is also known, estimates of the proportion of carcasses that have disappeared and were subsequently missed during the survey are straightforward, assuming that all toads present on the road during the survey were detected. In the roadkill survey we conducted, ignoring carcass persistence leads to underestimations of the

number of toad roadkill of about -50%, for a survey conducted 3 hours after amphibian crossing at this particular location. A similar survey conducted the next morning (t=12h after road crossing window) would have under-estimated the casualties by about 70%. Aquatic breeding amphibians are particularly suited to this example of roadkill counts correction because roadkill is synchronized at sunset, allowing for estimations of the time elapsed between the road crossings and the survey, and because road crossings are localized in space, allowing for on-foot surveys where the detection rate of carcasses is higher than surveys done by car.

Correcting roadkill estimates for carcass persistence is much less straightforward when animal-vehicle collisions happen continuously. Teixeira et al. (2013) developed a theoretical framework of carcass persistence correction for roadkill monitoring surveys which we applied to citizen science data of passerine roadkill. We estimated a total of 7000 collisions between small passerines and vehicles in the AuRA region. Not all small passerine species present in AuRA were present in the roadkill reports for 2022, meaning that this number is likely under-estimated. Roadkill rates ranged from 0.9 (house sparrow *Passer domesticus* and European robin *Erithacus rubecula)* to 0.01 (long-tailed tit *Aegithalos caudatus)* collision per 100km of road and per year. Roadkill rates are likely linked to the local abundance of species (Seiler & Helldin, 2006). Despite having no current estimate of these species' abundance in the AuRA region, *P. domesticus* and *E. rubecula* are the most reported small passerines in Faune-AuRA, and they are reported 5 times more than *A. caudatus* (resp. 562 577, 681 000 and 164 600 direct observations of living specimens between 2000 and 2023). This shows that patterns of species abundance in the AuRA region could be a driving factor in the inter-specific differences in roadkill rates, along with species traits and behaviors (Grilo et al., 2020; Teixeira et al., 2013).

However, while we estimate the persistence time on the road for these species, we have little information about the conversion rate of roadkill carcasses into reported roadkill. Indeed, following a collision with a vehicle a passerine might never be detected by contributors (detection probability) or be detected but never reported (reporting probability), because they forgot or could not identify the species with certainty. Additionally, an unknown proportion of passerines could be projected into the roadside vegetation at the moment of impact. Very little work has been done on roadkill detection, although we know that detection rates of roadkill from a car (which encompasses the majority of reports into Faune-AuRA) is significantly lower than when surveying carcasses on foot (Teixeira et al., 2013). Reporting probabilities in citizen science roadkill projects are even less documented. We estimated the cumulative number passerine roadkill for the 21 reported species using a range of plausible values for the detection and reporting probabilities in figure A2. Using an estimate of 1% of report for passerine collisions with vehicles (*i.e.,* 1% of the passerines killed by a vehicle are detected, identified and reported by a

contributor) and after correcting for passerine persistence time on the road, we estimate about 700 000 small passerines killed by vehicles in 2022 in the AuRA region, a surface of 70 000 km². In other words, the roadkill citizen science reports only give us a glimpse into a much larger issue, as we multiplied the number of reports by a factor of 3500. Currently, no estimates of the abundance of passerine species in the region are available to put these estimates into perspective. The French Breeding Bird Survey (a standardized protocol for bird populations tracking, Julliard & Jiguet, 2002) reports alarming declines of up to -50% in wild small passerine french populations over the last two decades (European greenfinch *Chloris chloris*, -50%; European serin *Serinus serinus*, -41.7%*;* yellowhammer *Emberiza citrinella*, -53.6%). Although wild passerine populations face multiple anthropogenic threats from farmland practices (Broyer et al., 2016; Moreau et al., 2021; Rigal et al., 2023), road mortality could be an important and under-estimated driver of biodiversity loss that needs investigating.

Conclusion

By conducting daily or bi-daily surveys, an observer would miss an important part of the road mortality for small-bodied birds and amphibians. Adapting the periodicity of roadkill surveys to minimize the number of missed carcasses is not a viable option (unless we monitor road continuously). Instead, we should focus on quantifying the persistence of carcasses and correct the data gathered during surveys. Our estimations of the number of killed animals by collisions with vehicles illustrate the huge gap between raw counts of carcasses on roads and how many animals were actually lost. Common toads casualties 3 hours after they crossed the road were already underestimated by half, which has severe consequences in the quantification of the impact of road mortality in amphibian biodiversity loss. Assuming a collision-report rate of 1% in the citizen science project *Faune-Auvergne-Rhône-Alpes*, we estimate 700 000 individuals killed each year in a surface of 70 000 km², which could play a part in the national decline in small passerine population observed over the last two decades.

Acknowledgments

We thank the wildlife rehabilitation center Le Tichodrome for their help in providing small passerine carcasses and Benoit Vallas for his contribution to the data record. We would also like to thank Julien Girard-Claudon and the LPO Auvergne-Rhône-Alpes for their help in acquiring and analyzing biodiversity data, as well as all the Faune-AuRA project contributors.

Funding

This work was supported by French Ministry of Research and Higher Education funding (PhD grant 2020-2023) and the SR3A.

REFERENCES

Anderson-Bergman, C. (2017). icenReg: Regression Models for Interval Censored Data in R. *Journal of Statistical Software*, *81*, 1–23. https://doi.org/10.18637/jss.v081.i12

Antworth, R. L., Pike, D. A., & Stevens, E. E. (2005). Hit and run: Effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist*, *4*(4), 647–656. https://doi.org/10.1656/1528-7092(2005)004[0647:HAREOS]2.0.CO;2

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., & Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation*, *222*(November 2017), 146–153. https://doi.org/10.1016/j.biocon.2018.04.014

Beebee, T. J. C. (2013). Effects of Road Mortality and Mitigation Measures on Amphibian Populations: Amphibians and Roads. *Conservation Biology*, *27*(4), 657–668. https://doi.org/10.1111/cobi.12063

Brand, L., Hussey, M., & Taylor, J. (2003). Decay and Disarticulation of Small Vertebrates in Controlled Experiments. *Journal of Taphonomy*, *1*.

Broyer, J., Sukhanova, O., & Mischenko, A. (2016). How to sustain meadow passerine populations in Europe through alternative mowing management. *Agriculture, Ecosystems & Environment*, *215*, 133–139. https://doi.org/10.1016/j.agee.2015.09.019

Costantini, D., Gustin, M., Ferrarini, A., & Dell'Omo, G. (2017). Estimates of avian collision with power lines and carcass disappearance across differing environments. *Animal Conservation*, *20*(2), 173–181. https://doi.org/10.1111/acv.12303

Erritzoe, J., Mazgajski, T. D., & Rejt, Ł. (2003). Bird Casualties on European Roads—A Review. *Acta Ornithologica*, *38*(2), 77–93. https://doi.org/10.3161/068.038.0204

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1998), 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R. L., Goldman, C. R., Heanue, K., Jones, J., Swanson, F., Turrentine, T., & Winter, T. C. (2003). *Road Ecology: Science and Solutions*. Island Press.

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2008). Vertebrate road mortality predominantly impacts amphibians. *Herpetological Conservation and Biology*, *3*(1), 77–87.

Goosem, M. (2007). Special section : Asian biodiversity crises. Fragmentation impacts caused by roads through rainforests. *Current Science*, *93*(11), 1587–1595.

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., Koroleva, E., Ferreira, F. Z., Gagné, S. A., Wang, Y., & González-Suárez, M. (2021). Conservation threats from roadkill in the global road network. *Global Ecology and Biogeography*, *30*(11), 2200–2210. https://doi.org/10.1111/geb.13375

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, *18*(6), 323–328. https://doi.org/10.1002/fee.2216

Guinard, É., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties: Carcasses surveys and scavenging bias. *Biological Conservation*, *147*(1), 40–51. https://doi.org/10.1016/j.biocon.2012.01.019

Helldin, J. O., & Petrovan, S. O. (2019). Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. *PeerJ*, *7*, e7518. https://doi.org/10.7717/peerj.7518

Hels, T., & Buchwald, E. (2001). The effect of road kills on amphibian populations. *Biological Conservation*, *99*(3), 331–340. https://doi.org/10.1016/S0006-3207(00)00215-9

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*, 112664. https://doi.org/10.1016/j.jenvman.2021.112664

Julliard, R., & Jiguet, F. (2002). Integrated monitoring of common bird species in France. *Alauda*, *70*, 137–147.

Lagerwerff, J. V., & Specht, A. W. (2002, May 1). *Contamination of roadside soil and vegetation with cadmium, nickel, lead, and zinc* (world) [Research-article]. ACS Publications; American Chemical Society. https://doi.org/10.1021/es60042a001

Lengagne, T. (2008). Traffic noise affects communication behavior in a breeding anuran, *Hyla arborea*. *Biological Conservation*, *141*(8), 2023–2031. https://doi.org/10.1016/j.biocon.2008.05.017

Lesbarrères, D., & Fahrig, L. (2012). Measures to reduce population fragmentation by roads: What has worked and how do we know? *Trends in Ecology & Evolution*, *27*(7), 374–380. https://doi.org/10.1016/j.tree.2012.01.015

Martin, A. E., Graham, S. L., Henry, M., Pervin, E., & Fahrig, L. (2018). Flying insect abundance declines with increasing road traffic. *Insect Conservation and Diversity*, *11*(6), 608–613. https://doi.org/10.1111/icad.12300

Meek, R. (2009). Patterns of reptile road-kills in the Vendée region of western France. *Herpetological Journal*, *19*(3), 135–142.

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations: A systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12942

Moreau, J., Monceau, K., Crépin, M., Tochon, F. D., Mondet, C., Fraikin, M., Teixeira, M., & Bretagnolle, V. (2021). Feeding partridges with organic or conventional grain triggers cascading effects in life-history traits. *Environmental Pollution*, *278*, 116851. https://doi.org/10.1016/j.envpol.2021.116851

Morelli, F., Rodríguez, R. A., Benedetti, Y., & Delgado, J. D. (2020). Avian roadkills occur regardless of bird evolutionary uniqueness across Europe. *Transportation Research Part D: Transport and Environment*, *87*, 102531. https://doi.org/10.1016/j.trd.2020.102531

Nunes, L. J. R., Meireles, C. I. R., C.j, P. G., & N.m.c, A. R. (2020). Propagation Model of Invasive Species: Road Systems as Dispersion Facilitators. *Research in Ecology*, *2*(1), Art. 1. https://doi.org/10.30564/re.v2i1.1054

Ogletree, K. A., & Mead, A. J. (2020). What Roadkills Did We Miss in a Driving Survey? A Comparison of Driving and Walking Surveys in Baldwin County, Georgia. *Georgia journal of science: official publication of the Georgia Academy of Science.* 78. 1-10.

Parris, K. M., & Schneider, A. (2009). Impacts of Traffic Noise and Traffic Volume on Birds of Roadside Habitats. *Ecology and Society*, *14*(1). https://www.jstor.org/stable/26268029

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., … Walpole, M. (2010). Scenarios for Global Biodiversity in the 21st Century. *Science*, *330*(6010), 1496–1501. https://doi.org/10.1126/science.1196624

Pollock, L. J., O'Connor, L. M. J., Mokany, K., Rosauer, D. F., Talluto, M. V., & Thuiller, W. (2020). Protecting Biodiversity (in All Its Complexity): New Models and Methods. *Trends in Ecology & Evolution*, *35*(12), 1119–1128. https://doi.org/10.1016/j.tree.2020.08.015

Prosser, P., Nattrass, C., & Prosser, C. (2008). Rate of removal of bird carcasses in arable farmland by predators and scavengers. *Ecotoxicology and Environmental Safety*, *71*(2), 601–608. https://doi.org/10.1016/j.ecoenv.2007.10.013

Prunier, J. G., Kaufmann, B., Léna, J.-P., Fenet, S., Pompanon, F., & Joly, P. (2014). A 40-year-old divided highway does not prevent gene flow in the alpine newt *Ichthyosaura alpestris*. *Conservation Genetics*, *15*(2), 453–468. https://doi.org/10.1007/s10592-013-0553-0

Puky, M. (2005). *Amphibian road kills: A global perspective*. https://escholarship.org/uc/item/7j7546qv

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Radke, B. R. (2003). A demonstration of interval-censored survival analysis. *Preventive Veterinary Medicine*, *59*(4), 241–256. https://doi.org/10.1016/s0167-5877(03)00103-x

Ratton, P., Secco, H., & da Rosa, C. A. (2014). Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research*. https://doi.org/10.1007/s10344-014-0798-z

Reijnen, R., & Foppen, R. (1994). The Effects of Car Traffic on Breeding Bird Populations in Woodland. I. Evidence of Reduced Habitat Quality for Willow Warblers (*Phylloscopus trochilus*) Breeding Close to a Highway. *Journal of Applied Ecology*, *31*(1), 85–94. https://doi.org/10.2307/2404601

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J. C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., … Devictor, V. (2023). Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences*, *120*(21), e2216573120. https://doi.org/10.1073/pnas.2216573120

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417–427. https://doi.org/10.1007/s11284-014-1235-1

Rytwinski, T., & Fahrig, L. (2015). The Impacts of Roads and Traffic on Terrestrial Animal Populations. In *Handbook of Road Ecology* (pp. 237–246). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118568170.ch28

Santos, R. A. L., & Ascensão, F. (2019). Assessing the effects of road type and position on the road on small mammal carcass persistence time. *European Journal of Wildlife Research*, *65*(1). https://doi.org/10.1007/s10344-018-1246-2

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0025383

Santos, S. M., Marques, J. T., Lourenço, A., Medinas, D., Barbosa, A. M., Beja, P., & Mira, A. (2015). Sampling effects on the identification of roadkill hotspots: Implications for survey design. *Journal of Environmental Management*, *162*, 87–95. https://doi.org/10.1016/j.jenvman.2015.07.037

Schwartz, A. L. W. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1–7. https://doi.org/10.1093/jue/juy006

Seiler, A., & Helldin, J. O. (2006). *Mortality in wildlife due to transportation*. 165–189. https://doi.org/10.1007/1-4020-4504-2_8

Sharanowski, B. J., Walker, E. G., & Anderson, G. S. (2008). Insect succession and decomposition patterns on shaded and sunlit carrion in Saskatchewan in three different seasons. *Forensic Science International*, *179*(2), 219–240. https://doi.org/10.1016/j.forsciint.2008.05.019

Shepard, D. B., Dreslik, M. J., Jellen, B. C., & Phillips, C. A. (2008). Reptile Road Mortality around an Oasis in the Illinois Corn Desert with Emphasis on the Endangered Eastern Massasauga. *Copeia*, *2008*(2), 350–359. https://doi.org/10.1643/CE-06-276

Slater, F. M. (2002). An assessment of wildlife road casualties—The potential discrepancy between numbers counted and numbers killed. *Web Ecology*, *3*, 33–42. https://doi.org/10.5194/we-3-33-2002

Smith, F. A., & Lyons, S. K. (Eds.). (2013). *Animal Body Size: Linking Pattern and Process across Space, Time, and Taxonomic Group*. University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/A/bo15233198.html

Taylor, B. D., & Goldingay, R. L. (2009). Can Road-Crossing Structures Improve Population Viability of an Urban Gliding Mammal? *Ecology and Society*, *14*(2). JSTOR. http://www.jstor.org/stable/26268299

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates: Effects of sampling methods and carcass removal. *Biological Conservation*, *157*, 317–323. https://doi.org/10.1016/j.biocon.2012.09.006

Teixeira, F. Z., Coelho, I. P., Esperandio, I. B., Rosa Oliveira, N., Porto Peter, F., Dornelles, S. S., Rosa Delazeri, N., Tavares, M., Borges Martins, M., & Kindel, A. (2013). Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis*, *17*(1), 36–47. https://doi.org/10.4257/oeco.2013.1701.04

Testud, G. (2020). *Étude de la perméabilité de la LGV Bretagne – Pays de la Loire (BPL) aux déplacements des amphibiens* [PhD thesis, Université Paris sciences et lettres]. https://www.theses.fr/2020UPSLP043

Troïanowski, M., Mondy, N., Dumet, A., Arcanjo, C., & Lengagne, T. (2017). Effects of traffic noise on tree frog stress levels, immunity, and color signaling. *Conservation Biology*, *31*(5), 1132–1140. https://doi.org/10.1111/cobi.12893

Valladares, F., Tena, D., Matesanz, S., Bochet, E., Balaguer, L., Costa-Tenorio, M., Tormo, J., & García-Fayos, P. (2008). Functional traits and phylogeny: What is the main ecological process determining species assemblage in roadside plant communities? *Journal of Vegetation Science*, *19*(3), 381–392. https://doi.org/10.3170/2008-8-18378

Van Langevelde, F., & Jaarsma, C. F. (2005). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, *19*(8), 895–907. https://doi.org/10.1007/s10980-005-0464-7

Wise, S. (2007). Studying the ecological impacts of light pollution on wildlife: Amphibians as models. *Starlight: A Common Heritage*, 209–218.

Supplementary material

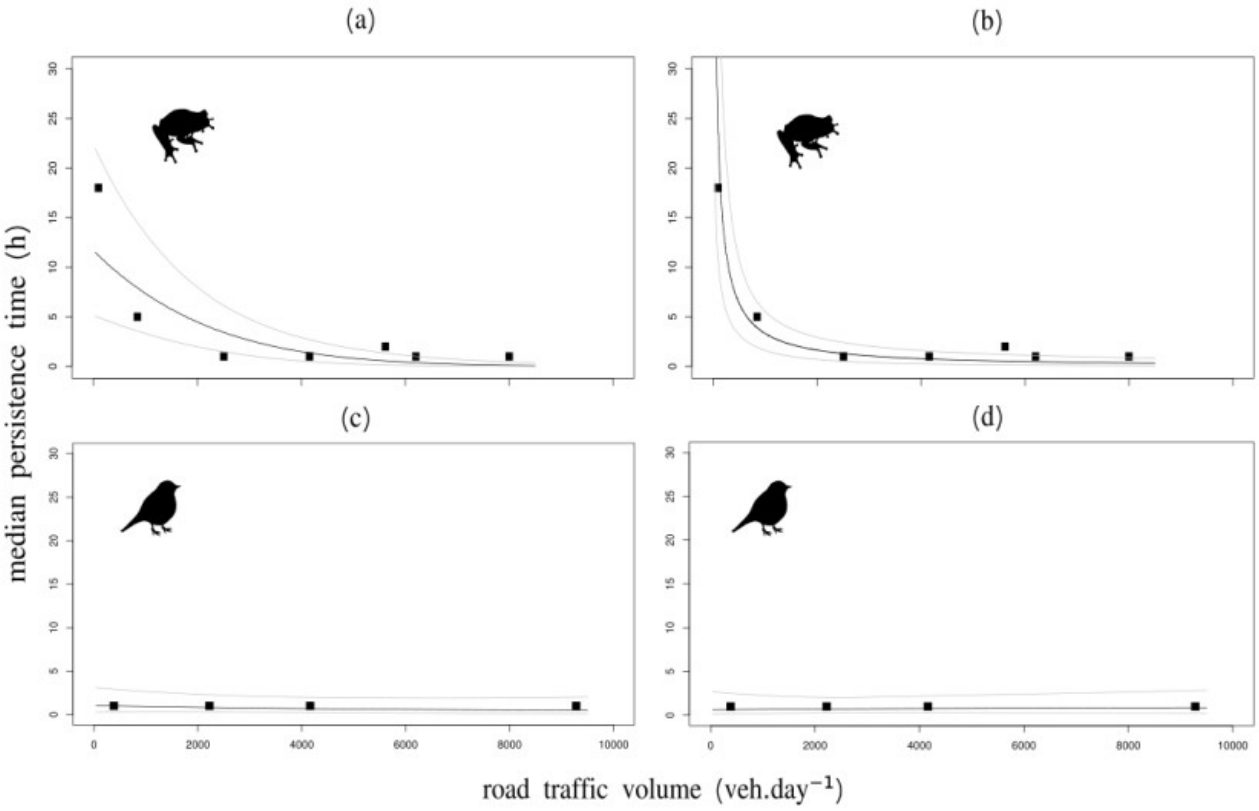


Fig. A1: **Survival model predictions of carcass persistence.** We represent the median persistence time (■; time for half of the carcasses to disappear) of amphibian (a, b) and small passerine (c, d) carcasses on roads of different volumes of traffic. We fitted parametric survival models for both taxa, including road traffic volume as one of the covariables. The predictions of the models are represented as black lines (grey lines: 95% confidence interval). Road traffic volume was either modeled as a linear (a, c) or log-linear (b, d) covariable, and we selected the best option based on the visual fit between the median persistence on each road and the model predictions. Amphibian persistence was modeled using a log-linear effect of traffic (b) and passerine persistence was modeled using a linear effect (c).

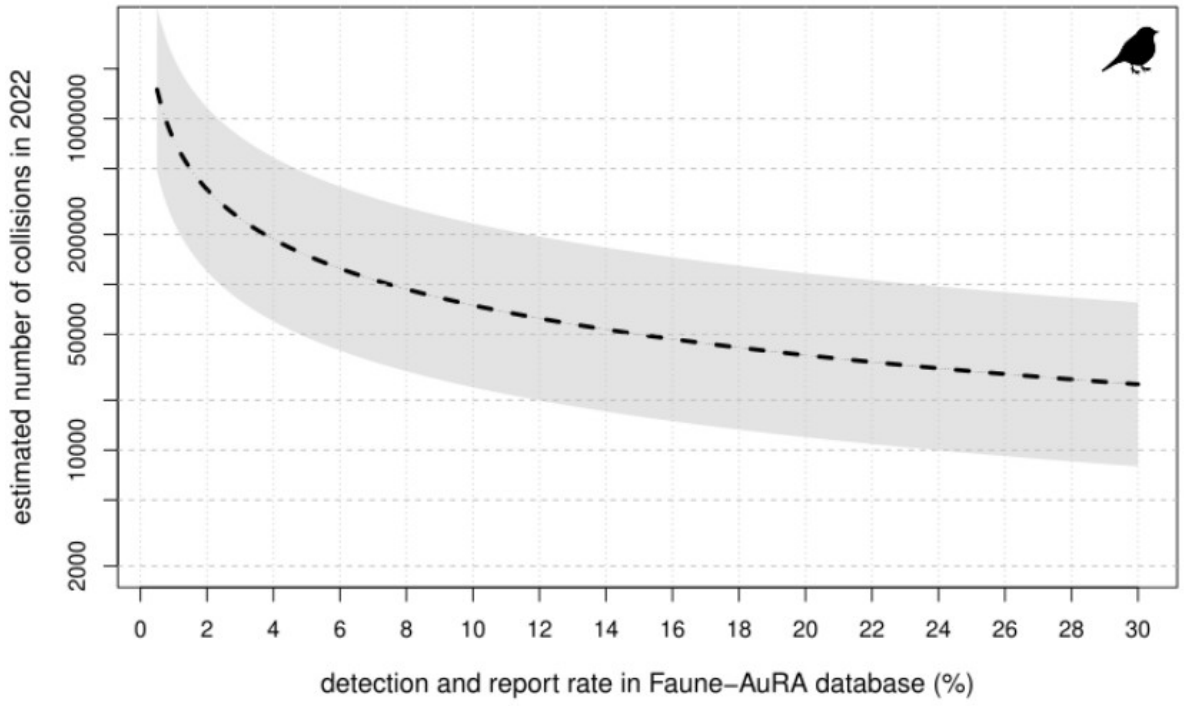


Fig. A2: **Passerine roadkill estimates in 2022.** Estimated number of collisions (gray area: 95% confidence interval) between 21 small passerine species (< 20g) and road vehicles in 2022 in the region Auvergne-Rhône-Alpes (AuRA), France, based on reports from citizen science database Faune-AuRA. Roadkill reports were first adjusted to account for carcass persistence time on the road (tested experimentally with fresh carcasses) following Teixeira et al. (2013). Then, following the assumption that only a small proportion of small-bodied carcasses present on the road are both seen and reported by users in citizen science roadkill reporting projects, we show here the estimated number of actual collisions if between 0.5 and 30% of passerines carcasses present on the road surface end up in the database. For example, if 1% of the visible small passerine roadkill is reported, we estimate 709 100 actual collisions in AuRA in 2022.

Complete list of small passerines species reported in Faune-AuRA in 2022: *Aegithalos caudatus, Carduelis carduelis, Carduelis chloris, Cyanistes caeruleus, Emberiza cirlus, Emberiza citrinella, Erithacus rubecula, Fringilla coelebs, Fringilla montifringilla, Motacilla alba, Motacilla flava flava, Parus major, Passer domesticus, Phoenicurus ochruros, Phoenicurus phoenicurus, Phylloscopus trochilus, Prunella modularis, Saxicola rubetra, Saxicola rubicola, Serinus serinus, Sylvia atricapilla, Sylvia borin, Sylvia communis, Sylvia melanocephala, Troglodytes troglodytes.*

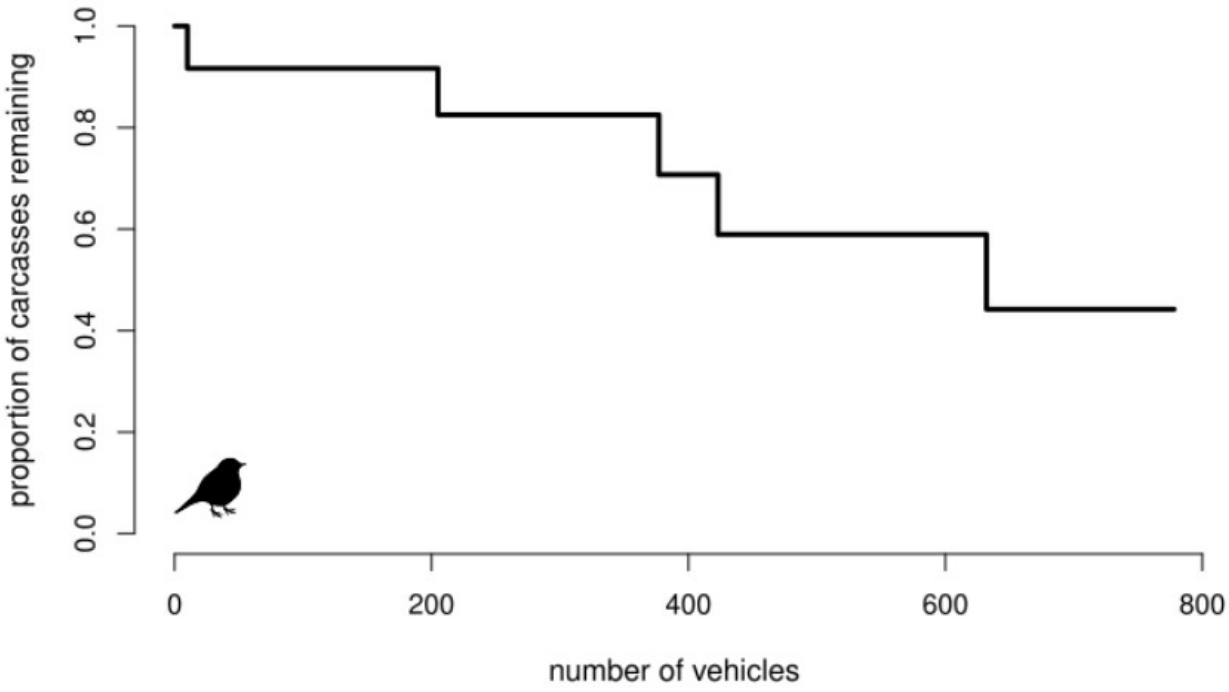


Fig. A3: **Kaplan-Meier curve of passerine persistence on a road**. We conducted an additional experiment where we placed 12 small passerine carcasses on a dry road surface (8000 veh.day^{-1}) and continuously counted the number of passing vehicles until the carcasses disappeared (i.e. carcass can't be detected on foot during a road survey or species is no longer identifiable). The experiment was conducted on an urban road with a 50 km.h^{-1} speed limit, during a day with no rainfall. Passerines were placed randomly on the road surface using a random number generator. Half of the carcasses had disappeared after 632 vehicles, and 58% were still visible when the experiment was ended after 2 hours. All carcass disappearances were the result of repeated crushing by vehicle wheels. All birds (100%) were crushed at least once during the experiment, including carcasses placed in parts of the road lane that vehicles were unlikely to reach, either because the turbulence of passing vehicles had displaced the carcasses, or because some vehicles swerved on the lane to avoid obstacles. The rates of carcass removal during the first 2 hours are lower here than in the experiments conducted in the main body of this article, which hints at a possible involvement of other mechanisms of carcass removal beyond mechanical crushing by tires.

An experimental measurement of carcass persistence time and sources of removal as revealed by camera-traps (in preparation)

Annaëlle Bénard, Thierry Lengagne and Christophe Bonenfant

CONTEXT

Roadkill carcasses observed on roads are often used as an approximation of road mortality. However, the actual number of wildlife-vehicle collisions is likely higher than the raw count of detected carcasses, because they can disappear from the road within a few days or even hours. Previous estimates of roadkill persistence only have a resolution of 24 hours, and the mechanisms implicated in roadkill removal are deduced without any direct evidence.

OBJECTIVES

Using camera-traps, continuously track the removal of medium to large bird and mammal carcasses from roads to:

- Refine existing estimates of roadkill persistence,

- Document the mechanisms by which roadkill is removed and explore the interactions between these mechanisms, the species involved, and the volume of traffic.

KEY RESULTS

- Roadkill was typically removed within an average of 18 hours, mostly through the movement of vehicle tires and the actions of road users.

- The contribution of carrion-feeders to the removal of carcasses appears to be relatively small.

- The most probable mechanism of removal varied depending on the species and the amount of road traffic, but we did not find any statistical evidence that these factors increase or decrease the persistence time.

CONCLUSIONS

Short persistence time (< 24h) of roadkill suggests that even daily monitoring of roads may underestimate the true extent of wildlife-vehicle collisions. Furthermore, the current literature may overestimate occurrences of roadkill removal by scavengers, while overlooking the role of road users in carcass removal.

Persistence time was not affected by road traffic or species' body mass, leading to a single estimate of roadkill persistence encompassing all tested species and roads, but extending this estimate to other species and other types of roads will require further work.

Abstract

Roadkill rates are often under-estimated because a proportion of the roadkill disappears from the road before it can be counted. Studies have estimated the persistence of roadkill carcasses on roads and its relationship with factors such as species and road traffic. However, little attention has been given the different mechanisms of roadkill removal, how often they occur and how they affect the relationships between carcass persistence, road traffic and species. The overall spatial and specific patterns of roadkill persistence are the result of the contrasting patterns occurring within each source of removal, and we need to know how it is being removed in order to understand how fast it will disappear. We placed 86 fresh wild carcasses of birds and mammals on roads with varying volumes of traffic, and positioned a camera-trap on each of them to follow the disappearance of the carcasses. We were able to determine the source of removal in 61% of cases, and we find that people removed roadkill at least 30% of the time, and more often targeted large species on less frequented roads, while small carcasses placed on frequented roads were crushed by vehicles until they are no longer visible (28% of photographed removals). However, we only witnessed 3% of carcasses being removed by scavengers, which is less than what is assumed to occur during most roadkill persistence studies. Roadkill removal through the action of road users, often considered anecdotal in studies, can represent a significant proportion of the removals with people removing the largest species (previously thought to have the longest persistence) in an average of only 5 hours.

1. Introduction

The ever-expanding global road network encompasses all the major drivers of biodiversity loss identified by the IPBES (Díaz et al., 2019). While terrestrial transportation contributes to global greenhouse gases emissions (European Environment Agency, 2019), roadsides accumulate chemical pollutants such a heavy metals and salts, impacting the fauna and flora of the surrounding habitats (Seiler, 2001). In addition, roads and road traffic generate acoustic and light pollution, habitat destruction and fragmentation that disrupt ecological processes and are detrimental to the viability of many species (Forman & Alexander, 1998). Collisions between wildlife and terrestrial transports is a substantial source of mortality for many species (Moore et al., 2023) that amounts to an estimated 220 million birds and mammals in Europe annually (Grilo et al., 2020).

Roadkill data is often used as proxy to mortality, therefore serving as a basis to identify roadkill hot-spots (Girardet et al., 2015; Gomes et al., 2009; Teixeira et al., 2013) and to implement mitigation measures such as crossing structures or fences (Aresco, 2005; Rytwinski et al., 2016). Roadkill data is usually obtained from periodic surveys of animal carcasses along sampled roads. The raw number of detected carcasses is, however, an under-estimation of the real number of wildlife-vehicle collisions because of carcass detection and persistence (Teixeira et al., 2013). Carcass detectability is strongly influenced by the size of the animal (Barrientos et al., 2018), the position of the animal carcass on the road (Guinard et al., 2012) and the travel speed and level of experience of the observers (Collinson et al., 2014; Guinard et al., 2023; Langen et al., 2007; Paraguassu-Chaves et al., 2020). The biases emerging from undetected carcasses can be addressed by selecting the most appropriate survey methodology for the species, such as conducting the surveys on foot (Santos et al., 2016), lowering the travel speed of the observer (Collinson et al., 2014) or with ad-hoc data corrections using detection rate estimates (Gerow et al., 2010).

However, an animal can also be hit and then disappear from the road anytime between the collision and the survey, and in consequence, a portion of the mortality from vehicular traffic can never be counted during surveys (Guinard et al., 2012). Several studies have produced estimate of roadkill carcasses persistence times (Antworth et al., 2005; Henry et al., 2021; Ratton et al., 2014; Santos & Ascensão, 2019; Stewart, 1971). The most comprehensive study of roadkill persistence was published in 2011 by Santos *et al.*, who show that not only does roadkill remain on the road for short windows of time (usually a few days at most), but persistence time is also variable across areas, species, body mass, road traffic, weather, and season. Large-bodied species persist longer on roads (see also Teixeira et al., 2013), and the persistence of roadkill is negatively linked with the volume of traffic (see also Santos & Ascensão, 2019). Yet, these results are not always replicated, and the complexity of roadkill persistence on roads and its dependence on spatio-temporal predictors remains poorly understood (Bénard et al., 2023).

These results have substantial implications for roadkill monitoring: road surveys that are not conducted every few days likely miss an important part of the mortality (Teixeira et al., 2013), and roadkill monitoring schemes that cover multiple species, large temporal or large spatial scales will be inconsistently biased following the variations in carcass persistence (Santos et al., 2015). The mechanisms by which the carcasses disappear from roads remain the most likely drivers for the observed variations in roadkill persistence, *e.g.*, road traffic volume influences the speed of disappearance when carcasses are repeatedly crushed by vehicle tires, or the season and geographical location impact the rates of roadkill consumption by carrion-feeders (Santos et al., 2011).

Despite several studies estimating carcass persistence on roads, little effort has been produced regarding these mechanisms of roadkill carcass disappearance. Roadkill carcasses can disappear through a limited number of mechanisms: the action of scavengers (Antworth et al., 2005), mechanical crushing of tissues from vehicle tires (Beckmann & Shine, 2015; Bénard et al., 2023), picked up or displaced by people (Abbate, 2019). Because roadkill carcasses seldom persist beyond a few days on roads (Santos et al., 2011), disappearances from the road surface and shoulder through decomposition by microorganisms may be marginal (Brand et al., 2003). A few studies have focused on the communities of scavengers that feed on roadkill with the help of sand to analyze footprints (Antworth et al., 2005; Beckmann & Shine, 2015; Slater, 2002), but the majority of authors deduce the mechanisms of removal at play *ad-hoc* based on the observed patterns of carcass persistence (Hubbard & Chalfoun, 2012; Ratton et al., 2014; Santos et al., 2011).

Because of this, it appears essential to (1) quantify the relative frequencies of carcass removal by scavengers, by people, and through the mechanical crushing of vehicle tires, (2) to explore the relationships between the source of removal and factors such as body mass and road traffic and (3) to explore the relationships between the persistence time of roadkill, its body mass, and the traffic volume for the three putative mechanisms. Existing hypotheses covering the relationships between the source of disappearance, traffic volume and body mass include: when smaller carcasses disappear faster, roadkill is likely removed by vehicles as small animals are probably more easily torn apart by tires (Santos et al., 2011), and high volumes of traffic deter scavengers, which would explain that roadkill usually has shorter persistence times on roads with less traffic (Ratton et al., 2014; Santos et al., 2016; Santos et al., 2011; Slater, 2002). However, if roadkill is crushed by vehicles until it disappears, then we would expect that higher volumes of traffic shorten the persistence of roadkill on roads (Stewart, 1971), and if scavengers are responsible for roadkill disappearance, we would expect that smaller animals have longer persistence times because (1) larger carcasses would be more visible to scavengers (Antworth et al., 2005) and (2) scavenging on roadkill is a dangerous activity for carrion feeders (Erritzoe et al., 2003) and

the risk-benefits balance for feeding on roadkill suggests that small-sized carcasses would not be preferred (optimal foraging theory, Stephens et al., 2007; also suggested by Hastings et al., 2019).

In cases where roadkill is removed by people, which is seldom described in the literature, we would also expect the largest animals to have the shortest persistence, because they are the most visible to drivers (Barrientos et al., 2018). Predicting the persistence of roadkill that people remove in relation to traffic volume is less straightforward: on the one hand roads with high traffic offer an increased likelihood that a driver willing to removed roadkill carcasses will drive by, but at the same time smaller roads might offer more possibilities for stopping and safe parking in order to handle the carcass. It is likely that, in any given case, several sources are concurrently responsible for roadkill disappearance (Hubbard & Chalfoun, 2012), such that part of the roadkill is eaten by scavengers, part is crushed by vehicles and part is removed by people. The relationships between carcass body mass, road traffic and the persistence of roadkill on roads is therefore the outcome of multiple mechanisms that are poorly understood.

In this study, we aimed at identifying the sources of disappearance, measure persistence time of carcasses by placing fresh carcasses on roads equipped with camera traps and assess the relationships between road traffic volume, carcass' species' body mass and persistence. We predict that roadkill is removed by several sources, and that body mass and the volume of traffic can predict the probability of disappearance through each of the sources. In addition, we predict that carcass body mass and road traffic impact the persistence time of roadkill in contrasting ways, depending on the way it was removed from the road (Table 1).

Table 1: Predictions of the relationships between the possible sources of removal of roadkill carcasses from roads, the size of the carcass, and the volume of traffic of the roads. We make predictions for the probabilities of a carcass being either picked up or displaced by someone, being consumed by scavengers, or being crushed by the tires of passing vehicles until it is no longer visible. In addition, we make predictions for the persistence time (speed of disappearance) of carcasses under each possible source of removal. 1. Santos et al. 2011 – 2. Ratton et al., 2014; Santos et al., 2016; Santos et al., 2011; Slater, 2002 – 3. Stewart, 1971 – 4. Antworth et al., 2005.

	Source	Effect of carcass size	Effect of road traffic volume
Frequency of removal mechanism	People	Positive - *large animals disappear more often because of people than smaller ones because of increased detectability*	Positive - *more people driving by the carcass increase probability of removal* or Negative - *easier to park a vehicle on a road with less traffic*
	Scavengers	Positive - *large animals more detectable[4] and preferred by scavengers under optimal foraging theory*	Negative - *scavengers avoid roads with high traffic volumes[2]*
	Crushed by tires	No prediction	Positive – *high traffic deters scavengers and people, leaving carcasses to be crushed*
Persistence time	People	Negative - *the bigger the animal, the quicker it will get detected[4]*	No prediction
	Scavengers		Negative - *the less traffic, the more accessible to scavengers[2]*
	Crushed by tires	Positive - *dismemberment by tires is quicker for small carcasses[1]*	Negative - *more vehicles means less time for carcass to be entirely crushed[3]*

2. Material and Methods

2.1 Study location and experimental design

We conducted all the experiments in the south of the Ain department, central-east France, between October and March. This area is dominated by agricultural (56.2%) and forested or semi natural (43.6%) landscapes (CORINE Land Cover, 2018) with a road density of 0.88 km per km² (fig. A1). Our area of study contained the Dombes, a mosaic of ponds and wetland (Ramsar, 2023) with high species richness (Bernard & Lebreton, 2007). We selected 15 roads in peri-urban or rural areas covering a range of traffic of 500 to 14 000 vehicles per day, representative of the diversity of traffic of the road network in south-east France (French Ministry of Ecological Transition, 2023). Very high traffic roads (>14 000 vehicles/day^{-1}) were not included due to safety reasons of the observers (AB). To our knowledge, police and road patrols (Direction Départementale des Territoires, Direction Interdépartementale des Routes) are not instructed by law to remove the roadkill they encounter.

We set up “Cuddeback 1279” camera-traps with a “Black Flash” module (night vision without a visible flash) at 31 locations on the 15 roads (fig. A1). We ensured that traps on the same road were located at least 2km from one from the other, and selected the most appropriate locations on the road based on accessibility and ability to hide the trap from people. We placed the traps on a tree on the verge of the road, such that the entire width of the road was in the field of view of the camera. We programmed the traps to take 3 photographs at each movement triggering the sensors, plus an additional time-lapse photo every 3 hours. This camera setting ensured that, should the trap not trigger as expected when the animal was removed from the road, we could estimate the persistence from the time-lapse with a minimal accuracy of 3h. Because the traps were difficult to set-up and the appropriate locations were limited, we used the same traps for consecutive experiments by placing new carcasses once the previous carcass had disappeared, alternating birds and mammals, as well as small and large species.

We obtained 79 bird and mammal carcasses from a wildlife rehabilitation center, stored at -20°C and thawed for 24h before the experiments. The 38 mammalian specimens ranged from brown rat (*Rattus norvegicus*, 300g) to roe deer (*Capreolus capreolus*, 25kg), and the 41 birds from blue tit (*Cyanistes caeruleus*, 20g) to Eurasian eagle-owl (*Bubo bubo,* 2.5kg). The complete list of specimens is made available in appendix A1. We retrieved the average body mass of each species from publicly accessible databases (Ocampo et al., 2021; Tobias et al., 2022). We placed the animals on the road surface in front of a camera trap, alternating between the center of the lane and the border between the road and shoulder. Note that we placed carcasses >5kg in weight (fox, badger, and roe deer) on the shoulder and not on the

lane due to safety concerns for drivers. We checked each location on foot every 1 to 3 days for camera-trap maintenance and noted whether the carcass was still present on each occasion.

2.2 Data analysis

We analyzed the photographs to estimate the time of carcass disappearance from the road (*photographed removal*), the interval of removal if the trap did not trigger (*interval disappearance*), or the moment the trap stopped functioning (*monitoring stop*). Note that the source of disappearance (scavenger, mechanical crushing of tissues by vehicles, active removal by people) could only be determined in the first case. We considered an animal 'disappeared' from the road once it could no longer be detected by a observer driving on the road (see Bénard et al., 2023, for a similar approach).

Sources of disappearance

We classified three possible sources of disappearance for carcasses on the road: the mechanical action of vehicle tires, the removal by one or several people, and scavenger activity, plus cases with an unknown source of disappearance (*e.g.*, if the trap failed during the experiment). Because of the low rate of roadkill consumption we observed (N=2), we did not include scavenging as a source of disappearance in the analyses. Therefore, each of the animal carcass had an assigned source of disappearance with no relevant alternative, and we used a multinomial logistic regression (Agresti, 2012) to determine the relationship between the 3 sources of disappearance (by people, by vehicles, undetermined), the body mass of species (continuous variable, based on the species' average body mass, see section 2.1) and the traffic of the road (continuous variable). We added the camera trap location as a random variable. This model analyzes the probability of each source of disappearance depending on the species' body mass and the traffic, which allows to test the hypotheses that some situations (namely, species and road traffic) are more conducive to some sources of removal (Table 1).

Animal persistence on the road

We programmed the traps for time-lapse photos to obtain the persistence time of each carcass, even if a trap did not trigger during the removal. Consequently, some of the survival data is interval-censored, meaning the only information available is that the carcass disappeared sometime between the last

photograph and the next time-lapse photo. Ignoring interval-censoring in survival models will lead to biased survival estimates in either direction and confidence intervals biased downwards (Radke, 2003). Therefore, we used survival models that can incorporate interval-censoring to model the persistence time of the animals on the road (Lindsey & Ryan, 1998). We implemented Cox proportional hazards (thereafter: CoxPH) interval-censored survival models (Anderson-Bergman, 2017) to estimate the persistence time of the carcasses and to test the effects of body mass of species (continuous variable), traffic volume of the road (continuous variable) for all observations. In a second model, we tested the hypotheses summarized in Table 1 by specifying two-way interaction terms between the source of disappearance (three levels categorical variable: removed by people, removed by vehicles, undetermined disappearance) and body mass, and source of disappearance and road traffic. Survival models also allow to estimate the median survival time, which in our case is defined as the time at which 50% of the carcasses have disappeared from the road. Note that the notion of survival is translated differently when applied to roadkill persistence : the event of interest (“death”) is the disappearance of the animal from the road, and the time-to-event (“survival”) is the persistence of the carcass.

To our best knowledge, there is no implemented function for conducting mixed interval-censored survival analysis in R, we therefore were not able to include the trap location as a random effect in the survival models. We used packages *mclogit* (multinomial logistic regression, Elff, Martin, 2022) and *icenReg* (survival models, Anderson-Bergman, 2017) for the R statistical software (R Core Team, 2021).

3. Results

We placed 79 animal carcasses in 31 locations equipped with camera traps. The median persistence on the road was 10h36 (95% CI: 5h52, 42h36). After 24 hours on the road, 34% of the animals were still visible. We could not obtain the source of disappearance for 31 animals: either traps did not trigger at the moment of removal, were stolen during the experiment, stopped working, or the animal carcass was pushed by the wind of passing vehicles out of the frame of the photographs.

Sources of disappearance

We could not ascertain the source of disappearance for 39.1% of the animals: 13.5% were right-censored (either the animal was moved out of frame by vehicles: 5%; or the trap failed or was stolen: 8.8%) and in the remaining 25.3%, the trap did not trigger at the time of removal. Failure to determine the source of disappearance is explored in more detail in appendix 2. 30.4% of the animal carcasses were moved or picked up by people. In many cases of removal by people, the animal would be simply be placed in a ditch or hidden in the vegetation of the road shoulder (fig. A3). Finally, 27.8% were removed by the mechanical action of vehicles. Only 2 scavenger removals (2.5%) were evidenced: a European badger (*Meles meles)* removed a common swift (*Apus apus*) from a road of medium frequentation (3 180 vehicles.day^{-1}); and a red fox (*Vulpes vulpes)* and common buzzards (*Buteo buteo)* consumed the carcass of a European rabbit (*Oryctolagus cuniculus)* from a small road (931 vehicles.day^{-1}). We did not record / capture other instances of scavengers feeding on carcasses.

Using the removal by mechanical crushing as a baseline, a 1kg-increase of the body mass of the carcass' species increased the odds of being removed by people (Odd ratio (OR) = (95% CI: 1.12;1.38), z=-2.42, p=0.016), but did not change the odds of the removal source being undetermined (OR: 0.91 (95% CI: 0.82, 1.01), z=-0.89, p=0.38). A 100-vehicles increase in the daily road traffic volume decreased the odds of a removal by someone (OR = 0.96 (95% CI: 0.95;0.98), z=-2.42, p=0.016) and did not change the odds of an undetermined disappearance (OR: 0.99 (95% CI: 0.98, 1.005), z=-0.428, p=0.67; fig. 2). Using undetermined disappearance as a baseline, a 1kg-increase of the body mass increased the odds of the carcass being removed by someone (OR = 1.36 (95% CI: 1.22;1.51), z=2.91, p=0.003, fig. 1). A 100-vehicles increase in the daily road traffic volume decreased the odds of removal by someone (OR = 0.96 (95% CI: 0.95;0.98), z=-2.22, p=0.03).

In summary, larger animals and smaller roads were associated with increased odds of removal by people. Conversely, bigger roads were associated with increased odds of either removal by vehicles or a removal mechanism we were not able to ascertain. This is in support of our hypotheses that: people remove animals more often when the animal is bigger (positive link between body mass of the species and odds of human removal), and the probability of carcass disappearance through mechanical crushing is (1) negatively linked with body mass and (2) positively linked with the volume of traffic of the road (Table 1).

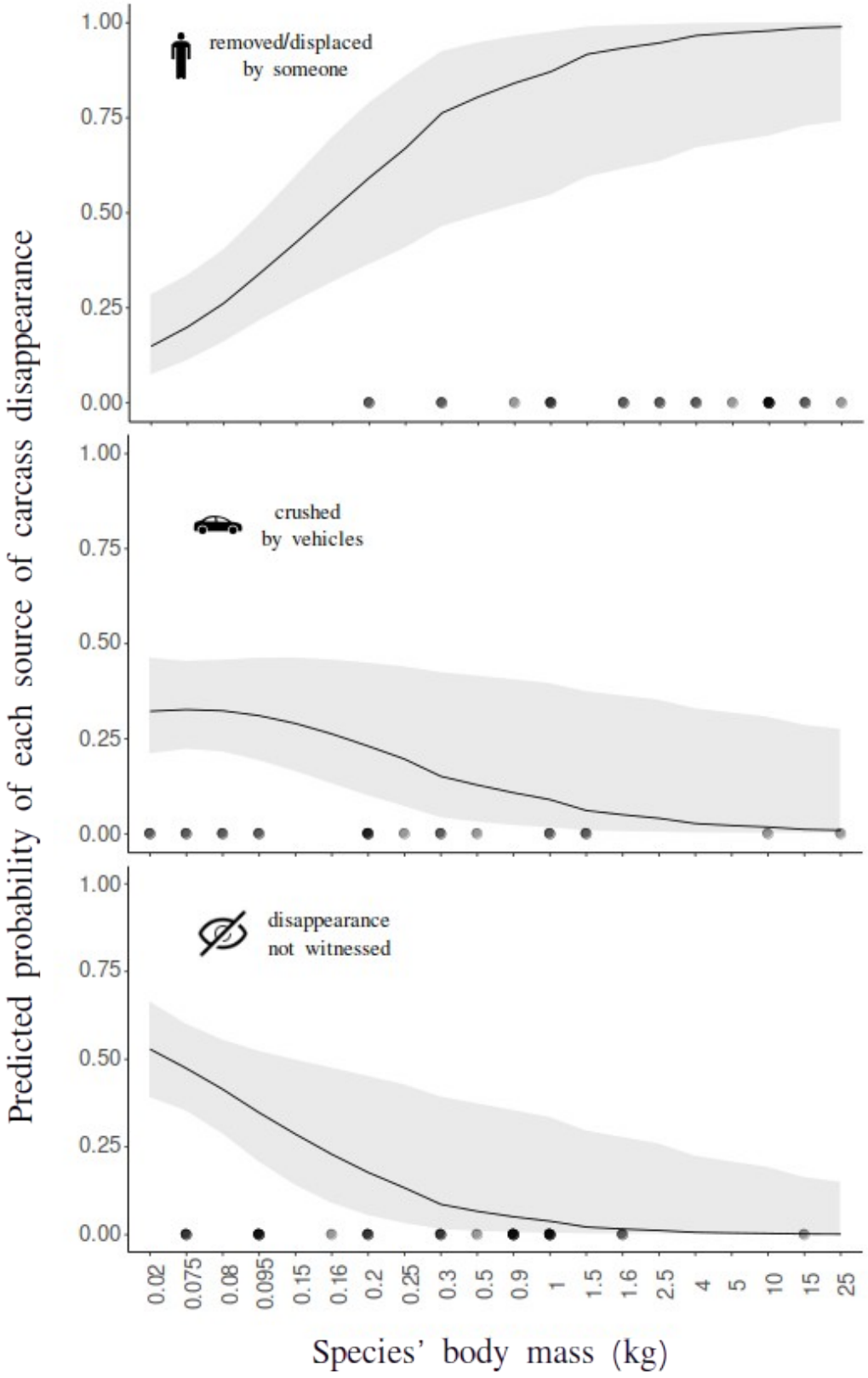


Fig. 1: We placed animal carcasses on roads in south-east France and quantified the sources of disappearance: removed or displaced by people (top) or crushed by vehicles until it was no longer visible (middle). Scavenging was rare (2.5% of cases) and is not represented here. In a number of cases, we were unable to determine the source of removal (bottom). The prediction for probability of occurrence of each source of disappearance in relation to body mass of the species placed on the road are represented (grey: 95% CI), along with the data points at the bottom of each graph.

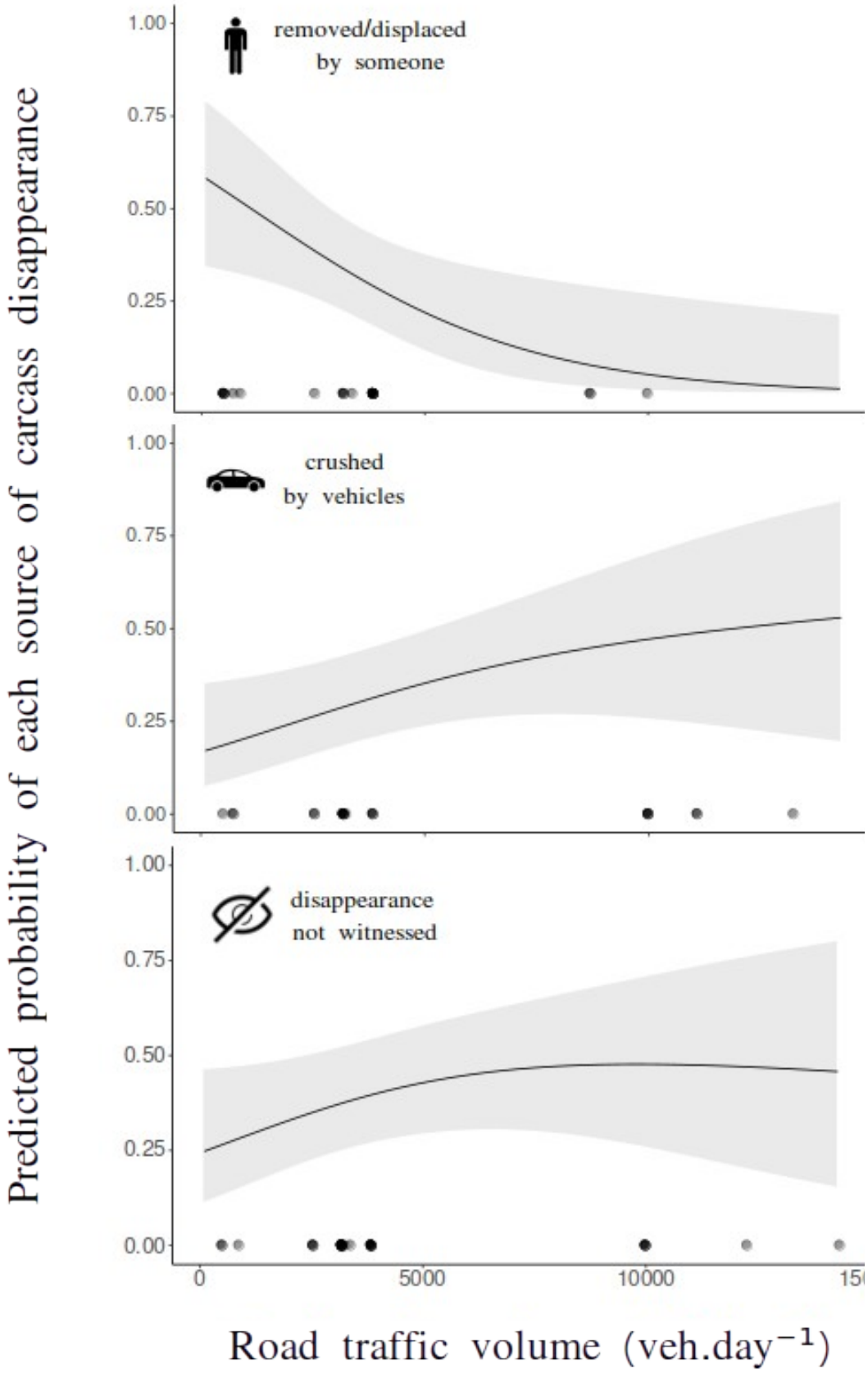


Fig. 2: We placed animal carcasses on roads in south-east France and quantified the sources of disappearance: removed or displaced by people (top) or crushed by vehicles until it was no longer visible (middle). Scavenging was rare (2.5% of cases) and is not represented here. In a number of cases, we were unable to determine the source of removal (bottom). The prediction for probability of occurrence of each source of disappearance in relation to the traffic of the road are represented (grey: 95% CI), along with the data points at the bottom of each graph.

Animal persistence on the road

We obtained the exact time of removal for 38% of the animal carcasses, a time of removal contained within a known interval for 40% of the carcasses and the remaining 22% were right-censored either due to the trap failure, theft, or the animal being moved out of the frame of the photographs. The median persistence of animals removed by people was 5h27 (95% CI: 2h16, 23h42), while animals removed by vehicles persisted on average 20h28 (95% CI: 10h40, 83h) and undetermined removal cases persisted for 20h52 (95% CI: 4h43, 411h30, fig. 3). Note that the upper limit of the confidence interval for the undetermined disappearances is very high, a consequence of the high proportion of these observations being right-censored.

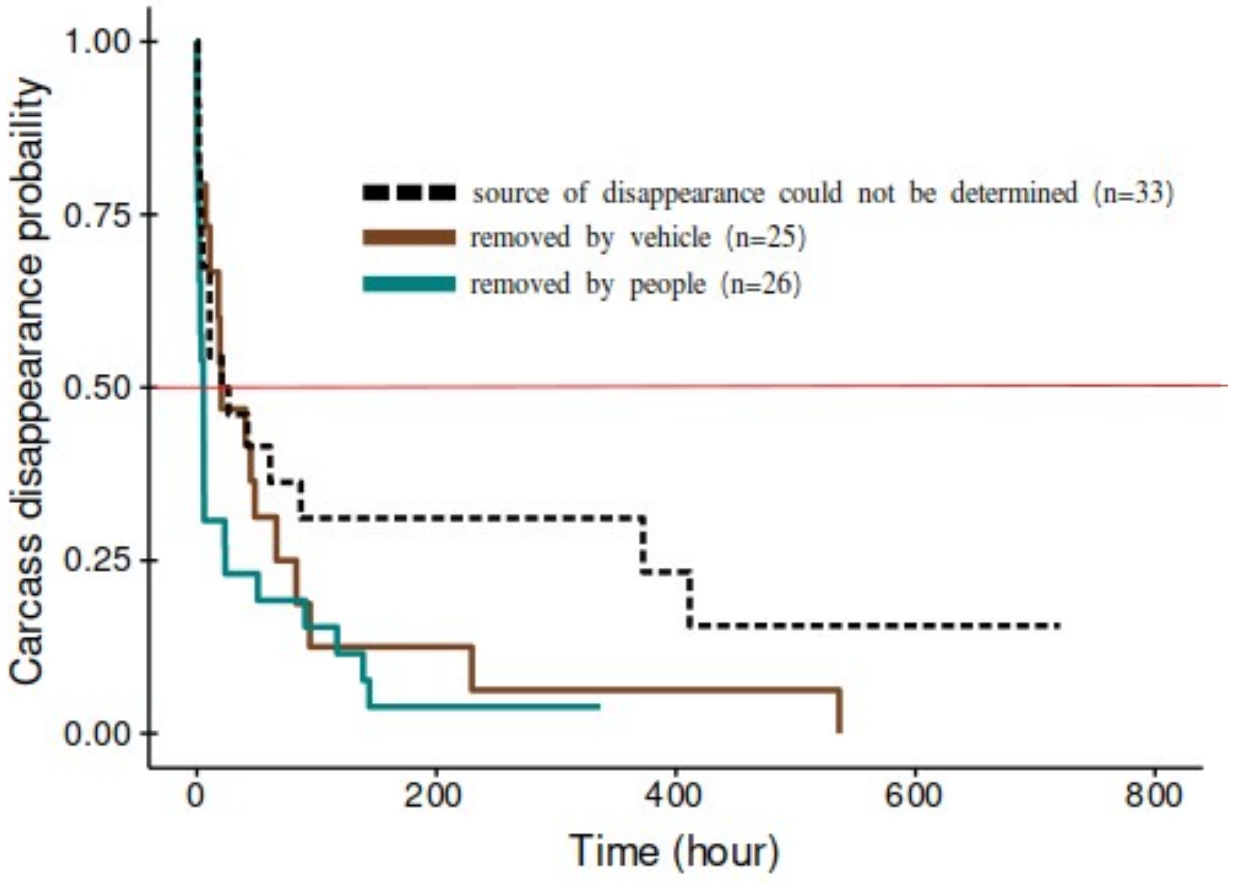


Fig. 3: Kaplan-Meier survival curves of the persistence of roadkill carcasses on the road. We identified three sources of removal for roadkill: scavengers eating the carcass, people removed the carcass and vehicle crushing the carcass until complete removal, plus 33 cases where we could not determine the source of disappearance. Scavenger-related removal is not shown here as there was only 2 occurrences. The median persistence time (time for 50% of carcasses to be removed, red line) is shorter for animals removed by people (about 5h30) than by vehicles (about 20h30) and undetermined cases (about 21h). These differences were not found to be statistically significant. The 95% confidence interval of the Kaplan-Meier curves are not represented here for clarity.

There was no effect of the species' body mass (Hazard Ratio=0.997 (95% CI: 0.991,1.0), z=-0.68, p=0.49) nor the volume of traffic of the road (Hazard Ratio=1.001 (95% CI: 0.96,1.04), z=0.028, p=0.97) on the persistence of carcasses on the road.

Including the source of disappearance in two-way interaction terms, the second interval-censored CoxPH model (fig. 4) showed no significant differences in the hazard ratios (HR) of removals by people vs. vehicles (HR=1.60 (95% CI: 0.83, 3.06), *z*=0.72, p=0.47), undetermined vs. vehicles (HR=1.36 (95% CI: 0.66, 2.81), z=0.43, p=0.66) or undetermined vs. people (HR=0.85 (95% CI: 0.36,2.01), z=-0.18, p=0.85). In other words, expected persistence times for roadkill are not statistically different between each source of disappearance.

A 1kg-increase in the carcass' species body mass had a tendency to increase the persistence of animals removed by vehicles (HR=0.75 (95% CI: 0.48,1.17), z=0.72, p=0.47, reference level: *people*) and decreased the persistence when removed by people (HR=1.46 (95% CI: 0.93,2.29), z=1.66, p=0.096, reference level: *vehicle*) but these trends are not statistically significant. Only small sized species disappeared faster than larger ones in cases where the disappearance was not witnessed, using cases where the carcass was removed by people as the reference level (HR=0.25 (95% CI: 0.10, 0.64), z=0.72, p=0.02). An increase in road traffic (unit of increase: 100 vehicles.day^{-1}) was not associated to the persistence time of animals, whatever the source of removal we considered (people removal: HR=0.99 (95% CI: 0.96,1.01), z=-1.29, p=0.20, reference level: *vehicle*; vehicle removal: HR=1.01 (95% CI: 1.001,1.02), z=1.26, p=0.2, reference level: *people*; undetermined removal: HR=1.01 (95% CI: 0.98,1.03), z=1.03, p=0.30, reference level: *people*).

In summary, we found no statistical support for the predicted relations between the volume of traffic, the source of disappearance and the time during which the animal persisted on the road, nor between the body mass of the species, the source of disappearance and the persistence (Table 1).

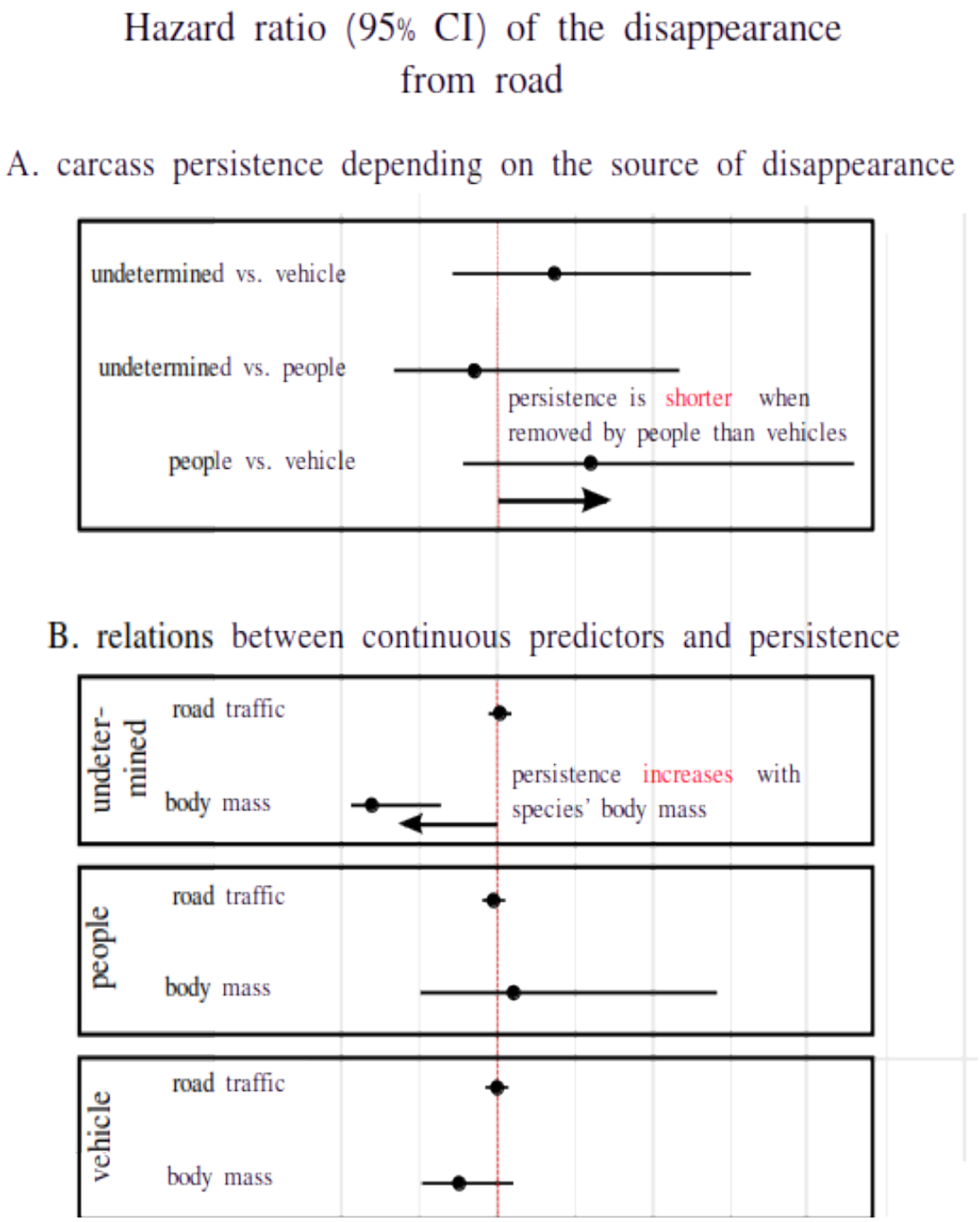


Fig. 4: Effects of road traffic volume (vehicles.day^{-1}) and carcass' species body mass (kg) on the persistence on the road in south-east France, tested between October and March. Interpretation of hazard ratios in the context of roadkill persistence is a follows: A. When comparing different sources of disappearance (removed by people, removed by the mechanical crushing of vehicle tires, undetermined source of disappearance), a hazard ratio (HR) > 1 means a shorter persistence on the road for the first category, and conversely for HR < 1. B. For continuous predictors, an increase of 1kg in the carcass' species body mass shortens the persistence if HR > 1, and increased the persistence HR < 1 (no impact if HR = 1). The same is true for an 100-vehicle increase in the daily volume of traffic of the road where the carcass was located.

Discussion

In this experiment, we document the mechanisms of disappearance of carcasses from roads, witnessing the disappearance of the carcass 60% of the time. Half of these carcasses were removed or displaced by people, and half were crushed by vehicle tires until they became invisible. Only 2 carcasses (2.5%) were consumed by scavengers. Larger carcasses and less frequented roads were more conducive to people removing the animals, in which case roadkill persisted on average about 5 hours. Smaller carcasses and bigger roads were more conducive to tires crushing the animals, or the source of disappearance being undetermined (average persistence time in both cases: 20 hours). The speed of disappearance, or persistence time, was not impacted by the volume of traffic or the species' body mass of the carcass both in general and when considering each source of disappearance separately.

The median persistence time for roadkill carcasses is generally estimated at 1 day, as few studies conduct experiments with a temporal resolution of less than 24 hours (Ratton et al., 2014; Santos et al., 2011; Slater, 2002). Through continuous monitoring with camera-traps, we refined this estimate to 10 hours on average. Short persistence times raise concerns for the interpretation of roadkill data collection, as monitoring scheme with a temporal resolution of >1 day are likely to miss an important proportion of the roadkill (Henry et al., 2021). In this study, 58% of the carcass had disappeared after 12 hours, and 66% after the first day, which implies that even daily roadkill surveys miss a significant part of the mortality on roads. However, increased frequencies in roadkill monitoring imply increased costs, and such expectations might not be realistic (Henry et al., 2021). In recent years, ad-hoc methods for roadkill data correction have emerged in response to these issues, which require robust estimates of persistence and thus a good understanding of the persistence of roadkill (Teixeira et al., 2013): using the results of this study, the correction factor (characteristic time T_R) for roadkill persistence, which we find to be constant across species and roads, is T_R=40h36 (95% CI: 10h37, 90h27).

Most of the studies estimating the persistence time of roadkill center around the idea that animals are removed by scavengers or by vehicle tires, and often construct experiments or hypotheses accordingly (Guinard et al., 2023; Ratton et al., 2014, 2014; Santos et al., 2011). In fact, roadkill removal by scavengers has been evidenced before using continuous observation and sand trays (Slater, 2002), yet we have observed few scavengers feeding on roadkill in this experiment. This is unexpected as we carried out most experiments during late fall, winter and early spring (October to early March), which is known to be a time of the year during which scavenging rates increase, as opportunistic scavengers switch to carrion-feeding when other food resources become scarce (Prosser et al., 2008; Selva et al., 2005). Others have suggested however that season is a poor proxy for scavenger activity levels (Barrientos et al., 2018; Ponce et al., 2010). In addition, we used the carcasses of wild individuals, which are thought to be more

attractive to scavengers than domestic species (Prosser et al., 2008) and conducted most of the observations in a rural area with high biodiversity in which one would expect a rich community of scavengers (carrion crow *Corvus corone*, Eurasian magpie *Pica pica*, red fox *Vulpes vulpes*, Schwartz et al., 2018).

We have been unable to ascertain the source of removal for a third of the observations, so part of these observations could be the result of scavenging, and we have also artificially placed carcasses on roads which mean they likely did not follow hotspots of roadkill presence expected by scavengers in the area (Santos et al., 2011). Interestingly, Winton et al. (2018) monitored snake roadkill consumption by scavengers with camera traps and reported undermined cases similar to this study, where the snake would be present on one photograph and absent on the next. Considering they had mostly recorded terrestrial scavengers, they theorized that undetermined cases could be the result of avian scavengers dropping on the road and flying off with the carcass. However, in this case we recorded very few scavengers, mammalian and avian alike. We still obtained similar persistence estimates compared to previous work (Ratton et al., 2014; Santos et al., 2011), suggesting the role played by scavenger activity in roadkill persistence may not be as important as previously thought and that the removal of roadkill through tires and people could be responsible for the observed persistence of roadkill in south-east France.

In this study, we have shown that roadkill may disappear from the road through different mechanisms: removed by people, removed by the action of vehicle tires, and in a few cases, scavenging. The frequencies of each of these removals is, however, markedly dependent on the size of the animal, which means the source of disappearance from the road is likely species-dependent. Roadkill removal by vehicles followed similar patterns to disappearances from undetermined sources: it concerned mostly smaller animals, and roadkill persistence time decreased with animal body mass (significant only for undetermined cases) with a median persistence time on the road of about 20 hours in both cases. As discussed in appendix A2, failure to determine the source of disappearance could be explained by different types of issues (no trigger, trap theft...), all of which were equally probable across all road traffic volumes and species' body mass (fig. A2).

In particular, traps not triggering could be the result of (1) animals moved out of frame by vehicles that did not trigger the camera trap sensors (not all vehicles triggered the traps, AB's personal obs.), such that the animal was visible on one photograph and not on the next, (2) vehicles crushing the animal until it disappeared, and none of these vehicles triggered the sensors, (3) scavengers feeding entirely on the animal without triggering the sensors and finally (4) people removing the animal without triggering the traps. The lack of association between non-trigger events and the species' body mass and road suggests that it is unlikely these events were specifically associated to one type of removal, except for scavenger

activity for which we have no knowledge of the facilitating factors. We lack the ability to give a definitive explanation on this subject, although it should be noted that camera traps' ability to trigger can be dependent on the temperature, battery level, and could be reduced when the subjects are moving too fast (Marcus Rowcliffe et al., 2011). In particular, vehicles moved on the road at high speeds and did not always trigger the traps.

Small fauna on roads was often removed by the action of vehicle tires, which can lead to very short persistence times (Stewart, 1971). In addition to short persistence times, small-bodied animals are more difficult to detect during surveys (Barrientos et al., 2018; Ogletree & Mead, 2020; Santos et al., 2016) which would make them the most under-estimated species in roadkill datasets. As we expected, the probability of disappearance through repeated crushing by vehicles was higher on more frequented roads, possibly because few people and scavengers will approach carcasses when there are too many vehicles (Erritzoe et al., 2003), leaving time for vehicles to crush the carcasses repeatedly. In addition, it is possible that a carcass that has been damaged by a vehicle (even though it is still very visible), which may happen quickly when the flow of traffic is high, may discourage members of the public from displacing it. However, our results did not show that road traffic influenced the speed at which the animal disappeared, due to more vehicles crushing them (Stewart, 1971). Although we did not include highways in our experiment as Stewart (1971) did, our experiment covered a wide range of traffic from 500 to 14 000 vehicles.day^{-1} (mean: 4862 vehicles.day^{-1}) such that volumes of traffic that were too low are an unlikely reason for the lack of effect observed here (fig. 4). Carcass persistence being significantly shorter on highly frequented roads was previously evidenced for amphibian roadkill, but small passerines disappearance remained unaffected by the volume of traffic (Bénard et al., 2023). In this experiment, nearly all small passerines (80%) disappeared from all roads in 2 hours or less. It is possible that we lack a proper understanding of the mechanisms behind carcass removal by vehicles, and the importance of species characteristics, such as size, morphology, or bone density.

We found high rates of removal by people, especially for large carcasses, likely owed to their visibility for drivers (Barrientos et al., 2018). Drivers were more likely to remove carcasses on smaller roads, although the traffic of the road did not in itself affect the persistence of the animal. This could be the result of the need for stopping and parking on roads to displace the carcass, easier to do when traffic is low, and raises the question of fine temporal variations of roadkill removal by people as traffic volumes also tend to vary throughout the day (Van Langevelde & Jaarsma, 2005). Carcasses removed by people were also the fastest to be removed, persisting an average of only 5 hours on the road. In addition, when removed by people, bigger carcasses had a tendency to disappear even faster. This is in direct contradiction with the findings of Santos et al. (2011) where smaller animals disappeared faster, and the

heaviest animals (“carnivores”; Santos et al., 2011) had a median persistence time of 9 days. Their study however did not include animals over 10 kg, when we had animals as heavy as 25kg. It is possible that removals rates are area-dependent, and/or that their sample did not include animals large enough to warrant being removed by people, either because roadkill for these species are not frequent in the area they studied, or because large animals were killed and removed from roads fast enough to never be counted during their daily road surveys.

The value of roadkill as an ethical source of meat for human consumption has been a subject of debate in recent years (Abbate, 2019; Wright, 2019), and some have suggested displacing carcasses is an act of respect or mourning (first author’s personal communications, and see Calarco, 2023; Kopnina & Shoreman-Ouimet, 2013; Lunney, 2013). Carcasses left on the road also pose the threat of secondary collisions when attracting scavengers (Klöcker et al., 2006; Vidal-Vallés et al., 2018), which could drive people to want to remove them. Despite these possible explanations for roadkill removal by people, we lack a good understanding of how widespread this behaviour is, or how it is affected by culture or local laws. As demonstrated in this study, it can be a frequent occurrence that has a significant impact on roadkill persistence times and patterns, and thus warrants more interest from the scientific community.

Our results shed a new light on the complexities of roadkill persistence on roads. Because different sources of removal affect the relations between animal body mass and persistence, it is possible that overall relationships between persistence time and body mass are non-linear, with large and small animals being removed more quickly (*e.g.*, Guinard et al., 2012). Our results challenge the common perception that a significant part of roadkill removal is the result of scavenging activity (Antworth et al., 2005; Guinard et al., 2012; Schwartz et al., 2018), and explore the previously ignored impact of members of the public displacing and removing roadkill, making it invisible to observers during roadkill surveys. People removing roadkill impacts mostly larger animals, previously thought to stay the longest on roads, and their removal of roadkill appears faster than the action of vehicles.

Ethical statement

In compliance with the General Data Protection Regulation (GDPR) guidelines, articles 6 and 89, photographs of people captured in public spaces constitute personal data that was necessary to carry out the experiments presented in this paper. We have collected no other identifying information. Photographs showing faces, vehicle plates and other identifying information will not be shared.

Acknowledgments

We would like to thank the Syndicat de la rivière d'Ain Aval et de ses affluents (SR3A) and the Ligue de Protection des Oiseaux (LPO) Auvergne-Rhône-Alpes for their help in conducting the experiments. We also thank the Tichodrome wildlife rehabilitation center for supplying animal carcasses.

Funding

This work was supported by French Ministry of Research and Higher Education funding (PhD grant 2020-2023) and the SR3A.

REFERENCES

Abbate, C. (2019). Save the Meat for Cats : Why It's Wrong to Eat Roadkill. *Journal of Agricultural and Environmental Ethics*, *32*(1), 165-182. https://doi.org/10.1007/s10806-019-09763-6

Agresti, A. (2012). *Categorical Data Analysis*. John Wiley & Sons.

Anderson-Bergman, C. (2017). icenReg : Regression Models for Interval Censored Data in R. *Journal of Statistical Software*, *81*, 1-23. https://doi.org/10.18637/jss.v081.i12

Antworth, R. L., Pike, D. A., & Stevens, E. E. (2005). Hit and run : Effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist*, *4*(4), 647-656. https://doi.org/10.1656/1528-7092(2005)004[0647:HAREOS]2.0.CO;2

Aresco, M. J. (2005). Mitigation Measures to Reduce Highway Mortality of Turtles and Other Herpetofauna at a North Florida Lake. *The Journal of Wildlife Management*, *69*(2), 549-560. https://doi.org/10.2193/0022-541X(2005)069[0549:MMTRHM]2.0.CO;2

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., & Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation*, *222*(November 2017), 146-153. https://doi.org/10.1016/j.biocon.2018.04.014

Beckmann, C., & Shine, R. (2015). Do the numbers and locations of road-killed anuran carcasses accurately reflect impacts of vehicular traffic? *The Journal of Wildlife Management*, *79*(1), 92-101. https://doi.org/10.1002/jwmg.806

Bénard, A., Bonenfant, C., & Lengagne, T. (2023). *Influence of traffic and weather on carcass persistence time of small wildlife on roads* (p. 2023.06.01.543226). bioRxiv. https://doi.org/10.1101/2023.06.01.543226

Brand, L., Hussey, M., & Taylor, J. (2003). Decay and Disarticulation of Small Vertebrates in Controlled Experiments. *Journal of Taphonomy*, *1*.

Calarco, M. (2023). Subjects of Roadkill. In M. Calarco (Éd.), *Reflections on Roadkill between Mobility Studies and Animal Studies : Altermobilities* (p. 57-69). Springer International Publishing. https://doi.org/10.1007/978-3-031-30578-8_4

Collinson, W. J., Parker, D. M., Bernard, R. T. F., Reilly, B. K., & Davies-Mostert, H. T. (2014). Wildlife road traffic accidents : A standardized protocol for counting flattened fauna. *Ecology and Evolution*, *4*(15), 3060-3071. https://doi.org/10.1002/ece3.1097

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Erritzoe, J., Mazgajski, T. D., & Rejt, Ł. (2003). Bird Casualties on European Roads—A Review. *Acta Ornithologica*, *38*(2), 77-93. https://doi.org/10.3161/068.038.0204

European Environment Agency. (s. d.). *Greenhouse gas emissions by aggregated sector* [Data Visualization]. Visited on August 3rd, 2023 at https://www.eea.europa.eu/data-and-maps/daviz/ghg-emissions-by-aggregated-sector-5#tab-dashboard-02

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1998), 207-231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Gerow, K., Kline, N., Swann, D., & Pokorny, M. (2010). Estimating annual vertebrate mortality on roads at Saguaro National Park, Arizona. *Human-Wildlife Interactions*, *4*(2), 283-292.

Girardet, X., Conruyt-Rogeon, G., & Foltête, J.-C. (2015). Does regional landscape connectivity influence the location of roe deer roadkill hotspots? *European Journal of Wildlife Research*, *61*(5), 731-742. https://doi.org/10.1007/s10344-015-0950-4

Gomes, L., Grilo, C., Silva, C., & Mira, A. (2009). Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. *Ecological Research*, *24*(2), 355-370. https://doi.org/10.1007/s11284-008-0515-z

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, *18*(6), 323-328. https://doi.org/10.1002/fee.2216

Guinard, E., Billon, L., Bretaud, J.-F., Chevallier, L., Sordello, R., & Witté, I. (2023). Comparing the effectiveness of two roadkill survey methods on roads. *Transportation Research Part D: Transport and Environment*, *121*, 103829. https://doi.org/10.1016/j.trd.2023.103829

Guinard, É., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties : Carcasses surveys and scavenging bias. *Biological Conservation*, *147*(1), 40-51. https://doi.org/10.1016/j.biocon.2012.01.019

Hastings, H., Barr, J., Bateman, P. W., Hastings, H., Barr, J., & Bateman, P. W. (2019). Spatial and temporal patterns of reptile roadkill in the north-west Australian tropics. *Pacific Conservation Biology*, *25*(4), 370-376. https://doi.org/10.1071/PC18082

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*, 112664. https://doi.org/10.1016/j.jenvman.2021.112664

Hubbard, K. A., & Chalfoun, A. D. (2012). An experimental evaluation of potential scavenger effects on snake road mortality detections. *Herpetological Conservation and Biology*, *7*(2), 150-156.

Kemp, F. (2003). Modern Applied Statistics with S. *Journal of the Royal Statistical Society Series D: The Statistician*, *52*(4), 704-705. https://doi.org/10.1046/j.1467-9884.2003.t01-19-00383_22.x

Klöcker, U., Croft, D. B., Ramp, D., Klöcker, U., Croft, D. B., & Ramp, D. (2006). Frequency and causes of kangaroo–vehicle collisions on an Australian outback highway. *Wildlife Research*, *33*(1), 5-15. https://doi.org/10.1071/WR04066

Kopnina, H., & Shoreman-Ouimet, E. (2013). *Environmental Anthropology : Future Directions*. Routledge.

Langen, T. A., Machniak, A., Crowe, E. K., Mangan, C., Marker, D. F., Liddle, N., & Roden, B. (2007). Methodologies for Surveying Herpetofauna Mortality on Rural Highways. *The Journal of Wildlife Management*, *71*(4), 1361-1368. https://doi.org/10.2193/2006-385

Lindsey, J. C., & Ryan, L. M. (1998). Methods for interval-censored data. *Statistics in Medicine*, *17*(2), 219-238. https://doi.org/10.1002/(SICI)1097-0258(19980130)17:2<219::AID-SIM735>3.0.CO;2-O

Marcus Rowcliffe, J., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps : An adapted distance sampling approach. *Methods in Ecology and Evolution*, *2*(5), 464-476. https://doi.org/10.1111/j.2041-210X.2011.00094.x

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations : A systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12942

Ocampo, D., Borja-Acosta, K. G., Lozano-Flórez, J., Cifuentes-Acevedo, S., Arbeláez-Cortés, E., Bayly, N. J., Caguazango, Á., Coral-Jaramillo, B., Cueva, D., Forero, F., Gómez, J. P., Gómez, C., Loaiza-Muñoz, M. A., Londoño, G. A., Losada-Prado, S., Pérez-Peña, S., Ramírez-Chaves, H. E., Rodríguez-Posada, M. E., Sanabria-Mejía, J., … Acevedo-Charry, O. (2021). Body mass data set for 1,317 bird and 270 mammal species from Colombia. *Ecology*, *102*(3), e03273. https://doi.org/10.1002/ecy.3273

Ogletree, K. A., & Mead, A. J. (2020). What roadkills did we miss in a driving survey? A comparison of driving and walking surveys in Baldwin County, Georgia. *Georgia Journal of Science,* 78(2), 8.

Paraguassu-Chaves, C. A., Izidorio, A. de O., da Silva Júnior, N. P., Filho, A. K. D. B., Pereira, L. S., de Almeida, F. M., Neto, J. V. F., Barata, C. da S., Cavalcante, F. R. C., & Casara, H. N. (2020). Monitoring of Wildlife Mortality on a State Road in Rondônia, Western Amazon. *International Journal of Advanced Engineering Research and Science*, *7*(8), 208-221. https://doi.org/10.22161/ijaers.78.21

Ponce, C., Alonso, J.C., Argandona, G., Garcia Fernandez, A., & Carrasco, M. (2010). Carcass removal by scavengers and search accuracy affect bird mortality estimates at power lines. *Animal Conservation, 13(6), 603-612.*

Prosser, P., Nattrass, C., & Prosser, C. (2008). Rate of removal of bird carcasses in arable farmland by predators and scavengers. *Ecotoxicology and Environmental Safety*, *71*(2), 601-608. https://doi.org/10.1016/j.ecoenv.2007.10.013

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Ratton, P., Secco, H., & da Rosa, C. A. (2014). Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research*. https://doi.org/10.1007/s10344-014-0798-z

Rovero, F., Zimmermann, F., Bersi, D., & Meek, P. (2013). « Which camera trap type and how many do I need? » A review of camera features and study designs for a range of wildlife research applications. *Hystrix*.

Rytwinski, T., Soanes, K., Jaeger, J. A. G., Fahrig, L., Findlay, C. S., Houlahan, J., Van Ree, R. D., & Van Der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill ? A meta-analysis. *PLoS ONE*, *11*(11), 1-25. https://doi.org/10.1371/journal.pone.0166941

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass Persistence and Detectability : Reducing the Uncertainty Surrounding Wildlife-Vehicle Collision Surveys. *PLoS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road ? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0025383

Santos, S. M., Marques, J. T., Lourenço, A., Medinas, D., Barbosa, A. M., Beja, P., & Mira, A. (2015). Sampling effects on the identification of roadkill hotspots : Implications for survey design. *Journal of Environmental Management*, *162*, 87-95. https://doi.org/10.1016/j.jenvman.2015.07.037

Schwartz, A. L. W. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1-7. https://doi.org/10.1093/jue/juy006

Seiler, A. (2001). Ecological Effects of Roads : A review. *Uppsala: Swedish University of Agricultural Sciences*.

Selva, N., Jędrzejewska, B., Jędrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, *83*(12), 1590-1601. https://doi.org/10.1139/z05-158

Slater, F. M. (2002). An assessment of wildlife road casualties—The potential discrepancy between numbers counted and numbers killed. *Web Ecology*, *3*, 33-42. https://doi.org/10.5194/we-3-33-2002

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). *Foraging : Behavior and Ecology*. University of Chicago Press.

Stewart, P. A. (1971). Persistence of Remains of Birds Killed on Motor Highways. *The Wilson Bulletin*, *83*(2), 203-204.

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates : Effects of sampling methods and carcass removal. *Biological Conservation*, *157*, 317-323. https://doi.org/10.1016/j.biocon.2012.09.006

Teixeira, F. Z., Coelho, I. P., Esperandio, I. B., Rosa Oliveira, N., Porto Peter, F., Dornelles, S. S., Rosa Delazeri, N., Tavares, M., Borges Martins, M., & Kindel, A. (2013). Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis*, *17*(1), 36-47. https://doi.org/10.4257/oeco.2013.1701.04

Teixeira, F. Z., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, *54*(5), 1544-1551. https://doi.org/10.1111/1365-2664.12870

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET : Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581-597. https://doi.org/10.1111/ele.13898

Van Langevelde, F., & Jaarsma, C. F. (2005). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, *19*(8), 895-907. https://doi.org/10.1007/s10980-005-0464-7

Vidal-Vallés, D., Pérez-Collazos, E., & Rodríguez, A. (2018). Bird roadkill occurences in Aragon, Spain. *Animal Biodiversity and Conservation, (*41.2) .https://digital.csic.es/handle/10261/169416

Wright, J. (2019). Roadkill - It's What's for Dinner : How Eating Roadkill May Help Reduce Automobile Accidents. *University of the Pacific Law Review*, *51*, 301.

Appendix

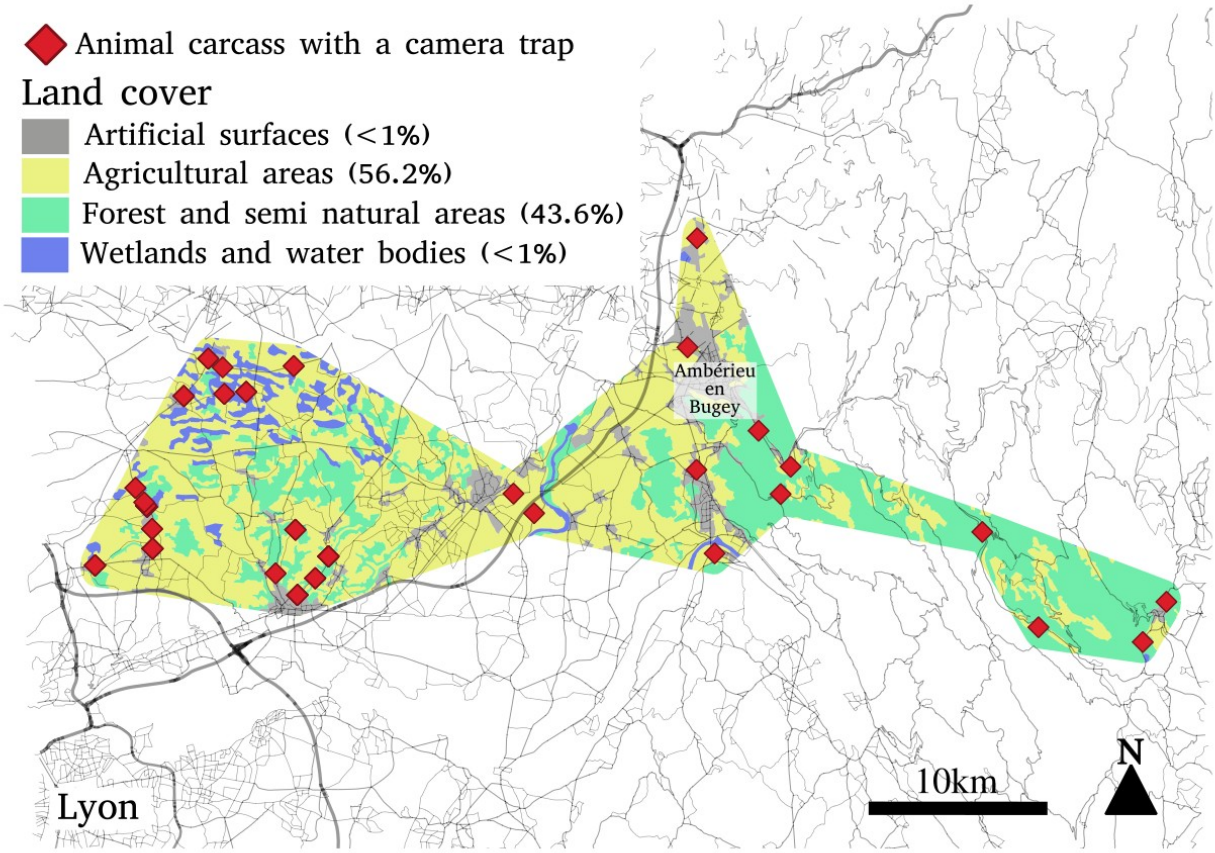


Fig. A1: Map of the area in which we conducted the carcass persistence experiments between October and March 2022 and 2023. We used Corine Land Cover data and nomenclature to characterize the study area (Corine Land Cover, 2018). Each red point represents an animal carcass we placed on the road surface or shoulder, with an infra-red camera trap installed in the road side vegetation such that the animal is visible on the photographs. We used a total of 26 species donated by a wildlife rehabilitation center:

Mammals

1 Least weasel *(Mustela nivalis)*
3 European badger *(Meles meles)*
4 Roe deer *(Capreolus capreolus)*
4 Red squirrel *(Sciurus vulgaris)*
11 European hedgehog (*Erinaceus europaeus*)
2 European rabbit (*Oryctolagus cuniculus*)
4 Pine marten (*Martes martes*)
1 Coypu (*Myocastor coypus*)
1 Brown rat (*Rattus norvegicus*)
7 Red fox *(Vulpes vulpes)*

Birds

1 swift (*Apodidae spp*.)
7 Common buzzard (*Buteo buteo*)
1 Common kestrel (*Falco tinnunculus)*
1 Carrion crow (*Corvus corone*)
5 European starling *(Sturnus vulgaris)*
1 Common pheasant *(Phasianus colchicus)*
1 Eurasian jay *(Garrulus glandarius)*
2 Great horned owl *(Bubo bubo)*
7 Common blackbird *(Turdus merula)*
1 Long-eared owl *(Asio otus)*
2 Passerine *(Passeriformes spp.)*
1 Green woodpecker *(Picus viridis)*
1 Great spotted woodpecker *(Dendrocopos major)*
2 Eurasian magpie *(Pica pica)*
4 Common pigeon *(Columba livia domestica)*
4 Common wood pigeon *(Columba palumbus)*

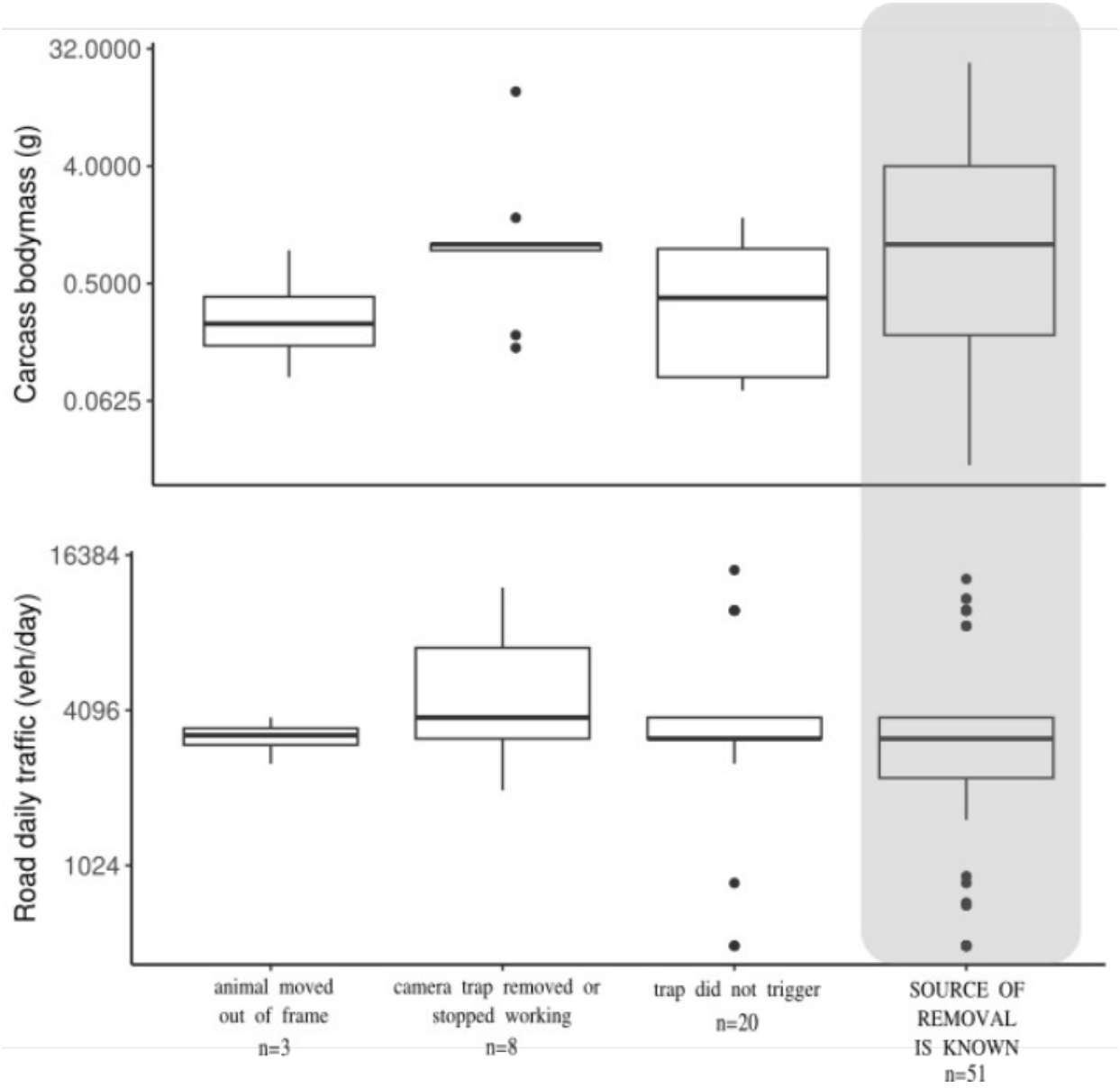


Fig. A2: We placed animal carcasses on roads equipped with camera-traps. In some cases, the source of disappearance of the carcass could not be ascertained because the trap failed or had been stolen, the trap did not trigger at the moment of removal, or the animal was displaced out of frame by passing vehicles. To explore possible biases in our results due to traps not triggering, we represent here the distribution of carcass body mass in each category compared to distribution in cases with known removal source (top) and the distribution of road traffic volumes (bottom).

A multinomial logistic regression including the trap's position as a random effect showed that the species' body mass and the traffic volumes had no significant influence on the type of issue we faced. Nonetheless, animals displaced out of frame by vehicles appear to be mostly smaller animals, meaning that particular care should be given to the positioning of the traps with small species as to photograph a wide area. Note that traps not triggering can be due to a variety of reasons, such as low battery and weather conditions (which can affect the sensors' sensitivity, Rowcliffe et al., 2011).

Fig. A3: **Examples of roadkill removal evidenced with camera-traps.**

Top left: European rabbit removal by scavengers.

Top right: Adult roe deer (intact carcass) removed by someone and placed in the forest 5 meters away from the road. The animal was not visible by drivers.

Bottom: Red fox progressive disappearance from mechanical crushing by vehicle tires. The moment of removal is defined as the moment when the species is no longer recognizable.

Case study: informing roadkill persistence time with citizen science

CONTEXT

Roadkill persistence is an essential factor for accurate study of wildlife-vehicle collisions. Research has shown that various spatio-temporal factors impact this persistence, making it challenging to extend existing persistence estimates to new roadkill monitoring projects. However, citizen science initiatives, which currently enable the monitoring of roadkill across broad spatio-temporal ranges at a fraction of the effort required for professional surveys, may also be a promising avenue for estimating roadkill persistence in new contexts.

OBJECTIVES

- Formulate a methodology to assess the persistence of roadkill, relying on citizen sciences.

- Estimate persistence, along with the impacts of two previously investigated predictors – species' body mass and road traffic volume – and a newly introduced predictor: season.

RESULTS

This preliminary experiment achieved reasonable spatio-temporal scales, yielding results that demonstrated a notable impact of traffic volume on persistence. This outcome, which differs from previous results, could be attributed to the inclusion of highways as a novel road type in the dataset. Furthermore, the persistence estimates obtained through this methodology aligned with previous findings, and no effect of the season on roadkill persistence is evidenced.

CONCLUSIONS

Citizen science proves a viable approach for estimating roadkill persistence and investigating its spatial, temporal, and biological predictors. This cost-effective method has enabled us to expand the scope of our experiments, both in terms of time and locations, which has led to new insights.

The straightforward nature of this experimental design makes it well-suited for implementation alongside existing citizen science roadkill monitoring programs or as stand-alone research projects.

Introduction

In the two previous manuscripts, we worked toward estimates of the persistence of roadkill on roads by (1) placing fresh carcasses in front of camera traps, and (2) by following the disappearance of carcasses at intervals of 2 hours. We encompassed a wide range of species' sizes, from great tit *Pajus major* to roe deer *Capreolus capreolus,* and of road traffic volumes, from 500 to over 15 000 vehicles.day^{-1}. In both of these studies, we found generally short persistence times for all species, with most of the roadkill disappearing in less than 24 hours. We also found evidence of a spatial distribution in the persistence of amphibians, as persistence was strongly influenced by the volume of traffic of the road. In addition, in the previous manuscript, road users were seen removing a third of the carcasses we placed on the road, after an average of 6h (95% CI: 2h,24h), which was much shorter than disappearance through mechanical crushing (about 20h) and other average persistence estimates found in the literature (see next paragraph). There might be a spatial component to the removal of carcasses by people, as we do not know yet if this habit is widespread or specific to certain areas and cultures (other documented evidence of this behaviour: Calarco, 2023; Kopnina & Shoreman-Ouimet, 2013). We have lightly touched on temporal variations (rainfall) in roadkill persistence, but have yet to explore seasonal effects, which have previously been demonstrated in Portugal (Santos et al., 2011)

Another indication of the possible presence of a spatio-temporal structure in roadkill persistence is the disparity in the persistence estimates presented in published studies. We found an overall median persistence time of 10 hours (95% CI: 5h, 42h) for a wide range of mammal and bird species and sizes of roads (previous manuscript). Santos et al. (2011) found substantially longer median persistence times than we did for hedgehogs (4.5 [3,7] days), birds of prey[5] (6 [4,9] days) and mammalian carnivores (9 [5,19] days). Henry et al. (2021) found a median persistence of 8 (0,17) days for large mammals[6], and 2 (0,4) days for passerines and small mammals[6]. Ruiz-Capillas et al. (2015) found an average persistence of 6.65 (6.24,7.06) days for small rodents. Conversely, Stewart (1971) found that house sparrows (*Passer domesticus*) carcasses deposited on an interstate highway persisted on average less than 90 minutes, and chick carcasses placed by Ratton et al. (2014) on highways and dirt roads persisted an average of 12h. The persistence of roadkill, useful to calibrate survey methodologies, appears highly variable depending on the species but also presumably on locations, weather, or the distribution of road traffics.

5 Birds of prey: diurnal and nocturnal; accipitriforms and strigiforms (Santos et al., 2011)

6 Large mammals: 4.5 to 40 kg; Passerines: all passerine species; Small mammals: < 70g (Henry et al., 2021)

Consequently, estimates of roadkill persistence that aim at correcting a roadkill dataset should ideally be obtained in the context of the roadkill monitoring scheme, in order to match the geographical, cultural and ecological parameters of the area where the roadkill data is collected. Methods for estimating persistence can be implemented concurrently to the regular monitoring of roads with capture-recapture approaches, which means leaving the carcasses on the road during surveys and noting the presence or absence of each carcass during each consecutive survey (see Guinard et al., 2012 for an application of this methodology). However, in the context of roadkill monitoring with citizen sciences, this approach is not as straightforward: citizen science roadkill monitoring schemes usually continuously monitor roadkill within a wide geographical area (Vercayie & Herremans, 2015).

Two options are possible for roadkill counts correction in the context of citizen science: estimating the persistence of roadkill at a smaller scale (*i.e.,* a limited geographical area and period) and upscale these estimates at the larger scale of the monitoring project (as we have attempted in sections 1 and 2 of this chapter), or estimating persistence at a much larger scale by relying on the project contributors themselves, who can cover spatial and temporal ranges comparable to the monitoring project they take part in. In other words, roadkill persistence experiments have the potential to be carried out through citizen science, serving as a supplementary activity for participants alongside their usual roadkill reporting duties. In this case study, we explore the feasibility of roadkill persistence monitoring using Faune-AuRA contributors and compare the results obtained with this methodology to the two previous manuscript dealing with roadkill persistence as well as published results.

Methods

Volunteer contributors recruitment

We recruited volunteer contributors with announcements through the LPO communication channels (many LPO members also take part in the Faune-AuRA monitoring), as well as via a local newspaper[7]. Volunteers provided us with a set of roads they accepted to cover by car at least daily, either because it

7 "Des volontaires recherchés pour évaluer la mortalité des animaux sur les routes de l'Ain" – 05/05/2022, Bugey Côtière [url]

was their daily itinerary to and from work, or because they lived in the area. They were tasked with monitoring roadkill carcasses present in their area at least every 24h: taking a picture and sending it to the author's phone number, along with a comment on the visibility of the animal from the road (whether it was visible to drivers or not). The volunteers could either detect a fresh carcass themselves, or be asked to monitor a carcass that had been reported in Faune-AuRA by another contributor. For this second option, we monitored the Faune-AuRA database bi-daily to signal new roadkill reports.

The recruitment of volunteers required the disclosure of personal information such as names, contact, and places of residence. Particular care was given to inform participants of their rights under the GDPR (General Data Protection Regulation) guidelines during this process.

Statistical analyses

We obtained daily observations of the presence or absence of roadkill carcasses, along with the species' body mass (continuous variable, obtained from manuscript n°3), the daily average traffic of the road (continuous variable, obtained from departmental councils and the Ministry of Ecological Transition, 2019) and the season (spring, summer and winter). This type of persistence data is very similar to data obtained by Santos et al. (2011), and we analyzed the data following the same methodology. We estimated the median roadkill persistence using a Kaplan-Meier estimator, and constructed a mixed semi-parametric survival model (Cox-Ph model) to analyze the persistence probability of the carcasses in relation to the road traffic (continuous, see previous manuscript), season (categorical) and carcass' species body mass (continuous, see previous manuscript) with the ID of the observer as a random effect. In addition, we grouped the roadkill species into categories based on animal size and taxon and computed the survival curves for each group, to enable a comparison with Henry et al. (2021) and Santos et al. (2011) who presented their results in a similar manner. We used the packages *survival* (Therneau & Grambsch, 2000) and *coxme* (Therneau, 2022) for R (R Core Team, 2021).

Results

Volunteers turnout

We recruited a total of 12 volunteers who agreed to cover a total of 2886 km² of the AuRA region (4.14%), which amounted to 6.04% of the road network (fig. 1). In total, we obtained 55 observations of roadkill persistence covering the spring, summer, and winter of 2021. Volunteers were generally motivated to conduct the observations, although they could not always follow carcasses every day as required, which conducted 8 (14.5%) of the observations to be right-censored. As a side note, in another 14.5% of the observations, volunteers reported that the intact carcasses had been moved into the shoulder vegetation or in a ditch, making it likely the removal was the result of the intervention of someone.

Monitored roads covered a range of 400 to 14 044 vehicles.day^{-1}, with the notable inclusion of two highways (A6 and A89). We obtained observations for 19 species from 0.015 to 25kg. The observed species were: roe deer (*Capreolus capreolus)*, European badger (*Meles meles)*, red fox *(Vulpes vulpes)*, coypu (*Myocastor coypus)*, European hare (*Lepus europaeus)*, pine marten (*Martes martes)*, European rabbit (*Oryctolagus cuniculus)*, red squirrel (*Sciurus vulgaris*), brown rat (*Rattus norvegicus)*, common buzzard (*Buteo buteo)*, tawny owl (*Strix aluco)*, domestic pigeon (*Columba livia)*, Eurasian chaffinch (*Fringilla coelebs)*, common blackbird (*Turdus merula)* and European robin (*Erithacus rubecula*).

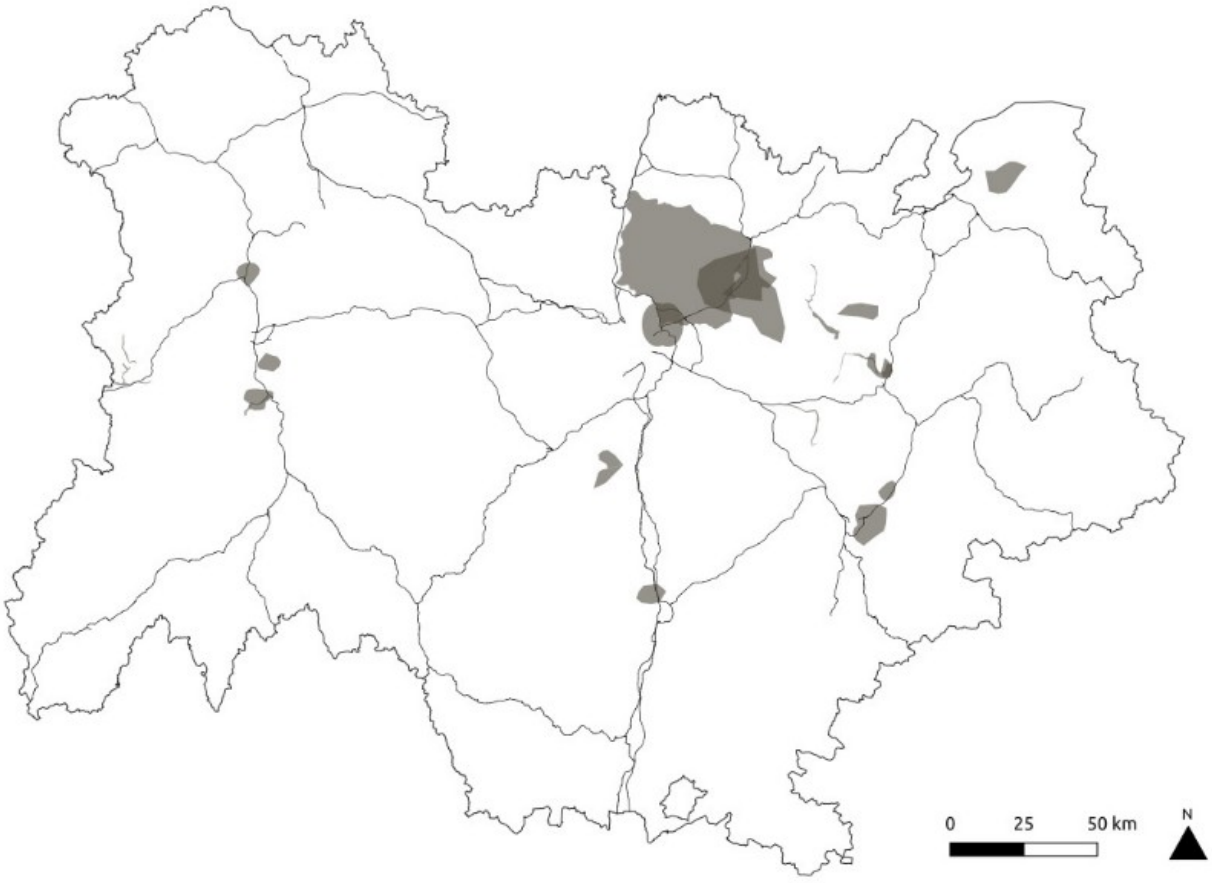


Fig. 1: Map of the Auvergne-Rhône-Alpes region with the area covered by the volunteers in the roadkill persistence experiment. Each volunteer provided an area in which they accepted to follow the disappearance of roadkill carcasses at least daily. Total coverage by volunteers represented about 4% of the region surface.

Persistence estimates

The median persistence time was estimated at 43h (95% CI: 24,62). The longest persistence was observed for small mammals (pine marten, red squirrel and brown rat) at 59h (95% CI: 24,NA) and the shortest median persistence was observed for non-birds of prey (23h (95% CI: 21.2,NA), common blackbird, European robin, domestic pigeon, Eurasian chaffinch, fig. 2). Note that 'NA' estimations with Kaplan-Meier estimators are a result of right-censoring (Goel et al., 2010).

The Cox-PH model showed no significant effect of the species' body mass (Hazard ratio (HR)=0.979 (95% CI: 0.95,1.001), z=-0.70, p=0.48) or season (*summer vs. spring:* HR= 0.52 (95% CI: 0.29,0.91), z=-1.15, p=0.25; *winter vs. spring*: HR= 0.56 (95% CI: 0.37,0.84), z=-1.43, p=0.15). Increasing the road traffic volume increased the persistence of the carcasses (HR=0.93 (95% CI: 0.89,0.96), z=-2.20, p=0.03).

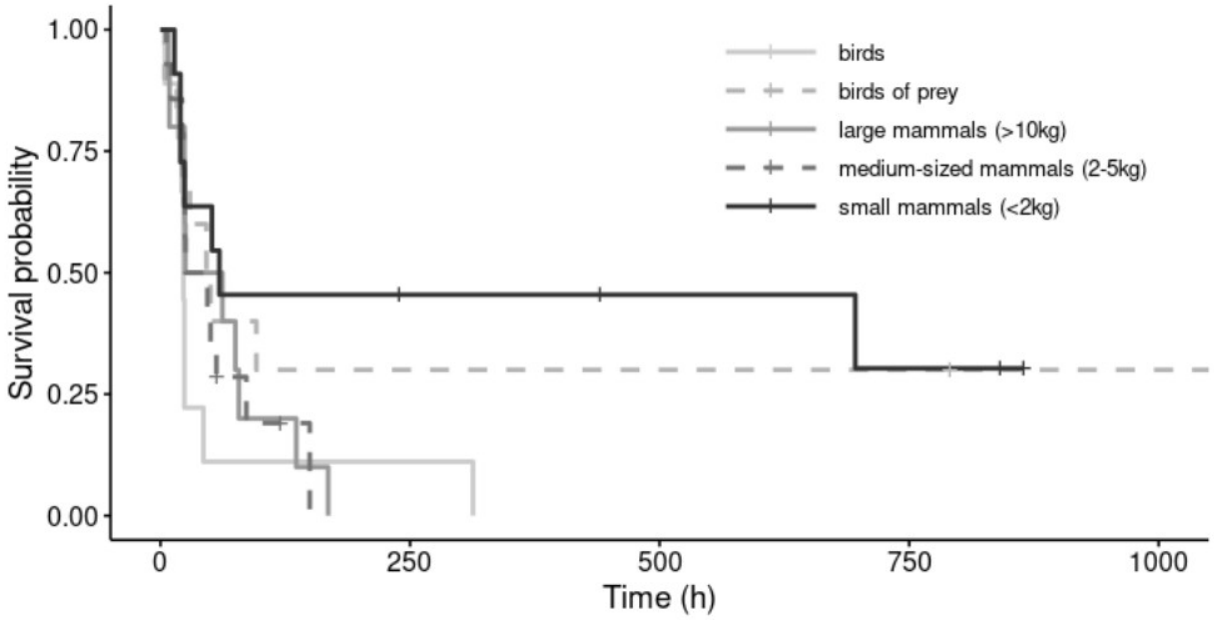


Fig. 2: **Survival curves of roadkill persistence on the road**.

Birds: domestic pigeon (*Columba livia*), Eurasian chaffinch (*Fringilla coelebs*), common blackbird (*Turdus merula*) and European robin (*Erithacus rubecula*), median persistence: 23h (95% CI: 21.2,NA);

Birds of prey: common buzzard (*Buteo buteo*), tawny owl (*Strix aluco*), median persistence: 48.1h (95% CI: 21.6,NA);

Large mammals: roe deer (*Capreolus capreolus*), European badger (*Meles meles*), red fox (*Vulpes vulpes*), median persistence: 43.5h (95% CI: 24,NA);

Medium-sized mammals: coypu (*Myocastor coypus*), European hare (*Lepus europaeus*), pine marten (*Martes martes*), European rabbit (*Oryctolagus* cuniculus), median persistence: 36 (95% CI: 24,NA);

Small mammals: red squirrel (*Sciurus vulgaris*), brown rat (*Rattus norvegicus*), median persistence: 59 (95% CI: 24,NA).

Discussion: is citizen science a viable method for estimating roadkill persistence?

In this short case study, we demonstrated a methodology for obtaining persistence estimates at large spatial scales using citizen science. We were successful in obtaining 55 reports of carcass persistence, covering a range of road traffic and species comparable to our previous experiments, but covering much larger geographical and temporal ranges. We estimated median persistence times of about 2 days across all species, which is comparable to published estimates (Henry et al., 2021; Ruiz-Capillas et al., 2015; Santos et al., 2011). However, while Santos et al. (2011) reported that small mammals and small birds disappeared faster than birds of prey, we found the reverse. We found no effect of the species' body mass on persistence, which is again in contradiction with Santos et al. (2011) and Henry et al. (2021), but is consistent with the conclusions of our previous manuscript. However, contrary to our previous findings, we found a significant effect of traffic volume on roadkill persistence, with roadkill persisting longer on more frequented roads (similar conclusions in Santos et al., 2011).

The volunteers sometimes reported that the animal had been placed in a ditch or in the vegetation of the road shoulder but had remained intact (14.5% of cases), which suggests that the roadkill removal by road users evidenced in the previous manuscript (limited to the Ain department) is also observed in other departments of the AuRA region (Isère, Loire, and Savoie departments). While season influenced roadkill persistence in other studies (Guinard et al., 2012; Santos et al., 2011), we did not find significant differences in roadkill persistence between summer, spring, and winter. It is often thought that seasonal differences in persistence are driven by scavenger presence and activity (Prosser et al., 2008; Santos et al., 2011), but we have uncovered little evidence of roadkill consumption by scavengers in the AuRA region (or at least the Ain department) in the previous manuscript.

The median persistence time of roadkill we estimated previously is lower than the results obtained in this experiment, with an overlap of the 95% confidence intervals (*manuscript n°3:* 10h36 (95% CI: 5h52,42h36); *citizen science approach*: 43h (95% CI: 24h,62h), fig. 3). However, there was no overlap between the confidence interval of the Kaplan-Meier survival curves for the first 24 hours, and we found a significative effect of the road traffic. The citizen science approach covered a larger area than we managed with more traditional experimental designs, with volunteers located in several departments of the region AuRA while we only conducted the camera-trap experiments in the south-east area of the Ain department. It is possible that roadkill persistence at the scale of the region is longer than what we observed in the Ain department.

There were also differences in methodology between the two studies: the *camera-trap* experiment (previous manuscript) involved placing animal carcasses on the road while the *citizen science* approach presented here only targeted roadkill that was either (1) detected by the volunteers or (2) reported by another contributor of the Faune-AuRA project. In consequence, there is a probable bias for animals with higher detectability and with longer persistence in the *citizen science* sample. Animals that disappear very quickly are less at risk of being selected for the citizen science approach, because the probability of being reported by a contributor was lower. In fact, some of the species placed on the road in the *camera-trap* experiment disappeared in a few minutes only, usually when they were located in the path of the vehicle's tires. This may also be the case in published studies of roadkill persistence which employ a capture-recapture method, as daily capture-recapture surveys may overlook the carcasses with very short persistence times (*i.e.*, a few hours or less). The heterogeneity in capture probability may result in positively biased estimates of persistence (Pledger et al., 2003).

In addition, this study managed to cover two highways of the region, which we did not include in the *camera-trap* experiment due to safety concerns. In this instance, removing the data collected on highways from the Kaplan-Meier estimates and Cox-PH model lowers the estimated median persistence to 27h12 (95% CI: 24h,59h), which overlaps the *camera-trap* estimates, and removes the significance of road traffic volume in the Cox-PH model (HR=0.93 (95% CI: 0.90,0.97), z=-1.76, p=0.08). Although the volume of traffic of these highways was comparable to some roads used in both manuscripts on roadkill persistence, highways in France differ from other roads by a few characteristics: they are mostly fenced, and it is not possible to park a car and step out on the road surface. Therefore, roadkill species and mechanisms of removal on these roads may differ from the rest of the road network. Guinard et al. (2012) found median persistencies of over a week for passerines and strigiforms carcasses on french highways.

Conclusions

Citizen sciences appear to be a viable way of obtaining persistence estimates for roadkill, covering large spatial scales at lower costs than experiments conducted by professionals. This preliminary experiment only involved a handful of volunteers and showed that they managed to produce exploitable data. Citizen science roadkill monitoring projects could use this method as a way to estimate persistence in the territory they cover by recruiting a sub-sample of volunteer contributors from the project. In this case, we were able to cover a new type of road with this approach (highways), which leads to novel conclusions about the spatio-temporal patterns of roadkill persistence.

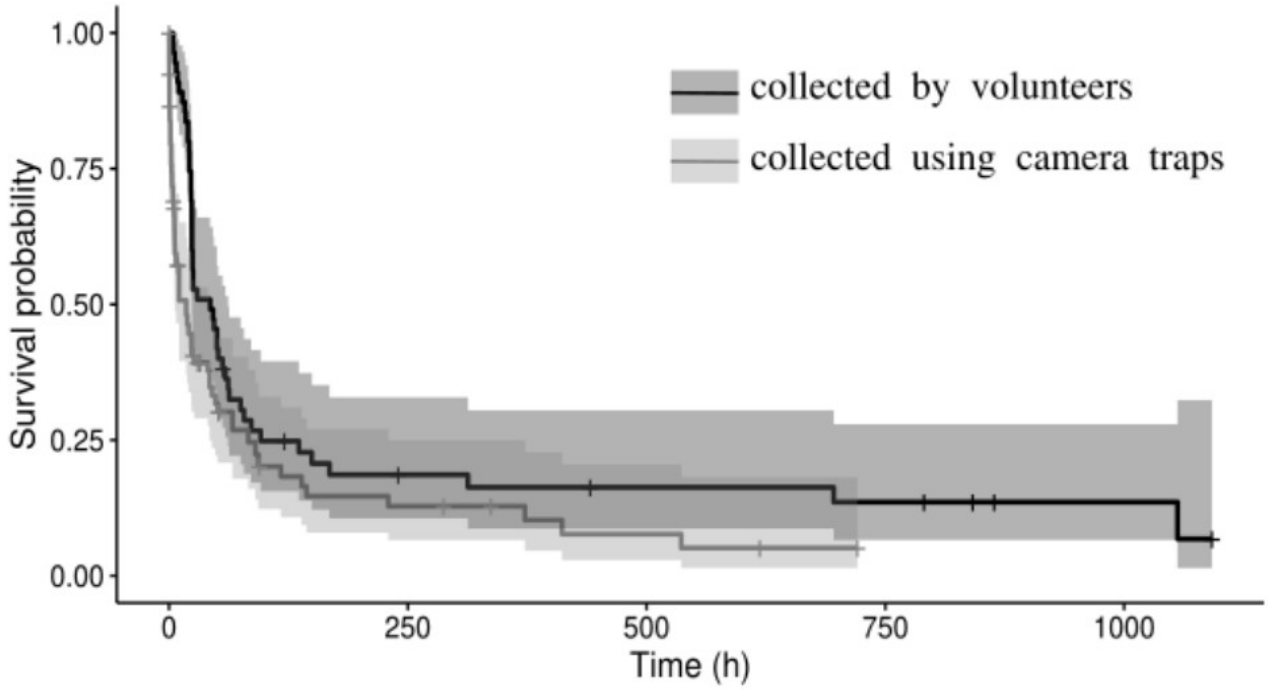


Fig. 3: Roadkill persistence survival curves and 95% confidence intervals using two methods of carcass monitoring: volunteers observers checking for the presence of the roadkill carcasses at least every 24 hours, or placing motion-triggered camera traps in front of the carcasses to capture the moment of removal. The first method (n=86) estimated the median persistence time of roadkill at 10h (95% CI: 6h07,42h36) and the second method 43h (95% CI: 24h,62h).

Ethical statement

In compliance with article 89 of the GDPR, we have received informed consent from the participants to use personal data. No personal data will be shared or stored after the end of this thesis project.

Acknowledgments

We would like to thank the volunteers that participated in this study, and in particular my colleague Prof. Y. Voituron for his enthusiastic regular reports of the state of the buzzard on highway A89. We would also like to thank the LPO Ain director, F. Bulliffon, as well as the LPO Auvergne-Rhône-Alpes as a whole for their help in recruiting volunteers. Finally, we are grateful for the implication of Bugey Côtière in the diffusion of our call to volunteers.

REFERENCES

Calarco, M. (2023). *Reflections on Roadkill between Mobility Studies and Animal Studies : Altermobilities*. Springer International Publishing.

Goel, M. K., Khanna, P., & Kishore, J. (2010). Understanding survival analysis: Kaplan-Meier estimate. *International Journal of Ayurveda Research*, *1*(4), 274–278. https://doi.org/10.4103/0974-7788.76794

Guinard, É., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties : Carcasses surveys and scavenging bias. *Biological Conservation*, *147*(1), 40-51.

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*, 112664.

Kopnina, H., & Shoreman-Ouimet, E. (2013). *Environmental Anthropology : Future Directions*. Routledge.

Pledger, S., Pollock, K. H., & Norris, J. L. (2003). Open Capture-Recapture Models with Heterogeneity: I. Cormack-Jolly-Seber Model. *Biometrics*, *59*(4), 786–794. https://doi.org/10.1111/j.0006-341X.2003.00092.x

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2015). How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecological Research*, *30*(3), 417-427.

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road ? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, *6*(9).

Shin, Y., Kim, K., Groffen, J., Woo, D., Song, E., & Borzée, A. (2022). Citizen science and roadkill trends in the Korean herpetofauna : The importance of spatially biased and unstandardized data. *Frontiers in Ecology and Evolution*, *10*.

Swinnen, K., Jacobs, A., Claus, K., Ruyts, S., Vercayie, D., Lambrechts, J., & Herremans, M. (2022). *'Animals under wheels' : Wildlife roadkill data collection by citizen scientists as a part of their nature recording activities*. Pensoft Publishers.

Therneau, T. M., & Grambsch, P. M. (2000). *Modeling survival data : Extending the Cox model*. Springer.

Vercayie, D., & Herremans, M. (2015). Citizen science and smartphones take roadkill monitoring to the next level. *Nature Conservation*, *11*, 29-40.

Chapter 3: Roadkill detection probabilities

Influence of animal size and driver attentiveness on roadkill detection rates (in preparation)

Annaëlle Bénard, Christophe Bonenfant and Thierry Lengagne

CONTEXT

Counting roadkill carcasses is an important aspect of understanding and reducing animal mortality on roadways. In recent years, citizen science has emerged as a valuable tool for gathering large-scale data of the spatio-temporal distribution of roadkill. However, both professional and citizen science methodologies underestimate the actual number of roadkill, as not all carcasses present on the road are detected. If roadkill detection has been studied in the context of professional surveys, we have yet to explore the search efficiency of contributors in citizen science projects.

OBJECTIVES

We conducted an experiment using taxidermied animals as roadkill decoys to:

- Estimate the rates of detection for roadkill based on the size of the carcass, the position of the observer in the vehicle, and the attentiveness of the observer,

- Illustrate the use of these estimated detection rates in the context of citizen science monitoring by correcting the roadkill reports from Faune-AuRA for two species of mammals (*Vulpes vulpes, Sciurus vulgaris)* and one bird species (*Buteo buteo).*

KEY RESULTS

- The probability of detecting a carcass increased with its size, but the observer's position in the car had no impact on detection,

- Attentive drivers (focused on counting roadkill, *e.g.*, professional monitoring) were found to have a much higher chance of detecting a carcass compared to inattentive drivers (*i.e.*, normal day-to-day driving, citizen science) with a 34-fold difference.

- Reported roadkill in Faune-AuRA may represent only 10% of the actual number of collisions for the red squirrel *Sciurus vulgaris*, 49% of the collisions for common buzzards *Buteo buteo* and 28% for the red fox *Vulpes vulpes.*

CONCLUSIONS

- Opportunistic roadkill reports tends to underestimate the true number of collisions due to the fact that not all carcasses are detected, and detection rates are even lower than in professional road surveys.

- Estimated ratios of reports-to-collisions in citizen science are alarming, especially considering the significant number of reports received by some of these projects (*e.g., 3*0 reports daily to Faune-AuRA across all species).

Abstract

Linear transportation infrastructures threaten the viability of many wildlife populations, most notably through directly mortality as a result of collisions with vehicles. Roadkill monitoring is a vital component of understanding and mitigating this mortality, and in recent years, citizen science monitoring has emerged as a way of obtaining large-scale datasets. However, in both professional and citizen science road monitoring, there is a possibility of under-estimating the number of roadkill because not all animals are detected, a bias that may be even greater in citizen science because contributors are not focused on searching for roadkill when driving. Using 20 taxidermied birds and mammals of varying sizes, we test the roadkill detection rates of drivers that were either tasked with detecting as much roadkill as possible, or that were unaware of the experiment at the time they drove by the decoys. We find that roadkill detectability increases with the size of the animal, and that drivers attentive to roadkill were 34 times more likely to detect carcasses than drivers that were not. We use the detectability estimates from inattentive drivers to correct roadkill reports from the citizen science database Faune-AuRA, and find that actual roadkill can be up to 9 times the number of reports present in the database. These results raise conservation concerns, considering that citizen science roadkill databases such as Faune-AuRA can receive hundreds of reports every day, many of them concerning endangered species.

1. Introduction

Terrestrial transportation contributes to the ongoing global biodiversity decline by jeopardizing the fitness of individuals (Forman & Alexander, 1998). In particular, building roads results in habitat loss and fragmentation that disrupt ecological processes (Seiler, 2001), and the acoustic, chemical and light pollution generated by road traffic are detrimental to the survival of many species (Bissonette & Rosa, 2009; Eigenbrod et al., 2009; Forman, 2000). Collisions between wildlife and vehicles are a direct source of mortality that potentially affects all terrestrial species (Olson et al., 2014; Swinnen et al., 2022) and threatens the persistence of populations (Grilo et al., 2021; Moore et al., 2023). The impact of road mortality could be as high as 194 million mammals and 29 million birds annually in Europe (Grilo et al., 2020). There is currently a need for reducing this impact, by identifying or the collisions hotspots and implementing mitigation measures. Fences can be used to prevent wildlife crossings roads, which also increases the fragmentation of habitats (Andrews, 2014). Structures such as underpasses and overpasses can be constructed to allow wildlife road crossing without the threat of encountering a vehicle (Bond et al., 2008). The high costs of these mitigation measures bring the need for accurate collision hotspot identification in order to target the most strategic locations (Teixeira et al., 2017).

For this reason, large-scale roadkill data is valuable. However, the collection of roadkill data in a territory requires regular monitoring of the entire road network, which is very costly (Henry et al., 2021). In recent years, ecologists have started to take advantage of the ubiquity of connected smartphones to ask road users to report the roadkill they encounter. Citizen science projects of roadkill monitoring have gained popularity in recent years, with some attaining thousands of contributors and 90 000 reports of roadkill (Swinnen et al., 2022). Although these projects allow the collection of roadkill data over large temporal and spatial scales, the reports from volunteer contributors often suffer from many biases. Incorrect species identification can introduce erroneous reports in datasets (J. L. Dickinson et al., 2010). Unevenly distributed sampling effort, both spatially and temporally, can introduce trends in roadkill reports that do not correspond to a biological reality (Hochachka et al., 2012). In addition, roadkill removal from roads by scavengers, people, or the passage of vehicles can prevent carcasses from ever being reported (Bénard et al., 2023). Finally, in most cases, not all roadkill is detected by contributors when they drive on the road (Collinson et al., 2014). Despite these issues, authors have argued that citizen science roadkill is useful for informing roadkill rates (Petrovan et al., 2020; Shin, Kim, Groffen, Woo, Song, & Borzee, 2022; Waetjen & Shilling, 2017).

In particular, detection probabilities for roadkill carcasses, which have received some attention from the perspective of roadkill survey conducted by professionals using standardized protocols (Collinson et al., 2014), are seldom addressed in citizen science. For standardized surveys, these detection rates can be

assessed by comparing the number of carcasses an observer can detect from a car to the number detected by observers on foot, which assumes that the latter can detect 100% of the carcasses present on the road (Teixeira et al, 2013). Roadkill detectability is better for observers on foot than in cars, increases with body size and differs depending on taxa (Collinson et al., 2014; Gerow et al., 2010; Santos et al., 2016; Teixeira et al., 2013, Table 1). Authors use these results to recommend optimal survey methods for maximum detection of roadkill (*e.g.*, prioritize surveys conducted on foot, Collinson et al., 2014). In the case of citizen science however, the reporting of roadkill is usually opportunistic and cannot be standardized in this way. Instead, *ad-hoc* corrections of the dataset appear to be the most promising avenue for integrating roadkill detection into these databases (Gerow et al., 2010). However, roadkill detection rates are most likely context-dependent: professional observers during standardized surveys are actively looking for roadkill while contributors to citizen science projects are most likely not, as they report opportunistic sightings of roadkill during day-to-day activities. Current estimates of roadkill detectability have always focused on active roadkill visual search, but there are (to our best knowledge) no available estimates of the detection rates for drivers that are not in a context of active roadkill search.

Standardized professional surveys are sometimes conducted from cars with one person driving and one passenger surveying the road (*e.g.*, Bright et al., 2015; Clevenger et al., 2002; Driessen, 2021), most likely for safety purposes, as it allows the driver to focus their full attention on the road. There is no clear evidence that passengers have higher roadkill detection rates when both are tasked with looking for roadkill (Collinson et al., 2014). In citizen science, we can make a different prediction: drivers typically focus their attention on the road ahead and to the left and right of the road (Chapman & Underwood, 1998; K. A. Miller et al., 2021), which is where roadkill is likely to be located, while we may expect passengers to be distracted or looking at the scenery. Therefore, there is a possibility that in this type of monitoring, drivers are in fact more efficient at detecting carcasses than their passengers.

In this study, we compare the detection rates of roadkill from a moving car in the context of citizen science, which means during non-active monitoring of roadkill, to rates in standardized roadkill surveys, which means drivers were tasked with detecting as much roadkill as possible. We used taxidermied mammals and birds as decoys to compare the detection scores of roadkill between both contexts, expecting that drivers in the context of citizen science will detect significantly fewer animals. Following current knowledge of the detectability of roadkill (Table 1), we expect decoy detectability to increase with its size in both contexts, and to differ according to the animal taxa. We also explore the differences in detection efficiency between the drivers and passengers of a vehicle during non-active monitoring, expecting better detection of roadkill from passengers. Finally, we demonstrate *ad-hoc* citizen science dataset correction by extracting roadkill reports from the citizen science database Faune-Auvergne-

Rhône-Alpes (Faune-AuRA) and using our estimates of the detection rates to account for the proportion of roadkill missed by the contributors of the citizen science project.

Table 1: Review of the roadkill detection probabilities during standardized professional road surveys. The detectability of roadkill from a moving vehicle can be estimated by either using decoys placed on the road or by comparing the results of surveys performed from a vehicle to surveys performed on foot, assuming that the latter represents a 100% detection probability. To the author's best knowledge, no estimates of detection probability are available for roadkill monitoring relying on citizen science.

Authors	**$P_{detection}$ (95% CI)**	**Method**
Collinson et al. (2014)	88.8% (83.8,92.8)	Painted pieces of rubber to simulate flattened roadkill placed on 1-km road transects on which observers drive
Gerow et al. (2010)	Amphibians: 4.8% (4,5.6) Reptiles: 3.7% (2.6,4.8) Birds: 34.5% (28.3,40.7) Mammals: 10.3% (7.6,13)	Comparing the number of carcasses recorded during a driving survey to the number recorded during a concurrent survey on foot
Santos et al. (2016)	7% (2,15) for animals <100g 13.3% (4,29) for animals >100g	
Teixeira et al. (2013)	Reptiles: 20% (7,33) Birds: 5% (4.3,5.7) Mammals: 47% (34,60)	

2. Material and Methods

2.1 Roadkill decoys

We chose to use animal taxidermy to represent roadkill. This method ensured that the species' size and coloration were comparable to fresh roadkill, while also allowing the comparison of informed and uninformed roadkill detection using the exact same decoys. In addition, artificially placing decoys on the road instead of counting roadkill that was already present ensured that the exact number of carcasses available to detection is known, leading to robust estimates of detection probability. We acquired 20 decoys of 11 species of birds and mammals from private collectors or by having fresh carcasses (donated by a wildlife rehabilitation center) taxidermied by a professional or the authors themselves, in a posture consistent with realistic fresh roadkill (complete list of species in appendix A1). We used the volume of the decoy as a variable instead of body mass (Santos et al., 2016), as it was likely that the size of the animal is the variable influencing its detectability. We computed decoy volume using measures of length (head to tail), width (measured at the thoracic cage) and height (from end of foot, hoof, or paw to animal back, perpendicularly). In addition, we accounted for unique postures: for example, we included wing

span in some birds that had been taxidermied with their wings stretched out, which means they appeared bigger than birds of the same body size with wings tucked along the body. During all experimental trials, we placed the decoys on the roads shoulders or at the junction between the road surface and shoulder, such that they were not hidden by the vegetation. We held the decoys in place using camping pegs. We did not place decoys directly on the lanes for safety purposes, as vehicles may drive over them.

2.2 Roadkill detectability experiments

Informed search

We conducted an experimental session on the road network of in the Ain department, central-east France. We defined a 28km circuit of roads, on which the volume of traffic varied between 9989 vehicles.day^{-1} to less than 500 vehicles.day^{-1} and the speed limits varied between 90km.h^{-1} and 50km.h^{-1} (Ain departmental council, 2023). We placed 20 roadkill decoys in random order (selected with a random number generator) on the circuit, always on the side of the road the volunteer would drive on (fig. A2). We did not place decoys at less than 700m from each other, and avoided urbanized road verges for decoys not to be displaced or stolen.

The experimental session took place on an overcast morning with medium rainfall (2 to 8mm.h^{-1}) and no fog. We recruited 17 volunteers with no previous experience in professional roadkill surveys by advertising with the Ligue de Protection des Oiseaux (*Bird Protection League*, thereafter: LPO) NGO and a student naturalist association. We asked volunteers to drive at speed limit along the circuit with their personal vehicle. We timed the departure and arrival of each volunteer and compared it to a reference travel time when driving at speed limit to ensure no driver drove significantly slower or faster than recommended. There was at least a 10 minutes interval between the departures of one volunteer and the next such that vehicles did not directly follow one another. Each participant was asked to fill out a form twice with the list of species detected, the first time at the mid-point of the road circuit (after driving by 11 decoys for 14 km) and a second time after they had completed the circuit (additional 11 decoys, 14 km). We split detected decoys recording in two occasions to reduce the possibility of under-estimating detection probability because of forgotten decoys.

Uninformed search

In order to assess the detection rate of drivers who were not actively looking for roadkill, we conducted two experimental sessions during the general assembly (first session, n=59 participants, June 2022) and meeting of the board of directors (second session, n=15 participants, October 2022) of the LPO of the Auvergne-Rhône-Alpes region (thereafter: LPO AuRA). Note that most of the contributors in the citizen science roadkill project Faune-AuRA are members of the LPO AuRA (Faune France, 2018). We placed decoys in the last 5 kilometers before the meeting locations of each event, covering every possible itinerary, at least 30 minutes before attendees were expected to arrive. We ensured that all attendees would drive by similar decoys (same set of species) no matter the itinerary they used (fig. A3).

The first session included decoys of squirrels (*Sciurus vulgaris)* and foxes (*Vulpes vulpes),* and the second session included squirrels, foxes, diurnal raptors (European honey buzzard *Pernis apivorus* and common buzzard *Buteo buteo*) and pigeons (*Columba livia).* At the start of each meeting, we asked attendees to fill out anonymous surveys, asking them to disclose their seat in the vehicle they arrived in (driver or passenger) and wether or not they had seen roadkill in the last 5km of their journey. Possible answers included each decoy placed on their itinerary plus a control species (Eurasian badger) that was not present on the road, in order to control for false reporting (Bhattacherjee, 2012).

2.3 Data analysis

All analyses were performed using R 4.3.1 (R Core Team, 2023).

Roadkill detectability in informed and uninformed searches

To evaluate the relations between decoy detectability, volume, taxa, and attentiveness of the observers, we constructed a mixed logistic regression (package *lme4,* Douglas et al, 2015). The response variable is the detection status after each encounter between a participant and a decoy (0: decoy was not detected, 1: decoy detected). Covariables included the volume of the decoy (continuous variable), the status of the observer (informed or uninformed observer) and the decoy taxa (bird or mammals), including all possible two-way interactions. We added the participant's ID nested within the experimental session as a random variable. We constructed models considering a linear and a log-linear relation between decoy volume and detectability, considering the hypothesis that detectability of a decoy does not increase linearly with its size, but rather increases at a fast rate for small to medium species, and approaches 100% detection at a

slower rate once animals are big enough to be detected by a large majority of the drivers. We compared these models to all possible nested models to select the best models.

The effect of the observer's seat in uninformed searches

To test the hypothesis that passengers are more efficient at detecting roadkill during uninformed searches, we constructed a mixed logistic regression (package *lme4*, Douglas et al, 2015) modelling the detection status after each encounter between a participant and a decoy (0: decoy was not detected, 1: decoy detected) during the *uninformed* experiment only. Covariables included the volume of the decoy (continuous variable), the taxa (bird or mammal) and the seat occupied by the observer in the vehicles (driver or passenger) as well as all possible two-way interactions. We included the participant ID nested within the session as a random variable in the models. As described above, we modeled the effect of decoy volume on detectability as linear and log-linear to account for the possibility that animal detectability does not increase linearly with size. We compared these models to all their nested models to select the best models describing the data.

Model selection approach

We used a model selection approach with Akaike's Information Criterion (AIC, Akaike, 1998). This method selects a best model (defined as the model with the lowest AIC) and a set of best models (models with a $\Delta AIC = AIC_{model}-AIC_{lowest} < 2$, Richards, 2005). The best models are the models that describe the data the best (goodness-of-fit) with as few covariates as possible (parsimony principle, Akaike, 1998). For each analysis, we report the 95% confidence set of the best models using AIC weights (Burnham et al., 2011). The selection of the best models was conducted using function *dredge* from package *MuMIn* (Bartoń K, 2023).

Estimating the number of animal-vehicle collisions using citizen science data

Faune-AuRA is a database administered by the LPO AuRA and contains over 90 000 reports of roadkill from 333 species of mammals, birds, reptiles, and amphibians. We extracted the daily roadkill reports for 2022 of the 4 species used in the *uninformed* experiments: red fox (*Vulpes vulpes*), red squirrel (*Sciurus vulgaris*), common buzzard (*Buteo buteo)*, and domestic pigeon (*Columba livia*). Following Teixeira et

al. (2013), the roadkill rate λ (collision.day^{-1}) can be estimated as $\lambda = \frac{N}{p.T_R}$, where N is the number of roadkill carcasses counted, p is the detection rate of the carcasses by the observer and T_R is a measure of the carcass persistence on the road defined as th*e* time needed to reduce the number of remaining carcasses on the road by $1 - \frac{1}{e^1} \sim 63\%$. We used the detection probability estimated for each of the species in the *uninformed* experiments, and previous estimates of carcass persistence to estimate T_R (Bénard et al., 2023).

3. Results

Roadkill detectability

In the *informed* experimental session, participants detected 59.9% (95% CI: 47.6, 72.1) of the decoys on average. In the *uninformed* sessions, a participant detected on average 10.1% (95% CI: 0, 31) of the decoys. None of the participants of the *uninformed* experimental session reported having seen the control decoy (not present on the road) in the surveys.

The set of best models included the decoy's volume (log-linear relationship), the observer's status (informed, uninformed), the taxa and interaction between decoy volume and status, and between decoy taxa and status (Table 2). The decoy volume and observer status were present in all the best models. The interaction between observer status and decoy taxa was not present in the set of best models. The top-ranked model included only the effects of decoy volume and observer status. In this model (intercept = 2.5e-4, 95% CI:8.2e-5,7.8e-4), the detectability of the decoys increased with the logarithm of their volume (Odds ratio (OR)=2.03, 95% CI: 1.80,2.28), and the odds of detecting a decoy when the participant was *informed* were 33.8 greater than when the participant was *uninformed* (95% CI: 23.2,49.3). The second-best model (ΔAIC=0.93) included an effect of the taxa, with greater odds of detection for mammals (OR=1.36, 95% CI: 1.01,1.82). The predictions of decoy detection score for *informed* and *uninformed* participants from the top-ranked models are represented in figure 1.

Table 2: 95% confidence set of the best models to describe the detection probability of roadkill decoys using Akaike's Information Criterion (AIC). Size = the volume of the decoy (continuous variable); IF = status of the observers, either looking for roadkill (*informed*) or not actively looking for roadkill (*uninformed*); Taxa = taxa of the decoy (bird or mammal). The last line gives the model that ranked last.

Model	**AICc**	**ΔAIC**	w_i	**acc** w_i
log(Size) + IF	468.68	-	0.210	0.205
log(Size) + IF + Taxa	469.61	0.93	0.128	0.33
log(Size) + IF + Taxa + log(Size) * IF + Taxa * IF	469.70	1.01	0.123	0.46
log(Size) + IF + Taxa + log(Size) * IF	469.72	1.03	0.122	0.58
log(Size) + IF + log(Size) * IF	469.81	1.13	0.117	0.69
log(Size) + IF + Taxa + Taxa * IF	470.05	1.36	0.104	0.79
log(Size) + IF + log(Size) * IF + log(Size) * Taxa + IF * Taxa (*full log-linear model)*	**471.28**	**2.60**	**0.057**	**0.85**
log(Size) + IF + log(Size) * Taxa	471.63	2.94	0.046	0.90
log(Size) + IF + log(Size) * IF + log(Size) * Taxa	471.73	2.94	0.044	0.95
~ 1 (null model)	571.34	102.65	$1.05e^{-23}$	1

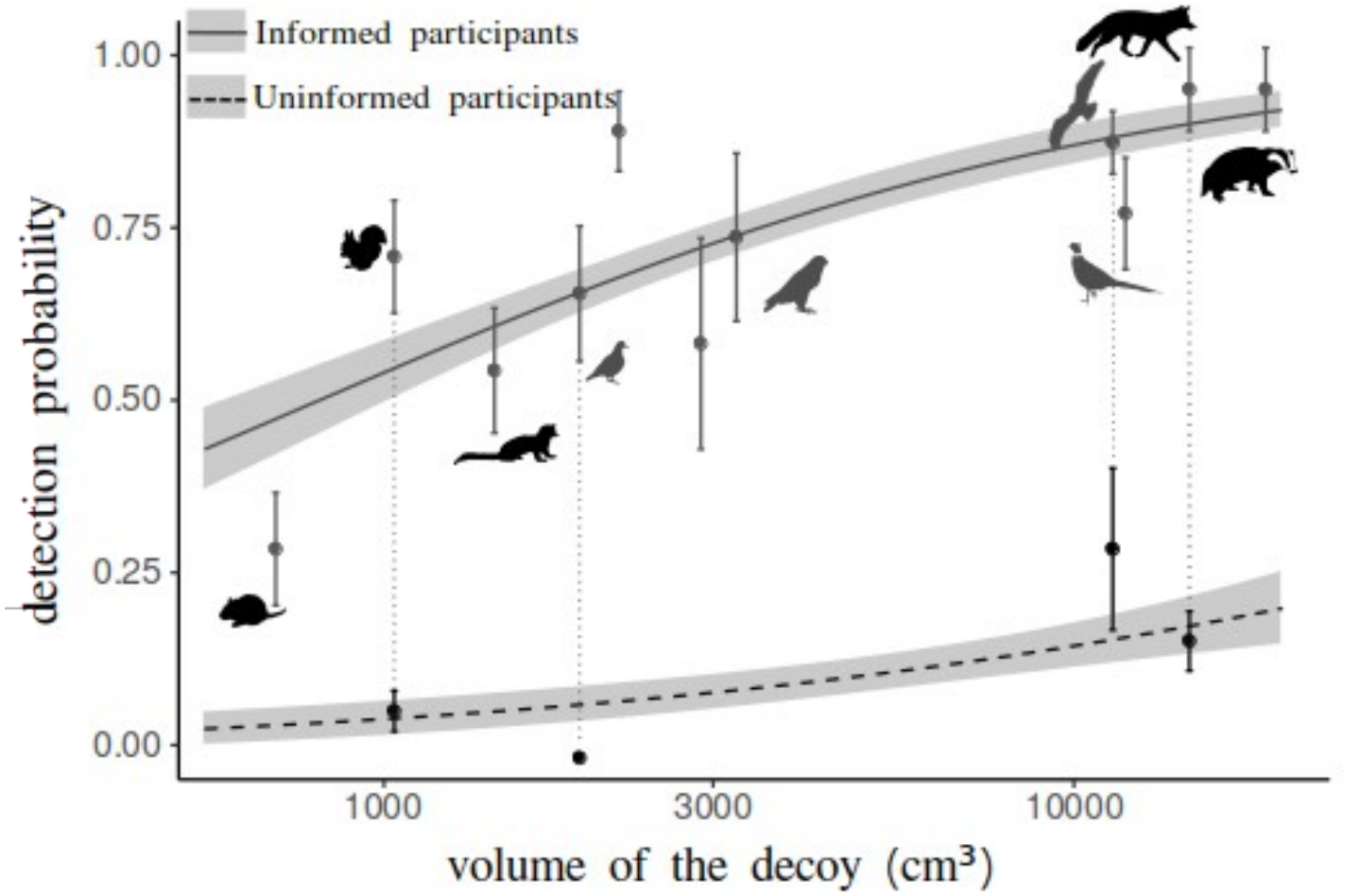


Fig. 1: The detection probabilities for roadkill decoys placed on roads of the Auvergne-Rhône-Alpes region, France, depending on the information status of volunteer observers. Volunteers were either actively looking for roadkill on a road circuit (*informed*), or the decoys were placed on roads without their knowledge (*uninformed*). A logistic regression shows that informed volunteers detected more roadkill decoys, and the detection probability of a decoy increases with its volume. The list of decoy species, represented here by silhouettes, is available in appendix 1.

Passenger versus driver searching efficiency

In total, 85.2% of the participants reported that they were driving the vehicle when going to the meetings, and the rest reported themselves as passengers. One participant reported going to the meeting on a motorcycle and was assigned to the *driver* category. The drivers detected on average 11.7% of the carcasses (95% CI: 0, 33.3) and the passengers detected 7.8% of the carcasses (95% CI: 0, 27.9).

All the best models included the effect of decoy size, and all the best models save two included the effect of taxa (Table 3). However, there was little statistical support for differences in detection scores between drivers and passengers, as the variable was not present in the top ranked model and only appeared in two of the 6 models present in the set of best models. Note that these models correspond to the linear and log-

linear versions of the same set of covariables. The top-ranked model (intercept: OR=0.08, 95% CI: 0.36,0.19) only included the effect of decoy volume and taxa. Decoy detectability increased with its size (OR=1.88; 95% CI: 1.46,2.44) and the odds of detecting mammal decoys were 1.53 higher than bird decoys (95% CI: 0.77,3.04). In the model including the observer's seat, the odds of a driver detecting a decoy were 1.42 higher than a passenger (95% CI: 0.86,2.33).

Table 3: 95% confidence set of the best models to describe the detection probability of roadkill decoys using Akaike's Information Criterion (AIC). Size = the volume of the decoy (continuous variable); Size = the size of the decoy (cm^3); Taxa = taxa of the decoy; Seat = seat of the observer in the vehicle (driver or passenger). The last line is the model that ranked last.

Model	**AICc**	**ΔAIC**	w_i	**acc** w_i
Size + Taxa + Size * Taxa	126.62	-	0.129	0.129
log(Size) + Taxa + log(Size) * Taxa	126.62	$4e^{-8}$	0.129	0.259
Size	127.29	0.671	0.093	0.352
log(Size)	127.89	1.269	0.069	0.421
Size + Seat + Taxa + Size * Taxa	128.25	1.626	0.057	0.478
log(Size) + Seat + Taxa + log(Size) * Taxa	128.25	1.626	0.057	0.478
Size + Seat + Taxa	128.97	2.349	0.040	0.617
log(Size) + Seat + Taxa	129.00	2.374	0.039	0.697
log(Size) + Taxa	129.11	2.478	0.038	0.734
log(Size) + Seat	129.51	2.885	0.031	0.765
log(Size) + Seat + Taxa + log(Size) * Taxa + Seat * Taxa + log(Size) * Seat *(full log-linear model)*	**129.77**	**3.150**	**0.027**	**0.792**
Size + Seat + Taxa + Size * Taxa + Seat * Taxa + Size * Seat *(full linear model)*	**130.00**	**3.377**	**0.024**	**0.816**
Size + Seat + Size * Seat	130.54	3.917	0.018	0.834
log(Size) + Seat + Taxa + log(Size) * Seat	132.12	5.491	0.008	0.947
Seat + Taxa	136.23	9.609	0.001	1

Roadkill rate estimates from citizen science data

We extracted 612 records of roadkill for *Vulpes vulpes*, 336 reports for *Sciurus vulgaris* and 276 reports for *Buteo buteo* from the Faune-AuRA database for the year 2022. Due to the lack of a detection rate estimate for pigeons *Columba livia* (none of the participants detected the pigeon decoy during the experiments), we did not compute estimates of the road mortality for this species. The characteristic time of carcass persistence on the road used here is 40h37 (95% CI: 10h37, 90h27) across all species (Bénard et al., 2023). Collisions estimates are presented in table 4.

Table 4: Estimated number of collisions with vehicles in the Auvergne-Rhône-Alpes region, France. We used citizen science reports of roadkill from the Faune-AuRA database for the 2022. Following Teixeira et al. (2013), we adjusted for the number of carcasses not reported with estimates of the detectability of animal carcasses in the context of citizen science derived from this study ($P_{detection}$) and of their persistence time on the road following a collision (T_R, Bénard et al., 2023).

Species	**$P_{detection}$ (95% CI)**	**T_R (95% CI)**	**Number of reports**	**Estimated number of collisions (95% CI)**
Vulpes vulpes	0.165 (0.123,0.207)	40h37 (10h37,90h27)	612	2196.7 (786.2, 11278.1) **0.81** (0.29,4.17) collisions per 100 km
Sciurus vulgaris	0.066 (0.037,0.094)		336	3016.6 (944.3,20422.7) collisions **1.12** (0.35,7.55) collisions per 100 km
Buteo buteo	0.294 (0.180,0.408)		276	554.3 (179.5,3459.6) collisions **0.21** (0.066,1.28) collision per 100 km

4. Discussion

Roadkill decoy detection rates were best explained by the size of the decoy and the information status of the observer. We confirmed that bigger decoys had higher detection rates by both observers actively looking for roadkill (*informed)* and observers not actively searching (*uninformed)*. In addition, for decoys of the same size, *uninformed* participants were about 34 times less likely to detect them compared to *informed* participants. We found little statistical support for the hypothesis that drivers are better at detecting roadkill than their passengers in the context of *uninformed* searches because they are more focused on the road.

In a context of active roadkill search, which can be assumed to represent standardized professional road surveys, we show that not all roadkill will be detected by drivers, including large species (European badger *Meles meles*, red fox *Vulpes vulpes*). Professional monitoring is therefore likely to miss an important part of the roadkill (see also Santos et al., 2016), although note that we used inexperienced volunteers and the level of experience of the observer may impact the probabilities of detection (Collinson et al., 2014). However, even for trained observers, the detection of all roadkill carcasses from a moving car is not always possible for small specimens (Gerow et al., 2010). Here, we find for example that brown rats *Rattus norvegicus* will be detected 3.2 times less often than badgers *Meles meles* during a survey. Santos et al. (2016) estimated that carcasses < 100g were 2 times less detectable than larger species (> 100g). In consequence, if differences in roadkill detectability are not addressed, the representation of species in roadkill datasets is likely to be biased according to their size, with smaller species being under-represented. Some small-bodied species such as amphibians or bats, which pose significant conservation concerns (Frick et al., 2020; Sterrett et al., 2019), are particularly vulnerable to the potential consequences of underestimating the impact of road mortality on their populations.

Many of the available estimations of detectability in the literature are derived from the comparison of carcass counts conducted by an observer on foot versus an observer in a vehicle and consequently, these estimations only hold true if on-foot surveys can achieve a flawless detection rate (Teixeira et al., 2013). The validity of this assumption was challenged by Winton et al. (2018) who found that their walking survey detected only 76% of the snake carcasses deliberately placed on the road. Although one study has produced unbiased estimations of detection rates by instead placing decoys on stretches of road (Collinson et al., 2014), they used rubber pieces to simulate flattened fauna and limited range of decoy sizes. Wildlife varies in size, shape, coloration and some species have unique features such as spikes or feathers that can influence their visibility. This study is, to our best knowledge, the first to use life-like decoys covering a wide range of sizes. However, if taxidermied animals can be seen as reasonable proxies of freshly killed fauna, they are not suitable for assessing the detection probabilities of older

roadkill carcasses that have for example been flattened by vehicles (Bénard et al, 2023). The choice of methodology may also impact the conclusion regarding the detectability of the taxa. The best model to describe our data did not include differences in detectability between birds and mammals, although decoy taxa was present within the set of best models, providing limited evidence that mammals were more often detected than birds. While it is in line with Teixeira et al. (2013) where mammals found 9 times more detectable than birds, it is in contradiction with Gerow et al., 2010 (birds 3 times more detectable than mammals). Our methodology differs from both of these studies, as the authors used real roadkill already present on the road. It is possible that some species characteristics, such as bird feathers or hedgehog spikes, remain highly visible on the road even after the carcass has been flattened (AB personal observations), which may account for differences in detectability depending on the taxa.

In citizen science roadkill monitoring projects, contributors are most likely not always actively looking for roadkill, but instead opportunistically report the animals they detected during their everyday journeys. We have demonstrated that the detection rates of roadkill in this context differ markedly from active monitoring. The substantial difference in efficiency between active and uninformed observers results in a decreased probability for roadkill carcasses to be reported in a citizen science database compared to a dataset acquired by professionals. We find collision estimates, after correcting for detection and persistence of the roadkill, that were 2 to 9 times the number of carcasses that had been reported by contributors. This is alarming considering that some citizen science datasets reach ten of thousand of reports a year. Citizen-science databases most likely represent a fraction of the true number of collisions in a territory. Once again, this may be particularly prevalent for smaller species (passerines, amphibians, bats, rodents...), which are both the least detectable but also the fastest to disappear from roads (Santos et al., 2011, Bénard et al., 2023). We found little statistical support for the hypothesis that drivers are better at detecting roadkill than their passengers, which simplifies the correction process of citizen science databases, as the position of the observer in the vehicle at the moment of detection is not an information typically required in monitoring schemes (Olson et al., 2014; Swinnen et al., 2022).

While citizen science datasets suffer from many biases, such as imperfect detection of roadkill, incorrect species identification and uneven sampling effort, they can still inform collision rates at much larger scales than other sources of roadkill data (Schwartz et al., 2020; Shin, Kim, Groffen, Woo, Song, & Borzee, 2022; Swinnen et al., 2022; Waetjen & Shilling, 2017). As demonstrated in this study, it is possible to approach more realistic collision rates by correcting citizen science data for biases such as imperfect detection rate and roadkill persistence rate. Of course, our estimates operate on the generous assumption that one contributor will drive on every road of the Auvergne-Rhône-Alpes region every day. While it may be true on average, this assumption does not hold at local scales on small roads. More

accurate estimates could be obtained by also accounting for the distribution of the observation pressure in the region. In addition, there is a possibility that even detected carcasses are not always reported by contributors, which would further widen the gap between the number of reports and the actual number of collisions between fauna and vehicles.

5. Conclusions

Roadkill detection probability varies greatly depending on the size of the animal, but also in which the observer. Driver that are actively looking for roadkill, for example during standardized professional roadkill monitoring, detect 34 times more animals on the road compared to drivers that are not in a context of active roadkill monitoring. In citizen science monitoring projects, most drivers are most likely in the latter category, which means that they only detect a fraction of the roadkill present on the road. The difference between the number of roadkill reports and the actual number of collisions in the Faune-AuRA citizen science datasets could be as high as 60 times, meaning that this database, which can reach hundreds of new reports every day, only paints a very partial picture of the true magnitude of road mortality in wildlife.

6. Ethical statement

The participants recruited in this experiment gave free and informed consent for their answers to be used for the purposes of this study, in compliance with article 89 of the GDPR. Surveys were entirely anonymous and no other identifying data was collected.

7. Acknowledgments

We thank the volunteers for participating in this study, as well as J. Barbe for helping in the *informed* experiment. We also thank the Tichodrome wildlife rehabilitation center for providing carcasses and J. Barbe, A. Salis and Y. Voituron for helping with the taxidermy process. In addition, we thank J. Gilbert for his taxidermy work and expert advice.

REFERENCES

Abbate, C. (2019). Save the Meat for Cats : Why It's Wrong to Eat Roadkill. *Journal of Agricultural and Environmental Ethics*, *32*(1), 165-182. https://doi.org/10.1007/s10806-019-09763-6

Agresti, A. (2012). *Categorical Data Analysis*. John Wiley & Sons.

Anderson-Bergman, C. (2017). icenReg : Regression Models for Interval Censored Data in R. *Journal of Statistical Software*, *81*, 1-23. https://doi.org/10.18637/jss.v081.i12

Antworth, R. L., Pike, D. A., & Stevens, E. E. (2005). Hit and run : Effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist*, *4*(4), 647-656. https://doi.org/10.1656/1528-7092(2005)004[0647:HAREOS]2.0.CO;2

Aresco, M. J. (2005). Mitigation Measures to Reduce Highway Mortality of Turtles and Other Herpetofauna at a North Florida Lake. *The Journal of Wildlife Management*, *69*(2), 549-560. https://doi.org/10.2193/0022-541X(2005)069[0549:MMTRHM]2.0.CO;2

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., & Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation*, *222*(November 2017), 146-153. https://doi.org/10.1016/j.biocon.2018.04.014

Bartoń K (2023). *MuMIn: Multi-Model Inference*. R package version 1.47.5. https://CRAN.R-project.org/package=MuMIn

Beckmann, C., & Shine, R. (2015). Do the numbers and locations of road-killed anuran carcasses accurately reflect impacts of vehicular traffic? *The Journal of Wildlife Management*, *79*(1), 92-101. https://doi.org/10.1002/jwmg.806

Bénard, A., Bonenfant, C., & Lengagne, T. (2023). *Influence of traffic and weather on carcass persistence time of small wildlife on roads* (p. 2023.06.01.543226). bioRxiv. https://doi.org/10.1101/2023.06.01.543226

Bénard, A., Bonenfant, C., & Lengagne, T. (2023).*Influence of animal size and driver attentiveness in roadkill detection rates (in preparation).*

Brand, L., Hussey, M., & Taylor, J. (2003). Decay and Disarticulation of Small Vertebrates in Controlled Experiments. *Journal of Taphonomy*, *1*.

Calarco, M. (2023). Subjects of Roadkill. In M. Calarco (Éd.), *Reflections on Roadkill between Mobility Studies and Animal Studies : Altermobilities* (p. 57-69). Springer International Publishing. https://doi.org/10.1007/978-3-031-30578-8_4

Collinson, W. J., Parker, D. M., Bernard, R. T. F., Reilly, B. K., & Davies-Mostert, H. T. (2014). Wildlife road traffic accidents : A standardized protocol for counting flattened fauna. *Ecology and Evolution*, *4*(15), 3060-3071. https://doi.org/10.1002/ece3.1097

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Erritzoe, J., Mazgajski, T. D., & Rejt, Ł. (2003). Bird Casualties on European Roads—A Review. *Acta Ornithologica*, *38*(2), 77-93. https://doi.org/10.3161/068.038.0204

European Environment Agency. (s. d.). *Greenhouse gas emissions by aggregated sector* [Data Visualization]. Consulted on August 3rd, at https://www.eea.europa.eu/data-and-maps/daviz/ghg-emissions-by-aggregated-sector-5#tab-dashboard-02

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1998), 207-231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Frick, W. F., Kingston, T., & Flanders, J. (2020). A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences*, *1469*(1), 5–25. https://doi.org/10.1111/nyas.14045

Gerow, K., Kline, N., Swann, D., & Pokorny, M. (2010). Estimating annual vertebrate mortality on roads at Saguaro National Park, Arizona. *Human-Wildlife Interactions*, *4*(2), 283-292.

Girardet, X., Conruyt-Rogeon, G., & Foltête, J.-C. (2015). Does regional landscape connectivity influence the location of roe deer roadkill hotspots? *European Journal of Wildlife Research*, *61*(5), 731-742. https://doi.org/10.1007/s10344-015-0950-4

Gomes, L., Grilo, C., Silva, C., & Mira, A. (2009). Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. *Ecological Research*, *24*(2), 355-370. https://doi.org/10.1007/s11284-008-0515-z

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, *18*(6), 323-328. https://doi.org/10.1002/fee.2216

Guinard, E., Billon, L., Bretaud, J.-F., Chevallier, L., Sordello, R., & Witté, I. (2023). Comparing the effectiveness of two roadkill survey methods on roads. *Transportation Research Part D: Transport and Environment*, *121*, 103829. https://doi.org/10.1016/j.trd.2023.103829

Guinard, É., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties : Carcasses surveys and scavenging bias. *Biological Conservation*, *147*(1), 40-51. https://doi.org/10.1016/j.biocon.2012.01.019

Hastings, H., Barr, J., Bateman, P. W., Hastings, H., Barr, J., & Bateman, P. W. (2019). Spatial and temporal patterns of reptile roadkill in the north-west Australian tropics. *Pacific Conservation Biology*, *25*(4), 370-376. https://doi.org/10.1071/PC18082

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, *291*, 112664. https://doi.org/10.1016/j.jenvman.2021.112664

Hochachka, W. M., Fink, D., Hutchinson, R. A., Sheldon, D., Wong, W.-K., & Kelling, S. (2012). Data-intensive science applied to broad-scale citizen science. *Trends in Ecology & Evolution*, *27*(2), 130–137. https://doi.org/10.1016/j.tree.2011.11.006

Hubbard, K. A., & Chalfoun, A. D. (2012). An experimental evaluation of potential scavenger effects on snake road mortality detections. *Herpetological Conservation and Biology*, *7*(2), 150-156.

Kemp, F. (2003). Modern Applied Statistics with S. *Journal of the Royal Statistical Society Series D: The Statistician*, *52*(4), 704-705. https://doi.org/10.1046/j.1467-9884.2003.t01-19-00383_22.x

Klöcker, U., Croft, D. B., Ramp, D., Klöcker, U., Croft, D. B., & Ramp, D. (2006). Frequency and causes of kangaroo–vehicle collisions on an Australian outback highway. *Wildlife Research*, *33*(1), 5-15. https://doi.org/10.1071/WR04066

Kopnina, H., & Shoreman-Ouimet, E. (2013). *Environmental Anthropology : Future Directions*. Routledge.

Langen, T. A., Machniak, A., Crowe, E. K., Mangan, C., Marker, D. F., Liddle, N., & Roden, B. (2007). Methodologies for Surveying Herpetofauna Mortality on Rural Highways. *The Journal of Wildlife Management*, *71*(4), 1361-1368. https://doi.org/10.2193/2006-385

Lindsey, J. C., & Ryan, L. M. (1998). Methods for interval-censored data. *Statistics in Medicine*, *17*(2), 219-238. https://doi.org/10.1002/(SICI)1097-0258(19980130)17:2<219::AID-SIM735>3.0.CO;2-O

Marcus Rowcliffe, J., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps : An adapted distance sampling approach. *Methods in Ecology and Evolution*, *2*(5), 464-476. https://doi.org/10.1111/j.2041-210X.2011.00094.x

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations : A systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12942

Ocampo, D., Borja-Acosta, K. G., Lozano-Flórez, J., Cifuentes-Acevedo, S., Arbeláez-Cortés, E., Bayly, N. J., Caguazango, Á., Coral-Jaramillo, B., Cueva, D., Forero, F., Gómez, J. P., Gómez, C., Loaiza-Muñoz, M. A., Londoño, G. A., Losada-Prado, S., Pérez-Peña, S., Ramírez-Chaves, H. E., Rodríguez-Posada, M. E., Sanabria-Mejía, J., … Acevedo-Charry, O. (2021). Body mass data set for 1,317 bird and 270 mammal species from Colombia. *Ecology*, *102*(3), e03273. https://doi.org/10.1002/ecy.3273

Ogletree, K. A., & Mead, A. J. (2020). What roadkills did we miss in a driving survey? A comparison of driving and walking surveys in Baldwin County, Georgia. *Georgia Journal of Science*, *78*(2), 8.

Olson, D. D., Bissonette, J. A., Cramer, P. C., Green, A. D., Davis, S. T., Jackson, P. J., & Coster, D. C. (2014). Monitoring Wildlife-Vehicle Collisions in the Information Age: How Smartphones Can Improve Data Collection. *PLoS ONE*, *9*(6), e98613. https://doi.org/10.1371/journal.pone.0098613

Paraguassu-Chaves, C. A., Izidorio, A. de O., da Silva Júnior, N. P., Filho, A. K. D. B., Pereira, L. S., de Almeida, F. M., Neto, J. V. F., Barata, C. da S., Cavalcante, F. R. C., & Casara, H. N. (2020). Monitoring of Wildlife Mortality on a State Road in Rondônia, Western Amazon. *International Journal of Advanced Engineering Research and Science*, *7*(8), 208-221. https://doi.org/10.22161/ijaers.78.21

Ponce, C., Alonso, J.C., Argandona, G., Garcia Fernandez, A., & Carrasco, M. (2010). Carcass removal by scavengers and search accuracy affect bird mortality estimates at power lines, *Animal Conservation, 13(6), 603-612.*

Prosser, P., Nattrass, C., & Prosser, C. (2008). Rate of removal of bird carcasses in arable farmland by predators and scavengers. *Ecotoxicology and Environmental Safety*, *71*(2), 601-608. https://doi.org/10.1016/j.ecoenv.2007.10.013

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ratton, P., Secco, H., & da Rosa, C. A. (2014). Carcass permanency time and its implications to the roadkill data. *European Journal of Wildlife Research*. https://doi.org/10.1007/s10344-014-0798-z

Rovero, F., Zimmermann, F., Bersi, D., & Meek, P. (2013). *«* Which camera trap type and how many do I need? » A review of camera features and study designs for a range of wildlife research applications. *Hystrix*

Rytwinski, T., Soanes, K., Jaeger, J. A. G., Fahrig, L., Findlay, C. S., Houlahan, J., Van Ree, R. D., & Van Der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill ? A meta-analysis. *PLoS ONE*, *11*(11), 1-25. https://doi.org/10.1371/journal.pone.0166941

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass Persistence and Detectability : Reducing the Uncertainty Surrounding Wildlife-Vehicle Collision Surveys. *PLoS ONE*, *11*(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road ? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0025383

Santos, S. M., Marques, J. T., Lourenço, A., Medinas, D., Barbosa, A. M., Beja, P., & Mira, A. (2015). Sampling effects on the identification of roadkill hotspots : Implications for survey design. *Journal of Environmental Management*, *162*, 87-95. https://doi.org/10.1016/j.jenvman.2015.07.037

Schwartz, A. L. W. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1-7. https://doi.org/10.1093/jue/juy006

Seiler, A. (2001). Ecological Effects of Roads : A review. *Uppsala: Swedish University of Agricultural Sciences*.

Selva, N., Jędrzejewska, B., Jędrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, *83*(12), 1590-1601. https://doi.org/10.1139/z05-158

Slater, F. M. (2002). An assessment of wildlife road casualties—The potential discrepancy between numbers counted and numbers killed. *Web Ecology*, *3*, 33-42. https://doi.org/10.5194/we-3-33-2002

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). *Foraging : Behavior and Ecology*. University of Chicago Press.

Sterrett, S. C., Katz, R. A., Brand, A. B., Fields, W. R., Dietrich, A. E., Hocking, D. J., Foreman, T. M., Wiewel, A. N. M., & Campbell Grant, E. H. (2019). Proactive management of amphibians: Challenges and opportunities. *Biological Conservation*, *236*, 404–410. https://doi.org/10.1016/j.biocon.2019.05.057

Stewart, P. A. (1971). Persistence of Remains of Birds Killed on Motor Highways. *The Wilson Bulletin*, *83*(2), 203-204.

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates : Effects of sampling methods and carcass removal. *Biological Conservation*, *157*, 317-323. https://doi.org/10.1016/j.biocon.2012.09.006

Teixeira, F. Z., Coelho, I. P., Esperandio, I. B., Rosa Oliveira, N., Porto Peter, F., Dornelles, S. S., Rosa Delazeri, N., Tavares, M., Borges Martins, M., & Kindel, A. (2013). Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis*, *17*(1), 36-47. https://doi.org/10.4257/oeco.2013.1701.04

Teixeira, F. Z., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, *54*(5), 1544-1551. https://doi.org/10.1111/1365-2664.12870

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET : Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581-597. https://doi.org/10.1111/ele.13898

Van Langevelde, F., & Jaarsma, C. F. (2005). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, *19*(8), 895-907. https://doi.org/10.1007/s10980-005-0464-7

Vidal-Vallés, D., Pérez-Collazos, E., & Rodríguez, A. (2018). Bird roadkill occurences in Aragon, Spain, *Animal Biodiversity and Conservation, 41(2): 379-388*

Wright, J. (2019). Roadkill - It's What's for Dinner : How Eating Roadkill May Help Reduce Automobile Accidents. *University of the Pacific Law Review*, *51*, 301.

Appendix

Appendix A1: **Complete list of the decoy species – volume of the decoy.** These decoys were used for the detectability experiments. Because the diurnal raptors (Red kite, Common buzzard, Honey buzzard, Marsh harrier) were very similar in coloration and volume, the participants could not accurately discriminate the species during the experiments. Consequently, their size was averaged, and they were pooled into a 'Diurnal raptor' category.

- 2 x Brown rat (*Rattus norvegicus) – 756 cm^3*
- Common buzzard *(Buteo buteo) – 9605 cm^3*
- 3x Common pheasant (*Phasianus colchicus) – 11 880 cm^3*
- 2x Domestic pigeon *(Columba livia) – 2025 cm^3*
- European badger (*Meles meles) – 18720 cm^3*
- 2x European hedgehog *(Erinaceus europaeus) – 633 cm^3*
- European honey buzzard (*Pernis apivorus) – 9500 cm^3*
- Eurasian jay (*Garrulus glandarius) – 3000 cm^3*
- 2x European pine marten (*Martes martes) – 1536 cm^3*
- Peregrine falcon (*Falco peregrinus) – 3366 cm^3*
- 2x Red fox *(Vulpes vulpes) – 14 620 cm^3*
- Red kite (*Milvus milvus) – 9410 cm^3*
- 2x Red squirrel (*Sciurus vulgaris) – 1110 cm^3*
- Western marsh harrier *(Circus aeruginosus) – 8902 cm^3*

Fig. A1: Roadkill decoys of a red fox (left) and red kite (right) placed on roads during the '*informed*' experiments and equipped with a camera-trap to discourage theft.

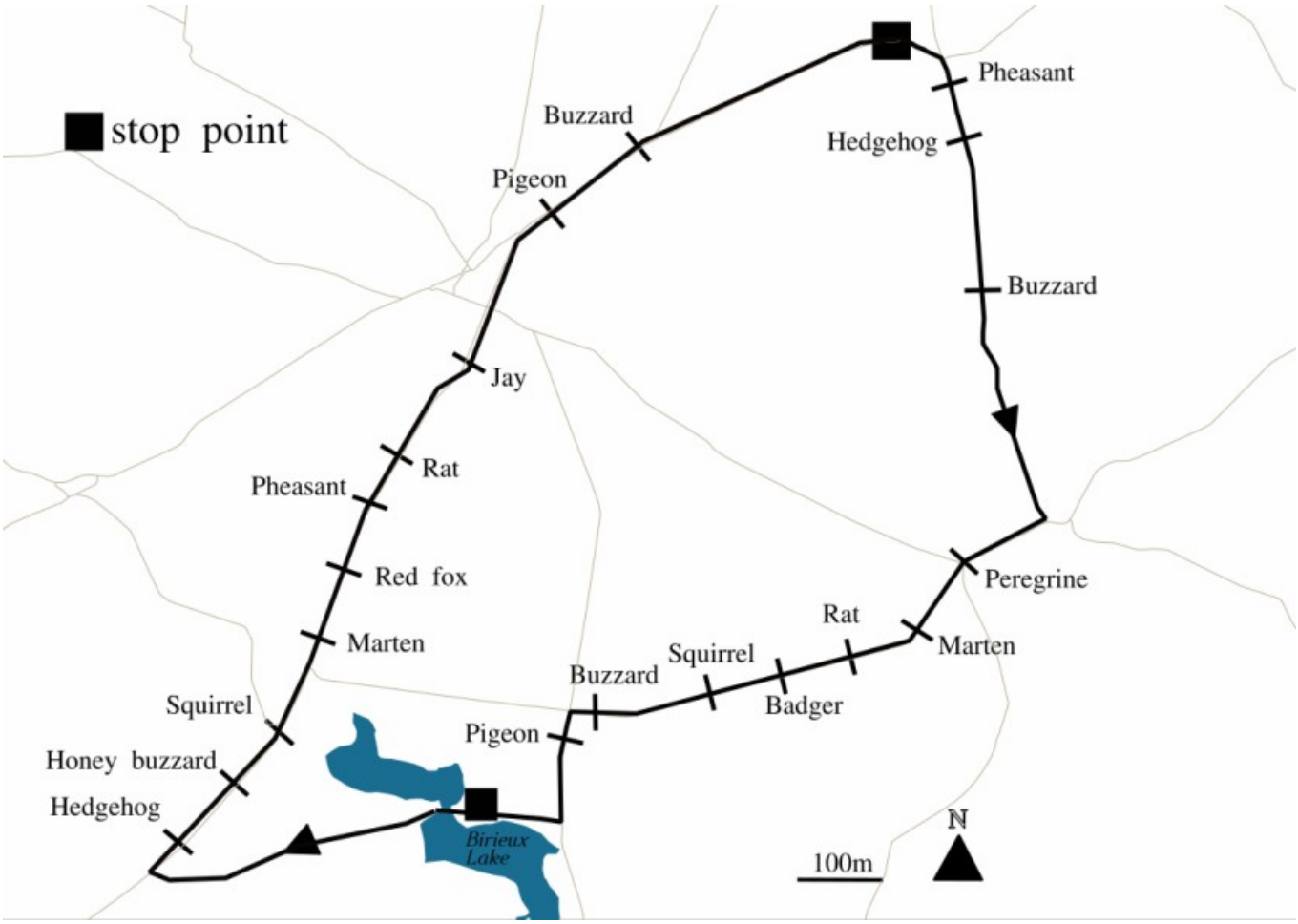


Fig. A2: **Map of the informed experiment.**

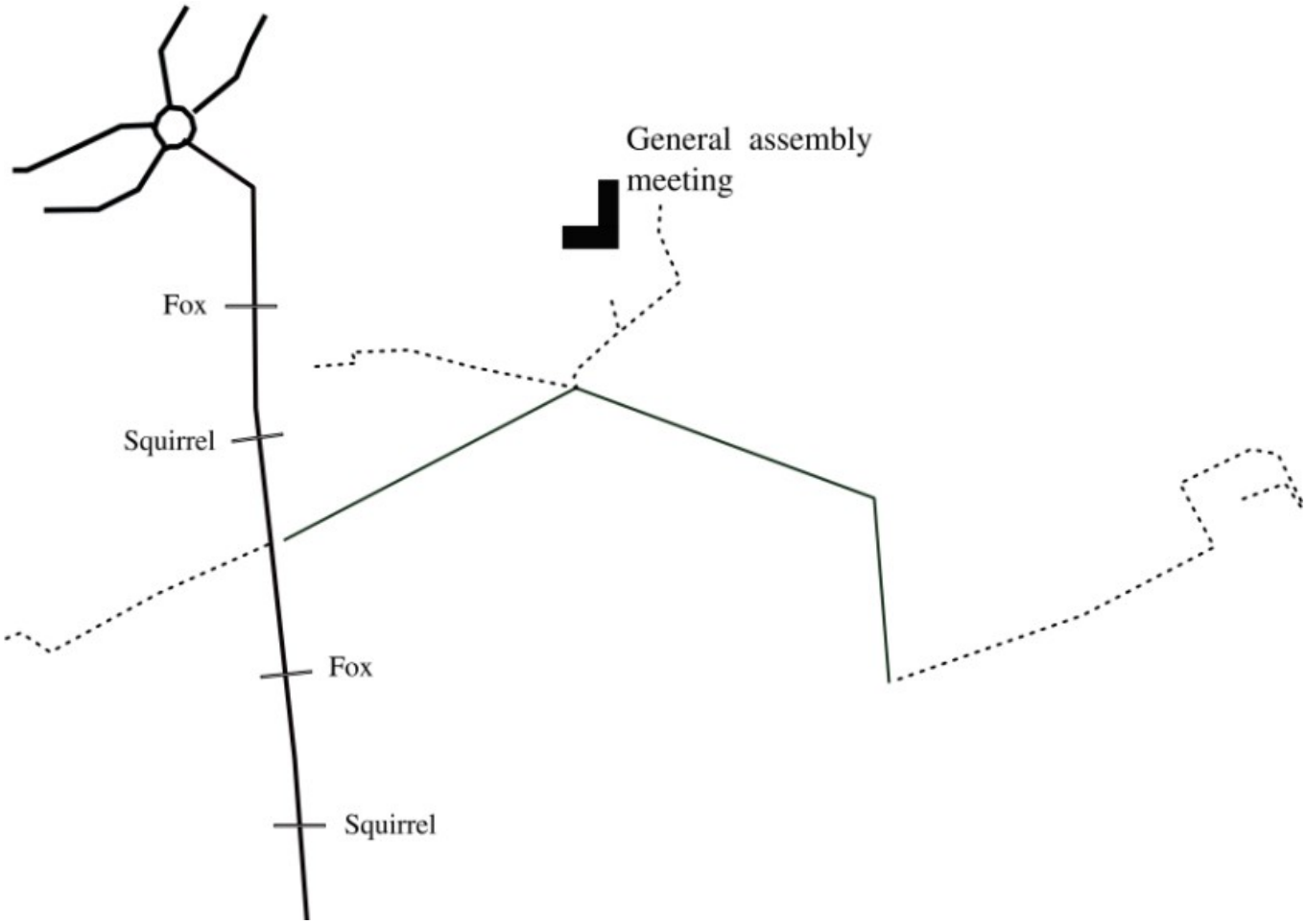
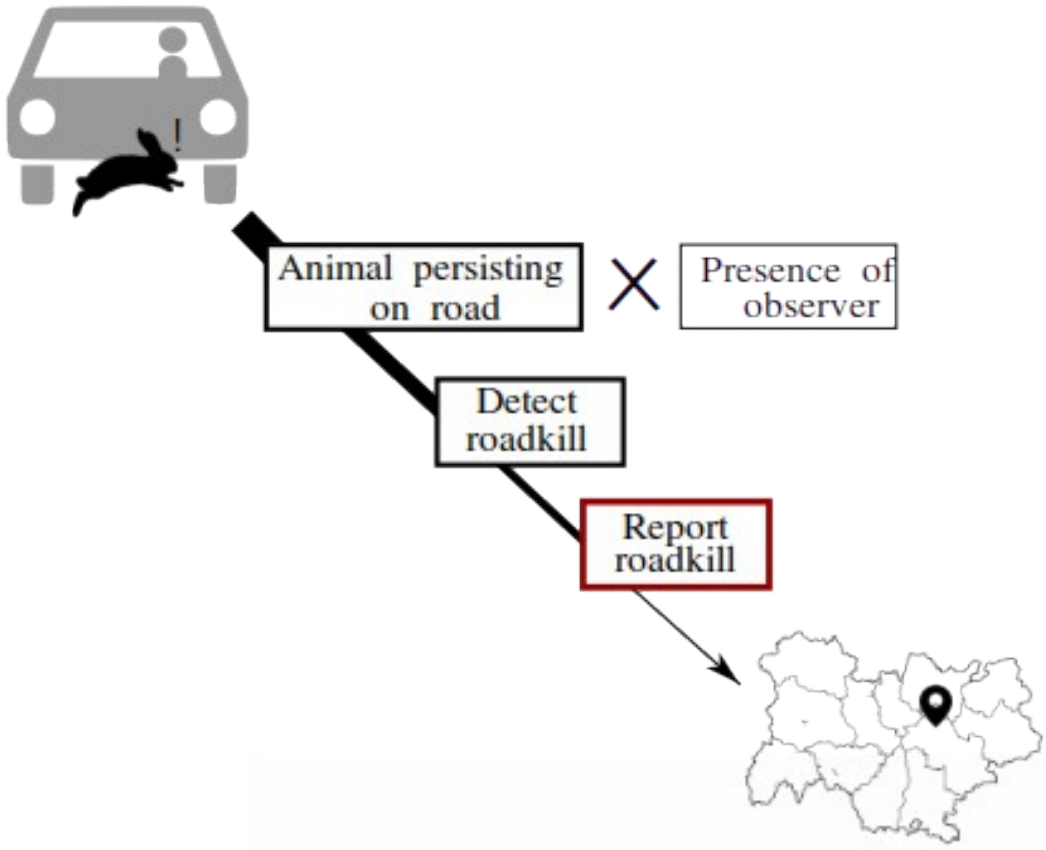


Fig. A3: **Map of the uninformed experiment (June session)**. Attendees of the general assembly meeting had no choice but to drive by a fox and a squirrel decoy on their way to the meeting location, which enabled the estimation of the detection probability of roadkill decoys without informing the drivers that roadkill would be present.

Chapter 4: Reporting probabilities in opportunistic roadkill monitoring



Case study: a methodology for estimating reporting probabilities in citizen science

CONTEXT

Most WVC monitoring schemes relying on citizen science gather data through the opportunistic reporting of carcasses. Contrary to more standardized surveys, this type of reporting does not ensure that contributors consistently report the carcasses they have detected. The lack of *willingness to report* has long been suspected of being a source of bias in citizen science, but has never been formally demonstrated in the case of roadkill reporting.

OBJECTIVES

- Estimate the conversion rate from detected to reported roadkill in opportunistic monitoring.

- Integrate this conversion rate into the Faune-AuRA dataset for select species to provide collision estimates.

RESULTS

Only a fraction of the detected roadkill is effectively reported by contributors of the Faune-AuRA project, which further widens the gap between reports and actual collisions.

Although the method presented here is promising, we encountered difficulties and were not able to test the existence of selective reporting biases for charismatic or rare species.

CONCLUSIONS

There is a reporting bias within Faune-AuRA where even identified carcasses go unreported. This concern may also extend to other citizen science monitoring initiatives, both regarding roadkill and biodiversity monitoring in general.

Methodological refinements are need to provide more precise estimates and confirm the existence of selective biases in the willingness to report.

Introduction

In the previous chapters, we have discussed monitoring roadkill by examining the impact of roadkill persistence and detectability on the reliability of the data. While the focus of this work is primarily on citizen science, both of these issues are equally relevant to professional roadkill monitoring schemes, and have received some attention from the scientific community (*e.g.,* Collinson et al., 2014; Santos et al., 2011). We have yet to address another potential source of bias that is seldom acknowledged in WVC citizen science research, and is inherent to opportunistic citizen science monitoring: the *willingness to report* roadkill. By *"willingness to report"*, I refer to the probability of effectively reporting roadkill that has been detected. Opportunistic reporting in ecology is not limited to roadkill, and studies have shown that reporting probabilities in other projects are not constant, often resulting in positive biases toward rarer species (Henckel et al., 2020; van Strien et al., 2013). In addition, citizen science projects sometimes focus on charismatic species in order to make the tasks more appealing and recruit more volunteers (Pocock et al., 2015; Steger et al., 2017). In roadkill datasets, some authors have expressed their concerns that charismatic or less common species seems to be over-represented (Swinnen et al., 2022; Vercayie & Herremans, 2015). However, it is important to note that the representation of species in datasets, which should describe the specific roadkill rates, is also influenced by factors such as carcass persistence and detectability (Teixeira et al., 2013). To my best knowledge, there is no published evidence that not all detected roadkill is reported by contributors in roadkill opportunistic reporting, or that selective biases exist within the reporting process.

Assessing biases such as in reporting only part of the roadkill can be achieved by asking the contributors to self-report their rate of carcass reporting through surveys. We have examples of this methodology to assess the selective biases towards certain species in citizen science projects (Henckel et al., 2020). Self-reporting is also often used in fields such as epidemiology (self-reporting of symptoms, *e.g.*, Menni et al., 2020) or social sciences (self-reporting emotions or behaviours, *e.g.,* Ben-Shakhar et al., 2007). However, self-reporting methods may prove inaccurate, especially when regarding variables that are difficult to estimate accurately (such as the proportion of detected roadkill that is forgotten by the contributor and therefore never reported) or variables that can provide "an incentive to misreport", *i.e.*, that may lead to contributors not being entirely truthful (Stone et al., 1999). In the case of roadkill reporting, there is a possible incentive to over-estimate the rates at which one reports detected roadkill, because of the perceived ecological and scientific importance of the data that is collected (Hsu & Lin, 2021). Therefore, accurate assessment of the willingness to report should not rely on self-reporting methods. In this case study, I will detail an experiment designed to assess the reporting probabilities in

the Faune-AuRA project without the need for self-reporting. The main hypothesis is that the detected-to-reported conversion rate is less than 100% (*i.e.*, not all detected carcasses are reported) for most contributors (Swinnen et al., 2022).

Material & Methods

Measuring reporting rates

The primary difficulty in accurately measuring the reporting rate of contributors in a citizen science roadkill monitoring scheme is that it cannot be achieved when the contributors are aware that their reporting rates are being assessed. For this reason, the experimental protocol presented here shares similarities with the *uninformed detection probability* experiment outlined in manuscript n°4.

We conducted experiments during multiple LPO AuRA meetings (May-July 2022). These meeting took place in several departments of the Auvergne-Rhône-Alpes region: Ain, Loire and Drôme and provided an opportunity for multiple LPO members (which constitute a majority of the Faune-AuRA users) to convene at a predetermined location. The meetings gave us access to a pool of Faune-AuRA contributors that would be used as subjects in the experiments. We exclusively selected events that met the following criteria: (1) we could inventory all the possible itineraries leading to the meeting location, (2) the last few kilometers of these itineraries were composed of roads accessible to the experimenters (*i.e.*, no highways or fenced roads), and (3) the meeting organizer agreed to cooperate in the experiment. Their cooperation involved providing the time and place of the meeting, as well as a restricted list of meeting attendees defined as “active Faune-AuRA roadkill contributors”, *i.e.*, meeting attendees who had reported sightings of carcasses on roads to Faune-AuRA at least 3 times during the past year.

We used roadkill decoys in the form of taxidermied birds and mammals. These decoys are the same as presented in manuscript n°4: we procured carcasses from a wildlife rehabilitation center, and asked for the help of a professional taxidermist. During the taxidermy process, we tried to mimic the posture of a freshly killed carcass to produce decoys that would be mistaken for actual roadkill. Before each meeting, we placed the three to five decoys within the last 5 km of all possible itineraries to the meeting place. We randomly selected the order of the decoys (using a random number generator) and situated them on the side of the road that the attendees would drive by, either at the junction between the road and the shoulder or on the road shoulder itself. No decoys were placed directly in a lane due to safety concerns

for drivers. All decoys were positioned at least 30 minutes before the expected time of arrival of the first attendees, and removed once the meeting commenced. This methodology ensured that all meetings attendees had unknowingly driven by several roadkill decoys on their way to the meeting.

In the week following the meeting, I then contacted each meeting attendee from the list of “active Faune-AuRA roadkill contributors” via phone. During these conversations, I introduced myself as LPO member interested in road mortality and proceeded to ask the contributors (1) which route they took to reach the meeting location and (2) if they had encountered any roadkill in the last few kilometers of their journey. Simultaneously, we monitored the Faune-AuRA database to determine which of the attendees had reported decoys as roadkill prior to being contacted. We did not include roadkill reported after the subject had been contacted, as the questions asked during the phone call may have artificially increased the motivation of the subject to report a decoy they had detected. Therefore, for each decoy placed on the road during the experiments, we had obtained the list of active contributors that had driven by, as well as which of these contributors had detected the decoy, and which had reported it to Faune-AuRA (fig. 1).

1.
Planned meeting where Faune-AuRA contributors will be present.

2.
Roadkill decoys placed on all possible itineraries to meeting.

3.
Faune-AuRA database is monitored for contributors reporting decoys as roadkill.

4.
Contributors are contacted and asked about their itinerary and whether they saw roadkill.

For each decoy:

list of contributors that drove by
↓
list of contributors that effectively detected decoy
↓
list of contributors that reported decoy to Faune-AuRA.

Fig. 1: Methodology of the experiment designed to measure the willingness to report from citizen science contributors of the Faune-AuRA roadkill monitoring scheme.

Roadkill reporting as a Markov process

A brief introduction to Markov chains

A Markov process refers to a system that transitions between different states based on the probabilities assigned to these transitions. It exhibits a property known as *memorylessness*, where the future state solely relies on the present state and remains unaffected by past events. This concept is also known as the *Markov property*, named after mathematician Andrey Markov. The observed sequence of states in a Markov process is named “Markov chain”. You may encounter example of Markov chains in daily life, such as when typing on a phone: the predictive text feature on a keyboard guesses the next word based on the word currently being typed[8]. Here, each word represents a state, the entire English dictionary acts as the collection of all possible states in the Markov process, and the sentence is the Markov chain – a sequence of states selected from the pool.

Markov chain models are used to describe ecological processes such as ecological successions (from pioneer species to a fully functioning ecosystem, Logofet & Lesnaya, 2000) or capture-recapture methods for population density estimation (Pradel, 2005). In this chapter, I will only focus on explicit discrete-time Markov chains, *i.e.,* Markov chains in which (1) the system transitions following discrete time steps $t = \{1,...,T\}$ and (2) all the states of the chain are known and observed.

The transition matrix of a Markov process contains all one-way transition probabilities between the states. In the earlier example of predictive text generation, the transition matrix would include the probability of transitioning from one word, such as "good," to another word, such as “morning”, and would also contain a different probability of transition from “morning” to “good”. In Markov models, an initial state is specified (*e.g,* the first word typed in a sentence), or a vector of initial probabilities for all possible states is used to randomly select the initial state.

8 This is a very basic form of predictive text generation. Modern predictive text features also rely on the general context of the text, or the typing habits of the user.

Describing roadkill reporting as a Markov process

We consider the possible states of a roadkill carcass in relation to a contributor participating in a citizen science monitoring project. Any time a contributor drives by a roadkill carcass present on a road, the carcass will be in one of the following states: not seen, detected by the contributor, reported by the contributor. I will refer to these states respectively as "*present*" (but not detected), "*detected*" (but not reported) and "*reported*" (fig. 2). The Markov chain transitions between states at each time step $t = \{1, 2, 3\}$.

The following chains are possible:

- {present, present, present}: the animal has not been detected or reported by the contributor
- {present, detected, detected}: the animal has been detected but not reported by the contributor
- {present, detected, reported}: the animal has been detected and reported by the contributor.

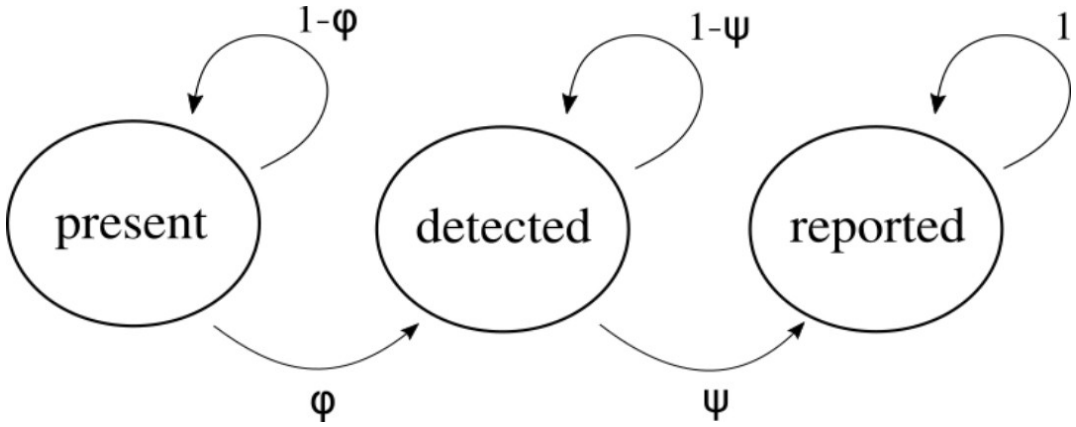


Fig. 2: State transition diagram of the Markov chain used to describe the reporting process of a roadkill carcass. The initial state is "present". The detection probability is denoted φ and the reporting probability is denoted ψ.

The initial state of the Markov chain is *present*. The transition matrix of the Markov process is defined as:

	present	detected	reported
present	1-φ	φ	0
detected	0	1-Ψ	Ψ
reported	0	0	1

Where φ is the detection probability of the carcass by the contributor, and Ψ is the reporting probability of said carcass conditional on its detection. Note that the probabilities for each individual row and column always sum to 1. The state *reported* is called an absorbing state, which means that once entered, it cannot be left.

Bayesian modelling of detection and reporting rates

We aim at estimating two independent parameters from the transition matrix: the detection probability (φ) and the reporting probability (ψ). To estimate the transition matrix, we constructed a Bayesian multinomial model describing the data obtained from the experiments. We assigned uniform priors ranging from 0 to 1 for the variables φ and ψ (uninformative priors). We ran three concurrent Monte-Carlo Markov Chains (MCMC) for 10000 iterations. We discarded the first 3000 iterations and applied a thinning value of 3 to reduce autocorrelation. To evaluate the MCMC chains, we conducted posterior checks by visualizing trace plots and Gelman-Rubin-Brooks plots (Brooks & Gelman, 1998). We implemented the model using NIMBLE (de Valpine et al., 2017) for R (R Core Team, 2021).

Integrating the reporting process in the Faune-AuRA database

The probabilities φ and ψ are useful to compute the conversion probability of an animal carcass present on the road into a data point in the Faune-AuRA database:

$$P_{conversion} = P_{detection} . P_{report|detected} = \phi . \psi$$

Following Teixeira et al. (2013), we can construct the function G(t) that represents the number of carcasses present on roads at time *t.* Therefore, we can write:

$$\frac{dG(t)}{dt} = \lambda - \frac{G(t)}{T_R}$$

, where λ is the roadkill rate (number of collisions per unit of time) and T_R is a characteristic time describing the persistence of carcasses on roads. This equation leads to the steady state solution $G(t \to \infty) = \lambda . T_R$, *i.e.* the number of roadkill carcasses present on roads is the product of the roadkill rate and the characteristic time of roadkill persistence.

Assuming that there are contributors present to report roadkill carcasses, the number of reported carcasses R(t) at time *t* is therefore defined as $R(t) = P_{conversion} . G(t)$. We can write:

$$R(t \to \infty) = P_{conversion} . G(t \to \infty) = \psi . \phi . \lambda . T_R$$

Using the methodology presented in manuscript n°3, we can estimate the roadkill rate λ of a species using the number of roadkill reported to the Faune-AuRA database on a daily basis, the characteristic time of the carcasses T_R (obtained from chapter 2) and the probabilities φ and ψ. With this approach, we assume that each road of the AuRA region is surveyed daily by project contributors.

We estimated the road mortality for the red fox *Vulpes vulpes*, the red squirrel *Sciurus vulgaris* and the common buzzard *Buteo buteo* using the detectability estimates for these species from manuscript n°4, table 4, the characteristic times of persistence presented in manuscript n°3, as well as the reporting probability ψ estimated in this chapter.

Results

Field experiments

We successfully obtained 76 observations regarding the detection and reporting rates of 7 different species of roadkill decoys (red squirrel *Sciurus vulgaris,* common buzzard *Buteo buteo,* domestic pigeon *Columba livia,* European hedgehog *Erinaceus europaeus*, pine marten *Martes martes*, brown rat *Rattus norvegicus* and ring-necked pheasant *Phasianus colchicus*) from 3 meetings (LPO departmental assemblies of the Ain, Drôme, and Loire departments). We interviewed a total of 27 contributors, who detected 5.2% of the decoys, resulting in only 1 report.

We encountered several challenges during the implementation of the experimental protocol. Despite regular patrols, some of the roadkill decoys were stolen from the road during the experiments. As a result, we were unable to determine which attendees had driven by the decoy, and had to exclude these observations from the dataset. Additionally, the number of active contributors reporting roadkill present at meetings was generally low (less than 10 individuals). Some contributors either did not disclose their contact information or could not be reached despite multiple attempts.

Detection (φ) and reporting (ψ) probabilities

The model estimated the detection probability φ at 0.0332 (95% credible interval: 0.0111,0.0661, rhat=1, N_{eff}=2951) and the reporting probability ψ at 0.3349 (95% credible interval: 0.0539,0.7216, rhat=1, N_{eff}=3016, fig. 3). Collision rate estimates are presented in Table 1.

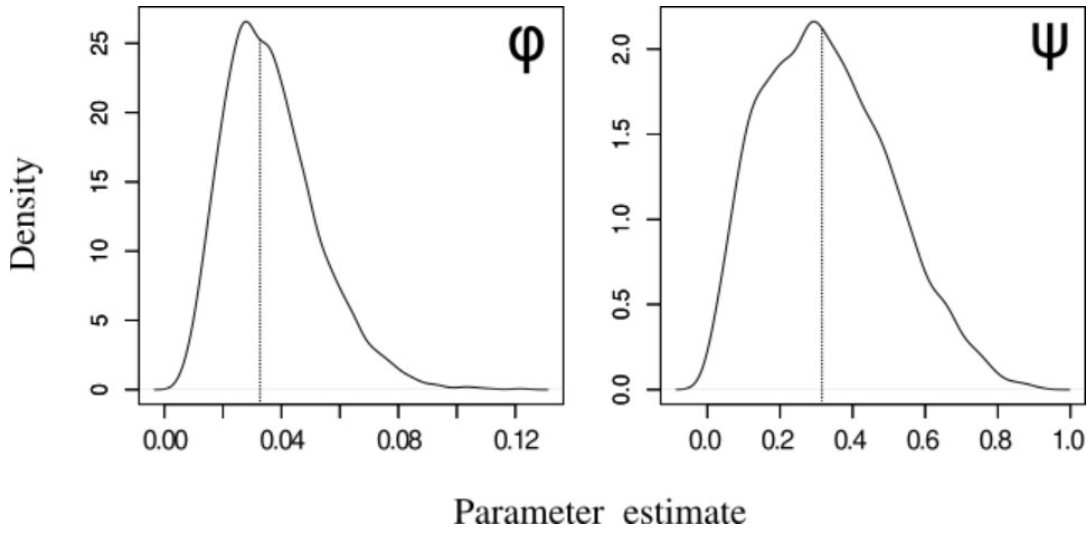


Fig. 3: Posterior distributions of the detection probability (φ) and the reporting probability conditional on the detection (Ψ) of roadkill decoys estimated with a Bayesian model of the Markov process.

Table 1: **Estimated number of collisions with vehicles in the Auvergne-Rhône-Alpes region, France.** We used citizen science reports of roadkill from the Faune-AuRA database for the 2022, and adjusted for the number of carcasses not reported with estimates of the detectability of animal carcasses in the context of citizen science ($P_{detection,}$ chapter 3), of their persistence time on the road following a collision ($T_{R,}$ chapter 2, manuscript n°3) and of the proportion of detected carcasses actually reported by contributors (ψ, or P_{report}).

Species	**$P_{detection}$ (95% CI)**	**T_R (95% CI)**	**P_{report} (95% CI)**	**Number of reports**	**Estimated number of collisions (95% CI)**
Vulpes vulpes	0.165 (0.123,0.207)	40h37 (10h37,90h27)	0.335 (0.054,0.722)	612	6557.3 (1088.9,208852.8) collisions **2.42** (0.40,77.16) collision per 100 km
Sciurus vulgaris	0.066 (0.037,0.094)			336	9004.7 (1307.8,378197.5) collisions **3.33** (0.48,139.7) collision per 100 km
Buteo buteo	0.294 (0.180,0.408)			278	1654.5 (248.6,64065.9) collisions **0.61** (0.09,23.67) collision per 100 km

Discussion and perspectives

We conducted this study in the Faune-AuRA project to obtain objective measures of the reporting rates using roadkill decoys and semi-structured interviews. Our findings revealed that approximately 33% of detected species were reported in the database, with a large 95% credible interval spanning 5% to 72%. In consequence, while the difference between the number of reports in Faune-AuRA and the estimated number of collisions varied between 6-fold (common buzzard *Buteo buteo)* to 27-fold (red squirrel *Sciurus vulgaris)*, the 95% confidence intervals around these estimates were wide enough to limit the relevance of these results.

Importance of reporting probabilities and biases in citizen science

Opportunistic reporting of species has gained significant popularity as a form of citizen science projects (*e.g.*, Faune-France, observation.org, artportalen.se, eBird), producing large quantities of data as well as "contribut[ing] to public engagement with the environment, potentially leading to behavioural change" (Pocock et al., 2018, see also Tulloch et al., 2013). The idea that not all species are reported by contributors is not novel (van Strien et al., 2013), but is often grouped with other issues regarding opportunistic monitoring, such as unevenly distributed sampling efforts (Knape et al., 2022; Mair & Ruete, 2016). However, the spatial distribution of the sampling effort is sometimes approximated with proxies such as population density or site accessibility (Geldmann et al., 2016; Sicacha-Parada et al., 2021), but the presence of an observer is not a guarantee of the effective reporting of the species present in the area. Failure to separate sampling effort and reporting probabilities may therefore result in introducing false-negatives to the models. In addition, selective biases may conduct contributors to report some species more often than they do others.

The fact that participants do not always report all the species they detect in biodiversity monitoring schemes without standardized reporting protocols ("*uncoordinated citizen science effort*", Klemann-Junior et al., 2017) is likely to extend to roadkill monitoring as well. We demonstrated here that not all detected roadkill will be reported to the Faune-AuRA database, which further widens the gap between the number of wildlife-vehicle collisions and the number of roadkill reports. Contributors may be occupied or time-constrained when they come across a carcass, resulting in a delayed reporting to the database. Consequently, it is highly probable that some of these encounters will be forgotten and remain unreported. Additionally, for contributors who typically wait until reaching their destination to report

roadkill, instances of forgetting or not having sufficient time or motivation to report the carcasses may also transpire.

Beyond general under-estimations of the number of roadkill, failure to report an animal may also impact the accuracy of roadkill datasets from citizen science projects through selective biases for species or taxa. Selective reporting has been described in other citizen science projects that focus on living specimens, with contributors preferring to report species that are rarer (Steen et al., 2019; van Strien et al., 2013), or in contrary, common species that are most likely more well-known and identifiable to contributors (Tiago et al., 2017). Selective reporting would result in roadkill datasets being biased toward certain species, that are readily identifiable to drivers through unique features, or that are perceived as conservation concerns by the general population. The existence and quantification of selective biases in roadkill monitoring is highly critical to proper exploitation of these databases, but has yet to warrant interest from the scientific community.

We initially set out to test the hypothesis that certain species were preferentially reported due to their charisma or conservation status (Swinnen et al., 2022) by selecting same-sized pairs of decoy species that would represent a charismatic or rare species, together with a more common, invasive or injurious species (*e.g.,* a peregrine falcon paired with a domestic pigeon, a honey buzzard paired with a ring-necked pheasant, and a red squirrel paired with a brown rat). However, some decoys from these pairs were stolen or removed during the experiments, limiting the number of contributors exposed to these pairs of species. In any case, having only one case of a decoy reported to the database, we are unable to draw any conclusions regarding the existence of a selective reporting bias in Faune-AuRA.

Assessment of the methodology

We discovered a significant disparity between the sampling effort initially anticipated and the actual effort required to gather data. The data collected provided limited examples of roadkill reporting, which had an impact on the predicting power of the Markov chain model. In consequence, the road mortality estimates for *Vulpes vulpes, Buteo buteo* and *Sciurus vulgaris* have large uncertainty margins. Roadkill reports for these species in Faune-AuRA could represent on average between 4% and 17% of the actual collisions, but confidence intervals (Table 1) are too large to draw meaningful conclusions. As a point of reference, Faune-AuRA receives on average 32 (± 9) roadkill reports daily across all species.

The estimated detection rates (3.3%, 95% credible interval: 1.1, 6.6) aligned with the *uninformed detection rates* presented in manuscript n°4, where we estimated detection rates ranging from 4.1% (95%

CI: 1.8, 6.3, brown rat *Rattus norvegicus*) to a maximum of 23% (95% CI: 15.8, 25.9, European badger *Meles meles*). The largest decoy used in this experiment was the red fox *Vulpes vulpes*. These low detection rates indicate the need for a substantial sampling effort to achieve an adequate number of detected decoys and determine reporting rates with reasonable accuracy. However, since both experiments were conducted simultaneously, we did not have this information at the time we designed this study. Another significant challenge we encountered was establishing contact with meeting attendees, which is a crucial step for constructing the complete sequence of states of the Markov chains. Eliminating the requirement for knowing the detection status of the decoy (and thus for contacting the contributors) would greatly enhance the efficiency of this protocol. Although we presented a methodology based on explicit Markov chains, it may be beneficial to explore hidden Markov chain models instead, which would allow the detection status to remain unobserved, removing the need for contacting the contributors (Glennie et al., 2023). Nevertheless, this study provides, to our best knowledge, the first formal demonstration that there is a detected-to-reported conversion rate of less than 100% in roadkill monitoring schemes involving volunteers, as well as one of the first demonstrations of this phenomenon across all unstandardized biodiversity monitoring schemes.

Ethical statement

This study involved collecting personal or identifying information. In compliance with article 89 of the GDPR, this data will not be stored or shared.

Acknowledgments

We thank the presidents of the Ain, Loire, and Drôme LPO for their help in conducting this experiments as well as the Tichodrome wildlife rehabilitation center and J. Gilbert for their help in procuring taxidermy decoys of wild species.

REFERENCES

en-Shakhar, G., Bornstein, G., Hopfensitz, A., & van Winden, F. (2007). Reciprocity and emotions in bargaining using physiological and self-report measures. *Journal of Economic Psychology*, *28*(3), 314-323. https://doi.org/10.1016/j.joep.2007.02.005

Bíl, M., Heigl, F., Janoška, Z., Vercayie, D., & Perkins, S. E. (2020). Benefits and challenges of collaborating with volunteers : Examples from National Wildlife Roadkill Reporting Systems in Europe. *Journal for Nature Conservation*, *54*(December 2019), 125798. https://doi.org/10.1016/j.jnc.2020.125798

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming with models : Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403-413. https://doi.org/10.1080/10618600.2016.1172487

Geldmann, J., Heilmann-Clausen, J., Holm, T. E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C., & Tøttrup, A. P. (2016). What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions*, 22(11), 1139–1149. https://doi.org/10.1111/ddi.12477

Henckel, L., Bradter, U., Jönsson, M., Isaac, N. J. B., & Snäll, T. (2020). Assessing the usefulness of citizen science data for habitat suitability modelling : Opportunistic reporting versus sampling based on a systematic protocol. *Diversity and Distributions*, *26*(10), 1276-1290. https://doi.org/10.1111/ddi.13128

Hess, B., Farahani, A. Z., Tschirschnitz, F., & von Reischach, F. (2012). Evaluation of fine-granular GPS tracking on smartphones. *Proceedings of the First ACM SIGSPATIAL International Workshop on Mobile Geographic Information Systems*, 33-40. https://doi.org/10.1145/2442810.2442817

Hsing, P.-Y., Bradley, S., Kent, V. T., Hill, R. A., Smith, G. C., Whittingham, M. J., Cokill, J., Crawley, D., Volunteers, M., & Stephens, P. A. (2018). Economical crowdsourcing for camera trap image classification. *Remote Sensing in Ecology and Conservation*, *4*(4), 361-374. https://doi.org/10.1002/rse2.84

Hsu, C.-H., & Lin, T.-E. (2021). Exploring the participation motivations of ongoing and former citizen scientists in Taiwan Roadkill Observation Network. *Journal for Nature Conservation*, *64*, 126055. https://doi.org/10.1016/j.jnc.2021.126055

Knape, J., Coulson, S. J., van der Wal, R., & Arlt, D. (2022). Temporal trends in opportunistic citizen science reports across multiple taxa. *Ambio,* 51(1), 183–198. https://doi.org/10.1007/s13280-021-01550-w

Kreling, S. E. S., Gaynor, K. M., & Coon, C. A. C. (2019). Roadkill distribution at the wildland-urban interface. *Journal of Wildlife Management*, *83*(6), 1427-1436. https://doi.org/10.1002/jwmg.21692

Logofet, D. O., & Lesnaya, E. V. (2000). The mathematics of Markov models : What Markov chains can really predict in forest successions. *Ecological Modelling*, *126*(2), 285-298. https://doi.org/10.1016/S0304-3800(00)00269-6

Mair, L., & Ruete, A. (2016). Explaining Spatial Variation in the Recording Effort of Citizen Science Data across Multiple Taxa. *PLoS ONE*, 11(1), e0147796. https://doi.org/10.1371/journal.pone.0147796

Menni, C., Valdes, A. M., Freidin, M. B., Sudre, C. H., Nguyen, L. H., Drew, D. A., Ganesh, S., Varsavsky, T., Cardoso, M. J., El-Sayed Moustafa, J. S., Visconti, A., Hysi, P., Bowyer, R. C. E., Mangino, M., Falchi, M., Wolf, J., Ourselin, S., Chan, A. T., Steves, C. J., & Spector, T. D. (2020). Real-time tracking of self-reported symptoms to predict potential COVID-19. *Nature Medicine*, *26*(7), Art. 7. https://doi.org/10.1038/s41591-020-0916-2

Merry, K., & Bettinger, P. (2019). Smartphone GPS accuracy study in an urban environment. *PLoS ONE*, *14*(7), e0219890. https://doi.org/10.1371/journal.pone.0219890

Pocock, M. J. O., Chandler, M., Bonney, R., Thornhill, I., Albin, A., August, T., Bachman, S., Brown, P. M. J., Cunha, D. G. F., Grez, A., Jackson, C., Peters, M., Rabarijaon, N. R., Roy, H. E., Zaviezo, T., & Danielsen, F. (2018). *Chapter Six—A Vision for Global Biodiversity Monitoring With Citizen Science. In D. A. Bohan, A. J. Dumbrell, G. Woodward, & M. Jackson (Eds.), Advances in Ecological Research (Vol. 59, pp. 169–223).* Academic Press. https://doi.org/10.1016/bs.aecr.2018.06.003

Pradel, R. (2005). Multievent : An Extension of Multistate Capture–Recapture Models to Uncertain States. *Biometrics*, *61*(2), 442-447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Shilling, F. M., & Collinson, W. J. (2017). Designing wildlife-vehicle conflict observation systems to inform ecology and transportation studies. *Biological Conservation.*

Sicacha-Parada, J., Steinsland, I., Cretois, B., & Borgelt, J. (2021). Accounting for spatial varying sampling effort due to accessibility in Citizen Science data: A case study of moose in Norway. *Spatial Statistic*s, 42, 100446. https://doi.org/10.1016/j.spasta.2020.100446

Steen, V. A., Elphick, C. S., & Tingley, M. W. (2019). An evaluation of stringent filtering to improve species distribution models from citizen science data. *Diversity and Distributions*, 25(12), 1857–1869. https://doi.org/10.1111/ddi.12985

Stone, A. A., Bachrach, C. A., Jobe, J. B., Kurtzman, H. S., & Cain, V. S. (1999). *The Science of Self-report : Implications for Research and Practice*. Psychology Press.

Swinnen, K., Jacobs, A., Claus, K., Ruyts, S., Vercayie, D., Lambrechts, J., & Herremans, M. (2022). *‘Animals under wheels’ : Wildlife roadkill data collection by citizen scientists as a part of their nature recording activities*. Pensoft Publishers. https://natureconservation.pensoft.net/article/72970/

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates : Effects of sampling methods and carcass removal. *Biological Conservation*, *157*, 317-323. https://doi.org/10.1016/j.biocon.2012.09.006

Tiago, P., Pereira, H. M., & Capinha, C. (2017). Using citizen science data to estimate climatic niches and species distributions. *Basic and Applied Ecology*, 20, 75–85. https://doi.org/10.1016/j.baae.2017.04.001

Tulloch, A. I. T., Possingham, H. P., Joseph, L. N., Szabo, J., & Martin, T. G. (2013). Realising the full potential of citizen science monitoring programs. *Biological Conservation*, 165, 128–138. https://doi.org/10.1016/j.biocon.2013.05.025

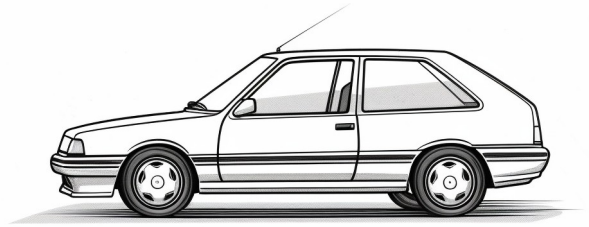
Van Eupen, C., Maes, D., Herremans, M., Swinnen, K. R. R., Somers, B., & Luca, S. (2022). Species profiles support recommendations for quality filtering of opportunistic citizen science data. *Ecological Modelling*, *467*, 109910. https://doi.org/10.1016/j.ecolmodel.2022.109910

van Strien, A. J., van Swaay, C. A. M., & Termaat, T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analyzed with occupancy models. *Journal of Applied Ecology*, *50*(6), 1450-1458. https://doi.org/10.1111/1365-2664.12158

Vercayie, D., & Herremans, M. (2015). Citizen science and smartphones take roadkill monitoring to the next level. *Nature Conservation*, *11*, 29-40. https://doi.org/10.3897/natureconservation.11.4439

Waetjen, D. P., & Shilling, F. M. (2017). Large Extent Volunteer Roadkill and Wildlife Observation Systems as Sources of Reliable Data. *Frontiers in Ecology and Evolution*, *5*. https://www.frontiersin.org/articles/10.3389/fevo.2017.00089

General discussion and perspectives



This thesis had for objective to work toward predictive models for wildlife-vehicle collisions on a large scale, both spatially and temporally.

In the first chapter, we developed a **mechanistic approach**, focusing on **animal and vehicle movement** and trajectories. The study successfully established **causal relationships** with factors that had previously been linked with wildlife-vehicle collision occurrences in empirical studies. Additionally, we concluded that factors relating to **animal movement** are more promising than road and traffic characteristics in **explaining and predicting collisions**.

Throughout the remainder of the thesis, we focused on **improving the precision of roadkill data**. While roadkill datasets serve as the foundation for predictive statistical models, they are also essential for validating mechanistic models.

We have focused on the citizen science Faune-Auvergne-Rhône-Alpes (Faune-AuRA) monitoring scheme to provide a **step-by-step investigation of the roadkill reporting process**, and work toward **robust correction parameters and methods** for the three main sources of bias we identified in opportunistic reporting. We conclude that the reports of roadkill present in the Faune-AuRA dataset paint a very partial picture of the magnitude of road mortality in the region.

1. On the value of citizen science for biodiversity monitoring

The challenges associated with roadkill monitoring, discussed in the introduction of this manuscript, are also relevant to all forms of biodiversity monitoring, where assessing the size and health of wild populations can prove costly and difficult (Schmeller et al., 2009). In response to these challenges, tools from citizen science tools have been explored as promising methods for data collection, including the collection of roadkill data. One notable example of the use of volunteer contributors to inform wildlife presence and characteristics is the Cornell Lab of Ornithology: for over 60 years, they have enlisted the help of volunteers to monitor bird species' presence, reproductive success and habits, while educating the public on the conservation issues faced by these species (Bonney et al., 2009; Dickinson, 2011). According to Donnelly et al. (2014), the earliest example of volunteers contributing to the data gathering process dates back to the 1900 (*Christmas bird count,* United States). Over the years, projects carried out by volunteers have yielded valuable information on species distributions (Klemann-Junior et al., 2017), the impact of global change on ecosystems (Larson et al., 2020), the monitoring of rare or elusive species (Robinson et al., 2018), and have helped to evaluate the efficiency of biodiversity conservation measures (Pellissier et al., 2020). These datasets may also hold value for decision-making in conservation (Newman et al., 2017). Therefore, the results presented in this manuscript have implications that extend beyond the specific issue of wildlife road mortality.

The challenges associated with working with biodiversity data collected through citizen science projects are quite extensive: erroneous reports, variations in species detectability, and biased selection of both sampling locations and species to report (Johnston et al., 2023). Opportunistic reporting is perhaps the most efficient method for collecting large quantities of data, but the presence-only data generated by this method presents significant challenges when it comes to modelling, compared to standardized surveys (Mengersen et al., 2017; Ver Hoef et al., 2021). Despite proving a valuable source of data in a number of occasions (Hall et al., 2021; Henckel et al., 2020; Klemann-Junior et al., 2017; Tiago et al., 2017), opportunistic citizen science data is sometimes regarded by authors as unreliable but yielding large datasets, while on the other hand, standardized sampling conducted by researchers is considered to be of higher quality, albeit with smaller datasets (Couvet et al., 2008; Elliott & Rosenberg, 2019). The existence of this trade-off between quantity and quality may be perceived as an inevitable outcome of involving volunteers in the data collection process. However, studies have shown that citizen science data can be effectively rectified to produce high-quality data (Bird et al., 2014; Cretois et al., 2021; Isaac et al., 2014; Robinson et al., 2018), a process which we have explored here in the context of opportunistic roadkill datasets.

Finally, one of the main challenges in managing citizen science monitoring schemes is to ensure the continued implication of its contributors, as the sampling effort is directly linked to the number of volunteers (Schmeller et al., 2009). Hsu & Lin (2021) showed that participants' motivations for taking part in such projects included the desire to contribute to scientific research, and that they may stop contributing in the project when they do not experience this sense of achievement (see also Thompson et al., 2023). Opportunistic monitoring schemes should therefore produce scientific knowledge in order to retain their contributors. In the case of Faune-AuRA, neither the roadkill dataset nor the larger species' presence dataset have been mentioned or used in scientific studies. The work that is presented in this manuscript can therefore potentially be the start of a virtuous cycle, where the recognition of the value of the data produced by volunteers, both through scientific publications but also public restitutions, can help ensure that the number of contributors remains sufficient for future contributions of the Faune-AuRA project to scientific knowledge and decision-making in conservation. In consequence, I have tried to during this project to ensure that the public, and in particular the project contributors, had access to the new knowledge produced, instead of focusing solely on publishing in peer-reviewed journals.

1.1. How biased are datasets from opportunistic roadkill monitoring?

We have explored three sources of bias in citizen science opportunistic roadkill datasets: roadkill persistence, probability of detection and probability of reporting. Citizen science monitoring schemes usually cover large spatial scales (Swinnen et al., 2022; Waetjen & Shilling, 2017) and operate in continuous time. In consequence, detecting spatio-temporal structures in these different sources of bias is also a major concern. While we have not been able to explore all the nuances in these sources of bias over the duration of this project, we have a better understanding of the roadkill reporting process in opportunistic citizen science, and can rely on existing literature to provide further insights on the subject (Table 1).

Table 1: Summary of the potential sources of bias present in opportunistic roadkill datasets and the factors influencing them. A green cell indicates that we have investigated the component and found a significative impact, a red cell indicates that we did not find any impact. White cell represent factors we did not cover in this project (green text: effect demonstrated by other authors, red text: no effect found in other studies, black text: hypothesis that remains to be investigated). The last column summarizes the estimates we have obtained (T_R = characteristic persistence time sensu Teixeira et al. (2013); $P_{detection}$ = roadkill detection probability; $P_{report \mid detected}$= reporting probability of detected roadkill by Faune-AuRA project contributors).

			Spatial	Temporal	Biological traits	Estimates (95% CI)
Persistence	Amphibians (anurans) (~35g)		Road traffic (100 – 8000 veh.day^{-1})	Rainfall	Body mass (Brzeziński et al., 2012)	**T_R = 24h30 (13h10,45h57) - 36 min (12 min,1h18)**
	Small passerines (~20g)		Road traffic	Rainfall	*Body mass?*	**T_R = 40 min (13 min, 1h07)**
	Birds and mammals (20g – 25kg)	*citizen science*	Road traffic	Season	Body mass	**T_R = 59h (46h,149.5h)**
		manuscript n°3	Road traffic	Time of day (Slater, 2002)		**T_R= 40h37 (10h37,90h27)**
Detection	Birds and mammals (160g – 15kg) *citizen science context*		Vehicle speed (50 – 90km.h^{-1})	Position of the sun (Collinson et al., 2014)	Body size (Eurasian Jay – European badger)	**$P_{detection}$ = 9% (6.5,11.4) -20.6% (15.7,25.5)**
Reporting	Birds and mammals (500g - 15kg)		*Influence of road traffic and configuration?*	-	*Positive bias toward charismatic species?*	**$P_{report \mid detected}$ = 33.5% (5.4,72.2)**

We assessed for the first time the *search efficiency* (*i.e.*, detection probability) of drivers in the context of citizen science, where observers are not trained professionals and opportunistically report roadkill (*i.e.*, they are not likely to be actively searching for roadkill while driving). We showed that detection probabilities are much lower in this context than during traditional road surveys (manuscript n°4). Focusing on the size of the animal as a continuous predictor of roadkill detectability (Barrientos et al., 2018), we constructed a model useful for predicting the detection probabilities of a wide range of species, both in the context of citizen science (*e.g.*, roe deer ~ 25kg: $P_{detection}$= 26.7%, 95% CI : 17.6%, 40.3%; small passerine ~ 20g: $P_{detection}$= 4.2%, 95% CI: 1.9%, 9.5%), but also for standardized surveys where drivers are actively searching for roadkill. In consequence, through lack of detection alone, citizen science datasets may underestimate the mortality of bigger species by about 75%, while we could have previously assumed that ungulate carcasses —such as the roe deer— were most likely always detected by

drivers. In addition to a general under-estimation of the total number of carcasses, differences in detectability between species or roads will introduce biases in the datasets. Therefore, modelling raw citizen science roadkill data without correcting for differences in detectability will likely result in inaccurate conclusions, as the relative frequencies of reports for each species do not represent the true ranking of collision rates (see also Collinson et al., 2014), and this also applies to surveys conducted by professionals (Teixeira et al., 2013). Differences in roadkill detectability may also be influenced by other spatio-temporal factors, such as the presence of vegetation on roadsides, road intersections or any configuration that may require the full attention of the driver, weather, and, of course, the amount of daylight. Although Collinson et al. (2014) found no effect of the position of the sun (which was thought to blind drivers depending on hours of the day), there has been, to the author's best knowledge, no attention given to these possible predictors of roadkill detectability, in the context of citizen science or otherwise. Further investigation of these predictors is therefore needed for accurate spatio-temporal modelling of WVC.

Following the detection of roadkill, drivers may not always immediately able to report the observation (usually *via* a mobile app) to the monitoring scheme, and, in some cases, they may forget the animal altogether. This issue is recognized in citizen science biodiversity monitoring schemes and often put under the umbrella of general issues with uneven monitoring pressure (Johnston et al., 2023). However, as explained in chapter 4, failure to discriminate between the two processes may lead to the incorrect inference of pseudo-absence data, which an approach classically employed for modelling opportunistic, presence-only, data of a species' presence (Mair & Ruete, 2016). The lack of *willingness to report* had, to the author's best knowledge, never been formally demonstrated with an experimental approach in citizen science projects with opportunistic sampling. We found that only 33.5% of the detections (95% CI: 5.4,72.2) are effectively reported to the Faune-AuRA database. By combining the probabilities for carcass detection and reporting, we can obtain the probability for an animal present on the road to be reported to the Faune-AuRA database. For example, the probability for a roe deer carcass (~ 25kg) to be reported to Faune-AuRA when a contributor drives by is $P_{detection} . P_{report \mid detected} = 0.267. 0.335 = 0.089$ (95% CI: 0.009, 0.29). Of course, we assume here that the probabilities are independent, *i.e.*, that the detectability of the animal does not impact its odds of being reported and vice versa.

In addition to a general under-reporting of the roadkill carcasses, authors have raised the issue of preferential reporting in opportunistic monitoring, where some species have a higher probability of being reported than others as they seem to be over-represented in roadkill datasets (Swinnen et al., 2022). This could possibly be the case for rare, endangered or charismatic species for which reports of mortality may be perceived as more critical. Preferential reporting of rarer species has been noted by Johnston et al. (2023) in the biodiversity monitoring scheme *eBird*, and in roadkill reporting by Périquet et al. (2018). However, contributors may instead prefer to report more easily identifiable species (Tiago et al., 2017). Selective reporting in opportunistic monitoring would have significant impacts on the accuracy of the data, for example for use in species distribution modelling (Tiago et al., 2017), and there is therefore a need for experimental designs that can detect and quantify the presence of this bias.

Proposing an experimental design to assess selective reporting biases in roadkill monitoring

An experimental design for detecting selective reporting biases can be built upon the design presented in chapter 4. By exposing naive contributors driving on the road to pairs of artificially placed roadkill, we can test whether they choose to report only one the carcasses from each pair. Selected pairs of species can vary in their (1) charisma (*e.g.*, Eurasian lynx), under the hypothesis that charismatic species are more often reported, or (2) abundance, under the hypothesis that the species contributors are most familiar with are also more frequently reported. If there is no prior information available on the detectability of each species, then effort should be made to standardize the detection probability of the pairs of species, through similar sizes and taxa (see manuscript n°4, Collinson et al., 2014; R. A. L. Santos et al., 2016; Teixeira, Coelho, Esperandio, & Kindel, 2013 for predictors of detectability). Of course, the level of charisma possessed by a species is an inherently subjective feature (Albert et al., 2018), and may need to first be assessed through surveys.

Roadkill dataset corrections in manuscript n° 2, 4 and in chapter 4 have made one important assumption regarding roadkill persistence: that all roads of the AuRA region were monitored daily by project contributors. In fact, it is not the persistence of roadkill alone, but the combination of persistence and of the presence of an observer that is relevant to roadkill monitoring. While in standardized monitoring the presence of observers is known with certainty (Teixeira et al., 2013), opportunistic citizen science frequently encounters challenges stemming from inconsistent and unbalanced sampling efforts, both in terms of location and time (Bíl, Heigl, et al., 2020; Geldmann et al., 2016). The resulting data is defined as "presence-only", with no immediate way to distinguish the true absence of a species from the lack of presence of an observer (Johnston et al., 2023). Although presence-only data may be useful for informing population trends and modelling species distributions (Horns et al., 2018; Tiago et al., 2017), these irregular sampling patterns can introduce detected trends in the data that do not reflect actual ecological realities (Isaac et al., 2014), such as variations in observer's efforts inducing temporal patterns in the number of record that are not related to changes in the species' abundance (Knape et al., 2022), or spatial patterns in reports that mirror the distribution of the observers' homes (Dennis & Thomas, 2000).

To address this issue, there is a limited number of methods that can be applied. For example, proxies of the sampling effort in citizen science biodiversity monitoring schemes can be used in order to correct the data (Cretois et al., 2021; Ver Hoef et al., 2021). Sampling effort in these projects has been shown to be reflected by the density of human populations and the accessibility of the sampling areas (Geldmann et al., 2016; Mair & Ruete, 2016; Sicacha-Parada et al., 2021). In addition, other observations made within the same citizen science project can be used: the length of the recorded list in list-based sampling (*i.e.*, listing all species sighted during a recording session, *e.g.*, ebird.org) can be introduced as a proxy of sampling effort (Horns et al., 2018), and, similarly, the reports submitted by an observer of species that are not the focal species in an area can be used to infer pseudo-absence points for said focal species (de Groot et al., 2022; Milanesi et al., 2020). In the case of opportunistic roadkill datasets, the potential biases introduced by inconsistencies in the sampling effort are often acknowledged, but seldom addressed (see Hiegl et al., 2016; Olson et al., 2014; Périquet et al., 2018; Shin, Kim, Groffen, Woo, Song, & Borzée, 2022; Yue et al., 2019). Some opportunistic roadkill monitoring schemes now offer the possibility to conduct standardized roadkill counts along transects, although it seems that even then, the overwhelming majority of reports remain opportunistic (Swinnen et al., 2022). Considering that most roadkill monitoring conducted by volunteers focuses on all roadkill, indiscriminately of the species, pseudo-absence points could be inferred for species of interest from the reports of other species on the

road (de Groot et al., 2022). Potential issues with this approach can arise if project contributors preferentially report certain species, which once again emphasizes the importance of detecting *selective reporting* biases in these datasets.

Proposing an experimental design for inferring pseudo-absence points in Faune-AuRA

Faune-AuRA is a unique example of a roadkill monitoring scheme that is part of a larger monitoring scheme, where contributors report the presence of all wild species. In consequence, the roadkill database is in fact a subsample of the reports contained within the Faune-AuRA project, for which the animals have been marked as “killed by a vehicle”. In this context, the sampling effort of contributors in reporting non-roadkill observations can be used to inform the monitoring pressure for roadkill. We show in figure 1 an example of the spatio-temporal distribution of the monitoring pressure in the Ain department, France. Figure 1a shows a map of the spatial distribution of the roadkill monitoring pressure, defined as the number of contributors that have reported at least one animal to Faune-AuRA in 2022 (excluding roadkill reports). Some areas of the department seem to have higher densities of active project contributors, and thus the frequency of road surveys in these hotspots is expected to much higher than in other areas. Figure 1b shows the temporal variations in the monitoring pressure with a similar approach. This type of data could lead to a spatially and temporally structured indicator of the monitoring pressure, describing the frequency of road surveys for roadkill in the AuRA region. This indicator of the monitoring pressure could then be integrated into the equation for roadkill reports correction presented in Chapter 4.

However, this type of approach needs further work to be reliable. For example, it is worth considering that, at finer spatial scales, more frequented roads have a higher probability of being used by contributors (Paul et al., 2014). In addition, contributor activity may sometimes misrepresent the monitoring pressure: there were two notable peaks in contributor activity on January 29th and 30th, 2022 (fig. 1b). These dates correspond to the national citizen science LPO reporting project “*Oiseaux des jardins*” (“*Garden birds”*), a national bird counting scheme which may draw many contributors that are not otherwise active in Faune-AuRA during the rest of the year. In general, it is worth considering that Faune-AuRA attracts many types of volunteer contributors, some of which may only be active in one-off monitoring schemes, and others that do not contribute to road mortality reports (as a more recent feature of the monitoring scheme, the mortality module is not known to all users). Therefore, a preliminary filtering of the contributors appears necessary to retain only users whose reporting activity for living specimens is likely to reflect their monitoring of roadkill.

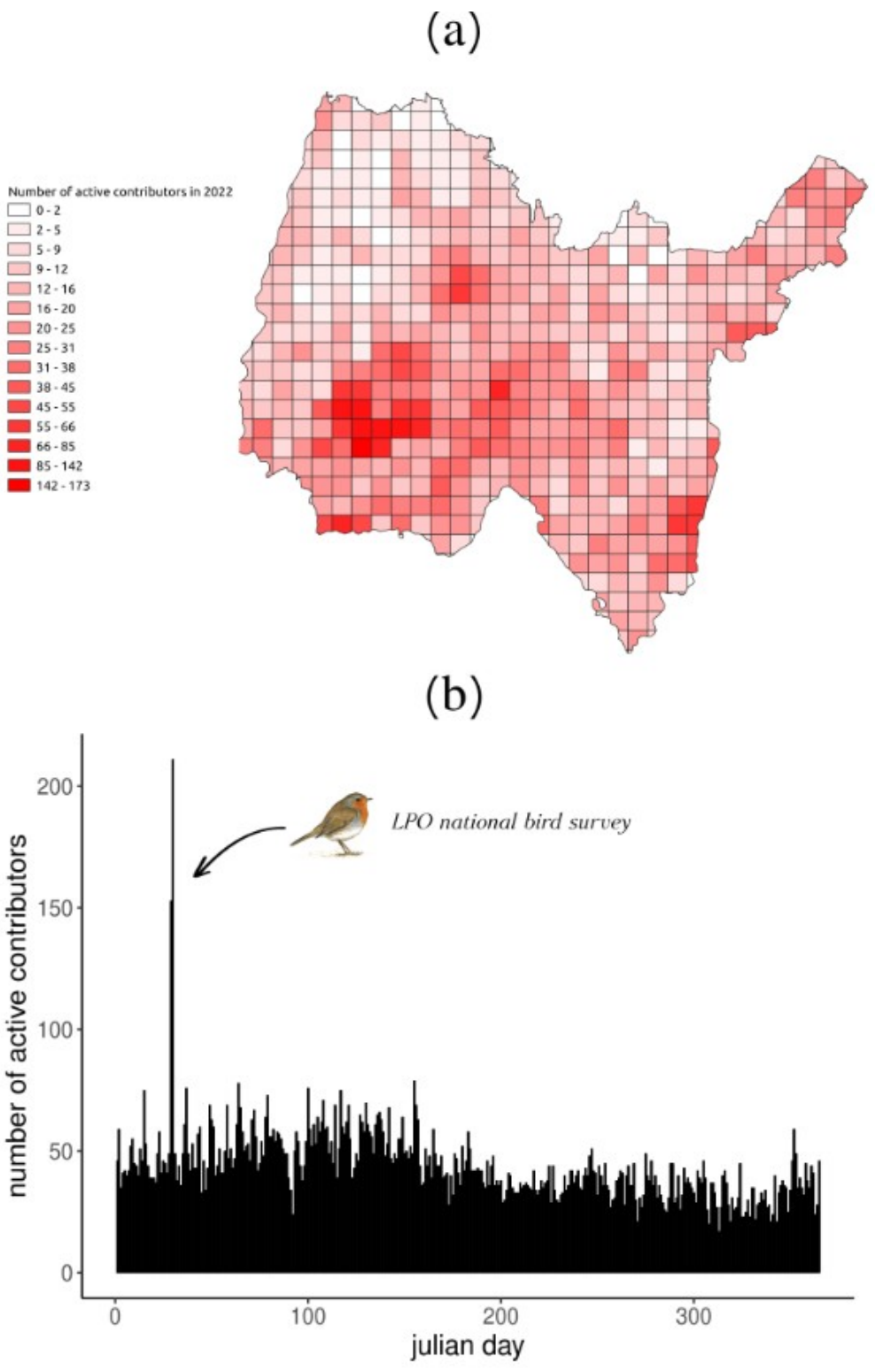


Fig. 1: **Spatial (a) and Temporal (b) distributions of active Faune-Ain contributors (2022) in the Ain department, AuRA region, France.** (a) in each 5km by 5km cell of the grid, we have computed the number of project contributors having submitted at least on report of a wildlife species (living specimens) to the Faune-Ain wildlife monitoring scheme; (b) the same type of approach has been applied to represent the number of active contributors (>1 contribution) for each day of the year.

1.2. Beyond citizen science: the problem of roadkill persistence

The short persistence of roadkill is a source of under-estimation in roadkill datasets that is not limited to citizen science monitoring schemes, but is instead transversal to all methods of roadkill monitoring (Santos et al., 2011). Most studies published to this day find that carcasses are not likely to remain visible for more than a few days on roads (Antworth et al., 2005; Guinard et al., 2012; Henry et al., 2021; Santos et al., 2011), which means that roadkill monitoring needs to be conducted frequently in order to avoid missing a large portion of the road mortality. The estimates of roadkill persistence presented in chapter 2 are consistent with previously published estimates, and we have been able to fine-tune these estimates of persistence for a number of species. We found characteristic persistence estimates (*i.e.,* time for 63% of the carcasses to be removed, Teixeira et al., 2013) ranging from less than 2 hours (small passerines, manuscript n°2) to 59 hours (medium to large-bodied birds and mammals, case study n°1). From these results, we can conclude that (1) roadkill available for detection to Faune-AuRA contributors only represents a small portion of the actual wildlife-vehicle collisions in the region, and (2) since removal rates differ between species, the most often reported species in the database are once again not necessarily the species most often killed on roads.

We considered road traffic volume, species' body mass, season, and rainfall as possible predictors for roadkill persistence in manuscripts n° 2 and 3, as well as in the case study presented in chapter 2. Although neither season nor rainfall modified the persistence of roadkill, we found that road traffic volume was a predictor of amphibian persistence; with longer persistence times on less frequented roads, but it had no impact on persistence for other species (manuscripts n°2 and 3). In contrast, the *citizen science* approach (case study n°1) revealed that medium to large avian and mammalian species' persistence was positively linked to traffic volume (consistent with Santos & Ascensão, 2019; Santos et al., 2011). Therefore, at first glance, we find no consistent answer to the existence and nature of the relation between road traffic volume and roadkill persistence.

However, some elements should be discussed regarding these results. The major difference between the experiment in case study n°1 (citizen science approach) and manuscript n°3 is that the former included observations on french highways, a type of road we could not access in manuscript n°3 for safety reasons. Highways in France are multi-lane roads, with fencing to prevent human and wildlife access to the road surface, and where only highway patrols are permitted to step out of a vehicle to, for example, remove roadkill carcasses. In this case, it seems that the persistence of roadkill was predicted by the type of road, more than it was by the volume of traffic itself, with carcasses persisting significantly longer on highways compared to the rest of the road network. Santos et al. (2019) have also found substantially

longer persistence for rodent roadkill on four-lane roads, compared to two-lane roads and dirt roads. Guinard et al. (2012) found median persistence times of about 10 days for small bird species on french highways, which is much higher than the results we obtained for these species on the rest of the road network (manuscripts n°2 and 3). In allowing us to expend the scale of our experiments to new types of roads at next to no financial costs, citizen sciences have showed considerable promise for the study of roadkill persistence. Finally, the differences in response to road traffic volume between amphibians and small passerines is less straightforward to explain, as both were tested on similar roads. Considering their size and low detectability, removal by members of the public is unlikely, and we found little evidence of scavenger activity for removing roadkill, making it plausible that some of these carcasses disappeared through repeated crushing by vehicles (see manuscript n°3). This result warrants a more in-depth analysis of the speed of disappearance of carcasses when repeatedly crushed, depending on their characteristics, such as morphology or bone density. Furthermore, we may have underestimated scavenging rates on small animals (see Antworth et al., 2005 for scavenging rates of small birds), as the experiments presented in manuscript n°3 showing little scavenger activity in the Ain department of AuRA focused on larger species.

Manuscript n°3 showed that road users play a significant part in the removal of roadkill in the Ain department, a phenomenon that may extend to other parts of the region according to case study n°1, where some carcass were found intact in ditches, suggesting displacement by a person. The cultural characteristics of the study area can possibly influence the prevalence of this habit, which is seldom considered as a potentially significant source of removal in current roadkill persistence studies (Santos et al., 2011). The extent of this phenomenon, which may lead to large carcasses being removed very quickly from roads, needs further attention, as is it relevant to both roadkill studies, but can also have significance for the way roadkill defines the relation between members of the public and wildlife (Lulka, 2008; Lunney, 2013). Therefore, roadkill persistence studies may have to draw insights from sociological studies, which may help explain and predict rapid roadkill removal by people.

Finally, the experiments presented in manuscript n°2 found that amphibian (~ 30g) and passerine (< 20g) carcasses disappeared between 2 and 100 times faster than the medium-to-large avian and mammalian species we used in manuscript n°3 and case study n°1. Although we conclude that there is no evidence of species' body mass being a predictor of roadkill persistence in medium-to-large species, it appears that this is not true for extreme values, such that very small species disappeared from roads significantly faster. Therefore, the generalization of the persistence estimates we have obtained throughout this project to other taxa (*e.g.,* reptiles) and species with extreme values of body mass (*e.g.,* bats, small rodents) is not straightforward. Although some authors have produced estimates of the median persistence times for

small rodents (Santos & Ascensão, 2019), and bats, lizards and snakes (Santos et al., 2011), we have also discussed throughout this manuscript that the context of each study seems to affect persistence estimates, and assessing the pertinence of these estimates for roadkill in the AuRA region may prove difficult. As an illustration, vipers *Crotalus oreganus* persisted about 48 hours in Winton et al. (2018), compared to 24 hours in other experiments (Santos et al., 2011). In conclusion, we find that, overall, roadkill persistence for most species remained largely unaffected by seasonal variations, rainfall patterns, or the volume of road traffic within the Auvergne-Rhône-Alpes region. This conclusion can be considered advantageous, as it greatly simplifies the dataset correction process by requiring a single correction parameter of roadkill persistence for all roads and times of year.

A note on the accuracy of reports from non-professional observers

The correction method presented in this manuscript (chapter 4) explicitly integrates the theoretical framework for roadkill reporting by volunteers following a wildlife-vehicle collision (*i.e.*, the carcass is still present on the road when a project contributor drives by, it is detected and it is reported). In consequence, it assumes that the roadkill reports that are made are accurate. In all citizen science projects focused on ecological surveys, there is a possibility of inaccurate reports due for example to contributors mistaking one species for another (Van Eupen et al., 2022). When it comes to roadkill, the challenge of species misidentification is heightened by the difficulty in identifying flattened remains (Bíl, Heigl, et al., 2020). To minimize the probability of erroneous reports in citizen science data, several measures can be implemented: allowing users to provide their level of confidence in identifying the species (*e.g.*, Kreling et al., 2019; Waetjen & Shilling, 2017); enabling community reviewing of the reports (note that multiple non-professional reviewers agreeing on the identification can provide high levels of confidence, Hsing et al., 2018); implementing reports reviewing by professionals (*e.g.*, Shilling & Collinson, 2017); flagging implausible reports (*e.g.*, Bonter & Cooper, 2012). For photographic data, automated verification methods with machine learning classifiers (*e.g.*, Rigoudy et al., 2023; Willi et al., 2019) may prove helpful, although not yet applied to roadkill data. Faune-AuRA implements automatic reviewing by professionals of the implausible reports (*i.e.*, rare species or reports outside of the expected spatio-temporal distribution of the species).

Another issue that can be considered in citizen science biodiversity monitoring is the level of spatio-temporal precision of reports. However, many monitoring schemes nowadays utilize the GPS capabilities of modern smartphones to accurately pinpoint the location of the animal (Vercayie & Herremans, 2015).

Typically, modern smartphones offer GPS horizontal accuracy within a range of 5 to 10 meters (Hess et al., 2012; Merry & Bettinger, 2019). Reports submitted through mobile apps also typically rely on the internal clock of the phone as the default timestamp. Although smartphones seem to be the current standard for roadkill reporting (Bíl, Heigl, et al., 2020), some monitoring projects rely on additional means of reporting data such as social media (*e.g., The Road Lab*, formerly *Project Splatter,* UK) may suffer from less accurate reports, which may interfere with the proper spatial and temporal modelling of the data.

1.3. Correcting opportunistic citizen science roadkill datasets and implications for wildlife conservation

In conclusion, how biased are datasets from opportunistic roadkill monitoring? Although issues regarding the monitoring pressure were beyond the scope of this project, we have successfully converted the number of reports into estimates of the wildlife-vehicle collisions in the Auvergne-Rhône-Alpes region for a select set of species. In order to achieve this, we rely on the assumption that roads are, on average, monitored daily by contributors, which may not be unreasonable when focusing on large spatial scales. We found little support for temporal structures in the correction parameters (persistence, detection, report) when we explored the effects of rain and season on roadkill persistence. In addition, we found little support for a spatial structure in these parameters, as road traffic volumes only affected the speed at which amphibian roadkill disappeared. Although there are several spatio-temporal predictors for these parameters that remain to be investigated, the information presently available to us leads to the conclusion that the spatial and temporal distributions of the roadkill reports in Faune-AuRA are representative of the true distribution of wildlife-vehicle collisions. However, we have left aside a central aspect of opportunistic monitoring schemes that may introduce significant spatial and temporal bias (Dennis & Thomas, 2000; Sauermann & Franzoni, 2015): the monitoring pressure. As a result, we are currently unable to produce spatial (map of wildlife-vehicle collision hotpots) or temporal (trends in WVC) distributions of roadkill.

Nevertheless, we find in chapter 4 that the reports in the database represented between 3.7% and 10.8% of the true extent of road mortality (respectively for the red squirrel *Sciurus vulgaris* and the red fox *Vulpes vulpes, c*hapter 4, table 1). In addition, the 21 species of small passerines presented in manuscript n°2 were estimated to be reported only 2.8% of the time *before* we corrected for detection and reporting probabilities. In the light of the rest of the results presented here, we can estimate the detection rate of

small passerines at 4.2% (chapter 3) and their reporting rate at 33.5% (chapter 4), which results in a final estimate of 504 000 collisions with vehicles in 2022 at the scale of the Auvergne-Rhône-Alpes region. Of course, the pertinence of these estimates is considerably weighted down by the large uncertainty surrounding the reporting probabilities (95% CI: 5%, 72%), which means that they range from reasonable (236 000 passerines killed on roads in 2022) to catastrophic (3 377 600 individuals killed). Based on the author's own experience as a Faune-AuRA contributor, along with other testimonies, small species such as passerines can only be identified after turning around, stopping the car and assessing the carcass on foot, which suggest that the lower tail of the confidence interval (probability of report: 5%) may not be absurd. In consequence, small passerine mortality in the region may be higher than current estimates and tend toward the catastrophic estimates of several million collisions annually, which is a major cause for concern for these populations. In addition, these testimonies add to the hypothesis that contributors may report selectively, based on the effort required for identification—which may be expressed in relation to the species' size, coloring, or other unique features—such that individuals are more likely to be reported when they can be identified at first glance (see also Tiago et al., 2017).

There are limited examples of calculated roadkill rates available in the literature to assess the plausibility of our results. Canova & Balestrieri (2019) estimated the annual roadkill rate of the red fox at 0.06 collision.km^{-1} in Italy, while we estimated 0.024 (95% CI: 0.004, 0.7) collisions.km^{-1}. However, annual common buzzard mortality, which we estimated at 0.006 collisions.km^{-1} (95% CI: 0.009,0.24), is comparable to estimated roadkill rate for *all* avian species in southern China (Wang et al., 2022). Of course, the comparison of the estimates of difficult as they often represent raw roadkill counts that are not corrected for roadkill persistence or detectability, and, as highlighted by the first chapter of this manuscript, characteristics of the landscape, population density, time of year, or even population-level behaviours may result in significant variations in the patterns of space-use of the individuals, and therefore, in the collision risks. In general, it is difficult to assess the conservation implications of the road mortality estimates that we have produced, as they need to be placed within the larger context of population demography. For examples, population sizes for foxes, squirrels, buzzards and small passerines are not currently available in France, which limits the conclusions we can draw regarding the impact of road mortality on these species.

Nevertheless, Hill et al. (2019) estimated that wildlife mortality resulting from collisions on transport infrastructures represented less than 10% of the total morality for most species (based on a meta-analysis of wildlife telemetry data), while legal harvest was the leading source of anthropogenic mortality. However, road mortality represents a source of mortality that is entirely accidental, whereas legal harvest or hunting are intentional and benefit the people involved. This means that road mortality can be reduced

with little repercussion for human populations, as next to no-one profits from roadkill (but see Abbate, 2019), and conservation efforts may turn toward road mortality as leverage for protecting endangered species. In fact, reducing wildlife mortality from vehicular collisions may be beneficial for societies in general, as collisions, particularly with large species, may pose significant risks for the safety of road users, and generate high costs when the vehicles are damaged (Seiler, 2005). In addition, several authors have expressed their concerns that the ubiquity of roadkill in everyday life may transform the relations between our societies and wildlife, specifically wildlife deaths (Lulka, 2008; Taylor, 2022), which may impact future conservation efforts.

2. Toward a predictive model for WVC

The initial objective of this thesis was to work toward a predictive model for wildlife-vehicle collisions. As explained in the introduction, predictive models can utilize observed patterns (statistical modelling) or focus on the underlying mechanics of the system under study (mechanistic modelling) to generate predictions (Denny & Benedetti-Cecchi, 2012). In both cases, reliable empirical data is essential for either constructing or validating the predictive model. Therefore, this project first focused on developing a mechanistic model of wildlife-vehicle collisions, which is an area that has received limited attention in the field of road ecology, and subsequently, efforts were made to obtain reliable data on wildlife-vehicle collisions through the improvement of an existing roadkill database.

2.1. Mechanistic approaches to WVC: what's around the bend?

The mechanistic model we presented can lead to several predictions for wildlife-vehicle collision (WVC) risks. Specifically, our model highlights the significance of animal movement and space use on WVC occurrences, which in turn helps identify animal behaviors, landscape configurations, and time windows that may correlate with higher road mortality in wildlife. In appendix C of the manuscript, we showed a strong association between the number of WVC reports in the Faune-AuRA database and the movement speed of male roe deer (*Capreolus capreolus*) obtained through GPS tracking, effectively validating one of the predictions made by the model. Our model is likely to produce three types of predictions: (i) certain species are more prone to being killed by vehicles due to specific behaviors they display (*e.g.*,

avian carrion-feeders that forage on roadkill are predicted to be at higher risks of collision compared to their terrestrial counterparts); and within a given population, (ii) there will be temporal variations in WVC occurrences that reflect changes in space-use and movement patterns, and (iii) there will be localized hotspots of collisions that reflect landscape configurations promoting animal mobility and contact with the road. While these broad categories of predictions may seem trivial when listed in that way, the strength of mechanistic modelling lies in providing precise predictions within each category.

However, testing these predictions will require either (i) comparing differences in WVC occurrences between species, (ii) analyzing temporal patterns in WVC, or (iii) investigating spatial patterns in WVC. As we previously mentioned, we have so far found little spatial and temporal structures in the correction parameters for the Faune-AuRA database, and suspect that a large part of the spatio-temporal biases are the result of the distributions of contributors, which are not currently integrated into the correction process. However, we have achieved reliable estimates for the overall number of collisions in the AuRA region for each species, and have applied this correction process in manuscripts n°2, 3 and 4 using small passerine species (< 20g), the red fox *Vulpes vulpes*, the common buzzard *Buteo buteo*, and the red squirrel *Sciurus vulgaris* as examples. In this context, we could consider correcting the Faune-AuRA database for select species to help validate or invalidate predictions of the mechanistic model. For instance, the diet of a species can provide insights into estimating the size of their home range, with carnivores occupying larger areas (Gittleman & Harvey, 1982). By comparing the collision rates across species with different diets, we could verify the model's prediction that species occupying larger home ranges may encounter higher risks of collisions. In fact, the link between diet and collision risks has been noted by other authors, although they found that carnivorous species were less often reported as killed by vehicles (Barthelmess, 2010; Cook & Blumstein, 2013; Ford & Fahrig, 2007), which means that, in this case, there is a discrepancy between the predictions of the model and empirical findings. This may result from some simplifying assumptions that we have made (such as the lack of avoidance behaviours from animals stepping on the road): failure to validate model predictions only leads to improving the accuracy of the model.

In general, the mechanistic model demonstrates that paradigms derived from movement ecology, such as the relations between home-range size and body mass (Makarieva et al., 2005), or diet (Gittleman & Harvey, 1982), the existence of territorial or mate-searching behaviours that may vary throughout the seasons (Potts & Lewis, 2014), the influence on animal trajectories of the distribution of resources (Pyke et al., 1977) and other characteristic of the landscape (*e.g.*, fire-prone habitats, Nimmo et al., 2019 and human-modified landscapes, Fahrig, 2007), as well as the role of cognition in the movements of animals (Fagan et al., 2013) should be at the forefront of future WVC research, both empirical and theoretical.

For example, a promising avenue for the study of collision risks is the movement ecology concept of *boundary responses*, which are responses of animals to encountering a boundary between the patch they are currently moving in, and the neighbouring patch (Fahrig, 2007). Boundary responses may result in animals remaining in the current patch and not crossing to the next. This response can be predicted by the species and type of habitat patch under consideration, with for example forested patches eliciting often stronger motivation in insects to stepping over the boundaries and access the neighbouring patches (Fahrig, 2007). The concept of boundary response echoes findings from empirical WVC studies, where the type of habitat predicted the risks of collisions: the probability of animals stepping on the road may vary according to the type of habitat that borders the road (Kreling et al., 2019; Malo et al., 2004; Pagany, 2020).

Perspectives for a more comprehensive mechanistic model of WVC

By definition, a model can never accurately represent the reality in all its complexity (Giere, 2004). In the case of the mechanistic model presented in chapter 1, we have approached the problem of wildlife-vehicle collisions through an agent-based model focusing on animal trajectories, which is reminiscent of the ideal gas model of molecule encounter rates (Hutchinson & Waser, 2007). However, if we have modelled both road encounter rate and collision rates, we have yet to address the second step of the wildlife-vehicle collision process as present in the conceptual model in the introduction of this manuscript (fig. 6). We described the collision probabilities for animals as resulting from three consecutive events: probability of encountering a road, probability of the animal making the decision to step on the road surface, and finally, probability of being hit while on the road. The mechanistic model has, so far, not addressed step 2: it has yet to include the behavioural reactions of an animal to encountering a road, save for a scenario of movement where we modelled a general avoidance of the road as a whole. In addition to the existing literature covering boundary responses in animal movement ecology, Jaeger et al. (2005) have presented a model for road-avoidance behaviours; noise avoidance, road surface avoidance, vehicle avoidance, all of which may prevent an animal from stepping onto the road surface.

The notable advantage of an agent-based simulatory approach to WVC modelling is that this type of model is both versatile and easily built-upon. For example, integrating decision-making processes into

the model to simulate road avoidance behaviours is relatively straightforward, such that the model may produce road mortality predictions for species whose cognitive abilities may help avoid collisions (Lima et al., 2015), or species that are easily deterred by the noise and disturbance produced by traffic (Forman et al., 2002). This type of extension of the model is a promising avenue for exploring the validity of the conceptual models, such as the model proposed by Seiler & Helldin (2006), where they postulate that high volumes of traffic are associated with reduced risks of collisions as animals do not attempt to cross these roads, a result that has been disputed by recent empirical studies (Grilo et al., 2015). In more concrete terms, implementing into the model a road avoidance parameter contingent upon the volume of traffic may help confirm the theoretical basis of this conceptual model, as well as identify which parameter values (both road traffic and strength of road avoidance) can lead to the expected results. In addition to animal behavioural reactions, the strength of this approach is that we may also build upon the behaviours of drivers: authors have suggested that some drivers may intentionally target select species when driving (Beckmann & Shine, 2012; Secco et al., 2014), but they may also swerve to intentionally avoid animals present on the road (de Resende Assis et al., 2022).

2.2. Advances toward statistical modelling of WVC

The advances we have made toward more robust roadkill datasets provided by opportunistic reporting have major implications for the future of predictive modelling in WVC. Indeed, this type of monitoring is a cost-efficient way of procuring large datasets that cover large spatial and temporal scales, but also a large diversity of species. Opportunistic monitoring may also be of particular interest for modelling rare events (Robinson et al., 2018), such as species that are rarely found in professional roadkill surveys, by allowing significant increases in the sampling effort. As previously discussed, although there are examples of the use of uncorrected datasets for statistical inference of roadkill risks (Červinka et al., 2015; dos Santos et al., 2017; Kreling et al., 2019), concerns regarding the robustness and accuracy of these datasets may have hampered their use in WVC modelling, even though roadkill datasets from citizen science projects are available in a number of different countries.

The level of precision in roadkill data correction for the Faune-AuRA database is currently insufficient for it to be a useful tool in checking mechanistic model predictions, or to be used in spatially or temporally explicit statistical models of roadkill risks. However, we have made significant advances in toward this goal, and believe that with continued effort, the challenges that remain can be overcome in the near future. Beyond wildlife-vehicle collisions, our work provides insights on the accuracy of

opportunistic datasets of species' presence, which we have found to paint a very partial picture of the reality in the case of road mortality. The methodologies we present should serve as a basis for extending correction processes of this type of data to other areas of ecology and conservation, thereby improving the accuracy of datasets that have tremendous potential for ecological research, but are currently not exploited to their full potential (Chandler et al., 2017). Additionally, the mechanistic model we presented is expected to mostly provide insights into the causal relations between animal movement and the probability of roadkill incidents, providing future orientations for empirical studies of collisions. Indeed, in ecology, there are often a wealth of potential predictors that can be explored for species distribution modelling, and in this case, roadkill distribution modelling, and challenges may reside in selecting the most promising predictors (Austin, 2002). In addition, we showed that many causal relations may not be linear, which should help construct better statistical model for describing roadkill data, as linear correlation are usually the default choice for many authors (Guinard et al., 2012).

3. General conclusions

We have addressed in this manuscript the issue of predictive modelling in wildlife-vehicle collisions through two complementary approaches: theoretical, or mechanistic modelling; and empirical, or statistical modelling. Although the current advancement of the correction process of the opportunistic roadkill dataset we have focused on is not sufficient to allow us to construct a statistical model of collision risks in the Auvergne-Rhône-Alpes region, we have made significant progress toward future application of statistical modelling techniques to opportunistic datasets, but also toward the exploitation of these datasets for hypothesis testing and model validation. In parallel, the mechanistic model of WVC we have presented yields predictions that are valuable to the issue of road mortality. This model allowed us to emphasize the importance of animal trajectories and therefore movement ecology in WVC research, and has for example helped predict that mitigation measures based on preventing animals from coming into contact with a road (crossing structures, fencing…) are more efficient than reducing the volume or speed of traffic.

Approaching more accurate estimates of the wildlife-vehicle collisions, especially at the scale of a region of about 70 000km², helps situate this source of mortality within the context of global change as one of the drivers of the current biodiversity decline. These estimates, and improvements in the accuracy of a dataset as extensive as Faune-AuRA, are helpful tools for future studies focusing on the demography of

wild populations (Moore et al., 2023), or the evolutionary pressures generated by the presence of roads in a landscape (Brady & Richardson, 2017). Wildlife mortality estimates may also lead to renewed efforts in implementing mitigation measures, and to new perspectives for the identification of endangered species. Beyond the issue of wildlife-vehicle collisions, mechanistic modelling is a promising tool for conservationists (Finke et al., 2008; Mokany & Ferrier, 2011; Thompson et al., 2021), which helps predict future response of populations to global change. Opportunistic monitoring on the other hand is becoming increasingly popular, especially for informing species distributions (Chandler et al., 2017). By examining the reporting process of one of these monitoring schemes, we promote their use for producing scientific knowledge, but we also contribute to make these projects more popular with the general public by demonstrating the usefulness work produced by volunteer contributors. Citizen sciences are also often recognized as valuable education tools for the public (Kelemen-Finan et al., 2018), which may be especially valuable in the light of the current biodiversity crisis.

Thank you for making it to the end of this manuscript.

Unless otherwise stated, all photographs credits belong to the author.

Chapters illustrations were generated using generative AI tool *Midjourney* and digitally edited by the author.

REFERENCES – Introduction and General discussion

Abbate, C. (2019). Save the Meat for Cats: Why It's Wrong to Eat Roadkill. *Journal of Agricultural and Environmental Ethics*, 32(1), 165–182. https://doi.org/10.1007/s10806-019-09763-6

Aguilar, R., Cristóbal-Pérez, E. J., Balvino-Olvera, F. J., de Jesús Aguilar-Aguilar, M., Aguirre-Acosta, N., Ashworth, L., Lobo, J. A., Martén-Rodríguez, S., Fuchs, E. J., Sanchez-Montoya, G., Bernardello, G., & Quesada, M. (2019). Habitat fragmentation reduces plant progeny quality : A global synthesis. *Ecology Letters*, 22(7), 1163-1173. https://doi.org/10.1111/ele.13272

Albert, C., Luque, G. M., & Courchamp, F. (2018). The twenty most charismatic species. *PLoS ONE*, 13(7), e0199149. https://doi.org/10.1371/journal.pone.0199149

Al-Zahrani, M. S., Ragab, K., & Haque, A. U. (2011). Design of GPS-based system to avoid camel-Vehicle collisions : A review. *Asian Journal of Applied Sciences*, 4(4), 362-377. https://doi.org/10.3923/ajaps.2011.362.377

Ansong, M., & Pickering, C. (2013). Are Weeds Hitchhiking a Ride on Your Car? A Systematic Review of Seed Dispersal on Cars. *PLoS ONE*, 8(11), e80275. https://doi.org/10.1371/journal.pone.0080275

Antworth, R. L., Pike, D. A., & Stevens, E. E. (2005). Hit and run : Effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist*, 4(4), 647-656. https://doi.org/10.1656/1528-7092(2005)004[0647:HAREOS]2.0.CO;2

Asari, Y. (2022). Decreased traffic volume during COVID-19 did not reduce roadkill on fenced highway network in Japan. *Landscape and Ecological Engineering*, 18(1), 121-124. https://doi.org/10.1007/s11355-021-00487-2

Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P., & Jackson, N. (2013). Wildlife–vehicle collision mitigation : Is partial fencing the answer? An agent-based model approach. *Ecological Modelling*, 257, 36-43. https://doi.org/10.1016/j.ecolmodel.2013.02.026

Ascensão, F., Ribeiro, Y. G. G., Campos, Z., Yogui, D. R., & Desbiez, A. L. J. (2022). Forecasting seasonal peaks in roadkill patterns for improving road management. *Journal of Environmental Management*, 321, 115903. https://doi.org/10.1016/j.jenvman.2022.115903

Austin, M. P. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecological Modelling*, *157*(2), 101–118. https://doi.org/10.1016/S0304-3800(02)00205-3

Baguley, T. (2004). Understanding statistical power in the context of applied research. *Applied Ergonomics*, 35(2), 73-80. https://doi.org/10.1016/j.apergo.2004.01.002

Baker, P. J., Dowding, C. V., Molony, S. E., White, P. C. L., & Harris, S. (2007). Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behavioral Ecology*, 18(4), 716-724. https://doi.org/10.1093/beheco/arm035

Balčiauskas, L. (2012). The Influence of Roadkill on Protected Species and Other Wildlife in Lithuania. *2011 International Conference on Ecology and Transportation (ICOET 2011)*

Balčiauskas, L., & Jasiulionis, M. (2012). Reducing the Incidence of Mammals on Public Highways Using Chemical Repellent. *The Baltic Journal of Road and Bridge Engineering*, 7(2), Art. 2. https://doi.org/10.3846/bjrbe.2012.13

Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C., & Pereira, H. M. (2021). The lost road : Do transportation networks imperil wildlife population persistence? *Perspectives in Ecology and Conservation*, 19(4), 411-416. https://doi.org/10.1016/j.pecon.2021.07.004

Barrientos, R., & Bolonio, L. (2009). The presence of rabbits adjacent to roads increases polecat road mortality. *Biodiversity and Conservation*, 18(2), 405-418. https://doi.org/10.1007/s10531-008-9499-9

Barrientos, R., Martins, R. C., Ascensão, F., D'Amico, M., Moreira, F., & Borda-de-Água, L. (2018). A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies. *Biological Conservation*, 222(November 2017), 146-153. https://doi.org/10.1016/j.biocon.2018.04.014

Barthelmess, E. (2010). The influence of body-size and diet on road-kill trends in mammals. *Biodiversity and Conservation.* https://doi.org/10.1007/s10531-010-9791-3

Bashore, T. L., Tzilkowski, W. M., & Bellis, E. D. (1985). Analysis of Deer-Vehicle Collision Sites in Pennsylvania. *The Journal of Wildlife Management*, 49(3), 769-774. https://doi.org/10.2307/3801709

Batty, M., & Torrens, P. M. (2001). Modelling complexity : The limits to prediction. *Cybergeo: European Journal of Geography.* https://doi.org/10.4000/cybergeo.1035

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-Winter Survival and Nest Site Selection of the West-European Hedgehog (*Erinaceus europaeus*) in Arable Dominated Landscapes. *Animals*, 10(9), Art. 9. https://doi.org/10.3390/ani10091449

Beckmann, C., & Shine, R. (2012). Do drivers intentionally target wildlife on roads? *Austral Ecology*, 37(5), 629-632. https://doi.org/10.1111/j.1442-9993.2011.02329.x

Bencin, H. L., Prange, S., Rose, C., & Popescu, V. D. (2019). Roadkill and space use data predict vehicle-strike hotspots and mortality rates in a recovering bobcat (*Lynx rufus*) population. *Scientific Reports*, 9(1), Art. 1. https://doi.org/10.1038/s41598-019-50931-5

Benten, A., Hothorn, T., Vor, T., & Ammer, C. (2018). Wildlife warning reflectors do not mitigate wildlife–vehicle collisions on roads. *Accident Analysis & Prevention*, 120, 64-73. https://doi.org/10.1016/j.aap.2018.08.003

Bíl, M., Heigl, F., Janoška, Z., Vercayie, D., & Perkins, S. E. (2020). Benefits and challenges of collaborating with volunteers : Examples from National Wildlife Roadkill Reporting Systems in Europe. *Journal for Nature Conservation*, 54 (December 2019), 125798. https://doi.org/10.1016/j.jnc.2020.125798

Bíl, M., Kušta, T., Andrášik, R., Cícha, V., Brodská, H., Ježek, M., & Keken, Z. (2020). No clear effect of odour repellents on roe deer behaviour in the vicinity of roads. *Wildlife Biology*, 2020(4), wlb.00744. https://doi.org/10.2981/wlb.00744

Bird, T. J., Bates, A. E., Lefcheck, J. S., Hill, N. A., Thomson, R. J., Edgar, G. J., Stuart-Smith, R. D., Wotherspoon, S., Krkosek, M., Stuart-Smith, J. F., Pecl, G. T., Barrett, N., & Frusher, S. (2014). Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation*, 173, 144-154. https://doi.org/10.1016/j.biocon.2013.07.037

Boarman, W. I., & Sazaki, M. (2006). A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). *Journal of Arid Environment*s, 65(1), 94-101. https://doi.org/10.1016/j.jaridenv.2005.06.020

Bonney, R., Cooper, C. B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V., & Shirk, J. (2009). Citizen Science : A Developing Tool for Expanding Science Knowledge and Scientific Literacy. *BioScience*, 59(11), 977-984. https://doi.org/10.1525/bio.2009.59.11.9

Bonter, D. N., & Cooper, C. B. (2012). Data validation in citizen science : A case study from Project FeederWatch. *Frontiers in Ecology and the Environment*, 10(6), 305-307. https://doi.org/10.1890/110273

Box, G. E. P. (1979). Robustness in the Strategy of Scientific Model Building. In R. L. Launer & G. N. Wilkinson (Éds.), *Robustness in Statistics* (p. 201-236). Academic Press. https://doi.org/10.1016/B978-0-12-438150-6.50018-2

Brady, S. P., & Richardson, J. L. (2017). Road ecology : Shifting gears toward evolutionary perspectives. *Frontiers in Ecology and the Environment*, 15(2), 91-98. https://doi.org/10.1002/fee.1458

Breiman, L. (1963). The Poisson Tendency in Traffic Distribution. *The Annals of Mathematical Statistics*, 34(1), 308-311. https://doi.org/10.1214/aoms/1177704267

Brieger, F., Kämmerle, J.-L., Hagen, R., & Suchant, R. (2022). Behavioural reactions to oncoming vehicles as a crucial aspect of wildlife-vehicle collision risk in three common wildlife species. *Accident Analysis & Prevention*, 168, 106564. https://doi.org/10.1016/j.aap.2021.106564

Bright, P. W., Balmforth, Z., & Macpherson, J. L. (2015). The effect of changes in traffic flow on mammal road kill counts. *Applied Ecology and Environmental Research*, 13(1), 171-179. https://doi.org/10.15666/aeer/1301_171179

Brown, C. R., & Bomberger Brown, M. (2013). Where has all the road kill gone? *Current Biology*, 23(6), R233-R234. https://doi.org/10.1016/j.cub.2013.02.023

Brown, G. P., Phillips, B. L., Webb, J. K., & Shine, R. (2006). Toad on the road : Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation*, 133(1), 88-94. https://doi.org/10.1016/j.biocon.2006.05.020

Brzeziński, M., Eliava, G., & Żmihorski, M. (2012). Road mortality of pond-breeding amphibians during spring migrations in the Mazurian Lakeland, NE Poland. *European Journal of Wildlife Research*, 58(4), 685-693. https://doi.org/10.1007/s10344-012-0618-2

Burgstahler, K., Isidro, J., Van Vuren, D. H., Collins, A. C., Aliperti, J. R., & Wells, C. P. (2023). Daily roadkill monitoring and long-term population census reveal female-biased mortality for a small mammal along a wildland-urban interface. *Biological Conservation*, 277, 109863. https://doi.org/10.1016/j.biocon.2022.109863

Callaghan, C. T., Poore, A. G. B., Hofmann, M., Roberts, C. J., & Pereira, H. M. (2021). Large-bodied birds are over-represented in unstructured citizen science data. *Scientific Reports*, 11(1), Art. 1. https://doi.org/10.1038/s41598-021-98584-7

Canova, L., & Balestrieri, A. (2019). Long-term monitoring by roadkill counts of mammal populations living in intensively cultivated landscapes. *Biodiversity and Conservation*, 28(1), 97-113. https://doi.org/10.1007/s10531-018-1638-3

Carr, L. W., Fahrig, L., & Pope, S. E. (2002). Impacts of Landscape Transformation by Roads. In K. J. Gutzwiller (Éd.), *Applying Landscape Ecology in Biological Conservation* (p. 225-243). Springer. https://doi.org/10.1007/978-1-4613-0059-5_13

Cassimiro, I. M. F., Ribeiro, M. C., & Assis, J. C. (2023). How did the animal come to cross the road? Drawing insights on animal movement from existing roadkill data and expert knowledge. *Landscape Ecology*, 38(8), 2035-2051. https://doi.org/10.1007/s10980-023-01671-5

Červinka, J., Riegert, J., Grill, S., & Šálek, M. (2015). Large-scale evaluation of carnivore road mortality : The effect of landscape and local scale characteristics. *Mammal Research*, 60(3), 233-243. https://doi.org/10.1007/s13364-015-0226-0

Chandler, M., See, L., Copas, K., Bonde, A. M. Z., López, B. C., Danielsen, F., Legind, J. K., Masinde, S., Miller-Rushing, A. J., Newman, G., Rosemartin, A., & Turak, E. (2017). Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, 213, 280-294. https://doi.org/10.1016/j.biocon.2016.09.004

Chyn, K., Lin, T.-E., Wilkinson, D. P., Tracy, J. L., Lawing, A. M., & Fitzgerald, L. A. (2021). Fine-scale roadkill risk models : Understanding the intersection of wildlife and roads. *Biodiversity and Conservation*, 30(1), 139-164. https://doi.org/10.1007/s10531-020-02083-6

Clarke, G. P., White, P. C. L., & Harris, S. (1998). Effects of roads on badger *Meles meles* populations in south-west England. *Biological Conservation*, 86(2), 117-124. https://doi.org/10.1016/S0006-3207(98)00018-4

Coleman, J. L., Ford, N. B., & Herriman, K. (2008). A Road Survey of Amphibians and Reptiles in a Bottomland Hardwood Forest. *Southeastern Naturalist*, 7(2), 339-348. https://doi.org/10.1656/1528-7092(2008)7[339:ARSOAA]2.0.CO;2

Colino-Rabanal, V. J., Langen, T. A., Peris, S. J., & Lizana, M. (2018). Ungulate : Vehicle collision rates are associated with the phase of the moon. *Biodiversity and Conservation*, 27(3), 681-694. https://doi.org/10.1007/s10531-017-1458-x

Collinson, W. J., Marneweck, C., & Davies-Mostert, H. T. (2019). Protecting the protected : Reducing wildlife roadkill in protected areas. *Animal Conservation*, 22(4), 396-403. https://doi.org/10.1111/acv.12481

Collinson, W. J., Parker, D. M., Bernard, R. T. F., Reilly, B. K., & Davies-Mostert, H. T. (2014). Wildlife road traffic accidents : A standardized protocol for counting flattened fauna. *Ecology and Evolution*, 4(15), 3060-3071. https://doi.org/10.1002/ece3.1097

Cook, T. C., & Blumstein, D. T. (2013). The omnivore's dilemma : Diet explains variation in vulnerability to vehicle collision mortality. *Biological Conservation*, 167, 310-315. https://doi.org/10.1016/j.biocon.2013.08.016

Coulson, G., Bender, H., Coulson, G., & Bender, H. (2019). Roadkill mitigation is paved with good intentions : A critique of Fox et al. (2019). *Australian Mammalogy*, 42(1), 122-130. https://doi.org/10.1071/AM19009

Couvet, D. (2002). Deleterious Effects of Restricted Gene Flow in Fragmented Populations. *Conservation Biology*, 16(2), 369-376. https://doi.org/10.1046/j.1523-1739.2002.99518.x

Couvet, D., Jiguet, F., Julliard, R., Levrel, H., & Teyssedre, A. (2008). Enhancing citizen contributions to biodiversity science and public policy. *Interdisciplinary Science Reviews*, 33(1), 95-103. https://doi.org/10.1179/030801808X260031

Cretois, B., Simmonds, E. G., Linnell, J. D. C., van Moorter, B., Rolandsen, C. M., Solberg, E. J., Strand, O., Gundersen, V., Roer, O., & Rød, J. K. (2021). Identifying and correcting spatial bias in opportunistic citizen science data for wild ungulates in Norway. *Ecology and Evolution*, 11(21), 15191-15204. https://doi.org/10.1002/ece3.8200

Crino, O. L., Johnson, E. E., Blickley, J. L., Patricelli, G. L., & Breuner, C. W. (2013). Effects of experimentally elevated traffic noise on nestling white-crowned sparrow stress physiology, immune function and life history. *Journal of Experimental Biology*, 216(11), 2055-2062. https://doi.org/10.1242/jeb.081109

Cukor, J., Havránek, F., Linda, R., Bukovjan, K., Painter, M. S., & Hart, V. (2018). First findings of brown hare (*Lepus europaeus*) reintroduction in relation to seasonal impact. *PLoS ONE*, 13(10), e0205078. https://doi.org/10.1371/journal.pone.0205078

D'Amico, M., Román, J., de los Reyes, L., & Revilla, E. (2015). Vertebrate road-kill patterns in Mediterranean habitats : Who, when and where. *Biological Conservation*, 191, 234-242. https://doi.org/10.1016/j.biocon.2015.06.010

de Groot, M., Ogris, N., van der Meij, M., & Pocock, M. J. O. (2022). Where to search : The use of opportunistic data for the detection of an invasive forest pest. *Biological Invasions*, 24(11), 3523-3537. https://doi.org/10.1007/s10530-022-02857-9

Deguines, N., Julliard, R., Flores, M. de, & Fontaine, C. (2012). The Whereabouts of Flower Visitors : Contrasting Land-Use Preferences Revealed by a Country-Wide Survey Based on Citizen Science. *PLoS ONE*, 7(9), e45822. https://doi.org/10.1371/journal.pone.0045822

Deletic, A., & Orr, D. W. (2005). Pollution Buildup on Road Surfaces. *Journal of Environmental Engineering*, 131(1), 49-59. https://doi.org/10.1061/(ASCE)0733-9372(2005)131:1(49)

Denneboom, D., Bar-Massada, A., & Shwartz, A. (2021). Factors affecting usage of crossing structures by wildlife – A systematic review and meta-analysis. *Science of The Total Environment*, 777, 146061. https://doi.org/10.1016/j.scitotenv.2021.146061

Dennis, R. L. H., & Thomas, C. D. (2000). Bias in butterfly distribution maps : The influence of hot spots and recorder's home range. *Journal of Insect Conservation,* 4(2), 73-77. https://doi.org/10.1023/A:1009690919835

Denny, M., & Benedetti-Cecchi, L. (2012). Scaling Up in Ecology : Mechanistic Approaches. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 1-22. https://doi.org/10.1146/annurev-ecolsys-102710-145103

de Resende Assis, J., Carvalho-Roel, C. F., Iannini-Custódio, A. E., Pereira, W. G., & Veloso, A. C. (2022). Snakes roadkill on highways in the Cerrado biome : An intentional conduct? *Studies on Neotropical Fauna and Environment,* 57(3), 198-205. https://doi.org/10.1080/01650521.2020.1844942

DeVault, T. L., Blackwell, B. F., Seamans, T. W., Lima, S. L., & Fernández-Juricic, E. (2014). Effects of Vehicle Speed on Flight Initiation by Turkey Vultures : Implications for Bird-Vehicle Collisions. *PLoS ONE,* 9(2), e87944. https://doi.org/10.1371/journal.pone.0087944

DeVivo, M. T., Cottrell, W. O., DeBerti, J. M., Duchamp, J. E., Heffernan, L. M., Kougher, J. D., & Larkin, J. L. (2011). Survival and cause-specific mortality of elk *Cervus canadensis* calves in a predator rich environment. *Wildlife Biology,* 17(2), 156-165. https://doi.org/10.2981/10-080

Dickinson, J. (2011, february 20). Citizen Science at the Cornell Lab of Ornithology. *American Association for the Advancement of Science 2011 Annual Meeting.*

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen Science as an Ecological Research Tool : Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics,* 41(1), 149-172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Donnelly, A., Crowe, O., Regan, E., Begley, S., & Caffarra, A. (2014). The role of citizen science in monitoring biodiversity in Ireland. *International Journal of Biometeorology*, 58(6), 1237-1249. https://doi.org/10.1007/s00484-013-0717-0

dos Santos, S. R., Davis Jr., C. A., & Smarzaro, R. (2017). Analyzing Traffic Accidents based on the Integration of Official and Crowdsourced Data. *Journal of Information and Data Management,* 8(1), 67-82.

Downs, J. A., & Horner, M. W. (2012). Enhancing Habitat Connectivity in Fragmented Landscapes : Spatial Modeling of Wildlife Crossing Structures in Transportation Networks. *Annals of the Association of American Geographers,* 102(1), 17-34. https://doi.org/10.1080/00045608.2011.600190

Driessen, M. M. (2021). COVID-19 restrictions provide a brief respite from the wildlife roadkill toll. *Biological Conservation,* 256, 109012. https://doi.org/10.1016/j.biocon.2021.109012

Dugan, H. A., & Arnott, S. E. (2023). The ecosystem implications of road salt as a pollutant of freshwaters. *WIREs Water,* 10(2), e1629. https://doi.org/10.1002/wat2.1629

EEA greenhouse gases — data viewer. (2023, May 08). Retrieved from https://www.eea.europa.eu/data-and-maps/data/data-viewers/greenhouse-gases-viewer

Eigenbrod, F., Hecnar, S., & Fahrig, L. (2009). Quantifying the Road-Effect Zone : Threshold Effects of a Motorway on Anuran Populations in Ontario, Canada. *Ecology and Society*, 14(1). https://doi.org/10.5751/ES-02691-140124

Elliott, K. C., & Rosenberg, J. (2019). Philosophical foundations for citizen science. *Citizen Science: Theory and Practice*, *4*(1).

Ellis, M. M. (1936). Erosion Silt as a Factor in Aquatic Environments. *Ecology*, 17(1), 29-42. https://doi.org/10.2307/1932951

Fagan, W. F., & Calabrese, J. M. (2014). The Correlated Random Walk and the Rise of Movement Ecology. *Bulletin of the Ecological Society of America*, 95(3), 204-206.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, 16(10), 1316-1329. https://doi.org/10.1111/ele.12165

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, 21(6), 1003-1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Farmer, R. G., & Brooks, R. J. (2012). Integrated risk factors for vertebrate roadkill in southern Ontario : Vertebrate Roadkill Risk Factors. *The Journal of Wildlife Management*, 76(6), 1215-1224. https://doi.org/10.1002/jwmg.358

Fey, K., Hämäläinen, S., & Selonen, V. (2016). Roads are no barrier for dispersing red squirrels in an urban environment. *Behavioral Ecology*, 27(3), 741-747. https://doi.org/10.1093/beheco/arv215

Finke, J., Strein, M., & Sonnenschein, M. (2008). A simulation framework for modeling anthropogenic disturbances in habitat networks. *Ecological Informatics*, 3(1), 26-34. https://doi.org/10.1016/j.ecoinf.2007.04.006

Ford, A. T., & Fahrig, L. (2007). Diet and body size of North American mammal road mortalities. *Transportation Research Part D: Transport and Environment*, *1*2(7), 498-505. https://doi.org/10.1016/j.trd.2007.07.002

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29(1998), 207-231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Forman, R. T. T., Reineking, B., & Hersperger, A. M. (2002). Road traffic and nearby grassland bird patterns in a suburbanizing landscape. *Environmental Management*, 29(6), 782-800. https://doi.org/10.1007/s00267-001-0065-4

Freedman, D. A. (2009). *Statistical Models : Theory and Practice*. Cambridge University Press.

Fu, B., Newham, L. T. H., & Ramos-Scharrón, C. E. (2010). A review of surface erosion and sediment delivery models for unsealed roads. *Environmental Modelling & Software*, 25(1), 1-14. https://doi.org/10.1016/j.envsoft.2009.07.013

Garcia-Gonzalez, C., Campo, D., Pola, I. G., & Garcia-Vazquez, E. (2012). Rural road networks as barriers to gene flow for amphibians : Species-dependent mitigation by traffic calming. *Landscape and Urban Planning*, 104(2), 171-180. https://doi.org/10.1016/j.landurbplan.2011.10.012

Geldmann, J., Heilmann-Clausen, J., Holm, T. E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C., & Tøttrup, A. P. (2016). What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions*, 22(11), 1139-1149. https://doi.org/10.1111/ddi.12477

George, L., Macpherson, J. L., Balmforth, Z., & Bright, P. W. (2011). Using the dead to monitor the living : Can road kill counts detect trends in mammal abundance? *Applied Ecology and Environmental Research*, 9(1), 27-41.

Gerow, K., Kline, N., Swann, D., & Pokorny, M. (2010). Estimating annual vertebrate mortality on roads at Saguaro National Park, Arizona. *Human-Wildlife Interactions*, 4(2), 283-292.

Giere, R. N. (2004). How Models Are Used to Represent Reality. *Philosophy of Science*, 71(5), 742-752. https://doi.org/10.1086/425063

Gippet, J., Rocabert, C., Fenet, S., Dumet, A., & Kaufmann, B. (2015). Modeling and evaluating human-mediated dispersal mechanisms at landscape scale : A study of road network and invasion parameters for Lasius neglectus ants invasive species. *World Conference on Natural Resource Modeling, Bordeaux, France.*

Girardet, X., Conruyt-Rogeon, G., & Foltête, J.-C. (2015). Does regional landscape connectivity influence the location of roe deer roadkill hotspots? *European Journal of Wildlife Research*, 61(5), 731-742. https://doi.org/10.1007/s10344-015-0950-4

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1), 57-63. https://doi.org/10.1007/BF00296396

Gladfelter, L. (1984). *Effect of wildlife highway warning reflectors on deer-vehicle accidents. (HR-210). Iowa. Highway Division.* https://rosap.ntl.bts.gov/view/dot/23945

Glista, D. J. (2008). Vertebrate Road Mortality Predominantly Impacts Amphibians. *Herpetological Conservation and Biology.*

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning*, 91(1), 1-7. https://doi.org/10.1016/j.landurbplan.2008.11.001

González-Suárez, M., Ferreira, F. Z., & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, 27(9), Art. 9. https://doi.org/10.1111/geb.12769

Grilo, C., Ascensão, F., Santos-Reis, M., & Bissonette, J. A. (2011). Do well-connected landscapes promote road-related mortality? *European Journal of Wildlife Research*, 57(4), 707-716. https://doi.org/10.1007/s10344-010-0478-6

Grilo, C., Bissonette, J. A., & Cramer, P. C. (2010). Mitigation measures to reduce impacts on biodiversity. In *Highways: Construction, Management, and Maintenance*.

Grilo, C., Borda-de-Água, L., Beja, P., Goolsby, E., Soanes, K., le Roux, A., Koroleva, E., Ferreira, F. Z., Gagné, S. A., Wang, Y., & González-Suárez, M. (2021). Conservation threats from roadkill in the global road network. *Global Ecology and Biogeography*, 30(11), 2200-2210. https://doi.org/10.1111/geb.13375

Grilo, C., Ferreira, F. Z., & Revilla, E. (2015). No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatio-temporal scale. *Environmental Impact Assessment Review*, 55, 54-58. https://doi.org/10.1016/j.eiar.2015.07.003

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, 18(6), 323-328. https://doi.org/10.1002/fee.2216

Grosman, P. D., Jaeger, J. A. G., Biron, P. M., Dussault, C., & Ouellet, J. P. (2009). Reducing moose-vehicle collisions through salt pool removal and displacement : An agent-based modeling approach. *Ecology and Society*, 14(2). https://doi.org/10.5751/es-02941-140217

Guinard, E., Billon, L., Bretaud, J.-F., Chevallier, L., Sordello, R., & Witté, I. (2023). Comparing the effectiveness of two roadkill survey methods on roads. *Transportation Research Part D: Transport and Environment*, 121, 103829. https://doi.org/10.1016/j.trd.2023.103829

Guinard, E., Julliard, R., & Barbraud, C. (2012). Motorways and bird traffic casualties : Carcasses surveys and scavenging bias. *Biological Conservation*, 147(1), 40-51. https://doi.org/10.1016/j.biocon.2012.01.019

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models : A review of current work and its application to transportation mitigation projects. *Journal of Environmental Management*, 92(4), 1074-1082. https://doi.org/10.1016/j.jenvman.2010.11.027

Gupta, S., Chand, D., & Kavati, I. (2021). Computer Vision based Animal Collision Avoidance Framework for Autonomous Vehicles. In S. K. Singh, P. Roy, B. Raman, & P. Nagabhushan (Éds.), *Computer Vision and Image Processing* (p. 237-248). Springer.

Gurrutxaga, M., Lozano, P. J., & Del Barrio, G. (2010). Assessing Highway Permeability for the Restoration of Landscape Connectivity between Protected Areas in the Basque Country, Northern Spain. *Landscape Research*, 35(5), 529-550. https://doi.org/10.1080/01426397.2010.504915

Hall, M. J., Martin, J. M., Burns, A. L., & Hochuli, D. F. (2021). Ecological insights into a charismatic bird using different citizen science approaches. *Austral Ecology*, 46(8), 1255-1265. https://doi.org/10.1111/aec.13062

Helldin, J. O. (2022). Are several small wildlife crossing structures better than a single large? Arguments from the perspective of large wildlife conservation. *Nature Conservation*, 47, 197-213. https://doi.org/10.3897/natureconservation.47.67979

Helldin, J. O., & Petrovan, S. O. (2019). Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. *PeerJ*, 7, e7518. https://doi.org/10.7717/peerj.7518

Hels, T., & Buchwald, E. (2001). The effect of road kills on amphibian populations. *Biological Conservation*, 99(3), 331-340. https://doi.org/10.1016/S0006-3207(00)00215-9

Henckel, L., Bradter, U., Jönsson, M., Isaac, N. J. B., & Snäll, T. (2020). Assessing the usefulness of citizen science data for habitat suitability modelling : Opportunistic reporting versus sampling based on a systematic protocol. *Diversity and Distributions*, 26(10), 1276-1290. https://doi.org/10.1111/ddi.13128

Henry, D. A. W., Collinson-Jonker, W. J., Davies-Mostert, H. T., Nicholson, S. K., Roxburgh, L., & Parker, D. M. (2021). Optimising the cost of roadkill surveys based on an analysis of carcass persistence. *Journal of Environmental Management*, 291, 112664. https://doi.org/10.1016/j.jenvman.2021.112664

Hess, B., Farahani, A. Z., Tschirschnitz, F., & von Reischach, F. (2012). Evaluation of fine-granular GPS tracking on smartphones. *Proceedings of the First ACM SIGSPATIAL International Workshop on Mobile Geographic Information Systems*, 33-40. https://doi.org/10.1145/2442810.2442817

Heigl, F., Stretz, C. R., Steiner, W., Suppan, F., Bauer, T., Laaha, G., & Zaller, J. G. (2016). Comparing road-kill datasets from hunters and citizen scientists in a landscape context. *Remote Sensing*, *8*(10), 832.

Hill, J. E., DeVault, T. L., & Belant, J. L. (2019). Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography*, 28(5), 680-689. https://doi.org/10.1111/geb.12881

Hobday, A. J., & Minstrell, M. L. (2008). Distribution and abundance of roadkill on Tasmanian highways : Human management options. *Wildlife Research*, 35(7), 712-726. https://doi.org/10.1071/WR08067

Hoermann, C. von, Pagany, R., Kirchner, K., Dorner, W., Heurich, M., & Storch, I. (2020). Predicting the Risk of Deer-vehicle Collisions by Inferring Rules Learnt from Deer Experience and Movement Patterns in the Vicinity of Roads. *2020 10th International Conference on Advanced Computer Information Technologies (ACIT)*, 368-373. https://doi.org/10.1109/ACIT49673.2020.9208843

Horns, J. J., Adler, F. R., & Şekercioğlu, Ç. H. (2018). Using opportunistic citizen science data to estimate avian population trends. *Biological Conservation*, 221, 151-159. https://doi.org/10.1016/j.biocon.2018.02.027

Hsing, P.-Y., Bradley, S., Kent, V. T., Hill, R. A., Smith, G. C., Whittingham, M. J., Cokill, J., Crawley, D., Volunteers, M., & Stephens, P. A. (2018). Economical crowdsourcing for camera trap image classification. *Remote Sensing in Ecology and Conservation*, 4(4), 361-374. https://doi.org/10.1002/rse2.84

Hsu, C.-H., & Lin, T.-E. (2021). Exploring the participation motivations of ongoing and former citizen scientists in Taiwan Roadkill Observation Network. *Journal for Nature Conservation*, 64, 126055. https://doi.org/10.1016/j.jnc.2021.126055

Huijser, M. P., Fairbank, E. R., Camel-Means, W., Graham, J., Watson, V., Basting, P., & Becker, D. (2016). Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife–vehicle collisions and providing safe crossing opportunities for large mammals. *Biological Conservation*, 197, 61-68. https://doi.org/10.1016/j.biocon.2016.02.002

Hutchinson, J. M. C., & Waser, P. M. (2007). Use, misuse and extensions of « ideal gas » models of animal encounter. *Biological Reviews*, 82(3), 335-359. https://doi.org/10.1111/j.1469-185X.2007.00014.x

Inbar, M., Shanas, U., & Izhaki, I. (2002). Characterization of road accidents in israel involving large mammals. *Israel Journal of Ecology and Evolution*, 48(3), 197-206. https://doi.org/10.1560/XGJB-VR67-RFEQ-N27A

Isaac, N. J. B., Strien, A. J., August, T. A., Zeeuw, M. P., & Roy, D. B. (2014). Statistics for citizen science : Extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, 5(10), 1052-1060. https://doi.org/10.1111/2041-210X.12254

Jaarsma, C. F. (1997). Approaches for the planning of rural road networks according to sustainable land use planning. *Landscape and Urban Planning*, 39(1), 47-54. https://doi.org/10.1016/S0169-2046(97)00067-4

Jaarsma, C. F., van Langevelde, F., & Botma, H. (2006). Flattened fauna and mitigation : Traffic victims related to road, traffic, vehicle, and species characteristics. *Transportation Research Part D: Transport and Environment*, 11(4), 264-276. https://doi.org/10.1016/j.trd.2006.05.001

Jacobson, S. L., Bliss-Ketchum, L. L., De Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, 7(4), 1-15. https://doi.org/10.1002/ecs2.1345

Jaeger, J. A. G. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., & Von Toschanowitz, K. T. (2005). Predicting when animal populations are at risk from roads : An interactive model of road avoidance behavior. *Ecological Modelling*, 185(2-4), 329-348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

Johnston, A., Matechou, E., & Dennis, E. B. (2023). Outstanding challenges and future directions for biodiversity monitoring using citizen science data. *Methods in Ecology and Evolution, 1*4(1), 103-116. https://doi.org/10.1111/2041-210X.13834

Jones, D. N., Griffiths, M. R., Griffiths, J. R., Hacker, J. L. F., & Hacker, J. B. (2014). Implications of upgrading a minor forest road on traffic and road-kill in southeast Queensland. *Australasian Journal of Environmental Management*, 21(4), 429-440. https://doi.org/10.1080/14486563.2014.944590

Kang, W., Minor, E. S., Woo, D., Lee, D., & Park, C.-R. (2016). Forest mammal roadkills as related to habitat connectivity in protected areas. *Biodiversity and Conservation*, 25(13), 2673-2686. https://doi.org/10.1007/s10531-016-1194-7

Kelemen-Finan, J., Scheuch, M., & Winter, S. (2018). Contributions from citizen science to science education : An examination of a biodiversity citizen science project with schools in Central Europe.

International Journal of Science Education, 40(17), 2078-2098. https://doi.org/10.1080/09500693.2018.1520405

Keller, I., & Largiadèr, C. R. (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1513), 417-423. https://doi.org/10.1098/rspb.2002.2247

Klemann-Junior, L., Vallejos, M. A. V., Scherer-Neto, P., & Vitule, J. R. S. (2017). Traditional scientific data vs. uncoordinated citizen science effort : A review of the current status and comparison of data on avifauna in Southern Brazil. *PLoS ONE*, 12(12), e0188819. https://doi.org/10.1371/journal.pone.0188819

Knape, J., Coulson, S. J., van der Wal, R., & Arlt, D. (2022). Temporal trends in opportunistic citizen science reports across multiple taxa. *Ambio*, 51(1), 183-198. https://doi.org/10.1007/s13280-021-01550-w

Koch, W., Hogeweg, L., Nilsen, E. B., & Finstad, A. G. (2022). Maximizing citizen scientists' contribution to automated species recognition. *Scientific Reports*, 12(1), Art. 1. https://doi.org/10.1038/s41598-022-11257-x

Kreling, S. E. S., Gaynor, K. M., & Coon, C. A. C. (2019). Roadkill distribution at the wildland-urban interface. *Journal of Wildlife Management*, 83(6), 1427-1436. https://doi.org/10.1002/jwmg.21692

Kroeger, S. B., Hanslin, H. M., Lennartsson, T., D'Amico, M., Kollmann, J., Fischer, C., Albertsen, E., & Speed, J. D. M. (2022). Impacts of roads on bird species richness : A meta-analysis considering road types, habitats and feeding guilds. *Science of The Total Environmen*t, 812, 151478. https://doi.org/10.1016/j.scitotenv.2021.151478

Kuipers, K. J. J., May, R. F., Graae, B. J., & Verones, F. (2019). Reviewing the potential for including habitat fragmentation to improve life cycle impact assessments for land use impacts on biodiversity. *The International Journal of Life Cycle Assessment*, 24(12), 2206-2219. https://doi.org/10.1007/s11367-019-01647-1

Lafortezza, R., & Chen, J. (2016). The provision of ecosystem services in response to global change : Evidences and applications. *Environmental Research*, 147, 576-579. https://doi.org/10.1016/j.envres.2016.02.018

Larson, E. R., Graham, B. M., Achury, R., Coon, J. J., Daniels, M. K., Gambrell, D. K., Jonasen, K. L., King, G. D., LaRacuente, N., Perrin-Stowe, T. I., Reed, E. M., Rice, C. J., Ruzi, S. A., Thairu, M. W., Wilson, J. C., & Suarez, A. V. (2020). From eDNA to citizen science : Emerging tools for the early detection of invasive species. *Frontiers in Ecology and the Environment*, 18(4), 194-202. https://doi.org/10.1002/fee.2162

Legagneux, P., & Ducatez, S. (2013). European birds adjust their flight initiation distance to road speed limits. *Biology Letters*, 9(5), 20130417. https://doi.org/10.1098/rsbl.2013.0417

Lehrer, E. W., Schooley, R. L., & Whittington, J. K. (2012). Survival and antipredator behavior of woodchucks (*Marmota monax)* along an urban–agricultural gradient. *Canadian Journal of Zoology*, 90(1), 12-21. https://doi.org/10.1139/z11-107

Lesbarrères, D., & Fahrig, L. (2012). Measures to reduce population fragmentation by roads : What has worked and how do we know? *Trends in Ecology & Evolution*, 27(7), 374-380. https://doi.org/10.1016/j.tree.2012.01.015

Lesbarrères, D., Pagano, A., & Lodé, T. (2003). Inbreeding and road effect zone in a *Ranidae :* The case of Agile frog, *Rana dalmatina Bonaparte*, 1840. *Comptes Rendus Biologies*, 326, 68-72. https://doi.org/10.1016/S1631-0691(03)00040-4

Lima, S. L., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2015). Animal reactions to oncoming vehicles : A conceptual review. *Biological reviews of the Cambridge Philosophical Society,* 90(1), 60-76. https://doi.org/10.1111/brv.12093

Litvaitis, J. A., & Tash, J. P. (2008). An approach toward understanding wildlife-vehicle collisions. *Environmental Management*, 42(4), 688-697. https://doi.org/10.1007/s00267-008-9108-4

Loraamm, R. W., & Downs, J. A. (2016). A wildlife movement approach to optimally locate wildlife crossing structures. *International Journal of Geographical Information Science,* 30(1), 74-88. https://doi.org/10.1080/13658816.2015.1083995

Loss, S. R., Will, T., & Marra, P. P. (2014). Estimation of bird-vehicle collision mortality on U.S. roads. *The Journal of Wildlife Management,* 78(5), 763-771. https://doi.org/10.1002/jwmg.721

Louvrier, J., Papaïx, J., Duchamp, C., & Gimenez, O. (2020). A mechanistic–statistical species distribution model to explain and forecast wolf (*Canis lupus*) colonization in South-Eastern France. *Spatial Statistics,* 36, 100428. https://doi.org/10.1016/j.spasta.2020.100428

LPO France (2021). *Séminaire: Bases de données citoyennes et biodiversité LPO.* January 2021.

Lulka, D. (2008). The intimate hybridity of roadkill : A Beckettian view of dismay and persistence. *Emotion, Space and Society,* 1(1), 38-47. https://doi.org/10.1016/j.emospa.2008.08.008

Lunney, D. (2013). Wildlife roadkill: Illuminating and overcoming a blind spot in public perception. *Pacific Conservation Biology*, *19*(4), 233–249. https://doi.org/10.1071/pc130233

Mair, L., & Ruete, A. (2016). Explaining Spatial Variation in the Recording Effort of Citizen Science Data across Multiple Taxa. *PLoS ONE*, 11(1), e0147796. https://doi.org/10.1371/journal.pone.0147796

Makarieva, A. M., Gorshkov, V. G., & Li, B. L. (2005). Why do population density and inverse home range scale differently with body size? : Implications for ecosystem stability. *Ecological Complexity*, 2(3), 259-271. https://doi.org/10.1016/j.ecocom.2005.04.006

Malo, J. E., Suárez, F., & Díez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? *Journal of Applied Ecology*, 41(4), 701-710. https://doi.org/10.1111/j.0021-8901.2004.00929.x

Manneri, A. (2002). Traffic mortality of small- and medium-sized vertebrates in finland. *Tiehallinnon selvityksia, finnra reports*, 26/2002(TIEH 3200758). https://trid.trb.org/view/685666

Mata, C., Hervás, I., Herranz, J., Suárez, F., & Malo, J. E. (2008). Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. *Journal of Environmental Management*, 88(3), 407-415. https://doi.org/10.1016/j.jenvman.2007.03.014

McLane, A. J., Semeniuk, C., McDermid, G. J., & Marceau, D. J. (2011). The role of agent-based models in wildlife ecology and management. *Ecological Modelling*, 222(8), 1544-1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020

Meek, R. (2009). Patterns of reptile road-kills in the Vendée region of western France. *Herpetological Journal*, 19(3), 135-142.

Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, 13(6), 064006. https://doi.org/10.1088/1748-9326/aabd42

Mengersen, K., Peterson, E. E., Clifford, S., Ye, N., Kim, J., Bednarz, T., Brown, R., James, A., Vercelloni, J., Pearse, A. R., Davis, J., & Hunter, V. (2017). Modelling imperfect presence data obtained by citizen science. *Environmetrics*, 28(5), e2446. https://doi.org/10.1002/env.2446

Merry, K., & Bettinger, P. (2019). Smartphone GPS accuracy study in an urban environment. *PLoS ONE*, 14(7), e0219890. https://doi.org/10.1371/journal.pone.0219890

Mestre, F., Lopes, H., Pinto, T., Sousa, L. G., Mira, A., & Santos, S. M. (2019). Bad moon rising? The influence of the lunar cycle on amphibian roadkills. European Journal of Wildlife Research, 65(4), 58. https://doi.org/10.1007/s10344-019-1285-3

Milanesi, P., Mori, E., & Menchetti, M. (2020). Observer-oriented approach improves species distribution models from citizen science data. *Ecology and Evolution*, 10(21), 12104-12114. https://doi.org/10.1002/ece3.6832

Miller, M. J., & Loaiza, J. R. (2015). Geographic Expansion of the Invasive Mosquito Aedes albopictus across Panama—Implications for Control of Dengue and Chikungunya Viruses. *PLoS Neglected Tropical Diseases*, 9(1), e0003383. https://doi.org/10.1371/journal.pntd.0003383

Ministère de la transition écologique et de la cohésion des territoires (2022). *Se déplacer en voiture : seul, à plusieurs ou en covoiturage ?* ISSN 2557-8510 . https://www.ecologie.gouv.fr/sites/default/files/DE_4p_covoiturage-v4-050722_SH_OK.pdf

Mokany, K., & Ferrier, S. (2011). Predicting impacts of climate change on biodiversity : A role for semi-mechanistic community-level modelling. *Diversity and Distributions*, 17(2), 374-380. https://doi.org/10.1111/j.1472-4642.2010.00735.x

Moore, L. J., Petrovan, S. O., Baker, P. J., Bates, A. J., Hicks, H. L., Perkins, S. E., & Yarnell, R. W. (2020). Impacts and Potential Mitigation of Road Mortality for Hedgehogs in Europe. *Animals*, 10(9), Art. 9. https://doi.org/10.3390/ani10091523

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations : A systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12942

Mumme, R. L., Schoech, S. J., Woolfenden, G. E., & Fitzpatrick, J. W. (2000). Life and Death in the Fast Lane : Demographic Consequences of Road Mortality in the Florida Scrub-Jay. *Conservation Biology,* 14(2), 501-512. https://doi.org/10.1046/j.1523-1739.2000.98370.x

Murphy, A., & Xia, J. (Cecilia). (2016). Risk analysis of animal–vehicle crashes : A hierarchical Bayesian approach to spatial modelling. *International Journal of Crashworthiness*, 21(6), 614-626. https://doi.org/10.1080/13588265.2016.1209823

Nathan, R., Safriel, U. N., & Noy-Meir, I. (2001). Field Validation and Sensitivity Analysis of a Mechanistic Model for Tree Seed Dispersal by Wind. *Ecology*, 82(2), 374-388. https://doi.org/10.1890/0012-9658(2001)082[0374:FVASAO]2.0.CO;2

Newman, G., Chandler, M., Clyde, M., McGreavy, B., Haklay, M., Ballard, H., Gray, S., Scarpino, R., Hauptfeld, R., Mellor, D., & Gallo, J. (2017). Leveraging the power of place in citizen science for effective conservation decision making. *Biological Conservation*, 208, 55-64. https://doi.org/10.1016/j.biocon.2016.07.019

Newmark, W. D., Boshe, J. I., Sariko, H. I., & Makumbule, G. K. (1996). Effects of a highway on large mammals in Mikumi National Park, Tanzania. *African Journal of Ecology,* 34(1), 15-31. https://doi.org/10.1111/j.1365-2028.1996.tb00590.x

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., … Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews*, 94(3), 981-998. https://doi.org/10.1111/brv.12486

Nunes, L. J. R., Meireles, C. I. R., C.j, P. G., & N.m.c, A. R. (2020). Propagation Model of Invasive Species : Road Systems as Dispersion Facilitators. *Research in Ecology*, 2(1), Art. 1. https://doi.org/10.30564/re.v2i1.1054

Oliver, R. M. (1961). A Traffic Counting Distribution. *Operations Research*, 9(6), 802-810. https://doi.org/10.1287/opre.9.6.802

Olson, D. D., Bissonette, J. A., Cramer, P. C., Green, A. D., Davis, S. T., Jackson, P. J., & Coster, D. C. (2014). Monitoring Wildlife-Vehicle Collisions in the Information Age : How Smartphones Can Improve Data Collection. *PLoS ONE,* 9(6), e98613. https://doi.org/10.1371/journal.pone.0098613

Oxley, D. J., Fenton, M. B., & Carmody, G. R. (1974). The Effects of Roads on Populations of Small Mammals. *Journal of Applied Ecology*, 11(1), 51-59. https://doi.org/10.2307/2402004

Padmanaba, M., & Sheil, D. (2014). Spread of the Invasive Alien Species *Piper Aduncum* via Logging Roads in Borneo. *Tropical Conservation Science*, 7(1), 35-44. https://doi.org/10.1177/194008291400700108

Pagany, R. (2020). Wildlife-vehicle collisions—Influencing factors, data collection and research methods. *Biological Conservation*, 251(August), 108758. https://doi.org/10.1016/j.biocon.2020.108758

Paul, K., Quinn, M. S., Huijser, M. P., Graham, J., & Broberg, L. (2014). An evaluation of a citizen science data collection program for recording wildlife observations along a highway. *Journal of Environmental Management*, 139, 180-187. https://doi.org/10.1016/j.jenvman.2014.02.018

Pellissier, V., Schmucki, R., Pe'er, G., Aunins, A., Brereton, T. M., Brotons, L., Carnicer, J., Chodkiewicz, T., Chylarecki, P., del Moral, J. C., Escandell, V., Evans, D., Foppen, R., Harpke, A., Heliölä, J., Herrando, S., Kuussaari, M., Kühn, E., Lehikoinen, A., … Julliard, R. (2020). Effects of Natura 2000 on nontarget bird and butterfly species based on citizen science data. *Conservation Biology*, 34(3), 666-676. https://doi.org/10.1111/cobi.13434

Périquet, S., Roxburgh, L., le Roux, A., & Collinson, W. J. (2018). Testing the value of citizen science for roadkill studies : A case study from South Africa. *Frontiers in Ecology and Evolution*, 6(FEB), 1-9. https://doi.org/10.3389/fevo.2018.00015

Peters, R. H., & Wassenberg, K. (1983). The effect of body size on animal abundance. *Oecologia*, 60(1), 89-96. https://doi.org/10.1007/BF00379325

Peterson, A. T., Papeş, M., & Soberón, J. (2015). Mechanistic and Correlative Models of Ecological Niches. *European Journal of Ecology*, 1(2), 28-38. https://doi.org/10.1515/eje-2015-0014

Petrovan, S. O., Vale, C. G., & Sillero, N. (2020). Using citizen science in road surveys for large-scale amphibian monitoring : Are biased data representative for species distribution? *Biodiversity and Conservation*, 29(6), 1767-1781. https://doi.org/10.1007/s10531-020-01956-0

Plante, J., Jaeger, J. A. G., & Desrochers, A. (2019). How do landscape context and fences influence roadkill locations of small and medium-sized mammals? *Journal of Environmental Management*, 235, 511-520. https://doi.org/10.1016/j.jenvman.2018.10.093

Pojar, T. M., Prosence, R. A., Reed, D. F., & Woodard, T. N. (1975). Effectiveness of a Lighted, Animated Deer Crossing Sign. *The Journal of Wildlife Management*, 39(1), 87-91. https://doi.org/10.2307/3800469

Pokorny, B., Cerri, J., & Bužan, E. (2021). Roadkill in a time of pandemic : The analysis of wildlife-vehicle collisions reveals the differential impact of COVID-19 lockdown over mammal assemblages. *EcoEvoRxiv*. https://doi.org/10.32942/osf.io/p3zft

Potts, J. R., & Lewis, M. A. (2014). How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society B: Biological Sciences*, 281(1784), 20140231. https://doi.org/10.1098/rspb.2014.0231

Proença, V., Martin, L. J., Pereira, H. M., Fernandez, M., McRae, L., Belnap, J., Böhm, M., Brummitt, N., García-Moreno, J., Gregory, R. D., Honrado, J. P., Jürgens, N., Opige, M., Schmeller, D. S., Tiago, P., & van Swaay, C. A. M. (2017). Global biodiversity monitoring : From data sources to Essential Biodiversity Variables. *Biological Conservation*, 213, 256-263. https://doi.org/10.1016/j.biocon.2016.07.014

Prunier, J. G., Kaufmann, B., Léna, J.-P., Fenet, S., Pompanon, F., & Joly, P. (2014). A 40-year-old divided highway does not prevent gene flow in the alpine newt *Ichthyosaura alpestris*. *Conservation Genetics*, 15(2), 453-468. https://doi.org/10.1007/s10592-013-0553-0

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal Foraging : A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, 52(2), 137-154. https://doi.org/10.1086/409852

Quiles, P. (2018). Are road-kills representative of wildlife community obtained from atlas data? *Hystrix, the Italian Journal of Mammalogy*, 29(2), 190-194. https://doi.org/10.4404/hystrix

Rastetter, E. B., Aber, J. D., Peters, D. P. C., Ojima, D. S., & Burke, I. C. (2003). Using Mechanistic Models to Scale Ecological Processes across Space and Time. *BioScience*, 53(1), 68-76. https://doi.org/10.1641/0006-3568(2003)053[0068:UMMTSE]2.0.CO;2

Raymond, S., Schwartz, A. L. W., Thomas, R. J., Chadwick, E., & Perkins, S. E. (2021). Temporal patterns of wildlife roadkill in the UK. *PLoS ONE*, 16(10), e0258083. https://doi.org/10.1371/journal.pone.0258083

Reid, L. M., & Dunne, T. (1984). Sediment production from forest road surfaces. *Water Resources Research*, 20(11), 1753-1761. https://doi.org/10.1029/WR020i011p01753

Reijnen, R., Foppen, R., Braak, C. T., & Thissen, J. (1995). The Effects of Car Traffic on Breeding Bird Populations in Woodland. III. Reduction of Density in Relation to the Proximity of Main Roads. *Journal of Applied Ecology*, 32(1), 187-202. https://doi.org/10.2307/2404428

Reynolds, C. W. (1987). Flocks, herds and schools : A distributed behavioral model. *Proceedings of the 14th annual conference on Computer graphics and interactive techniques*, 25-34. https://doi.org/10.1145/37401.37406

Riaz, F., & Niazi, M. A. (2016). Road collisions avoidance using vehicular cyber-physical systems : A taxonomy and review. *Complex Adaptive Systems Modeling*, 4(1), 15. https://doi.org/10.1186/s40294-016-0025-8

Rigoudy, N., Dussert, G., Benyoub, A., Besnard, A., Birck, C., Boyer, J., Bollet, Y., Bunz, Y., Caussimont, G., Chetouane, E., Carriburu, J. C., Cornette, P., Delestrade, A., Backer, N. D., Dispan, L., Barh, M. L., Duhayer, J., Elder, J.-F., Fanjul, J.-B., … Chamaillé-Jammes, S. (2023). The DeepFaune initiative : A collaborative effort towards the automatic identification of French fauna in camera-trap images (p. 2022.03.15.484324). *bioRxiv*. https://doi.org/10.1101/2022.03.15.484324

Riley, S. P. D., Pollinger, J. P., Sauvajot, R. M., York, E. C., Bromley, C., Fuller, T. K., & Wayne, R. K. (2006). FAST-TRACK : A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology*, 15(7), 1733-1741. https://doi.org/10.1111/j.1365-294X.2006.02907.x

Robertson, M. P., Peter, C. I., Villet, M. H., & Ripley, B. S. (2003). Comparing models for predicting species' potential distributions : A case study using correlative and mechanistic predictive modelling techniques. *Ecological Modelling*, 164(2-3), 153-167. https://doi.org/10.1016/S0304-3800(03)00028-0

Robinson, O. J., Ruiz-Gutierrez, V., & Fink, D. (2018). Correcting for bias in distribution modelling for rare species using citizen science data. *Diversity and Distributions*, 24(4), 460-472. https://doi.org/10.1111/ddi.12698

Rotholz, E., & Mandelik, Y. (2013). Roadside habitats : Effects on diversity and composition of plant, arthropod, and small mammal communities. *Biodiversity and Conservation*, 22(4), 1017-1031. https://doi.org/10.1007/s10531-013-0465-9

Rytwinski, T., Soanes, K., Jaeger, J. A. G., Fahrig, L., Findlay, C. S., Houlahan, J., Van Ree, R. D., & Van Der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill ? A meta-analysis. *PLoS ONE*, 11(11), 1-25. https://doi.org/10.1371/journal.pone.0166941

Ryu, M., & Kim, J. G. (2021). Coastal road mortality of land crab during spawning migration. *Scientific Reports*, 11(1), Art. 1. https://doi.org/10.1038/s41598-021-86143-z

Saad, W., & Alsayyari, A. S. (2020). Real Time IoT Based Camel-Vehicle Collision Avoidance System for KSA. *2020 3rd International Conference on Computer Applications & Information Security (ICCAIS)*, 1-4. https://doi.org/10.1109/ICCAIS48893.2020.9096714

Saint-Andrieux, C., Calenge, C., & Bonenfant, C. (2020). Comparison of environmental, biological and anthropogenic causes of wildlife–vehicle collisions among three large herbivore species. *Population Ecology*, 62(1), 64-79. https://doi.org/10.1002/1438-390X.12029

Santos, R. A. L., & Ascensão, F. (2019). Assessing the effects of road type and position on the road on small mammal carcass persistence time. *European Journal of Wildlife Research*, 65(1). https://doi.org/10.1007/s10344-018-1246-2

Santos, R. A. L., Mota-Ferreira, M., Aguiar, L. M. S., & Ascensão, F. (2018). Predicting wildlife road-crossing probability from roadkill data using occupancy-detection models. *Science of The Total Environment*, 642, 629-637. https://doi.org/10.1016/j.scitotenv.2018.06.107

Santos, R. A. L., Santos, S. M., Santos-Reis, M., Picanço de Figueiredo, A., Bager, A., Aguiar, L. M. S., & Ascensão, F. (2016). Carcass Persistence and Detectability : Reducing the Uncertainty Surrounding Wildlife-Vehicle Collision Surveys. *PLoS ONE*, 11(11), e0165608. https://doi.org/10.1371/journal.pone.0165608

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road ? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, 6(9). https://doi.org/10.1371/journal.pone.0025383

Santos, S. M., Lourenço, R., Mira, A., & Beja, P. (2013). Relative Effects of Road Risk, Habitat Suitability, and Connectivity on Wildlife Roadkills : The Case of Tawny Owls (*Strix aluco*). *PLoS ONE*, 8(11), e79967. https://doi.org/10.1371/journal.pone.0079967

Sauermann, H., & Franzoni, C. (2015). Crowd science user contribution patterns and their implications. *Proceedings of the National Academy of Sciences*, 112(3), 679-684. https://doi.org/10.1073/pnas.1408907112

Saxena, A., Gupta, D. K., & Singh, S. (2021). An Animal Detection and Collision Avoidance System Using Deep Learning. In G. S. Hura, A. K. Singh, & L. Siong Hoe (Éds.), *Advances in Communication and Computational Technology* (p. 1069-1084). Springer Nature. https://doi.org/10.1007/978-981-15-5341-7_81

Schmeller, D. S., Henry, P.-Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., Déri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Set[TEL]e, J., Van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E., & Henle, K. (2009). Advantages of Volunteer-Based Biodiversity Monitoring in Europe. *Conservation Biology,* 23(2), 307-316. https://doi.org/10.1111/j.1523-1739.2008.01125.x

Schmidt, B. R., & Zumbach, S. (2008). Amphibian Road Mortality and How to Prevent It : A Review. *Herpetological Conservation,* 3 (Cha, Art. 3)

Schwartz, A. L. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology,* 4(1), 1-7. https://doi.org/10.1093/jue/juy006

Seburn, D. C., & McCurdy-Adams, H. (2019). Do turtle warning signs reduce roadkill? *The Canadian Field-Naturalist,* 133(3), Art. 3. https://doi.org/10.22621/cfn.v133i3.2279

Secco, H., Ratton, P., Castro, E., da Lucas, P. S., & Bager, A. (2014). Intentional Snake Road-Kill : A Case Study using Fake Snakes on a Brazilian Road. *Tropical Conservation Science,* 7(3), 561-571. https://doi.org/10.1177/194008291400700313

Seiler, A. (2001). Ecological Effects of Roads : A review. *Uppsala: Swedish University of Agricultural Sciences.*

Seiler, A. (2005). Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology,* 42(2), 371-382. https://doi.org/10.1111/j.1365-2664.2005.01013.x

Seiler, A., & Helldin, J. O. (2006). Mortality in wildlife due to transportation. In *The ecology of transportation: Managing mobility for the environment* (pp. 165-189). Dordrecht: Springer Netherlands.

Selvan, M. (2012). Roadkill animals on national highways of Karnataka, India. *Journal of Ecology and The Natural Environmen*t, 4(14), 363-365. https://doi.org/10.5897/JENE11.068

Semlitsch, R. D., Ryan, T. J., Hamed, K., Chatfield, M., Drehman, B., Pekarek, N., Spath, M., & Watland, A. (2007). Salamander abundance along road edges and within abandoned logging roads in Appalachian forests. *Conservation Biology: The Journal of the Society for Conservation Biology*, 21(1), 159-167. https://doi.org/10.1111/j.1523-1739.2006.00571.x

Serieys, L. E. K., Rogan, M. S., Matsushima, S. S., & Wilmers, C. C. (2021). Road-crossings, vegetative cover, land use and poisons interact to influence corridor effectiveness. *Biological Conservation,* 253, 108930. https://doi.org/10.1016/j.biocon.2020.108930

Shanley, C. S., & Pyare, S. (2011). Evaluating the road-effect zone on wildlife distribution in a rural landscape. *Ecosphere,* 2(2), art16. https://doi.org/10.1890/ES10-00093.1

Sharma, S. U., & Shah, D. J. (2017). A Practical Animal Detection and Collision Avoidance System Using Computer Vision Technique. *IEEE Access*, 5, 347-358. https://doi.org/10.1109/ACCESS.2016.2642981

Shi, X. Z., Wang, K., Warner, E. D., Yu, D. S., Wang, H. J., Yang, R. W., Liang, Y., & Shi, D. M. (2008). Relationship between soil erosion and distance to roadways in undeveloped areas of China. *CATENA*, 72(2), 305-313. https://doi.org/10.1016/j.catena.2007.06.004

Shilling, F., Collinson, W., Bil, M., Vercayie, D., Heigl, F., Perkins, S. E., & MacDougall, S. (2020). Designing wildlife-vehicle conflict observation systems to inform ecology and transportation studies. *Biological Conservation*, *251*, 108797.

Shilling, F. M., & Waetjen, D. P. (2015). Wildlife-vehicle collision hotspots at US highway extents : Scale and data source effects. *Nature Conservation*, 11, 41-60. https://doi.org/10.3897/natureconservation.11.4438

Shin, Y., Kim, K., Groffen, J., Woo, D., Song, E., & Borzée, A. (2022). Citizen science and roadkill trends in the Korean herpetofauna : The importance of spatially biased and unstandardized data. *Frontiers in Ecology and Evolution*, 10. https://www.frontiersin.org/articles/10.3389/fevo.2022.944318

Sicacha-Parada, J., Steinsland, I., Cretois, B., & Borgelt, J. (2021). Accounting for spatial varying sampling effort due to accessibility in Citizen Science data : A case study of moose in Norway. *Spatial Statistics*, 42, 100446. https://doi.org/10.1016/j.spasta.2020.100446

Sidorovich, A. A. (2020). Road Mortality of Carnivores (*Mammalia, Carnivora*) in Belarus. *Zoodiversity*, 54(3), 211-220. https://doi.org/10.15407/zoo2020.03.211

Sijtsma, F. J., van der Veen, E., van Hinsberg, A., Pouwels, R., Bekker, R., van Dijk, R. E., Grutters, M., Klaassen, R., Krijn, M., Mouissie, M., & Wymenga, E. (2020). Ecological impact and cost-effectiveness of wildlife crossings in a highly fragmented landscape : A multi-method approach. *Landscape Ecology*, 35(7), 1701-1720. https://doi.org/10.1007/s10980-020-01047-z

Skórka, P., Lenda, M., Moroń, D., Martyka, R., Tryjanowski, P., & Sutherland, W. J. (2015). Biodiversity collision blackspots in Poland : Separation causality from stochasticity in roadkills of butterflies. *Biological Conservation*, 187, 154-163. https://doi.org/10.1016/j.biocon.2015.04.017

Slater, S. J., Maloney, D. M., & Taylor, J. M. (2022). Golden eagle use of winter roadkill and response to vehicles in the western United States. *The Journal of Wildlife Management*, 86(6), e22246. https://doi.org/10.1002/jwmg.22246

Spellerberg, I. (1998). Ecological effects of roads and traffic : A literature review. *Global Ecology & Biogeography Letters*, 7(5), 317-333. https://doi.org/10.1046/j.1466-822x.1998.00308.x

Steiner, W., Leisch, F., & Hackländer, K. (2014). A review on the temporal pattern of deer-vehicle accidents : Impact of seasonal, diurnal and lunar effects in cervids. *Accident Analysis and Prevention*, 66, 168-181. https://doi.org/10.1016/j.aap.2014.01.020

Steiner, W., Schöll, E. M., Leisch, F., & Hackländer, K. (2021). Temporal patterns of roe deer traffic accidents : Effects of season, daytime and lunar phase. *PLoS ONE*, 16(3), e0249082. https://doi.org/10.1371/journal.pone.0249082

Stevenson, E. R., Chitwood, M. C., Lashley, M. A., Pollock, K. H., Swingen, M. B., Moorman, C. E., & DePerno, C. S. (2016). Survival and Cause-Specific Mortality of Coyotes on a Large Military Installation. *Southeastern Naturalist*, 15(3), 459-466. https://doi.org/10.1656/058.015.0307

Středová, H., Podhrázská, J., Chuchma, F., Středa, T., Kučera, J., Fukalová, P., & Blecha, M. (2021). The Road Map to Classify the Potential Risk of Wind Erosion. I*SPRS International Journal of Geo-Information*, 10(4), Art. 4. https://doi.org/10.3390/ijgi10040269

Swanson, K., Land, D., Kautz, R., & Kawula, R. (2008). Use of least-cost pathways to identify key road segments for Florida panther conservation. *Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute*

Swinnen, K. R., Jacobs, A., Claus, K., Ruyts, S., Vercayie, D., Lambrechts, J., & Herremans, M. (2022). 'Animals under wheels': Wildlife roadkill data collection by citizen scientists as a part of their nature recording activities. *Nature Conservation*, *47*, 121-153.

Tatewaki, T., & Koike, F. (2018). Synoptic scale mammal density index map based on roadkill records. *Ecological Indicators*, 85, 468-478. https://doi.org/10.1016/j.ecolind.2017.10.056

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, 68(3), 571. https://doi.org/10.2307/3544927

Taylor, J. (2022). Roadkill Encounters and Affective Solidarity: Exploring Multispecies Fellowship through Disgust, Pain, and Mourning. *Sociální Studia / Social Studies*, 19(1), Art. 1. https://doi.org/10.5817/SOC2022-29553

Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., & Kindel, A. (2013). Vertebrate road mortality estimates : Effects of sampling methods and carcass removal. *Biological Conservation*, 157, 317-323. https://doi.org/10.1016/j.biocon.2012.09.006

Teixeira, F. Z., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, 54(5), 1544-1551. https://doi.org/10.1111/1365-2664.12870

Tennessen, J. B., Parks, S. E., & Langkilde, T. (2014). Traffic noise causes physiological stress and impairs breeding migration behaviour in frogs. *Conservation Physiology*, 2(1), cou032. https://doi.org/10.1093/conphys/cou032

Testud, G., Fauconnier, C., Labarraque, D., Lengagne, T., Le Petitcorps, Q., Picard, D., & Miaud, C. (2020). Acoustic enrichment in wildlife passages under railways improves their use by amphibians. *Global Ecology and Conservation*, 24, e01252. https://doi.org/10.1016/j.gecco.2020.e01252

Thel, L., Chamaillé-Jammes, S., Keurinck, L., Catala, M., Packer, C., Huebner, S. E., & Bonenfant, C. (2021). Can citizen science analysis of camera trap data be used to study reproduction? Lessons from Snapshot Serengeti program. *Wildlife Biology,* 2021(2), wlb.00833. https://doi.org/10.2981/wlb.00833

Thompson, B. K., Olden, J. D., & Converse, S. J. (2021). Mechanistic invasive species management models and their application in conservation. *Conservation Science and Practice,* 3(11), e533. https://doi.org/10.1111/csp2.533

Thompson, M. M., Moon, K., Woods, A., Rowley, J. J. L., Poore, A. G. B., Kingsford, R. T., & Callaghan, C. T. (2023). Citizen science participant motivations and behaviour : Implications for biodiversity data coverage. *Biological Conservation,* 282, 110079. https://doi.org/10.1016/j.biocon.2023.110079

Tiago, P., Pereira, H. M., & Capinha, C. (2017). Using citizen science data to estimate climatic niches and species distributions. *Basic and Applied Ecology,* 20, 75-85. https://doi.org/10.1016/j.baae.2017.04.001

Timothy, N., & Tagui Williams, E. (2019). Environmental Pollution by Heavy Metal : An Overview. *International Journal of Environmental Chemistry*, 3(2), 72. https://doi.org/10.11648/j.ijec.20190302.14

Valentin, C., Poesen, J., & Li, Y. (2005). Gully erosion : Impacts, factors and control. *CATENA,* 63(2), 132-153. https://doi.org/10.1016/j.catena.2005.06.001

Van der Ree, R., Jaeger, J. A. G., van der Grift, E. A., & Clevenger, A. P. (2011). Effects of roads and traffic on wildlife populations and landscape function : Road ecology is moving toward larger scales. *Ecology and Society*, 16(1). https://doi.org/10.5751/ES-03982-160148

Van Eupen, C., Maes, D., Herremans, M., Swinnen, K. R. R., Somers, B., & Luca, S. (2022). Species profiles support recommendations for quality filtering of opportunistic citizen science data. *Ecological Modelling*, 467, 109910. https://doi.org/10.1016/j.ecolmodel.2022.109910

Van Langevelde, F., & Jaarsma, C. F. (2005). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, 19(8), 895-907. https://doi.org/10.1007/s10980-005-0464-7

Van Langevelde, F., van Dooremalen, C., & Jaarsma, C. F. (2009). Traffic mortality and the role of minor roads. *Journal of Environmental Management*, 90(1), 660-667. https://doi.org/10.1016/j.jenvman.2007.09.003

Ver Hoef, J. M., Johnson, D., Angliss, R., & Higham, M. (2021). Species density models from opportunistic citizen science data. *Methods in Ecology and Evolution*, 12(10), 1911-1925. https://doi.org/10.1111/2041-210X.13679

Vercayie, D., & Herremans, M. (2015). Citizen science and smartphones take roadkill monitoring to the next level. *Nature Conservation*, 11, 29-40. https://doi.org/10.3897/natureconservation.11.4439

Villalobos-Hoffman, R., Ewing, J. E., & Mooring, M. S. (2022). Do Wildlife Crossings Mitigate the Roadkill Mortality of Tropical Mammals? A Case Study from Costa Rica. *Diversity,* 14(8), Art. 8. https://doi.org/10.3390/d14080665

Viscido, S. V., Miller, M., & Wethey, D. S. (2001). The Response of a Selfish Herd to an Attack from Outside the Group Perimeter. *Journal of Theoretical Biology*, 208(3), 315-328. https://doi.org/10.1006/jtbi.2000.2221

Waetjen, D. P., & Shilling, F. M. (2017). Large Extent Volunteer Roadkill and Wildlife Observation Systems as Sources of Reliable Data. *Frontiers in Ecology and Evolution*, 5. https://www.frontiersin.org/articles/10.3389/fevo.2017.00089

Walker, D. A., & Everett, K. R. (1987). Road Dust and its Environmental Impact on Alaskan Taiga and Tundra. *Arctic and Alpine Research*, 19(4), 479-489. https://doi.org/10.1080/00040851.1987.12002630

Walper, K. H., Ellenberg, H., Mueller, K., & Stottele, T. (1981). Ausgangssituationen-strassen-oekologie-auswirkungen von autobahnen und strassen auf oekosysteme deutscher landschaften. *Ökologie und Straße*.

Wang, Y., Yang, Y., Han, Y., Shi, G., Zhang, L., Wang, Z., Cao, G., Zhou, H., Kong, Y., Piao, Z., & Merrow, J. (2022). Temporal patterns and factors influencing vertebrate roadkill in China. *Transportation Research Interdisciplinary Perspectives*, 15, 100662. https://doi.org/10.1016/j.trip.2022.100662

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. T*rends in Ecology & Evolution*, 22(6), 323-330. https://doi.org/10.1016/j.tree.2007.03.007

Willi, M., Pitman, R. T., Cardoso, A. W., Locke, C., Swanson, A., Boyer, A., Veldthuis, M., & Fortson, L. (2019). Identifying animal species in camera trap images using deep learning and citizen science. *Methods in Ecology and Evolution*, 10(1), 80-91. https://doi.org/10.1111/2041-210X.13099

Williams, S. T., Collinson, W., Patterson-Abrolat, C., Marneweck, D. G., & Swanepoel, L. H. (2019). Using road patrol data to identify factors associated with carnivore roadkill counts. *PeerJ*, 7, e6650. https://doi.org/10.7717/peerj.6650

Woltz, H. W., Gibbs, J. P., & Ducey, P. K. (2008). Road crossing structures for amphibians and reptiles : Informing design through behavioral analysis. *Biological Conservation*, 141(11), 2745-2750. https://doi.org/10.1016/j.biocon.2008.08.010

Yue, S., Bonebrake, T. C., & Gibson, L. (2019). Informing snake roadkill mitigation strategies in Taiwan using citizen science. *The Journal of Wildlife Management*, 83(1), 80-88. https://doi.org/10.1002/jwmg.21580

Yulevitch, G., Danon, M., Krasovitov, B., Fominykh, A., Swet, N., Tsesarsky, M., & Katra, I. (2020). Evaluation of wind-induced dust-PM emission from unpaved roads varying in silt content by experimental results. *Atmospheric Pollution Research*, 11(2), 261-268. https://doi.org/10.1016/j.apr.2019.10.010

Zhang, W., Shu, G., Li, Y., Xiong, S., Liang, C., & Li, C. (2018). Daytime driving decreases amphibian roadkill. *PeerJ*, 6, e5385. https://doi.org/10.7717/peerj.5385