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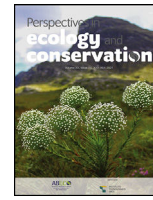

Research Letters

Factors influencing bat road casualties in a Neotropical savanna

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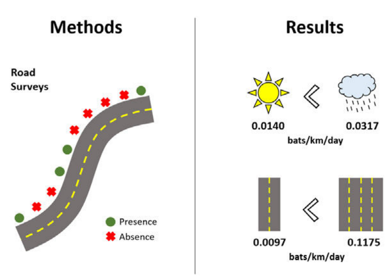
HIGHLIGHTS

- Estimation of over 4740 road-killed bats during a 5-year period.
- Phyllostomidae bats were the most affected by roadkill in the study area.
- Road casualties were more numerous during rainy season.
- Collisions occurred 12 times more in four-lane highways than in two-lane ones.
- Distance from water and presence of light were not significantly related to roadkill.

GRAPHICAL ABSTRACT



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ABSTRACT

Collision with vehicles is one of the main causes of death for many vertebrates; however, little is known about bat roadkill. Thus, in this study we described bat roadkill in an area of Neotropical savanna and evaluated factors potentially affecting its occurrence. We surveyed 114 km of roads on the margins of protected areas in the Brazilian Federal District for 5 years. We analysed bat roadkill on three types of roads (dirt roads, two-lane paved highways, and four-lane paved highways) and recorded distance from water and presence of artificial light. Bat roadkill was calculated for 2-km sections and analysed using generalized linear mixed models (GLMMs) with the following independent variables: season, road type, presence of light, and distance from water. We used section nested within road as a random effect. We estimated a total of 4740 roadkilled bats and identified individuals from three families. Bat road casualties were more numerous in the rainy season and on four-lane highways, whereas proximity to water and presence of artificial light were not related to roadkill number. The higher roadkill rate during the rainy season may be explained by higher bat activity due to the increased availability of resources. Regarding the influence of road type, four-lane highways have the highest traffic volumes in the area and the highest speed limits, which are associated with higher roadkill rates. Bats represent the most diverse order of mammals in the Cerrado, where they provide many important ecological services, which need to be preserved.

Introduction

Roadkill is the most obvious direct cause of wild vertebrate mortality related to habitat fragmentation by roads (Forman and

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Alexander, 1998; Prado et al., 2006). Although the number of road-killed bats is small compared with roadkill deaths of other vertebrates such as birds and amphibians (Glista et al., 2008; Russel et al., 2009), bats are more likely than most other mammalian species to be involved in vehicle collisions (González-Prieto et al., 1993). The annual mortality rate on roads near bat roosts is estimated to be 5% (Russel et al., 2009); however, the actual rate may be higher because bats look for minimum-cost paths for commuting (Pyke, 1984) and commonly use linear landscape features such as roads.

Because of their small body size, it can be challenging to detect bat carcasses on roads (Bafaluy, 2000). Moreover, small carcasses are easily removed by predators, destroyed during the vehicle collision, or thrown into the surrounding vegetation (Bafaluy, 2000; Slater, 2002, Prosser et al., 2008; Santos et al., 2011). This difficulty locating and identifying road-killed bats contributes to the underestimation of the number of individuals killed (Slater, 2002; Lesiński, 2008; Medinas et al., 2013), which hampers our understanding of the effect of vehicle collisions on bat populations (Bafaluy, 2000; Prosser et al., 2008).

Nevertheless, studies have shown that roads negatively impact bats (Schaub et al., 2008; Siemers and Schaub, 2011; Berthinussen and Altringham, 2012; Claireau et al., 2019) and may significantly reduce their populations (Schorcht et al., 2009). Road presence is also connected with reduced bat activity and diversity, which could affect population dynamics (Berthinussen and Altringham, 2012; Claireau et al., 2019; Medinas et al., 2013, 2019). Because chiropterans have low fecundity rates and later sexual maturity, the lasting effects of roadkill over bat populations makes population recovery harder (Medinas et al., 2013).

Although agile and manoeuvrable in flight, some bats species fly at low speeds (<20 km/h) and close to the ground (0–4 m) (Russel et al., 2009; Berthinussen and Altringham, 2012), particularly when crossing open spaces. These species, which are mainly adapted to forage in cluttered spaces or in fragment edges, may be more susceptible to road casualties than high-flying species (Lesiński, 2008). The risk of collision for open-space foraging high-flying species is considered negligible because they generally fly above vehicles (Zurcher et al., 2010). Moreover, edge-space foraging insectivorous bats can be attracted by insects around road lamps or car lights (Blake et al., 1994; Zortéa and Aguiar, 2001), leading to collision with vehicles on the road.

Other factors that may influence the risk of vehicle-bat collisions include features of the habitat surrounding the road (Lesiński, 2007; Medinas et al., 2013, 2021; Secco et al., 2017; Roemer et al., 2020). Roads near high-quality habitats are associated with higher bat roadkill rates (Medinas et al., 2013, 2021), whereas roads crossing open areas or suburban areas are associated with lower roadkill rates (Lesiński, 2007). Type of surround habitat can also influence on how roads affect bat activity, with lower activity near roads on forested areas and the opposite on open dry areas (Medinas et al., 2019). Similarly, Dean et al. (2019) observed that road verges are particularly hazardous for many vertebrates in arid areas. Although Medinas et al. (2013) also reported that higher traffic levels were associated with bat casualties, there are no published data regarding how road type affects the bat roadkill rate.

In the biodiverse country of Brazil, previous studies have evaluated roadkill of a range of vertebrate species (e.g., Prado et al., 2006; Braz and França, 2016), but few have evaluated bats (Alves et al., 2015; Ceron et al., 2017; Secco et al., 2017; Novaes et al., 2018), and little is known about how bat feeding habits are related to the likelihood of vehicle collision. In Brazilian Cerrado, bats represent the most diverse orders of mammals (Aguiar et al., 2016), and are important pollinators of economically valuable plants such as *Caryocar brasiliense* (Gribel and Hay, 1993) and play an important role in fruit dispersal, which is indispensable to the restoration of degraded areas (Kunz et al., 2011, Kuhlmann and Ribeiro, 2016). Therefore, the objective of this study is to describe bat roadkill on roads in a Neotropical savanna in Brazil and evaluate factors potentially influencing the roadkill rate. We tested the predictions that roadkill rates will be higher during rainy season and that four-lane highways, areas near water, and sites with artificial light have higher roadkill rates.

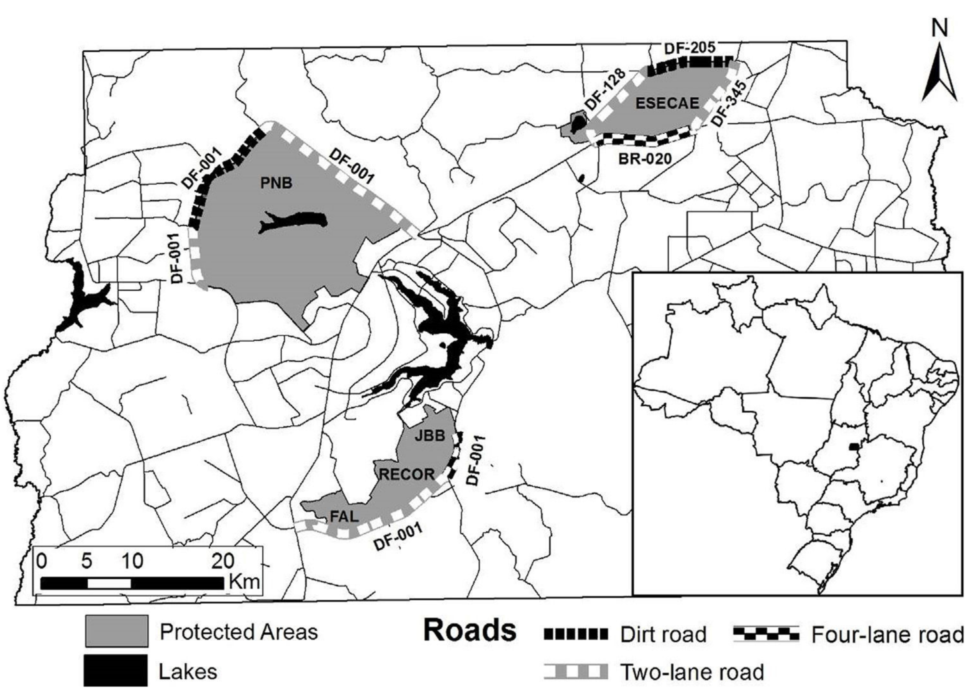

Fig. 1. Study area with locations of monitored roads and protected areas. ESECAE, Ecological Station of Águas Emendadas; FAL, Experimental Farm of the University of Brasília; JBB, Botanical Garden of Brasilia; PNB, Brasília National Park; RECOR, IBGE Biological Reserve.

Methods

We conducted this study in the Brazilian Federal District, located in the Cerrado biome of Central Brazil (Fig. 1). The vegetation in the study area is composed primarily of savanna forest ("Cerradão" and "Mata de Galeria") and open savanna ("Cerrado sensu stricto"), with small portions of grasslands and other less representative vegetation types (Fonseca, 2008). The Cerrado is the richest savanna in the world, and bats are the most diverse order of mammals in this biome. More than 100 species have been reported, and the following species are endemic to the Cerrado: *Lonchophylla dekeyseri*, *Lonchophylla bokermanni*, and *Glyphonycteris behnii*.

This study area is located near Brasília, the fourth most populated city in Brazil, with a population of approximately 3.1 million people (IBGE, 2019). In this area, over 1 million vehicles travel every day (DENATRAN, 2020), and most of the main roads are located near protected areas (Fig. 1). In this area, Brasília Environmental Institute (IBRAM) developed the Rodofauna Project, which aims to evaluate the impacts of roadkill in wild fauna (IBRAM, 2019). The results and data from this project are available online (http://www.ibram.df.gov.br/rodofauna-monitoramento-de-fauna-silvestre-atropelada/) and data from bat roadkill were used in this study.

Surveys were conducted along nine roads (total 114 km), including four-lane highways (BR-020 and DF-001; 16 km, speed limit: 80 km/h), two-lane highways (DF-001, DF-345, and DF-128; 74 km, speed limit: 60 km/h), and dirt roads (DF-205 and DF-001; 24 km, speed limit: 50 km/h) (Fig. 1). The four-lane and two-lane sections were paved (with shoulders), some of them with artificial lights in the median strip. These road sections delimit five protected areas, namely the Ecological Station of Águas Emendadas (ESECAE, 10,000 ha), Brasília National Park (PNB, 44,000 ha), Ecological Station of the Botanical Garden of Brasilia (EEJBB, 4000 ha), Experimental Farm of the University of Brasília (FAL/UnB, 4000 ha), and IBGE Biological Reserve (RECOR, 1300 ha) (Fig. 1). The United Nations Educational, Scientific and Cultural Organization (UNESCO) recognizes these protected areas as core areas of the Cerrado Biosphere Reserve in the Federal District.

Roadkill surveys were conducted every 2 days (except for weekends) from 7 a.m to 11 a.m. for 5 years, from April 2010 to March 2015, for a total of 484 roadkill surveys, 244 conducted on the dry season and 240 on the rainy reason. During each survey, all 114 km of roads surrounding the main protected areas in the area were inspected. Two observers and one driver searched for roadkill in a vehicle traveling at approximately 50 km/h. The observers identified each carcass to the lowest possible taxonomic level and collected data on its position on the road (lane or shoulder) and geographic coordinates using a handheld GPS device with 5-m accuracy. The observers also photographed bat individuals for species identification using the criteria of Díaz et al. (2016). Because there are no regular traffic counts for the studied roads (only yearly estimates), we used the road type (IBRAM, 2019) as a proxy of traffic volume.

We calculated roadkill rate estimates with Siriema v2.0 software (Coelho et al., 2014). This approach takes sampling effort, observer efficiency, and carcass persistence into consideration, resulting in a more reliable analysis. Because of the lack of data for observer efficiency and carcass persistence for bats, we used data from previous studies that were calculated for small individuals (<100 g). We used efficiency of 7% (Santos et al., 2016) and carcass persistence of 1 day (Santos et al., 2016), which may produce a still underestimated mortality rate.

To determine which factors had a greater effect on the bat roadkill rate, data regarding road characteristics and bat roadkill were collected for 2-km road section, totalling 57 sections. We recorded presence or absence of artificial light within each section. Before model construction, we removed outlier values with a cut-off value of 1 (Cook, 1977). We then constructed generalized linear mixed models (GLMMs) with negative binomial distribution due to the high number of 0s in our samples (Warton, 2005). We used number of road-killed bats per section as the dependent variable and all combinations of the following factors as independent variables: (i) season (dry or rainy), (ii) road type (dirt road, two-lane highway, or four-lane highway), (iii) artificial light (presence or absence), and (iv) linear distance between the centre of the road section and the closest source of water, which was calculated using shapefiles from Brazilian Foundation for Sustainable Development (FBDS). In all models constructed, we used section ID nested within road ID as random effects.

We checked models for multicollinearity using Variance Inflation Factor (VIF) values, with a cut-off value of VIF > 10, and for overdispersion by comparing the sum of squared Pearson residuals with the residual degrees of freedom (Venables and Ripley, 2002). We used the Akaike Information Criterion corrected for small samples (AICc) to rank models and select the most parsimonious models for each case based on ΔAICc (Table S1). We then used all models with ΔAICc < 2 to calculate average estimation and confidence intervals for the independent variables using multimodel inference (Burnham and Anderson, 2002). A variable was considered significant when its confidence intervals did not overlapped zero. The importance of each variable in the averaged model was estimated with the sum of the weights of models where they were present. We conducted all tests on R 3.2.2 (R Core Team, 2015) using packages "lme4" (Bates et al., 2015), "car" (Fox and Weisberg, 2019), "MASS" (Venables and Ripley, 2002) and "MuMIn" (Bartoń, 2019),

Table 1
Identified bat species involved in road casualties in Distrito Federal, Brazil from April 2010 to March 2015. NI = not identified.

Taxon	Foraging guild	Season	
		Dry	Rainy
Phyllostomidae: Stenodermatinae			
Artibeus spp.	Cluttered-space	1	1
Platyrrhinus spp.	Cluttered-space	1	1
Sturnira lilium	Cluttered-space	1	–
Phyllostomidae: Glossophaginae			
Glossophaga soricina	Cluttered-space	3	10
Phyllostomidae: NI			
NI	Cluttered-space	2	9
Molossidae: Molossinae			
Molossops temminckii	Edge-space	2	0
Molossidae: NI			
NI	–	4	4
Vespertilionidae: NI			
NI	–	0	1
NI	–	13	34
TOTAL		27	60

Results

During this 5-year study, we identified 87 individual bats from at least 3 families, 4 subfamilies, and 6 species, all of them considered as cluttered-space or edge-space foragers (Table 1). Phyllostomidae bats were the most common family recorded as roadkill, representing 72.5% of the identified individuals. Bats comprised 1.62% of the total number of individuals identified and were the second most abundant order of mammals in number of casualties, after Carnivora. We estimated a total of 4740 roadkilled bats during the 5-year period of the study, which represents a mortality rate

Table 2
Model averaged coefficients and standard error (MAC ± SE), confidence intervals (CI), relative importance, and significance values (p) for the variables of the most parsimonious models (ΔAICc < 2.00) for bat roadkill on roads in the Brazilian Federal District from April 2010 to March 2015.

Variable	MAC ± SE	CI		Importance
		2.50%	97.50%	
Intercept	1.08 ± 0.69	−0.30	2.46	
Season	0.76 ± 0.26	0.25	1.27	1
Road Type	−2.74 ± 0.53	−3.80	−1.68	1
Distance to Water	−0.01 ± 0.01	−0.01	0.01	0.69

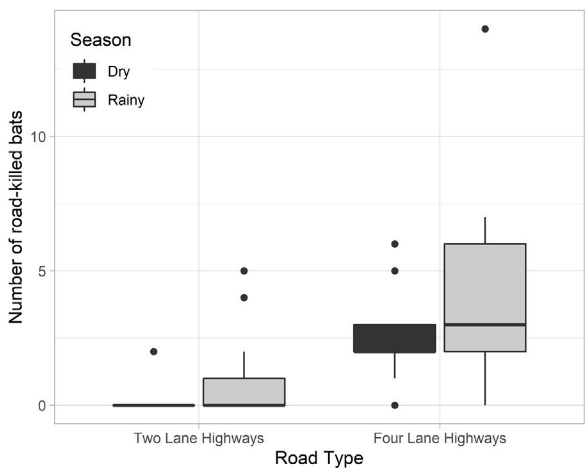

Fig. 2. Boxplot comparing the number of road-killed bats between two- and four-lane highways in both dry and rainy seasons in the Brazilian Federal District from April 2010 to March 2015.

of 0.023 roadkills/day/km. This estimate was over 54 times higher than the observed value.

Because we did not record any bats on dirt roads, we used only data from two-lane and four-lane highways in modelling. Two models including the variables season, road type, and distance from water had ΔAICc ≤ 2 and were therefore used for averaging. From those variables, distance from water was not considered significant as its confidence intervals overlapped zero (Table 2). Regarding bat roadkill seasonality, mortality rates were higher on the rainy season, with an estimation of 0.0317 bats/day/km, when compared to the dry season, with an estimated mortality rate of 0.0140 bats/day/km (Fig. 2). Estimated mortality rate for the rainy season presented, therefore, a 2.26-fold increase when compared to the one estimated for the dry season.

When considering impacts of road type on bat roadkill, four-lane highways represented larger roadkill danger for bats, with an estimated mortality rate over 12 times higher than the one estimated for two-lane highways (Fig. 2). When considering four-lane highways, estimated mortality rate was of 0.1175 bats/day/km, while estimated mortality rate for two-lane highways were of 0.0097 bats/day/km. Presence of artificial light on the roads was not included in any of the best models (Table S1).

Discussion

In this study we estimated over 4740 road-killed bats during a 5-year period. We identified individuals from at least three bat families, with Phyllostomidae bats most often involved in vehicle collisions. Significant predictors of the bat roadkill rate were season and road type, which supported our hypothesis that roadkill rates would be higher during the rainy season and at four-lane highways. Surprisingly, we did not observe any significant relationship between number of road-killed bats and distance to water or presence of artificial light.

In our study, we did not identify open-space foraging individuals, which could explain the lack of relationship between the presence of artificial light and bat roadkill rate, as open-space foragers are more likely to be attracted near roads by the higher resource availability provided by insects lured by streetlamps (Rydell, 1992; Nabli et al., 1999; Stone et al., 2015). Regarding cluttered-space foraging bats, most individuals fly at the height of the understory layer, which in the Cerrado is approximately 5 m (Lemos-Filho et al., 2010), and are slow-flying species (Kalko et al., 1996; Stockwell, 2001), which accounts for their greater likelihood to be involved in vehicle collisions. However, because of the lack of studies on abundance of different species in Brazilian Cerrado, it is not possible to draw any conclusion if those guilds are indeed more affected by roadkill.

Most studies of roadkill in Brazil have indicated that bats, considered as a single taxon, are not frequently involved in vehicle collisions (Coelho et al., 2008; Braz and França, 2016). Studies reporting bat roadkill have been conducted in all Brazilian biomes and have identified 46 species from seven bat families as casualties (Alves et al., 2015; Ceron et al., 2017; Secco et al., 2017; Novaes et al., 2018). Consistent with our results, previous studies reported that cluttered-space foragers, especially Phyllostomidae, are the most affected bat foraging guild, representing over 80% of the records (Novaes et al., 2018).

According to Medinas et al. (2013), the three main factors (other than season) that influence the bat roadkill rate are bat biology (e.g., species, sex, and age), road characteristics, and land features. Regarding road characteristics, higher traffic volume has been associated with increased bat mortality (Medinas et al., 2013). In our study we also observed that bat roadkill in the Brazilian Federal District occurred most often on four-lane paved highways, which are high-traffic roads. Similarly, studies in Portugal and Montenegro have reported higher levels of bat mortality on high-traffic roads (Medinas et al., 2013; Iković et al., 2014). Bafaluy (2000) reported that areas with higher speed limits had more bat casualties in Spain. Likewise, in our study, four-lane paved highways, which had the highest bat roadkill rates, also had higher speed limits than two-lane highways and dirt roads. In the present study, we did not observe any road-killed bats on dirt roads. Those roads are located mainly on more preserved areas and present lower traffic volumes, which provides higher scavengers' abundance and facilitated access to eventual road-killed individuals, thus reducing carcass persistence (Santos et al., 2016). Moreover, carcasses are more likely to be undetected in those roads, which suggests that the impacts of dirt roads on bat population are especially underestimated (Santos and Ascensão, 2019).

In our study, we observed more bat roadkill during the rainy season, especially in February and March. In the Brazilian Cerrado resource availability is higher in the rainy season, when many plant species are flowering or fruiting (Pilon et al., 2015) and insect abundance is higher (Pinheiro et al., 2012). Accordingly, the activity of insectivorous bats is approximately two times higher in the rainy season, and phyllostomid bats are usually captured in higher numbers in the rainy season than in the dry season (Willig, 1985; Sousa et al., 2013). Similarly, climactic conditions have been suggested to influence bat activity and roadkill in different areas, with higher activity and roadkill rates in rainy seasons and higher temperatures (Erickson and West, 2002; Bafaluy, 2000; Lesiński, 2007, 2008; Lesiński et al., 2011; Medinas et al., 2013; Iković et al., 2014). Moreover, in a study conducted in Brazilian Cerrado, Lira et al. (2020) observed that there was no seasonal difference in the number of carcass visits performed by scavengers, which suggests that higher roadkill rates observed during the rainy season reflects a factual higher mortality during this season.

Our results contrast with different data reported by previous studies carried out in Brazil. For example, in the Atlantic Forest in Rio de Janeiro, no difference in roadkill rates was observed between seasons (Secco et al., 2017); however, seasonal differences in weather are smaller in this region compared with the Cerrado (Secco et al., 2017). In a Cerrado area in the state of Minas Gerais, bat roadkill rates were higher in June and July than in the other months studied; however, this study was conducted during the dry season only (Alves et al., 2015). Thus, our study is the first to conduct a temporal analysis of roadkilled bats in areas of savanna.

Bats are generally thought to be less affected by vehicle collisions compared with other vertebrates (Ashley and Robinson, 1996), especially birds and amphibians (Glista et al., 2008; Russel et al., 2009). However, bat roadkill can be hard to detect, in part because bat carcasses persist on the roads for less than one day (Santos et al., 2011), with lower persistence time for smaller individuals (Santos et al., 2016; Barrientos et al., 2018). Surveys are often carried out during the day, which also hampers roadkill localization and identification (Lesiński, 2008), because the bat carcasses may have been removed or destroyed during the night, when bats are active, and the collisions are more likely to occur. Detectability of bat carcasses may be as low as 14% on walking searches and 7% on car searches (Arnett, 2006; Santos et al., 2016), further supporting the idea that bat roadkill is underestimated. Bat casualties on roads may affect up to 5% of a bat colony (Russel et al., 2009), which highlights the importance of studies evaluating bat-vehicle collisions and factors that may influence roadkill rates.

Estimates of bat roadkill are still scarce in Brazil and are often underestimated in many studies (Arnett, 2006), which suggests that mortality may be much higher than that generally reported. It is also important that new studies evaluate detectability of bat carcasses in driven surveys and how long bat carcass may persist in roads located on open habitats. Our results indicates that a high number of bats may have been killed during our search in the study area, approximately 950 individuals per year. However, because of the lack of those studies, this number may still be underestimated.

Based on previous studies, the most killed species on the roads are the most abundant in the areas (Medinas et al., 2013; Iković et al., 2014). Regardless, rare species' local populations can potentially be affected even by small mortality rates (Fensome and Mathews, 2016). As the knowledge about bat species present in Brazil is still scarce (Bernard et al., 2011), especially the rarest and insectivorous, and the Cerrado is one of the areas where new species can be found (Aguiar et al., 2020), it is urgent to mitigate the road impacts on bats. Roads may be interfering with movement routes, affecting individual survival, population dynamics, species distribution, and ecosystem functioning (Jeltsch et al., 2013); therefore, it's urgent that environmental agencies include bats in fauna monitoring in road infrastructures. We also suggest that more accurate estimates, which should include walking transects, are needed to recommend proper mitigation measures to reduce road impacts on bat population and prevent species' local disappearance.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pecon.2021.03.004.

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