An evaluation method of linear infrastructures permeability tested on the butterfly *Maniola jurtina* V8

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Abstract

Context.

Barrier effects of Large-scale Transportation Infrastructures (LTIs; roads, railways, *etc.*) are among the main factors contributing to the fragmentation of habitats. The reduction of dispersal across LTIs can drive small, local populations to extinction. To understand how LTIs modify dispersal, efficient and workable evaluation methods are required.

Objectives.

We developed a method based on Mark-Release-Recapture (MRR) surveys to estimate barrier effects of LTIs that could be easily applied in various landscape contexts and with any mobile species.

Methods.

Our method uses dispersal kernels of animal movements. Based on these kernels, we can calculate an expected probability of crossing any particular linear feature present in a landscape. The expected probability of crossing is then compared to empirical data (MRR crossing events) to estimate the barrier effect. We used simulations to test the reliability of our method and tested this framework on the butterfly *Maniola jurtina* in a landscape fragmented by four LTIs (a gas pipeline, a motorway, a power line and a railway).

Results.

Simulations showed that if the width of the infrastructure is smaller than 0.7 time the average movement capacity of organisms, our method was powerful enough to detect barrier effects. We suggest that this would be the case for most studied organisms. In our study case, this method was efficient to detect barrier effects, if present. Of the four infrastructures tested, only the motorway acted as a significant barrier to butterfly movements. Crossing events through the motorway were reduced by 5 times relative to natural habitats.

Conclusions.

This framework is of particular interest for conservation studies in order to detect where individual movements are modified by linear infrastructures at

local scale. Applying this framework may help landscape managers to design mitigation measures on existing infrastructures in order to offset the negative effects of fragmentation.

Key-words: barrier effects, butterfly, habitat fragmentation, large-scale transportation infrastructures, crossing probability, Mark-Release-Recapture, dispersal kernels

Introduction

Large-scale Transportation Infrastructures (LTIs) are any kind of linear infrastructures allowing the transportation of goods, vehicles and energy. They are expending considerably, creating dense transportation networks in growing anthropogenic landscapes (Dulac, 2013; Laurance et al., 2014). Despite their high impacts on natural ecosystems and their contribution to habitat fragmentation (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Balkenhol and Waits, 2009), methods are lacking to properly evaluate their barrier effects in landscapes.

Large-scale Transportation Infrastructures affect mobile organisms by direct vehicular collisions (Trombulak and Frissell, 2000). They also induce behavioural modifications of organisms; leading to infrastructure avoidance (Ascensao et al., 2016). Individuals may avoid LTIs due to traffic noise, modification of their natural habitat, perturbation of their reproductive success and perturbation of their physiological state (Trombulak and Frissell, 2000). All these perturbations may lead to barrier effects which limit dispersal (the movement of individuals that sustains gene flow within landscapes (Ronce, 2007)). Populations which are not linked by dispersal may suffer from geographical isolation (Fahrig and Rytwinski, 2009; Beyer et al., 2016). Isolated and small populations exhibit higher rates of inbreeding and genetic drift. It results in the decrease in heterozygosity and increases the population risk of extinction (McCauley, 1991; Fagan and Holmes, 2006).

The most common LTIs are roads, motorways, railways, power lines, pipelines and canals. Roads (including motorways) are the most studied infrastructures and are considered as strong barriers for a large range of animal species. Roads tend to have more negative than neutral or positive effects (Fahrig and Rytwinski, 2009). Railways can be barriers for certain species (Whittington et al., 2004; Bartoszek and Greenwald, 2009; Breyne et al., 2014), be neutral to movement (Vandevelde et al., 2012), increase species richness and abundance near infrastructures (Li et al., 2010) or create corridors (Penone et al., 2012). Power lines sometimes lead to avoidance behaviour (e.g. prairie grouse (Pruett et al., 2009)); but most studies reveal no effects of these infrastructures on animal movements (Latch et al., 2011; Bartzke et al., 2015; Jahner et al., 2016). Power lines are even attractive to some birds by providing perches for hunting activities (Morelli et al., 2014). The other types of LTIs (gas pipelines, canals, *etc.*) have been less studied and require more investigations (but see Dyer et al., 2002; Coulon et al., 2006; Breyne et al., 2014; Kaya Özdemirel et al., 2016).

For a given species, a particular type of infrastructure may act as a very strong barrier to movements while an other type might not. For example, in Norway, moose avoid crossing roads but power lines do not impede their movements (Bartzke et al., 2015). Similarly, gene flow of desert tortoises is affected by roads but not by power lines (Latch et al., 2011). Even with the same infrastructure type, effects can be landscape-specific. For example, Van Buskirk (2012) found that a motorway reduces gene flow of the alpine newt in Switzerland but Prunier et al. (2014) found that a similar motorway was not affecting gene flow of the same species in France.

Therefore, when trying to understand at the regional scale how a species travels through the landscape, it is crucial to determine the effects of the different infrastructure types present (Balkenhol and Waits, 2009). Those evaluations are particularly requested by local authorities to design mitigation measures (EEA, 2015).

In the past fifteen years, one of the most powerful tool to estimate landscape connectivity has been landscape genetics (Manel and Holderegger, 2013). Genetic studies have been widely used in order to estimate the effects of LTIs (Holderegger and Di Giulio, 2010). However, one major limit is the time-lag before detection of a barrier effect (Epps and Keyghobadi, 2015). Recent infrastructure may not have been in place for long enough to be able to detect any barrier effects on genetic metrics (e.g. Prunier et al., 2014). Furthermore, genetic methods can be expensive and difficult to implement for small local studies. Mark-Release-Recapture (MRR) methods provide a great alternative to follow individuals in a landscape. They are used to estimate population sizes and demographic parameters of populations (Lebreton et al., 1992). In addition, MRR methods provide information about individuals' mobility. They are an easy way to obtain shapes of the distribution of dispersal distances, called dispersal kernels (Baguette et al., 2013). Pépino et al. (2012) developed a method based on dispersal kernels to estimate the permeability of motorway crossing structures for fishes. However, this original method based on MRR data is currently restricted to stream environments (Pépino et al., 2012, 2016). Stream environments only host a portion of the global biodiversity and similar methods are lacking to study terrestrial organisms.

Our question was to know if the framework developed by Pépino et al. (2012) could be expanded on terrestrial organisms to estimate potential barrier effects of LTIs. Specifically, we developed a simple method consisting in evaluating the barrier effects of any kind of linear structures in a landscape. We assessed the reliability of our method with simulations. Finally, as an example of the method deployment, we applied it on a butterfly species within a landscape presenting multiple LTIs. We predicted that our method would be able to detect barrier effects, if present. In addition, we predicted that large infrastructures would limit, at least to some extant, crossing events of butterflies.

Method

0.1 Method framework

The first step of the method consists in obtaining data of individuals crossing or not crossing a LTI using Mark-Release-Recapture surveys. Ideally, the LTI is located in the middle of the study site and individuals monitored all around. Capture sessions must be close enough in time to obtain a relatively high number of recapture distances. In addition, in order to cover the entire range of distances travelled by the model species, the study site must be large enough to detect long distance dispersal events. During the surveys, each side of the LTI should be equally sampled for marked individuals that either crossed the LTI or stayed on the same side.

The second step of our method consists in measuring the distribution of dispersal distances (dispersal kernel) of the species under study. The dispersal kernel is a dispersal index calculated as the inverse cumulative proportion of individuals moving certain distances. Dispersal kernels are obtained by fitting mathematical curves to the empirical data. They are commonly used to compare dispersal abilities of species (e.g. Stevens et al., 2010). In our framework, the dispersal kernel is a proxy to estimate movement capacity of individuals. Therefore, we used a broad definition of dispersal kernel as a way to describe movement capacity instead of effective dispersal. Movement distances are obtained using Mark-Release-Recapture surveys. These data can either be based on existing literature or by using a neutral site where infrastructures are absent.

The third step consists in fitting the dispersal kernel to a theoretical distribution. Dispersal kernels are usually fitted to a large range of theoretical distributions; including log-normal (Skarpaas et al., 2005), leptokurtic (Pépino et al., 2012), negative exponential and inverse power distributions (Hill et al., 1996), among others. Once the best theoretical distribution is fitted to the data, the parameters derived from the theoretical distribution are used to calculate the expected crossing probability P_{cross} (probability for an individual to reach the other side of the LTI) as well as the expected non-crossing probability P_{stay}. P_{cross} and P_{stay} are calculated as if the LTI is completely permeable to individual movements (neutral model). A value of P_{cross} and P_{stay} is calculated for each individual recaptured on the study site. These expected probabilities are calculated based on the distance between the location of the captured individual and the LTI. The probability $P(d)$ for an individual captured at location C to be recaptured at a distance d is integrated on the geometry of the field site (Fig. 1). After capture, individuals can be recaptured either in area $A3$ (Fig. 1) with a certain probability (P_{cross}), or in $A1$ with the probability P_{stay}. $A2$ is the area corresponding to the probability to be on the LTI (P_{LTI}) and is usually inaccessible during MRR surveys (e.g. fenced motorways and railways).

In this framework, the only required parameter is the orthogonal distance from individual capture location to the infrastructure. The longer the distance to the LTI, the less chance the individual has to cross the infrastructure.

The last step consists in investigating the barrier effect of the LTI on individual movements. To do so, P_{cross} is compared with empirical data obtained in step 1. Empirical data provide a proportion of individuals either successfully crossing the LTI or staying. The probability of crossing (success) or staying (fail) follows a Bernoulli trial with a number of trials corresponding to the number of individuals recaptured on the study site. The ratio number of successes/number of trials observed is compared to the average expected probability of crossing (P_{cross}) using an exact binomial test. In addition, Odd Ratios are used to compute effect sizes, comparable among studies and organisms.

Our framework can be summarised as follow:

1. Using MRR, obtain empirical data of crossing/non-crossing events along the studied LTI portion.

2. Obtain the distribution of movements of the studied organism based on literature or based on a neutral site where movements are not disturbed.

3. Fit a theoretical distribution (kernel) on the dispersal distances and cal-

culate an expected probability of crossing the LTI (P_{cross}).

4. Assess LTI's permeability by comparing empirical data from step 1 against expected probabilities.

0.2 Simulations

In order to test the reliability of the method, we designed a simulation study using personal scripts. We simulated a study site of 1000x650 m crossed in the middle by a linear infrastructure, and 1000 random points representing the capture locations of individuals. Every point located on the infrastructure was discarded from the data set. Each individual was then assigned a random direction and a random movement distance sampled from a Negative Exponential Function (NEF) kernel distribution, obtained from an inverse transform sampling method (Devroye, 1986). We used NEF as it fits the distribution kernels of a wide range of organisms (e.g. Palomares et al., 2001; Byrne et al., 2014) and has been widely used for butterflies (Hill et al., 1996; Fric and Konvicka, 2007).

We recorded final destinations of individuals. If the final destination of an individual was located outside the study site or on the infrastructure, this sample was discarded from the data set. We recorded whether an individual stayed or crossed the structure and applied our method to calculate the average expected probability of crossing among all individuals.

We generated three scenarios depending on the barrier intensity of the infrastructure; strong barrier effect, weak barrier effect or no effect. The strong barrier effect was generated by applying a crossing cost equal to two times the average movement capacity ($2\text{x}1/\alpha$). For example, with an average kernel movement ($1/\alpha$) of 20 m, the final movement distance of an individual that was initially supposed to move over 100 m and to cross the infrastructure was reduced of 40 m. Thus, the final movement distance shrinks to 60 m, possibly preventing that individual from actually crossing the infrastructure. The weak barrier was defined with a cost of $(0.5x1/\alpha)$ and the neutral model with no cost.

We generated 5000 simulations per scenario. For each simulation, we randomly generated (i) the 1000 capture locations of individuals, (ii) the average movement distance $1/\alpha$ and (iii) the width of the infrastructure. Alpha was picked from a uniform distribution ranging from 0.002 (average movement distance of 500 m) to 0.1 (average movement distance of 10 m). Infrastructure width was picked from a uniform distribution ranging from 5 to 50 m, so that the ratio between the infrastructure width and the average movement distance $(1/\alpha)$ was lower than 1.5.

For each simulation, we compared the average expected probability of crossing and the actual number of crossing events to compute the magnitude (effect size) and the precision (95% confident interval) of the barrier effect. We first calculated the effect size in the form of a logOddsRatio as follows (Borenstein et al., 2009):

$$logOR = \ln\left(\frac{obs}{N - obs} \times \frac{N - pth \times N}{pth \times N}\right)$$

Where N is the total number of captured individuals, obs is the number of crossing events and pth is the average expected probability of crossing. We then computed the approximate variance of the effect size as follows:

$$V = \frac{1}{obs} + \frac{1}{N - obs} + \frac{1}{pth \times N} + \frac{1}{N - pth \times N}$$

We finally computed the upper and lower limits of the 95% CI as follows:

$$CI = logOR \pm 1.96 \times \sqrt{V}$$

0.3 Method application on the butterfly *Maniola jurtina*

0.3.1 Study site

The study site was located in the 'Périgord' region in the South-West of France, between Brive-La-Gaillarde and Périgueux (45°07'31.8"N; 0°58'56.9"E; Fig. 2).

The LTIs crossed a rural landscape composed of limestone plateaux with low human density. Habitats included crops, mowed meadows, deciduous forests and small villages. We monitored two sites (A & B), each crossed by two LTIs (Fig. 2). In total, four types of LTIs were tested for their potential barrier effects. Accordingly, site A (9.7 ha) was crossed by a medium size power line (20.8 m wide), and a gas pipeline (13.2 m wide). Site B (11.9 ha) was crossed by a motorway (50.6 m wide) and a low traffic single-track railway (8.2 m wide). The final shapes of site A and B were constrained by inadequate habitats surrounding meadows and forest edges were sampling took place. Inadequate habitats were mostly intensive crops where butterflies could not be easily sampled due to their 'direct flight' behaviour when crossing such landscape elements. The two sites were separated by approximately 6.7 km (Fig. 2). To avoid potential geographic and habitat bias, we chose LTIs that were in close vicinity, in a similar orientation, parallel to each other in a comparable habitat type.

0.3.2 Model species

A majority of studies estimating barrier effects of LTIs, focus on large animals. Invertebrates are dramatically under-represented (Fahrig and Rytwinski, 2009) despite their huge mortality due to collision with vehicles (Baxter-Gilbert et al., 2015; Skórka et al., 2015) and their drastic collapse in landscapes (Hallmann et al., 2017). Invertebrates also provide easily large data sets that are useful to investigate new methods such as the one we developed. We chose to test the method on a common species with high population abundances, good mobility capacities and generalist habitat requirements. These conditions were fulfilled by the meadow brown, *Maniola jurtina*, a common and widespread butterfly species in Europe. The ideal habitat for this species consists of open grasslands with medium to high vegetation cover. Median life span of adults is 6.55 days (Bubová et al., 2016). Flight period lasts about 67 days from June to September (Bubová et al., 2016). Caterpillars feed on a wide range of grass species with some preferences for *Poa spp.*, *Agrostis spp.* and *Lolium spp.* (Brakefield, 1982;

Thomas and Lewington, 1991).

0.3.3 Data collection

The mobility of *M. jurtina* was investigated with MRR surveys in summer 2015 on site A (13 July to 26 August) and in summer 2016 on site B (06 June to 16 August). We randomly walked through each entire study site during day time (9am to 6pm) and captured the maximum number of *M. jurtina* individuals following a robust sampling design (Pollock, 1982). Sites were surveyed for three consecutive days (secondary sampling events) every two weeks (primary sampling events). In total, sites A and B were surveyed during 12 and 18 days, respectively. Butterflies were captured with nets, sexed and individually marked with fine-tipped permanent ink pen on the underside of the left hind-wing. Date of capture (or recapture) and GPS locations were recorded (Garmin Etrex20, USA). See Fig. 2 for the sampling effort on each site. Care was taken to minimize butterflies handling and wing injuries. We sampled equally each side of the four infrastructures for new individuals and recaptured individuals.

0.3.4 Data analysis

When butterflies were recaptured, we calculated the euclidean distance between the locations of capture and recapture. We also determined the closest straight distance between capture location and both LTIs present on each site. Recapture events were classified either as 0 when butterflies remained on the same side of the LTI or as 1 when they crossed the LTI. Individuals recaptured within the same day were excluded from analyses to avoid any bias due to butterflies' altered behaviours facing capture events.

In order to determine whether recaptured butterflies followed random directions after capture event, we performed Rayleigh tests at the site level (pooling all recapture events from a given site).

The recapture events were used to calculate a dispersal kernel of *M. jurtina* on each site. The dispersal kernels were fitted using a negative exponential function (NEF : $P(d) = \beta e^{-\alpha d}$) and an inverse power function (IPF: $P(d) = \alpha d^{\beta}$), the two most commonly used theoretical distributions for butterflies' dispersal kernels (Hill et al., 1996). In both distributions, the probability to travel a certain distance $P(d)$ depends on the distance (d) and the constants β and α. Preliminary results showed that on both sites, NEF gave a better fit than IPF ($R^2 = 0.84$ (IPF) and 0.91 (NEF) on site A and $R^2 = 0.69$ (IPF) and 0.98 (NEF) on site B). Therefore, we used NEF to model *M. jurtina* dispersal kernel. In NEF, α is a synthetic descriptor of the kernel and $1/\alpha$ corresponds to the average distance travelled by the butterfly (Stevens et al., 2010). On the two studied sites, we found an average movement distance ($1/\alpha$) of 116 m on site A and 64 m on site B. These values may underestimate the true dispersal capacity of *M. jurtina* due to the presence of the infrastructures on the two study sites. This would be particularly the case on site B where the motorway and the railway are present. Therefore, the movement capacity of *M. jurtina* was based on existing literature. We identified nine published studies where the average movement distances travelled by *M. jurtina* were reported or could be calculated. In these studies, the average mobility capacity ranged from 39 m to 428 m (Brakefield, 1982; Munguira and Thomas, 1992; Lörtscher et al., 1997; Merckx and Van Dyck, 2002; Schneider et al., 2003; Valtonen and Saarinen, 2005; Grill et al., 2006; Öckinger and Smith, 2007; Ouin et al., 2008) with an average of 127 m (suppFile) resulting in a value of α of 0.0079. We used this value to calculate P_{cross}. As illustrated in Fig. 1, P_{cross} corresponded to the probability of recapturing an individual captured in C in the $A3$ area (volume occupied by the dispersal kernel behind the LTI and covering $A3$). Hence:

$$P_{cross} = \gamma \int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} \int_{d_i+e}^{\infty} P(d) d^2 dr.d\theta \qquad (1)$$

Where d_i the shortest straight distance between the initial capture location (C) and the LTI. θ the angle between d_i and the intersection between the radius and the LTI and e the LTI's width (Fig. 1). P_{cross} is bounded between 0 and 1 while NEF is defined on R^*. Thus, γ corresponds to the adjustment parameter insuring that probability ranges between 0 and 1. γ was estimated by considering the specific case where $d_i + e = 0$, then $P_{cross} = 0.5$ leading to $\gamma = \frac{\alpha}{2\beta\Pi}$.

Consequently:

$$P_{cross} = \frac{1}{2\Pi}\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} e^{-\alpha\frac{d_i+e}{cos\theta}} d\theta \tag{1'}$$

In situations where the area $A2$ cannot be sampled (individuals on the infrastructure), the probability of crossing (P_{cross}) is corrected (CP_{cross}) with the inaccessibility of the LTI. Therefore, we estimated (P_{LTI}), the probability that an individual is located on the infrastructure area:

$$P_{LTI} = 1 - (P_{cross} + P_{stay}) \tag{2}$$

Where P_{stay} corresponds to the probability of recapturing an individual captured in C in the $A1$ area (volume occupied by the dispersal kernel before the LTI and covering $A1$). It can be estimated as follow:

$$P_{stay} = 1 - \gamma\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}}\int_{d_i}^{\infty} P(d)d^2dr.d\theta \tag{3}$$

Leading to:

$$P_{stay} = 1 - \frac{1}{2\Pi}\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} e^{-\alpha\frac{d_i}{cos\theta}} d\theta \tag{3'}$$

Finally, the corrected probability of crossing is calculated as follow:

$$CP_{cross} = \frac{P_{cross}}{1 - P_{LTI}} \tag{4}$$

Comparison between CP_{cross} and empirical data were made using binomial tests and effect sizes were evaluated using log Odd Ratios. All analyses including simulations were performed with R V3.2.3 (R Core Team, 2015) and QGIS (V.

2.8). Results were given with standard errors unless specified.

Results

0.4 Simulations

Simulated data revealed that our method was able to detect barrier effects when ratios were small (Fig. 3). Small ratios reflected narrow infrastructure widths in comparison to the average movement capacity of the studied organism. A ratio of 1 corresponded to an infrastructure width equals to the averaged distance moved by the studied organism. Based on the 95% confident intervals, we found that when the infrastructure has a strong barrier effect, we were able to detect the effect up to a ratio of 0.7. With a 50 m-wide LTI, this means that we can always detect the effect if the average distance moved by the studied organism is larger than 70 m. For weak barriers, we observed the same pattern but the effect could be detected only for ratio lower than 0.27. With a barrier of 50 m, this corresponded to an averaged distance moved by the studied organism larger than 200 m. When the infrastructure was permeable to movements, our method did not detect any artefactual barrier effect (Fig. 3).

0.5 Survey on the butterfly *Maniola jurtina*

A total of 3182 *Maniola jurtina* butterflies were captured and marked, 1035 on site A of which 92 were recaptured (8.9%), and 2147 on site B of which 155 were recaptured (7.2%).

The greatest measured distance between two capture sessions was 504 m within a 14 days interval but a 409 m distance was recorded in a single day interval (site A) showing that some individuals were able to cover large distances rapidly. Butterflies were recaptured on average after 4.12 ± 0.45 days on site A and 5.99 ± 0.80 days on site B. Longest recapture intervals were 29 days and 59 days on site A and B, respectively. Both were females. We captured similar numbers of males and females in site A (percentage of males: 44.6%, $\chi^2(1) =$

1.17, $p = 0.25$) but more males than females in site B (percentage of males: 63.6%, $\chi^2(1) = 7.40$, $p = 0.006$).

On site A, we did not detect any deviation from a uniform (random) directionality in butterfly movements (Rayleigh test = 0.054, $p = 0.74$). On site B, a weak deviation from a uniform distribution of movement directions was detected (Rayleigh test = 0.14, $p = 0.042$). Butterflies recaptured on site B had a tendency to follow a West to East direction (alternative Rayleigh test with specified mean direction = 0.14, $p = 0.006$).

When applying our method on this study case, we found that the ratios infrastructure widths/average movement capacity ranged between 0.06 for the railway (8.2/127) to 0.40 for the motorway (50.6/127). Therefore, we were always able to detect a barrier effect if it was present.

On site A, butterfly movements were not affected by the two LTIs present. Eight (7.8%) butterflies crossed the gas pipeline. Based on our method, 12 crossing events were expected (Fig. 4). Although we observed less crossing events than expected, this result was not significant (logOddsRatio -0.46 [95% CI -1.41–0.48]; binomial test $p = 0.28$). On the same site, a higher number of butterflies crossed the power line than expected by our method (11 (10.7%) crossing events against 6 expected). This difference was also not significant (logOddsRatio 0.64 [95% CI -0.37–1.66]; binomial test $p = 0.065$; Fig. 4).

On site B, we detected a strong barrier effect of the motorway (logOddsRatio -1.80 [95% CI -2.79– -0.81]; binomial test $p < 0.0001$). Our method expected 24 crossing events but only 5 (2.9%) were recorded. This represents a 5 times diminution of crossing events through the motorway. On the same site, our method expected 35 crossing events through the railway. During the field surveys, 29 crossing events were recorded, suggesting a neutral effect of the railway (logOddsRatio -0.32 [95% CI -0.86–0.23]; binomial test $p = 0.22$; Fig. 4).

Discussion

Understanding how animal movements are affected by LTIs is a key issue in applied ecology. The framework we propose in this study is a simple way of estimating the permeability of large-scale transportation infrastructures on a wide range of terrestrial species. Our method highlights new applications in terrestrial environments by following individuals in two dimensions. This is an improvement of already existing methods restricted to linear features such as in stream environments (Pépino et al., 2012, 2016).

Based on simulations, we found that our method was performing well to detect barrier effects when ratios were small. Ratios represent the relationship between the infrastructure width divided by the average movement distances of the studied organism. When the ratios were larger than 0.7, our method showed a lack of power to detect barrier effects.

Considering these results, we believe that our method is particularly suitable for organisms with good mobile capacities such as mammals, birds or flying invertebrates. However, this method may be unsuitable for organisms with low mobile capacities such as ground invertebrates, amphibians or reptiles. This statement is strongly context-specific and depends on the width of the infrastructure studied. With a 5 m-wide strong barrier, the method will be able to detect the barrier effect if the studied organisms has an average movement capacity of 7 meters or more. This will be the case for most organisms including small invertebrates, amphibians or snakes. Detecting barrier effects of wide infrastructures such as motorways would be complicated for animals with reduced movement capacities. However, for such structures, ecologists and managers are usually more interested in the connectivity of large animals such as wolfs or deer (Fahrig and Rytwinski, 2009). For example, the average movement distance capacity of a badger is 1.7 km (Byrne et al., 2014). With a wide infrastructure of 50 m, the ratio would be 0.03. This value would allow to detect barrier effects with a great power (Fig. 3), even if the barrier effect is weak.

In this study, data on the butterfly *M. jurtina* on four types of LTIs were used to illustrate the method framework. The ratio infrastructure width/average movement capacity was always smaller than 0.7 and therefore, our method could be considered powerful enough to detect a barrier effect if it was present.

We found that the motorway was the only studied LTI with a significant barrier effect on the mobility of butterflies. Five crossing events were recorded, as against 24 expected crossing events. The barrier effect detected can arise from two causes. Butterflies might avoid crossing the structure or be killed while trying. Avoidance behaviour due to LTIs has been demonstrated in previous studies (Munguira and Thomas, 1992; Polic et al., 2014). Butterflies might be able to perceive the danger of flying over the motorway. Danger perception to fly over inadequate habitats suggests that movements are not random and that butterfly behaviours are influenced by landscape structures (Dover and Settele, 2009). Avoidance might also be due to the physical characteristics of the motorway preventing butterflies to cross. These characteristics may include aerial turbulences due to traffic, changes in thermal conditions, edge configuration, and noise generated by traffic. In our study, avoidance behaviour was supported by field observations where individuals were observed heading back when reaching the motorway. Alternatively, butterfly might be killed while trying to cross the motorway due to collision with vehicles. Road-kill is known to affect tremendously butterflies (Baxter-Gilbert et al., 2015; Skórka et al., 2015) and to participate greatly to the large-scale decline of invertebrates (Hallmann et al., 2017). Both causes (avoidance and mortality) might drive together the barrier effect detected. In order to disentangle the two causes, behaviour monitoring of butterflies along the infrastructures could help understand which cause is the most influential in driving the barrier effect.

The railway was not acting as a barrier to butterfly movements (Fig. 4). The railway we studied is a small single rail structure with low traffic density (less than 10 trains per day). This result is consistent with Vandevelde et al. (2012) who found a neutral effect of a high speed railway on a butterfly with similar life history traits as *M. jurtina*.

On site A, the two infrastructures present (power line and gas pipeline) were not affecting the mobility of *M. jurtina*. These results were concordant to expectations when considering the structural features of these two infrastructures. Along these two LTIs, utility right-of-ways are created to prevent vegetation interference with power lines and gas pipelines. Utility right-of-ways can be beneficial to a wide range of species, including bees (Russell et al., 2005) and grassland species (Lampinen et al., 2015). These alternative habitats provided by right-of-ways may be used by butterflies in a way similar to surrounding meadows.

Butterflies' movements on site B differed slightly from a random distribution, meaning that some directions were preferred. We found that there was a tendency of butterflies to follow preferentially West to East directions. Dominant winds in the region in summer are from W, N-W. Butterflies' movements might be affected by the wind because they spend more energy when flying against dominant winds. However, winds in the region are weak and we did not find a similar pattern on site A, which was less than 7 km apart from site B. Both sites have similar habitat types and site A is 50 m higher in elevation, located at the top of a small hill. Because butterflies' movements are random on site A, we believe that wind has a limited influence on individual movements. On site B, both LTIs (the motorway and the railway) are also arranged in a West-East direction (Fig. 2). The preferred direction of butterflies could thus be better explained by the perturbation due to the barrier effect of the motorway.

Our method is limited by the availability of existing literature of the species under study in order to build the dispersal kernel. In cases where there is no information on the movement capacity of the studied species, dispersal kernels can be estimated on a control site where infrastructures are absent. Estimating the dispersal kernel directly with data from the studied site (with the presence of the studied infrastructure) might shrink the dispersal kernel due to the potential barrier effect of the infrastructure. In our case, averaged movements based on dispersal kernels was 116 m on site A. This value was similar to the average value of 127 m found in the literature (supp file). This is probably due to the fact that the gas pipeline and the power line present on that site have no barrier effects. However, on site B, average movement was twice lower (64 m). This value could be biased due to the presence of the motorway.

Conclusion

We were able to develop a method that estimates barrier effects due to linear infrastructures on a wide range of terrestrial species. We showed that this method is powerful to detect barrier effects, especially for organisms with good mobile capacities. We encourage managers to adapt this framework when looking at the connectivity of populations within landscapes fragmented by LTIs, notably when landscape genetic approaches are not worth considering. This could be used to set up mitigation programs on existing infrastructures and to propose conservation management strategies for species particularly at risk. Finally, while flying invertebrates, such as *Maniola jurtina*, already suffer drastic declines, we revealed that motorways can limit their dispersal by creating barriers in landscapes.

1 Authors' contributions

JR, EC and SM contributed to the conception and design of the study. EC and JR collected the data. EC, JR and JGP performed data analysis. JGP designed the simulation study, ran simulations and analysed simulated data. JR wrote the manuscript. All authors participated in critical revisions of the manuscript.

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Data accessibility

Butterfly field data for the two sites: uploaded as online supporting information (Table S1). R scripts to perform analysis and simulations: uploaded as online supporting information (Appendix S1).

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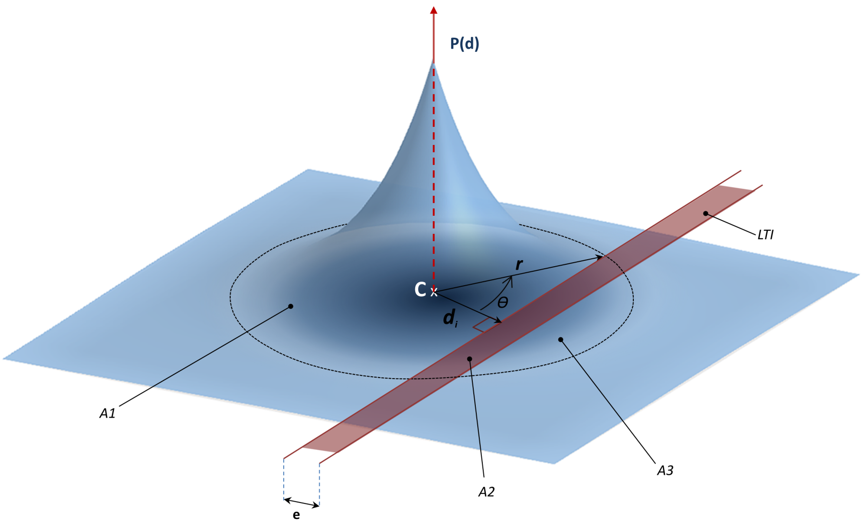

Figure 1: Three-dimensional representation of the conceptual framework used to calculate expected probabilities of crossing a Large-scale Transportation Infrastructure (LTI)(see text). Empirical data on movement is used to fit the P(d) function (dispersal kernel). The higher the distance between the capture location (C) and the infrastructure (d_i) and the width of the infrastructure (e), the lower the chance individuals have to cross the infrastructure. The distance r and the angle θ are used to estimate the area A1 (staying) and A3 (crossing).

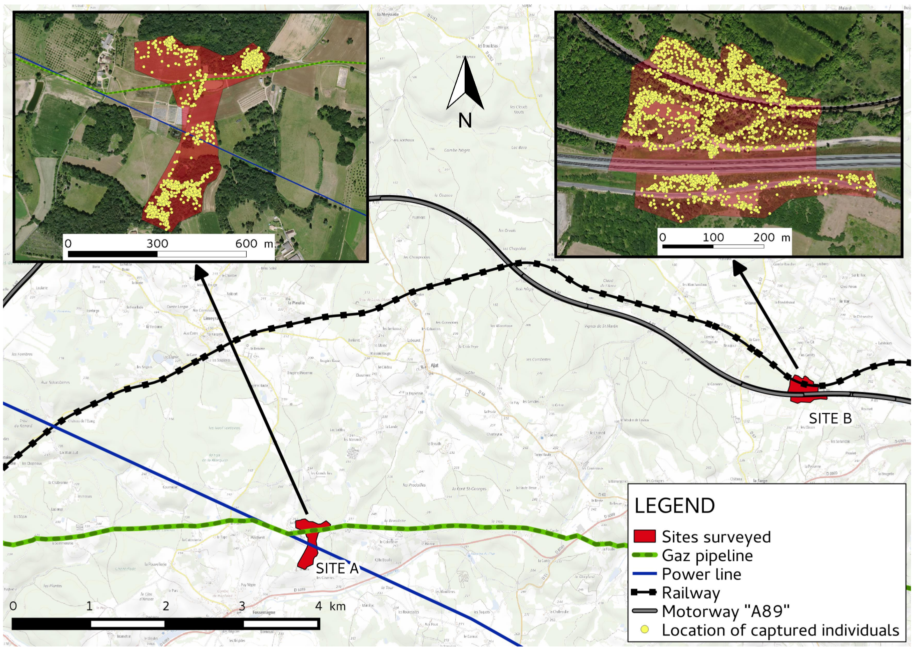

Figure 2: Study sites in the 'Périgord' region in the South-West of France. Site A was surveyed in 2015 and site B in 2016. Two different LTIs crossed each site.

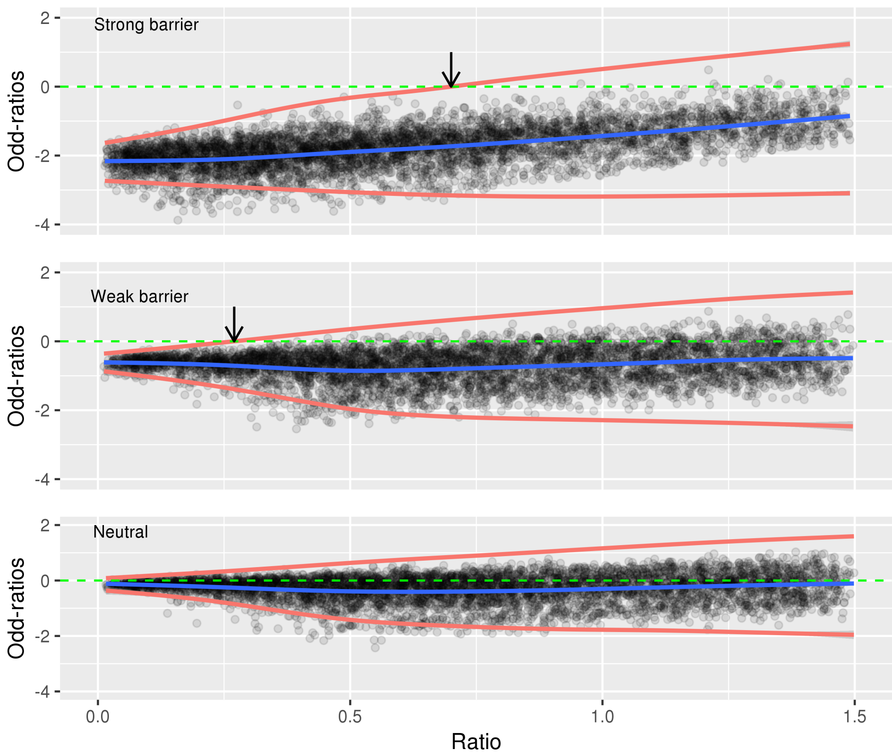

Figure 3: Method application on 5000 simulated data per scenario type. We simulated three scenarios: a strong barrier, a weak barrier and a neutral model. Various barrier sizes (from 5 to 50 m) and various movement capacities (mean distance capacity from 10 to 500 m) were also simulated. This two components were synthesized in a single ratio (= barrier width divided by average distance capacity). A ratio of 1 corresponds to a barrier size equal to the average distance capacity of the organism. Blue lines represent log Odd-Ratios and red lines the 95% confident interval. If the dashed green line is inside the 95% confident interval, no barrier effect could be detected with our method. Arrows represent the thresholds where our method was able to detect a barrier effect.

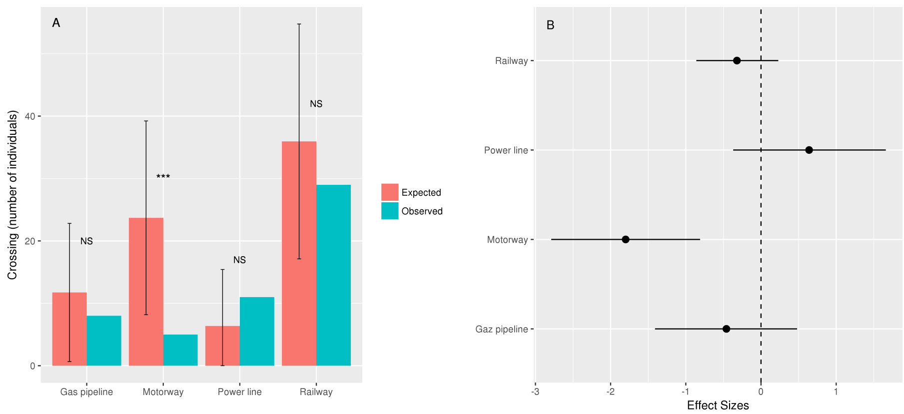

Figure 4: Comparison between expected and observed probability that *Maniola jurtina* crosses four types of LTIs in the study sites. Expected probabilities were calculated from a theoretical distribution fitted to a dispersal kernel as if LTIs were completely permeable. Panel A shows the comparison between expected and observed number of crossing events. Error bars represent mean $\pm$ SD. Significances were based on binomial tests. NS: Non Significant, *** : $p \leq 0.001$. Panel B shows effect sizes (logOddsRatio) $\pm$ 95% confident intervals.