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5 authors, including:

Jonathan Remon
French National Centre for Scientific Research

Chevallier Emmanuelle
AgroParisTech

Jerome G. Prunier
Station d’Ecologie Théorique et Expérimentale du CNRS à Moulis

Michel Baguette
Muséum National d'Histoire Naturelle

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Jonathan Remon[1,2*] Emmanuelle Chevallier[2] Jérôme G. Prunier[2]
Michel Baguette[2,3] Sylvain Moulherat[1]

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*Corresponding author: jonathan.remon@wanadoo.fr

[1] TerrOïko, 14 Rue Ferlus, BP 26, 81540 Sorèze, France

[2] CNRS-Université Paul Sabatier, UMR 5321, Station d'Ecologie Théorique & Expérimentale, 2 Route du CNRS, 09200 Moulis, France

[3] Museum National d'Histoire Naturelle, UMR 7205, Institut de Systématique, Evolution, Biodiversité, Rue St Hillaire, 75005 Paris, France

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Running headline: A METHOD TO DETECT BARRIER EFFECTS OF INFRASTRUCTURES

Abstract

Context.

Barrier effects of Large-scale Transportation Infrastructures (LTIs) 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 surveys to estimate barrier effects of LTIs that could be easily applied in various landscape contexts and on any mobile species.

Methods.

Our method uses dispersal kernels of animal movements to calculate an expected probability of crossing any particular linear feature. This probability is then compared to observed crossing events to estimate the barrier effect. We used simulations to test the reliability of our method and applied this framework on the butterfly *Maniola jurtina* in a landscape fragmented by a motorway and a railway.

Results.

Simulations showed that our method was able to detect efficiently even weak barrier effects given that enough data are available. When sample size was reduced, our method was able to detect barrier effects only when the infrastructure width was small in comparison to the average movement capacity of organisms. In our case study, both infrastructures acted as significant barriers.

Conclusions.

The power of our method is to use MRR data which are more representative of population processes than telemetry monitoring and are not limited by time-lag involved in genetic studies. This framework is of particular interest for conservation studies in order to assess how individual movements are modified by linear infrastructures.

Key-words: barrier effects; butterfly; habitat fragmentation; 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 or 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 because of 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 that 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 risk of population extinction (McCauley, 1991; Fagan and Holmes, 2006).

In practice, LTIs effects are not always negative and are context dependent. 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 few studies revealed 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 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 in the alpine newt in Switzerland but Prunier et al. (2014) found that a similar motorway did not affect gene flow in the same species in France.

Therefore, when trying to understand 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 infrastructures may not have been in place for long enough to allow detecting effects on genetic metrics (e.g. Prunier et al., 2014). Furthermore, genetic methods can be expensive and deterrent for small local studies. Direct monitoring using telemetry or Mark-Release-Recapture (MRR) data provides an interesting alternative to follow individual movements within a landscape. Telemetry framework have been previously developed to assess barrier effects of infrastructures (e.g. Shepard et al., 2008; Colchero et al., 2011; Beyer et al., 2016). However, telemetry data might be tricky to obtain for small organisms, they require costly equipment and generally concern a small fraction of the population. Alternatively, MRR data are cost effective, a large portion of the populations can be monitored and they can be applied to small species for which other monitoring techniques are inappropriate (e.g. small butterflies). MRR data are used to estimate population sizes and demographic parameters of populations (Lebreton et al., 1992) but provide additional information about individuals' mobility. They are an easy way to obtain dispersal kernels (the shape of the distribution of dispersal distances (Baguette et al., 2013)). Dispersal kernels can be used in modelling frameworks in order to predict the movement of individuals across specific barriers. The comparison between the predicted number of individuals crossing the barrier and direct crossing observations can be achieved using MRR data. So far, such modelling frameworks have been used only in one dimension environments (rivers) to estimate barrier effects of infrastructures (Pépino et al., 2012, 2016). Specifically, Pépino et al. (2012) used dispersal kernels and observation data to estimate the permeability of motorway-crossing structures for fishes. However, stream environments only host a portion of the global biodiversity and similar methods are lacking to study terrestrial organisms.

We aimed at developing a modelling framework where the dispersal kernels of organisms can be used to assess barrier effects in two-dimension landscapes. This would allow the application of this framework to a wide number of species in various landscape configurations.

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 decline in Europe (Hallmann et al., 2017). Invertebrates also make it easy to collect large data sets that are useful to investigate new methods such as the one we developed here. Therefore, as an example of the method deployment, we applied our framework to study a butterfly species within a landscape crossed by a motorway and a railway. We predicted that the motorway would limit, at least to some extent, crossing events of butterflies due to vehicular collisions (Baxter-Gilbert et al., 2015) but that the railway would be neutral to movements (Vandevelde et al., 2012).

Method

Method framework

The first step of the 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. Movement distances are obtained using Mark-Release-Recapture surveys. Because kernels might vary due to landscape settings (e.g. Baguette and Van Dyck, 2007), their shapes might be biased by infrastructures. Therefore, dispersal kernels should be estimated on a control site with no LTI (or LTIs known as neutral) but with similar habitat configuration and similar time frame to the site under study. 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.

The second step of our method consists in obtaining data of individuals crossing or not crossing a LTI using Mark-Release-Recapture surveys on the study site. 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. 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 third step consists in fitting the dispersal kernel (obtained at the first step on a control site) to a theoretical distribution and to estimate the expected crossing probability across the LTI on the study site. 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 for each recaptured individual under the hypothesis that the LTI is completely permeable to individual movements (neutral model). Expected probabilities are based only on recaptured individuals as these values are later compared to crossing observations which are available only for recaptured individuals. Expected probabilities are computed as a function of the orthogonal distance between an individual capture location and the infrastructure (insuring that this individual was later recaptured). The longer the distance to the LTI, the lower the probability that the individual may cross the infrastructure. Figure 1 provides a three-dimensional representation of the conceptual framework used to calculate expected probabilities of crossing a LTI. The probability $P(x)$ for an individual captured at location C to be recaptured at a distance x is integrated on the geometry of the field site. A recaptured individual can be recaptured either in area $A3$ 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).

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 2. Empirical data provide the proportion of individuals that either successfully crossed the LTI or stayed on the same side. 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 observed ratio between the number of successes and the number of trials is compared to the average expected probability of crossing (P_{cross}) using an exact binomial test. In addition, OddsRatios are used to compute the magnitude and the precision of effect sizes, comparable among studies and organisms.

Simulations

In order to test the reliability of the method, we designed a simulation study using personal R-scripts. We simulated a study site with a linear infrastructure of 1000 m in length. As in real study design, we adapted the sampling area to the movement abilities of the studied species: on each side of the infrastructure, the width of the studied area was set as 95% of the dispersal kernel maximum distance. We simulated two specific cases with 100 or 500 points randomly distributed on the study site, respectively. These points represented the capture locations of individuals that we defined as being recaptured in our framework. We choose 100 points as it corresponded to the number of recapture events available in our empirical case and 500 to represent a scenario with a larger data set. In both cases, each individual was then assigned a random direction and a random movement distance sampled from a Negative Exponential Function (NEF: $P(x) = \beta e^{-\alpha x}$) 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). 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).

We recorded the final destination coordinates of each individual. 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. In such cases, additional simulations were performed to insure to the targeted number of data was obtained (100 or 500 individuals). 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 four times the average movement capacity ($4 \times 1/\alpha$). 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 80 m. Thus, the final movement distance shrinks to 20 m, possibly preventing that individual from actually crossing the infrastructure. The weak barrier was defined with a cost of ($1 \times 1/\alpha$) and the neutral model with no cost.

We generated 5000 simulations per scenario. For each simulation, we randomly generated (i) the average movement distance $1/\alpha$, (ii) the corresponding kernel distribution and the subsequent width of the study area on each side of the barrier (95% of the kernel distribution maximum distance), (iii) the

100 or 500 capture locations of individuals, respectively and (iv) 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 (W) and the average movement distance $1/\alpha$ (D) was lower than 1.5 (W/D ratio).

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% confidence interval) of the barrier effect. Here, effect sizes were computed in the form of logOddsRatios, following Borenstein et al. (2009) (equations 5.8 and 5.9).

Odd-ratios were computed as the ratio of observed to theoretical odds of crossing events. With N the total number of recaptured individuals, obs the number of observed crossing events and P_{cross} the average expected probability of crossing, observed odd was computed as the ratio of observed crossing events (obs) to observed non-crossing events ($N - obs$), whereas theoretical odd was computed as the ratio of theoretical crossing events ($N \times P_{cross}$) to theoretical non-crossing events ($N - N \times P_{cross}$). Hence:

$$OR = \frac{obs}{N - obs} \times \frac{N - N \times P_{cross}}{N \times P_{cross}} \tag{1}$$

And

$$logOR = \ln(OR) \tag{2}$$

The approximate variance V and 95% confidence interval CI of logOddsRatio were then respectively computed as follows (Borenstein et al., 2009) (equations 5.10 and 5.11):

$$V = \frac{1}{obs} + \frac{1}{N - obs} + \frac{1}{N \times P_{cross}} + \frac{1}{N - N \times P_{cross}} \tag{3}$$

And

$$CI = logOR \pm 1.96 \times \sqrt{V} \tag{4}$$

LogOddsRatios range from $-\infty$ to $+\infty$. A null logOddsRatio indicates that the observed odd of crossing is equal to the theoretical one. A barrier effect would thus be detected when the upper bound of the 95% CI is strictly negative, indicating that observed crossing events are way scarcer than expected.

Application of the method to the butterfly *Maniola jurtina*

Study site and biological model

The study area was located in the 'Périgord' region in South-Western France, between Brive-La-Gaillarde and Périgueux (45°07'31.8"N; 0°58'56.9"E; Fig. 2). The studied LTIs crossed a rural landscape composed of limestone plateaux with low human density. The landscape included crops, mowed meadows, deciduous forests and small villages. We monitored two sites: a control site and a study site (Fig. 2). The control site (9.7 ha) was used to estimate the dispersal kernel of the studied organism. The study site (11.9 ha) was crossed by a motorway (50.6 m wide) and a low traffic single-track railway located within a trench (8.2 m wide and 4 m deep). The shapes of the control and the study sites were constrained by inadequate landscape features surrounding meadows and forest edges where sampling took place. Inadequate landscape features were mostly non-habitat annual crops impracticable for experimenters (Delattre et al., 2010), in addition to hosting low *M. jurtina* densities (Ouin et al., 2008). The two sites were separated by approximately 6.7 km (Fig. 2) and comprised similar landscape elements. On the control site, a power line and a gas pipeline crossed the area but they were considered as having no effects on butterflies' movements (buried gas nozzles and aerial electric lines; see Appendix 1 for a detailed rationale behind this statement).

We chose to test the method on a mobile and generalist species with large demographic densities. 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 in open grasslands with medium to high vegetation cover. Based on MRR data, a median residence time of adults of 6.55 days was reported in Bubová et al. (2016) but under specific conditions, residence time can reach much higher values (Grill et al., 2013; Haeler et al., 2014). Flight period lasts in average 67 days (Bubová et al., 2016) but vary considerably between mid-May to October depending on geographic location, altitude and climate (Grill et al., 2013). 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).

Data collection

The mobility of *M. jurtina* was investigated with MRR surveys in summer 2015 on the control site (from 13 July to 26 August) and in summer 2016 on the study site (from 04 July to 16 August). Each site was surveyed for a time length of 44 and 43 days, respectively. We applied a similar sampling scheme on both sites: we randomly walked through each entire 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). This protocol is similar to a previous MRR study performed on the same species in Switzerland

(Lörtscher et al., 1997). The protocol was standardised and performed in the same way on both sites to insure that dispersal kernel obtained on the control site could be applied to the movements of butterflies on the study site. The variation of dispersal kernels in time is plausible (Schtickzelle et al., 2012) but because weather conditions, landscape settings and sex-ratio were similar on both sites (see results), there was no indication that movements of butterflies in 2015 should differ from 2016.

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 (re)capture and GPS locations were recorded (Garmin Etrex20, USA). See Fig. 2 for the sampling effort on each site. Care was taken to minimise butterflies handling and wing injuries. On the study site, we sampled equally each side of the two infrastructures for new individuals and recaptured individuals. To compare weather conditions between the two sites, we retrieved climatic data (temperatures and wind speed) for the periods July-August 2015 and 2016 from the nearest weather station at Gourdon (ca. 52 km from the study site, Météo-France).

Data analysis

When butterflies were recaptured, we measured both the euclidean distance and the direction of the observed trajectories from capture to recapture locations. To determine whether the average direction of observed trajectories were random or showed a direction trend, we performed Rayleigh tests at the site level (pooling all recapture events from a given site). On the study site, we also determined the shortest orthogonal distances between capture location and both LTIs. 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 short after capture events.

The recapture events on the control site were used to generate the dispersal kernel of *M. jurtina*. The dispersal kernel was fitted using a negative exponential function (NEF : $P(x) = \beta e^{-\alpha x}$) and an inverse power function (IPF: $P(x) = \alpha x^{\beta}$), 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 $P(x)$ depends on the distance x and the constants β and α. Preliminary results showed that NEF gave a better fit than IPF ($R^2 = 0.84$ (IPF) and 0.91 (NEF)). Therefore, we used NEF to model *M. jurtina* dispersal kernel. The value of α was used to calculate P_{cross}. As illustrated in Fig. 1, P_{cross} corresponded to the probability of recapturing an individual captured at C in the $A3$ area (volume occupied by the dispersal kernel behind the LTI and covering $A3$). Hence:

$$P_{cross} = \gamma \int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} \int_{d_i+e}^{\infty} P(x)dx.d\theta \qquad (5)$$

With d_i the shortest orthogonal 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 from 0 to 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:

$$P_{cross} = \frac{1}{2\Pi}\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} e^{-\alpha\frac{d_i+e}{cos\theta}} d\theta \tag{5'}$$

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:

$$P_{LTI} = 1 - (P_{cross} + P_{stay}) \tag{6}$$

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

$$P_{stay} = 1 - \gamma\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}}\int_{d_i}^{\infty} P(x)dx.d\theta \tag{7}$$

Leading to:

$$P_{stay} = 1 - \frac{1}{2\Pi}\int_{\frac{-\Pi}{2}}^{\frac{\Pi}{2}} e^{-\alpha\frac{d_i}{cos\theta}} d\theta \tag{7'}$$

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

$$CP_{cross} = \frac{P_{cross}}{1 - P_{LTI}} \tag{8}$$

Comparison between CP_{cross} and empirical data were made using binomial tests and effect sizes were computed using logOddsRatios. We provided a R-script with the function that we developed (NEFbarrDetect) which enables the calculation of these probabilities and the barrier effect statistics and effect sizes based on a data fame of recapture events (Supplementary file). All analyses including simulations were performed in R 3.2.3 (R Core Team, 2015) and QGIS (V. 2.8). Results were given with standard errors unless specified.

Results

Simulations

The ability of our method to detect barrier effects depended on the W/D ratio. Small W/D ratios reflect a narrow infrastructure width in comparison to the average movement capacity of the studied organism. A W/D ratio of 1 corresponds to an infrastructure width equal to the averaged distance moved by the studied organism.

When the infrastructure was permeable to movements, our method did not detect any artefactual barrier effect in the N = 100 or N = 500 scenario whatever the W/D ratio (less than 5% of detection errors, Fig. 3). For N = 100, simulated data revealed that our method was able to detect barrier effects when W/D ratios were small (Fig. 3). Based on the 95% confidence intervals, we found that when the infrastructure had a strong barrier effect, we were able to detect the effect only for W/D ratios smaller than 0.2. 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 250 m. The barrier effect could be detected up to W/D ratios of 0.5, but in such cases, the proportion of detection failures was high (Fig. 3). For weak barriers, our method lacked power to detect the barrier effect for the N = 100 scenario.

Our method was much more powerful when the sample size increased (N = 500 scenario). In the strong barrier case, our method was able to detect efficiently the barrier effect whatever the W/D ratio. In the weak barrier case, our method was still powerful enough to detect the barrier for W/D ratios lower than 0.5. With a barrier of 50 m, this corresponded to an average distance moved by the studied organism larger than 100 m.

Survey on the butterfly *Maniola jurtina*

A total of 2182 *Maniola jurtina* butterflies were captured and marked, 1035 on the control site of which 92 were recaptured at least once (8.9%), and 1147 on the study site of which 77 were recaptured at least once (6.7%).

The temperatures and wind speed between the sampling periods in 2015 and 2016 were similar (Temperatures: 2015 = 26.0 ± 0.3°C; 2016 = 25.5 ± 0.3°C; t(487) = 1.02; $p = 0.31$; Wind speed: 2015 = $2.43 \pm 0.07 m.s^{-1}$; 2016 = $2.30 \pm 0.05 m.s^{-1}$; t(470) = 1.47; $p = 0.14$).

The largest 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 (control site) showing that some individuals were able to cover large distances rapidly. Butterflies were recaptured on average after 4.12 ± 0.45 days on the control site and 4.47 ± 0.89 days on the study site. Longest recapture intervals were 29 days and 42 days on control and study site, respectively, and both individuals were females.

We recaptured more females than males on both the control and the study sites (Control site: 58

females as against 34 males, $\chi^2(1) = 6.26$, $p = 0.012$; Study site: 51 females as against 26 males, $\chi^2(1) = 8.12$, $p = 0.0044$). On both sites, the movement of butterflies did not deviate from a uniform (random) directionality (Control site: Rayleigh test = 0.054, $p = 0.74$; Study site: Rayleigh test = 0.164, $p = 0.11$).

Based on the kernel estimated on the control site, we found an average movement distance ($1/\alpha$) of 116 m. We found that males were more mobile than females with an average movement distance ($1/\alpha$) of 166 m for males and 104 m for females. Because, the sample size was already limited on the study site and because sex ratio was similar on both sites, we decided to analyse male and female data sets simultaneously and to use the value of $1/\alpha = 116$ m to build the dispersal kernel. When applying our method on this case study, we found that the W/D ratios ranged from 0.07 for the railway (8.2/116) to 0.44 for the motorway (50.6/116).

On the study site, two butterflies crossed the motorway as against 12 expected crossing events, and 7 butterflies crossed the railway as against 15 expected crossing events. The motorway was identified as a strong barrier (logOddsRatio -2.02 [95% CI -3.55– -0.48]; binomial test $p = 0.0007$; Fig. 4) with a sixfold diminution of crossing events. In the same way, the railway was identified as a barrier to butterflies movements (logOddsRatio -1.02 [95% CI -1.97– -0.06]; binomial test $p = 0.015$; Fig. 4) with a twofold reduction in crossing events. None of the butterfly crossed both infrastructures.

Discussion

Understanding how animal movements are affected by LTIs is a key issue in applied ecology. Dispersal kernels based on MRR data has been used to estimate barrier effects of infrastructures in one-dimensional environments (Pépino et al., 2012, 2016). But so far, a method applicable to two-dimensional landscape was lacking. Our framework proposes a simple way of estimating the permeability of linear LTIs on a wide range of terrestrial species. Compared to Pépino et al. (2012) whose framework relies on the use of both observation data and dispersal kernels corrected for the expected barrier permeability, our modelling framework is only based on dispersal kernels. It is therefore analogous to Rodríguez (2010) and does not require any a-priori information on the barrier effect of the studied infrastructure.

We found that our method performed well in detecting barrier effects as soon as an important data set is available (N = 500 scenario). For smaller sample sizes (N = 100 scenario), our method proved to detect barrier effects when the width of the infrastructure is small in comparison to the average movement capacity of the studied organism (small W/D ratio) and/or the effect of the barrier is strong.

Considering these results, we believe that our method is particularly suitable for organisms with good mobile capacities such as mammals, birds or flying invertebrates. If the barrier effect is weak and the sample size reduced, our method might be unsuitable for organisms with low mobility or low locomotor capacities such as ground invertebrates, amphibians (Trochet et al., 2014) or reptiles (Grimm et al., 2014), except when the considered infrastructure is narrow enough to counterbalance the lack of power associated with low average movement distances. With an only 5 m-wide barrier and a sample size of 500 individuals, the method will still be able to detect weak barrier effects as soon as the studied organism shows an average movement capacity of 10 meters or more. This will be the case for most organisms including small invertebrates, amphibians or reptiles. Detecting barrier effects of wide infrastructures such as motorways would be complicated for animals with reduced movement capacities and small data sets. However, for such structures, ecologists and managers are usually more interested in the connectivity of large animals such as wolves or deer (Fahrig and Rytwinski, 2009). For example, the average movement distance capacity of a badger is 1.7 km (based on 474 movement records) (Byrne et al., 2014). With a wide infrastructure of 50 m like a motorway, the corresponding W/D ratio would be 0.03, providing great power to detect even weak barrier effects (Fig. 3).

In this study, data on the butterfly *M. jurtina* along two types of LTIs were used to illustrate the method. The estimated kernel calculated with butterflies from the control site (average movement capacity = 116 m) was very similar to the kernel estimated in a previous MRR study performed on the same species in western France (average movement capacity on three sites = 100 m) (Ouin et al., 2008).

The W/D ratio was high for the motorway (0.44) suggesting that a barrier effect, if present, would have been hard to detect considering the reduced sample size in our study. Yet, we found that the number of crossing through the motorway was sixfold reduced. We were able to detect this effect probably because the motorway had a strong barrier effect that would have not been detected if the barrier effect was weaker. Concerning the railway, the W/D ratio was small (< 0.1) and therefore, our method can be considered powerful enough to detect a strong barrier effect if present (Fig. 3). We detected an effect of this infrastructure although we were expecting a neutral effect because the studied railway is a small single rail structure with low traffic density. Our results differ from Vandevelde et al. (2012) who found a neutral effect of a high speed railway on a butterfly with life history similar to *M. jurtina*.

The barrier effects detected can arise from two causes. Butterflies might avoid crossing the structures 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 or the railway. Danger perception to fly over inadequate features suggests that movements are not random and that butterfly behaviours are influenced by landscape structures (Dover and Settele, 2009). Avoidance might be due to the physical characteristics of these two LTIs 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, with individuals observed heading back when reaching the motorway. Alternatively, butterfly might be killed while trying to cross these LTIs due to collision with vehicles. Given the low traffic density on the railway, mortality due to collision is supposed to be of limited intensity. It is more likely that edge configuration and/or changes in thermal conditions explain the barrier effect of the railway. For instance, the steep change in slope characterising the railway trench might act as an edge barrier to dispersal, although further investigation are now needed to confirm this hypothesis. However, mortality due to collision on the motorway may be substantial as 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 detected barrier effect of the motorway. In order to disentangle the two causes, behaviour monitoring of butterflies along the infrastructure could help understand which cause is the most influential in driving the barrier effect.

Seasonal variation in the movements of butterflies (and any type of organism in general) is likely to occur (Schtickzelle et al., 2012). For example, butterflies tend to be less active during the hottest month of summer with reduced travelled distances than earlier or later in the season (Grill et al., 2013). As a consequence, the dispersal kernel estimated might vary depending on the sampling period on the control site. This implies that, besides similar landscape characteristics, similar sampling time periods are to be considered between the control and the study site: the species dispersal kernel might otherwise be under- or overestimated, with possible spurious conclusions as to the barrier effects of studied infrastructure (see Appendix 2 for details). For the same two reasons, we discourage the use of data from the literature to compute the dispersal kernel. Our method is also limited by sample size. We believe that data sets with 500 recapture events or more are optimal to apply our method. Depending on the species, this number might be difficult to achieve but would provide solid conclusions. Our method also implies that the LTI under study is linear across the study site as it considerably simplifies the equations. A potential improvement of our method would be to broaden the equations to account for non-linear LTIs. Yet, linear LTIs are most often encountered in landscapes due to obvious cost reasons and our method should be applicable in most cases. Although our method may be used to assess the cumulative barrier effect of several contiguous LTIs, our empirical dataset did not allow us to test for this as no butterfly crossed both the railway and the motorway (at least one crossing event is necessary to calculate logOddRatios).

Conclusion

We developed a method that allows estimating 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 investigating 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. We recommend to collect large data sets (ideally 500 recapture events) with similar time frame and landscape characteristics between the study and the control sites in order to build solid conclusions when applying this framework. Finally, while flying invertebrates, such as *Maniola jurtina*, already suffer drastic declines, we revealed that motorways and railways can constrained organism home ranges and represent an additional threat to small wildlife.

Authors' contributions

JR, EC, SM and MB 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.

Data accessibility

Butterfly empirical data (motorway.csv and railway.csv) and R-scipts are uploaded as online supporting information. We provided a standalone R function (NEFbarrDetect.R) that estimate the barrier effect of any linear feature based on our method. Supplementary material (Appendix 1 and 2) is uploaded as online supporting information.

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References

Ascensao, F., Mata, C., Malo, J. E., Ruiz-Capillas, P., Silva, C., Silva, A. P., Santos-Reis, M. and Fernandes, C. (2016). Disentangle the causes of the road barrier effect in small mammals through genetic patterns, *PLoS ONE* **11**(3): e0151500. doi:10.1371/journal.pone.0151500.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. and Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks, *Biological Reviews* **88**(2): 310–326. doi:10.1111/brv.12000.

Baguette, M. and Van Dyck, H. (2007). Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal, *Landscape Ecology* **22**(8): 1117–1129. doi:10.1007/s10980-007-9108-4.

Balkenhol, N. and Waits, L. P. (2009). Molecular road ecology: Exploring the potential of genetics for investigating transportation impacts on wildlife, *Molecular Ecology* **18**(20): 4151–4164. doi:10.1111/j.1365-294X.2009.04322.x.

Bartoszek, J. and Greenwald, K. R. (2009). A population divided: Railroad tracks as barriers to gene flow in an isolated population of marbled salamanders (Ambystoma opacum), *Herpetological Conservation and Biology* **4**(2): 191–197.

Bartzke, G. S., May, R., Solberg, E. J., Rolandsen, C. M. and Røskaft, E. (2015). Differential barrier and corridor effects of power lines, roads and rivers on moose (Alces alces) movements, *Ecosphere* **6**(4): art67. doi:10.1890/ES14-00278.1.

Baxter-Gilbert, J. H., Riley, J. L., Neufeld, C. J. H., Litzgus, J. D. and Lesbarrères, D. (2015). Road mortality potentially responsible for billions of pollinating insect deaths annually, *Journal of Insect Conservation* **19**(5): 1029–1035. doi:10.1007/s10841-015-9808-z.

Beyer, H. L., Gurarie, E., Börger, L., Panzacchi, M., Basille, M., Herfindal, I., Van Moorter, B., R. Lele, S. and Matthiopoulos, J. (2016). 'You shall not pass!': Quantifying barrier permeability and proximity avoidance by animals, *Journal of Animal Ecology* **85**(1): 43–53. doi:10.1111/1365-2656.12275.

Borenstein, M., Hedges, L. V., Higgins, J. P. and Rothstein, H. R. (2009). Introduction to Meta-Analysis, *Introduction to Meta-Analysis*, John Wiley & Sons, Chichester, U.K.

Brakefield, P. M. (1982). Ecological Studies on the Butterfly Maniola Jurtina in Britain. I. Adult Behaviour, Microdistribution and Dispersal, *Journal of Animal Ecology* **51**: 713–726. doi:10.2307/4000.

Breyne, P., Mergeay, J. and Casaer, J. (2014). Roe deer population structure in a highly fragmented landscape, *European Journal of Wildlife Research* **60**(6): 909–917. doi:10.1007/s10344-014-0859-3.

Bubová, T., Kulma, M., Vrabec, V. and Nowicki, P. (2016). Adult longevity and its relationship with conservation status in European butterflies, *Journal of Insect Conservation* **20**: 1021–1032. doi:10.1007/s10841-016-9936-0.

Byrne, A. W., Quinn, J. L., O'Keeffe, J. J., Green, S., Paddy Sleeman, D., Wayne Martin, S. and Davenport, J. (2014). Large-scale movements in European badgers: Has the tail of the movement kernel been underestimated?, *Journal of Animal Ecology* **83**(4): 991–1001. doi:10.1111/1365-2656.12197.

Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A. and Ceballos, G. (2011). Jaguars on the move: Modeling movement to mitigate fragmentation from road expansion in the Mayan Forest, *Animal Conservation* **14**(2): 158–166. doi:10.1111/j.1469-1795.2010.00406.x.

Coulon, A., Guillot, G., Cosson, J.-F., Angibault, J. M. A., Aulagnier, S., Cargnelutti, B., Galan, M. and Hewison, A. J. M. (2006). Genetic structure is influenced by landscape features: empirical evidence from a roe deer population, *Molecular Ecology* **15**(6): 1669–1679. doi:10.1111/j.1365-294X.2006.02861.x.

Delattre, T., Burel, F., Humeau, A., Stevens, V. M., Vernon, P. and Baguette, M. (2010). Dispersal mood revealed by shifts from routine to direct flights in the meadow brown butterfly Maniola jurtina, *Oikos* **119**(12): 1900–1908. doi:10.1111/j.1600-0706.2010.18615.x.

Devroye, L. (1986). Complexity questions in non-uniform random variate generation, *Non-Uniform Random Variate Generation*, Springer, New York, USA.

Dover, J. and Settele, J. (2009). The influences of landscape structure on butterfly distribution and movement: A review, *Journal of Insect Conservation* **13**(1): 3–27. doi:10.1007/s10841-008-9135-8.

Dulac, J. (2013). Global Land Transport Infrastructure Requirements: Estimating road and railway infrastructure capacity and costs to 2050, *Technical report*, International Energy Agency.

Dyer, S. J., O'Neill, J. P., Wasel, S. M. and Boutin, S. (2002). Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta, *Canadian Journal of Zoology* **80**(5): 839–845. doi:10.1139/z02-060.

EEA (2015). The European environment - state and outlook 2015: synthesis report, European Environment Agency, Copenhagen, *Technical report*.

Epps, C. W. and Keyghobadi, N. (2015). Landscape genetics in a changing world: Disentangling historical and contemporary influences and inferring change, *Molecular Ecology* **24**: 6021–6040. doi:10.1111/mec.13454.

Fagan, W. F. and Holmes, E. E. (2006). Quantifying the extinction vortex, *Ecology Letters* **9**(1): 51–60. doi:10.1111/j.1461-0248.2005.00845.x.

Fahrig, L. and Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis, *Ecology and Society* **14**(1): 21.

Forman, R. T. and Alexander, L. E. (1998). Roads and their major ecological effects, *Annual Review of Ecology, Evolution, and Systematics* **29**: 207–231. doi:10.1002/9781444355093.ch35.

Fric, Z. and Konvicka, M. (2007). Dispersal kernels of butterflies: Power-law functions are invariant to marking frequency, *Basic and Applied Ecology* **8**(4): 377–386. doi:10.1016/j.baae.2006.06.005.

Grill, A., Cerny, A. and Fiedler, K. (2013). Hot summers, long life: egg laying strategies of Maniola butterflies are affected by geographic provenance rather than adult diet, *Contributions to Zoology* **82**(1): 27–36.

Grimm, A., Prieto Ramírez, A. M., Moulherat, S., Reynaud, J. and Henle, K. (2014). Life-history trait database of European reptile species, *Nature Conservation* **9**: 45–67. doi:10.3897/natureconservation.9.8908.

Haeler, E., Fiedler, K. and Grill, A. (2014). What prolongs a butterfly's life?: Trade-offs between dormancy, fecundity and body size, *PLoS ONE* **9**(11): e111955. doi:10.1371/journal.pone.0111955.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. and de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas, *PloS ONE* **12**(10): e0185809. doi:10.1371/journal.pone.0185809.

Hill, J. K., Thomas, C. D. and Lewis, O. T. (1996). Effects of Habitat Patch Size and Isolation on Dispersal by Hesperia comma Butterflies: Implications for Metapopulation Structure, *Journal of Animal Ecology* **65**(6): 725–735. doi:10.2307/5671.

Holderegger, R. and Di Giulio, M. (2010). The genetic effects of roads: A review of empirical evidence, *Basic and Applied Ecology* **11**(6): 522–531. doi:10.1016/j.baae.2010.06.006.

Jahner, J. P., Gibson, D., Weitzman, C. L., Blomberg, E. J., Sedinger, J. S. and Parchman, T. L. (2016). Fine-scale genetic structure among greater sage-grouse leks in central Nevada, *BMC Evolutionary Biology* **16**: 127. doi:10.1186/s12862-016-0702-4.

Kaya Özdemirel, B., Turak, A. S. and Bilgin, C. C. (2016). Impact of large scale dam construction on movement corridors of mammals in Artvin, north- eastern Turkey, *Applied Ecology and Environmental Research* **14**(3): 489–507. doi:10.15666/aeer/1403_489507.

Latch, E. K., Boarman, W. I., Walde, A. and Fleischer, R. C. (2011). Fine-scale analysis reveals cryptic landscape genetic structure in desert tortoises, *PLoS ONE* **6**(11): e27794. doi:10.1371/journal.pone.0027794.

Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Goosem, M., Venter, O., Edwards, D. P., Phalan, B., Balmford, A., Van Der Ree, R. and Arrea, I. B. (2014). A global strategy for road building, *Nature* **513**: 229–232. doi:10.1038/nature13717.

Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. (1992). Modeling Survival and Testing Biological Hypotheses Using Marked Animals : A Unified Approach with Case Studies, *Ecological Monographs* **62**(1): 67–118.

Li, Z., Ge, C., Li, J., Li, Y., Xu, A., Zhou, K. and Xue, D. (2010). Ground-dwelling birds near the Qinghai-Tibet highway and railway, *Transportation Research Part D: Transport and Environment* **15**(8): 525–528. doi:10.1016/j.trd.2010.07.004.

Lörtscher, M., Erhardt, A. and Zettel, J. (1997). Local movement patterns of three common grassland butterflies in a traditionally managed landscape, *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **70**: 43–55.

Manel, S. and Holderegger, R. (2013). Ten years of landscape genetics, *Trends in Ecology and Evolution* **28**(10): 614–621. doi:10.1016/j.tree.2013.05.012.

McCauley, D. E. (1991). Genetic consequences of local population extinction and recolonization, *Trends in Ecology and Evolution* **6**(1): 5–8.

Morelli, F., Beim, M., Jerzak, L., Jones, D. and Tryjanowski, P. (2014). Can roads, railways and related structures have positive effects on birds? - A review, *Transportation Research Part D: Transport and Environment* **30**: 21–31. doi:10.1016/j.trd.2014.05.006.

Munguira, M. L. and Thomas, J. A. (1992). Use of Road Verges by Butterfly and Burnet Populations, and the Effect of Roads on Adult Dispersal and Mortality, *Journal of Applied Ecology* **29**(2): 316–329.

Ouin, A., Martin, M. and Burel, F. (2008). Agricultural landscape connectivity for the meadow brown butterfly (Maniola jurtina), *Agriculture, Ecosystems and Environment* **124**: 193–199. doi:10.1016/j.agee.2007.09.010.

Palomares, F., Miguel, D., Revilla, E., Calzada, J. and Fedriani, J. M. (2001). Spatial Ecology of Iberian Lynx and Abundance of European Rabbits in Southwestern Spain, *Wildlife Monographs* **148**(1): 1–36.

Penone, C., Machon, N., Julliard, R. and Le Viol, I. (2012). Do railway edges provide functional connectivity for plant communities in an urban context?, *Biological Conservation* **148**(1): 126–133. doi:10.1016/j.biocon.2012.01.041.

Pépino, M., Rodríguez, M. A. and Magnan, P. (2012). Fish dispersal in fragmented landscapes: A modeling framework for quantifying the permeability of structural barriers, *Ecological Applications* **22**(5): 1435–1445. doi:10.1890/11-1866.1.

Pépino, M., Rodriguez, M. A., Magnan, P. and Heino, J. (2016). Assessing the detectability of road crossing effects in streams: mark-recapture sampling designs under complex fish movement behaviours, *Journal of Applied Ecology* **53**(6): 1831–1841. doi:10.1111/1365-2664.12725.

Polic, D., Fiedler, K., Nell, C. and Grill, A. (2014). Mobility of ringlet butterflies in high-elevation alpine grassland: effects of habitat barriers, resources and age, *Journal of Insect Conservation* **18**: 1153–1161. doi:10.1007/s10841-014-9726-5.

Pollock, K. H. (1982). A Capture-Recapture Design Robust to Unequal Probability of Capture, *The Journal of Wildlife Management* **46**(3): 752–757.

Pruett, C. L., Patten, M. A. and Wolfe, D. H. (2009). Avoidance behavior by prairie grouse: Implications for development of wind energy, *Conservation Biology* **23**(5): 1253–1259. doi:10.1111/j.1523-1739.2009.01254.x.

Prunier, J. G., Kaufmann, B., Léna, J. P., Fenet, S., Pompanon, F. and 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. doi:10.1007/s10592-013-0553-0.

R Core Team (2015). *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.

Rodríguez, M. A. (2010). A Modeling Framework for Assessing Long-Distance Dispersal and Loss of Connectivity in Stream Fish, *American Fisheries Society Symposium* **73**: 263–279.

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution, *Annual Review of Ecology, Evolution, and Systematics* **38**: 231–253. doi:10.1146/annurev.ecolsys.38.091206.095611.

Schtickzelle, N., Turture, C. and Baguette, M. (2012). Temporal variation in dispersal kernels in a metapopulation of the bog fritillary butterfly (Boloria eunomia), *Dispersal Ecology and Evolution*, Oxford University Press, chapter 18, pp. 231–239.

Shepard, D. B., Kuhns, A. R., Dreslik, M. J. and Phillips, C. A. (2008). Roads as barriers to animal movement in fragmented landscapes, *Animal Conservation* **11**(4): 288–296. doi:10.1111/j.1469-1795.2008.00183.x.

Skarpaas, O., Shea, K. and Bullock, J. M. (2005). Optimizing dispersal study design by Monte Carlo simulation, *Journal of Applied Ecology* **42**(4): 731–739. doi:10.1111/j.1365-2664.2005.01056.x.

Skórka, P., Lenda, M., Moroń, D., Martyka, R., Tryjanowski, P. and Sutherland, W. J. (2015). Biodiversity collision blackspots in Poland: Separation causality from stochasticity in roadkills of butterflies, *Biological Conservation* **187**: 154–163. doi:10.1016/j.biocon.2015.04.017.

Stevens, V. M., Turlure, C. and Baguette, M. (2010). A meta-analysis of dispersal in butterflies, *Biological Reviews* **85**(3): 625–642. doi:10.1111/j.1469-185X.2009.00119.x.

Thomas, J. A. and Lewington, R. (1991). *The butterflies of Britain & Ireland*, Dorling Kindersley, London.

Trochet, A., Moulherat, S., Calvez, O., Stevens, V., Clobert, J. and Schmeller, D. (2014). A database of life-history traits of European amphibians, *Biodiversity Data Journal* **2**: e4123. doi:10.3897/BDJ.2.e4123.

Trombulak, S. C. and Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities, *Conservation Biology* **14**(1): 18–30.

Van Buskirk, J. (2012). Permeability of the landscape matrix between amphibian breeding sites, *Ecology and Evolution* **2**(12): 3160–3167. doi:10.1002/ece3.424.

Vandevelde, J. C., Penone, C. and Julliard, R. (2012). High-speed railways are not barriers to Pyronia tithonus butterfly movements, *Journal of Insect Conservation* **16**(5): 801–803. doi:10.1007/s10841-012-9513-0.

Whittington, J., St. Clair, C. C. and Mercer, G. (2004). Path tortuosity and the permeability of roads and trails to wolf movement, *Ecology and Society* **9**(1): 4.

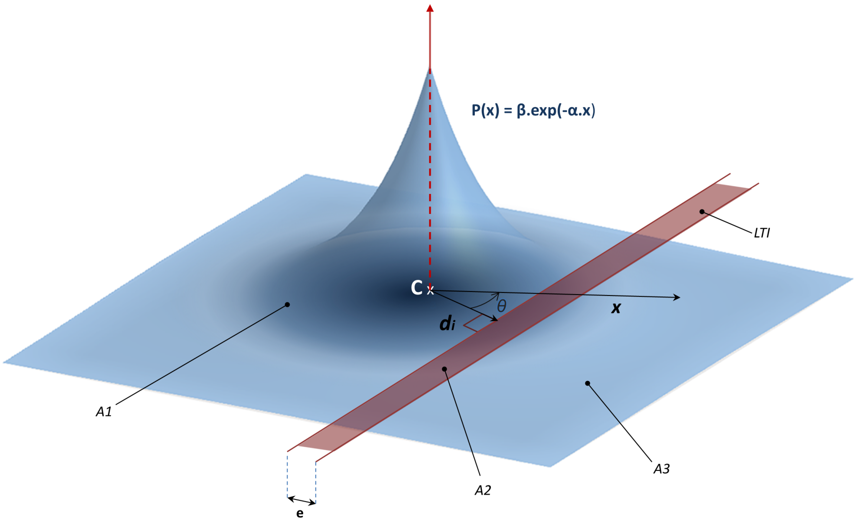

Figure 1: Three-dimensional representation of the conceptual framework used to calculate expected probabilities of crossing a Large-scale Transportation Infrastructure (LTI)(see text). Empirical data on movement are used to fit the negative exponential function $P(x) = \beta e^{-\alpha x}$ (dispersal kernel). The longer the distance between the capture location (C) and the infrastructure (d_i) and the width of the infrastructure (e), the lower the probability that the individual may cross the infrastructure. The distance x and the angle θ are used to estimate the area A1 (staying) and A3 (crossing).

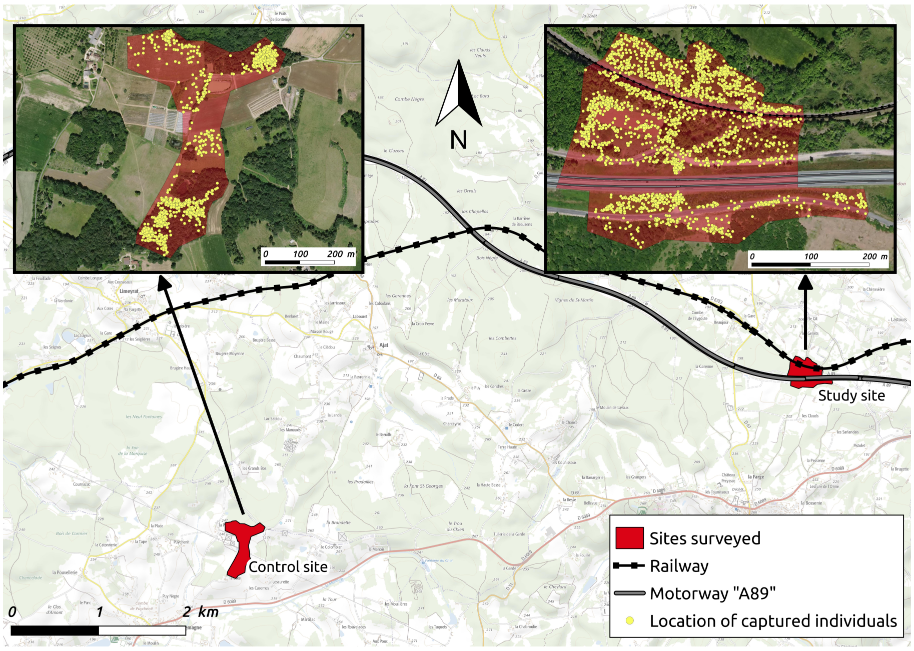

Figure 2: Study area in the 'Périgord' region in the South-West of France. The control site was surveyed in 2015 and the study site in 2016. On the study site, two infrastructures were studied for their barrier effects: a railway and a motorway.

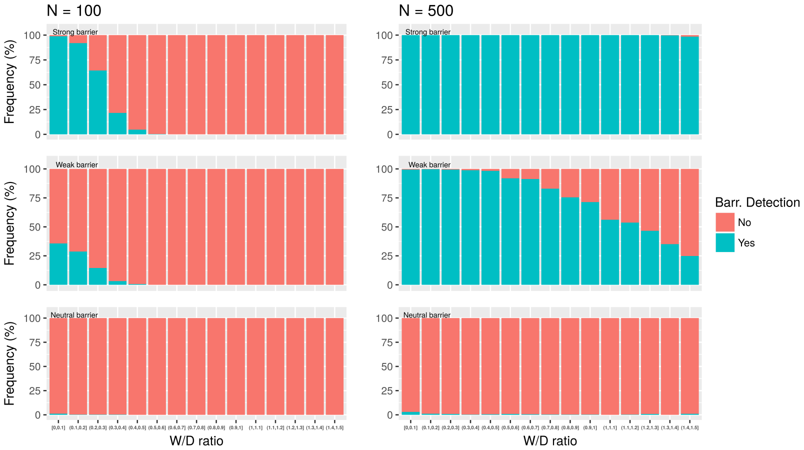

Figure 3: Method application on 5000 simulated data per scenario type. We simulated two specific study cases with either 100 or 500 recaptured individuals. For each case, three scenarios were simulated: a strong barrier, a weak barrier and a neutral barrier. Various barrier sizes (from 5 to 50 m) and various movement capacities (mean distance capacity from 10 to 500 m) were also simulated. These two components were synthesised into a single ratio (W/D ratio = barrier width divided by average distance capacity). A W/D ratio of 1 corresponds to a barrier width equal to the average distance capacity of the organism. Barrplots represent the frequency of simulations that either detect a barrier effect or not according to logOddsRatios 95% CI.

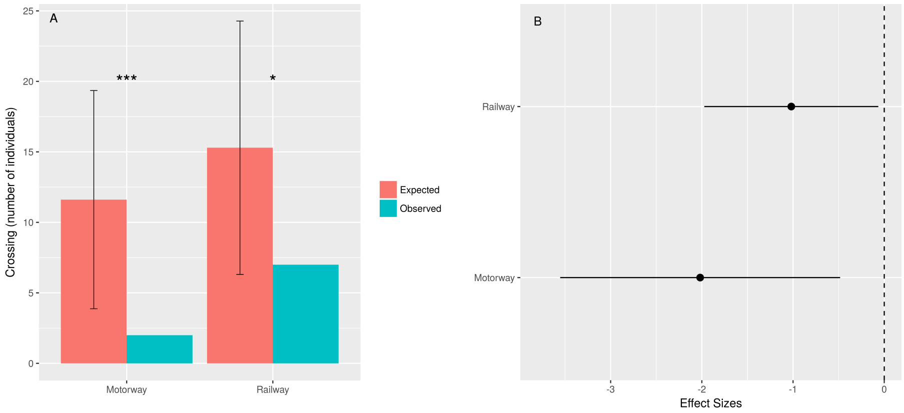

Figure 4: Comparison between expected and observed probability that *Maniola jurtina* individuals cross two types of LTIs on the study site. Expected probabilities were calculated from a theoretical distribution fitted to a dispersal kernel as if LTIs were completely permeable. Panel A shows the comparison between expected and observed number of crossing events. Error bars represent mean ± SD. Significance was based on binomial tests. * : $p \leq 0.05$, *** : $p \leq 0.001$. Panel B shows effect sizes (logOddsRatio) ± 95% confidence intervals.