

# Are the nesting probabilities of the red-backed shrike related to proximity to roads?

Federico Morelli<sup>1</sup>

<sup>1</sup> DiSTeVA, University of Urbino, 61029 Urbino, Italy

Corresponding author: *Federico Morelli* ([federico.morelli@uniurb.it](mailto:federico.morelli@uniurb.it))

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## Abstract

Roads are a pervasive feature in the landscape, and their ecological effects on vertebrate wildlife have been well documented. The main types of effect described are mainly negative consequences on birds and other vertebrates. The major impact of roads on birds includes habitat fragmentation, traffic noise and direct mortality from road kills. However, some passerines, such as the Red-backed Shrike, seem to often use areas close to roads for nesting and hunting purposes.

The aim of this paper is to study the importance of road proximity for the selection of suitable shrubs for nesting by the Red-backed Shrike in the farmland landscapes of central Italy. To achieve this goal, the hierarchical partitioning procedures of Generalized Linear Models (GLM) are applied in order to quantify the relative effects of a number of independent variables.

At least 77% of the nests we identified were positioned less than 25 meters from roads. The mean distance from the nest to the nearest road was  $12.9 \pm 18.1$  m. The analysis of the relative importance of each variable revealed that “road distance” is one of variables most associated with nesting probability in suitable shrubs. It is reasonable to argue that suitable shrubs and the presence of open spaces for hunting, both of which exist close to countryside roads, might represent the favourable components of the breeding habitat selections of Red-backed Shrikes. Our results can provide useful indications for census techniques and for the planning of conservation measures for the species in agricultural landscapes.

## Keywords

Road, *Lanius collurio*, occurrence, nest, suitable shrub, GLM

## Introduction

Roads constitute a pervasive feature in the landscape, and their ecological effects on vertebrate wildlife have been well documented (Van der Zande et al. 1980, Bennett 1991, Forman 1995, Forman and Alexander 1998, Spellerberg 1998, Forman and Deblinger 2000, Trombulak and Frissell 2000). However, the main types of effect have mainly negative consequences on birds and other vertebrates (Kociolek et al. 2011). The major impact of roads on birds includes habitat fragmentation during and after road construction (Reed et al. 1996), displacement caused by traffic noise (Reijnen et al. 1995a, 1995b, 1996, Forman and Deblinger 2000), and direct mortality from road kills (Mumme et al. 2000). Reduced reproductive success associated with increasing human interference has been also reported, although some birds seem to be unaffected by the presence of roads (Trombulak and Frissell 2000). For example, some passerines, such as the Red-backed Shrike, *Lanius collurio*, often seem to use areas close to roads for nesting and hunting purposes (Bechet et al. 1998, Morelli 2012, Morelli et al. 2012), possibly because the hedgerows and shrubs alongside roads can increase prey abundance and constitute good perches for hunting (Farkas et al. 1997; Tryjanowski et al. 2000).

The Red-backed Shrike is an endangered bird species whose populations have recently been in decline almost all over the world (Yosef 1994, PECBMS 2008). It is present in all regions of Italy, both as a regular migrant and a breeding species during the summer months (Foschi and Gellini 1987, Meschini and Frugis 1993, Dinetti 1997). The species mainly prefers to breed in the transition zones between woods and grassland, lines of trees, and the thick hedgerows that often border roads. They also use open farmland with shrub or tree cover as well as high meadows (Guerriere and Castaldi 2006, Morelli 2012, Morelli et al. 2012). The Red-backed Shrike is a carnivorous bird that primarily hunts invertebrates and insects, but also reptiles, amphibians, micromammals and other birds, using observation posts or perches for this purpose (Lefranc 1993).

The aim of this work is to study if the selection of suitable shrubs for nesting by Red-backed Shrike is related to road proximity in the farmlands of central Italy.

## Materials and methods

The study was conducted in a breeding territory of the Red-backed Shrike in the River Foglia catchment area in central Italy (43°45'8.43"N, 12°37'47.10"E). The bird data was collected during the 2009 breeding season by recording the presence and occupancy for nesting of each suitable shrub in an area of 600ha. First, all of the contacts obtained within the study areas were recorded on detailed aerial photographs (scale 1:1000). Following methods used elsewhere and the census of the species in Italy (Brambilla et al. 2007; Morelli 2012), and by considering the marked territoriality of the species (Tryjanowski and Golawski 2004), a variation of the formal mapping procedure mentioned by Bibby et al. 1997 was used and adjusted to gathering informa-

tion on nest locations in the study area. When breeding behaviour was detected (particularly, males and females together, singing males, aggressive encounters, pairs showing courtship routines, copulating or any nesting behaviour), the observations were increased to identify the core of the breeding territory and the most commonly used shrubs. Inspections of the occupied shrubs to verify nest presence were carried out, but contact with the breeding individuals was minimised (Tryjanowski and Kuzniak 1999), thereby avoiding more invasive collection methods (egg number counts, breeding success, etc.). All suitable shrubs were equally surveyed in the search for nests. The metrics on nest position were collected later, when the breeding season was over.

Each shrub was digitised and classified as “suitable” according to previous ecology studies of this species in the same region (Guerriere and Castaldi 2006, Morelli 2012, Morelli et al. 2011). The following were considered:

- Suitable vegetal species: Blackthorn *Prunus spinosa*, Dog rose *Rosa canina*, Elm-leaf Blackberry *Rubus ulmifolius*, and Common Hawthorn *Crataegus monogyna*.
- Suitable plant size: minimum height of suitable shrubs (fixed empirically at a minimum of 0.5m, based on previous studies in the same area; Morelli unpublished data); and
- Suitable density of foliage: mainly the shrubs with dense foliage and a strong branch structure that is suitable for positioning and protecting the nest.

The suitable shrubs were classified as “occupied” (when a nest was found inside them) or “unoccupied”. Only active nests were included in this analysis as “occupied”.

All of the data collected was mapped by means of ArcGIS 9 tools (ESRI 2009), which are also useful for calculating the following environmental parameters: altitude; distance to nearest road; shrub shape; shrub surface; shrub density (the density of the shrubs was calculated as the number of suitable shrubs around the occupied suitable shrub in a fixed radius of 50m as this corresponds approximately to the typical territory of the species (Lefranc 1993; Olsson 1995)); distance to nearest shrub; landscape fragmentation (as edge-density of land-use); and coverage proportion of each land-use category around 50m of each suitable shrub. All of the digitised data was further corrected during the surveys in the field. The large patches that were comprised of two or more shrubs, or were too near to or were intersected by roads, were adjusted by means of data collected in the field and then divided. The roads that were present in the study area were classified as paved, unpaved and pathway. Vehicular traffic intensity was also calculated for the monitored roads in terms of cars/hour (Table 1).

The relationships between nesting on suitable shrubs and environmental parameters were examined using Generalized Linear Models (McCullagh and Nelder 1989), with the dependent variable (shrub occupancy) modelled by specifying the logistic (binomial) family. The proportion of land-use coverage was transformed using the arcsine of square root transformation, as suggested by the Box-Cox plot (Box and Cox 1964). In order to minimise the multi-collinearity of variables, the parameters (regressors) with the strongest correlation between them ( $R > 0.8$ ) were eliminated manually. All

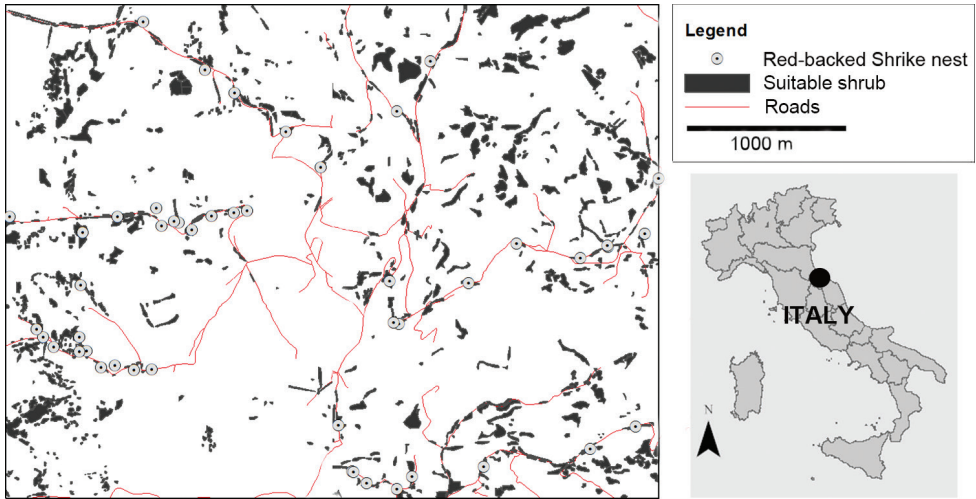
**Table 1.** Environmental parameters used to describe the study area and buffer zone around the suitable shrubs and for modelistic purposes.

Parameter	Level or type	Details	Variable used as regressor for model procedures
Altitude	landscape	Altitude of suitable shrub (m asl)	Yes
Roads	landscape	Presence and type of roads (paved, unpaved, pathway)	No
Nearest road distance	landscape	Distance in m from suitable shrub to nearest road	Yes
Power lines	landscape	Presence of power lines	Yes
Edge-density	landscape	Sum of the perimeters of all polygons contained in the buffer zone per number of land-use typologies	Yes
Shrub density	landscape	Calculated in a fixed radius of 50m around each suitable shrub	Yes
Nearest shrub distance	landscape	Distance in m from suitable shrub to nearest shrub	Yes
Shrub surface	-	Surface of suitable shrub, m <sup>2</sup>	Yes
Shrub shape	categorical	Classified as circle, rectangle or irregular	Yes
Traffic intensity	categorical	Cars/hour (classified then as low, medium, high)	No
Urban	land use	%	Yes
Forest	land use	%	Yes
Shrubs	land use	%	Yes
Uncultivated	land use	%	Yes
Badland	land use	%	Yes
Grassland	land use	%	Yes
Hedgerows	land use	%	Yes
Isolated trees	land use	%	Yes
Vineyards	land use	%	Yes
Olive	land use	%	Yes
Cultivated	land use	%	Yes

independent variables were standardised during the first run of the regression process in order to properly compare their coefficients. The decostand function of the vegan package in R was used and the “max” method was selected. This methodology works by transforming all variables in a range from 0 to 1, where the max values for each variable are 1 and the other values are calculated as a proportion thereof.

A stepwise backward procedure was followed in order to select the most significant variables using the Akaike Information Criterion (AIC) (Akaike 1974; Anon 1999). The predictive performance of the best model selected by the stepwise process was evaluated using a ROC plot and the AUC (area under the curve) (Fielding and Bell 1997). The AUC values ranged from 0.5 for models with no discrimination ability to 1 for the models with perfect discrimination.

In order to measure the effects of each independent variable on the occupancy of suitable shrubs, the hierarchical partitioning protocol (Chevan and Sutherland 1991) was used by means of HIER.PART package (Walsh and Mac Nally 2008) and allowed



**Figure 1.** Suitable shrubs, roads and nests of the Red-backed Shrike in the study area in central Italy.

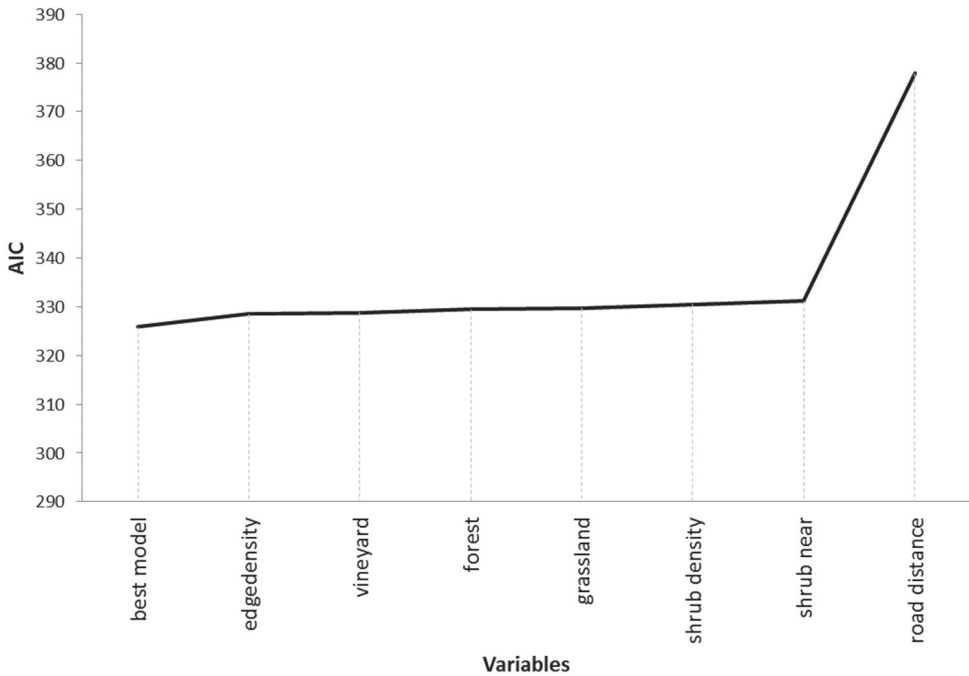
the estimation of both independent (I) and joint (J) explanatory power of each variable, considering all the 2K possible models (Mac Nally 2000). The relative importance values output is a numeric vector, named as the predictor variables, resulted from the sum of 'Akaike weights' over all models including the explanatory variable. All tests were performed using the R program (R Development Core Team 2011).

## Results

The roads present in the study area were: 75% paved, 23% unpaved and 2% pathway. All of the roads were characterized by low vehicular traffic, with fewer than five cars per hour.

A total of 739 suitable shrubs were identified and mapped in the study area (Fig. 1). The density of these shrubs was 1.23 shrubs/ha, and they were mainly distributed in cultivated, uncultivated and grassland land-use typologies. Circa 34% of the total number (occupied and unoccupied) of suitable shrubs were less than 100 metres from the roads. We found 46 nests belonging to Red-backed Shrikes in the study area. All of these were located on suitable shrubs, with a density of 0.76 pairs/10 ha. There were no cases of more than one nest per shrub. The mean distance from the occupied suitable shrubs to the nearest road was 12.9m (with a maximum of 98 and a minimum of 0.2 m). In 77% of the cases, the nests were positioned less than 25m from roads (Fig. 1).

From the initial model (AUC: 0.88), which considered all of the environmental variables, was selected the best model, with a compromise between goodness of fit and model complexity (MacNally 2000). This model produced an AUC score of 0.83. The presence of nests of Red-backed Shrikes in suitable shrubs seemed to be well explained by the seven variables set out in Figure 2. There were four parameters related to spatial distribution and landscape heterogeneity (nearest road distance, shrub density, nearest



**Figure 2.** Change in the goodness of fit of the best model when deleting each environmental variable.

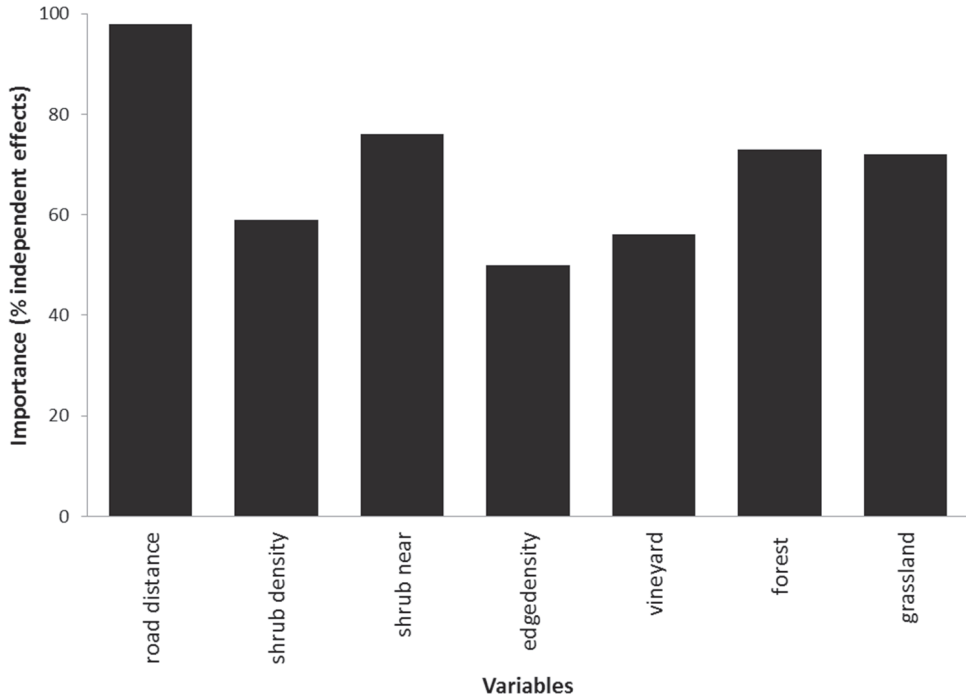
**Table 2.** Results of logistic regression for the best model related occurrence of Red-backed Shrike nests in suitable shrubs with environmental parameters in central Italy. The table shows the significant variables selected after a stepwise backward procedure using AIC criteria (p-values in bold). The AIC value of the best model was 327.9, which was the lowest figure if compared with the AIC value obtained by the initial model (336.2). AUC of best model: 83.0%.

Parameter	Estimate	SE	Z value	p-values
Farmlands (n=160)				
Nearest road distance	-0.0253	0.0052	-4.804	<b>1.55e-06</b> ***
Shrub density	-0.3096	0.1491	-2.077	<b>0.0378</b> *
Nearest shrub distance	-0.0317	0.0157	-2.019	<b>0.0435</b> *
Edge-density	3.2373	1.9718	1.642	0.1006
Vineyards	3.3881	1.8579	1.824	0.0682 .
Forest	-1.2244	0.6812	-1.797	0.0723 .
Grasslands	0.8670	0.4341	1.997	<b>0.0458</b> *
Intercept	-1.2114	0.5796	-2.090	<b>0.0366</b> *

Significance codes: '\*\*\*' p<0.001, '\*\*' p<0.01, '\*' p<0.05, '.' p<0.1

shrubs and edge-density), and three related to land-use typologies (vineyard, forest and grassland) (Table 2).

However, the relative importance of each variable on the probability of the occurrence of Red-backed Shrike nests on suitable shrubs was different. The result of the hierarchical partitioning procedures highlighted the importance of road distance for



**Figure 3.** Measure of the effects of the independent variables entered in the best model, as a contribution to all of the possible models (hierarchical partitioning regression results). In the Y axis the percentage of goodness of fit for each variable.

the selection of suitable shrubs for nesting (Fig. 3). The relative importance of variables selected in the best model, were ranged from a maximum close to 0.98 for road distance, to a minimum of 0.51 for edge-density.

## Discussion

Many studies on the breeding and feeding habitats of *Lanius collurio* have highlighted the importance of land use composition (Kuzniak and Tryjanowski 2000; Goławski and Goławska 2008, Girardello and Morelli 2012; Morelli 2012), with particular consideration given to patches' typology and their relative surface. However, the outcome of this work also highlighted the importance of landscape heterogeneity characteristics (shrub density, edge-density) and proximity to urban structures such as roads for the selection of the breeding habitats of species. The results of this work suggest that in extensive farmlands, the Red-backed Shrike seems to mainly select the shrubs nearest to roads for nesting. When available, the suitable shrubs that are closer to a road are chosen for this purpose. Other shrubs with similar characteristics (vegetal species, shape, surface, shrub density, proximity to other land use typologies, etc.), but which were

located away from roads, were not preferred. The hierarchical partitioning analysis demonstrated how road proximity made the greatest independent contribution when it comes to explaining the occupancy of suitable shrubs.

It is reasonable to argue that the presence of suitable shrubs and, at the same time, open spaces for hunting, both of which exist close to countryside roads, might represent the more favourable components for the breeding habitat selection of Red-backed Shrikes (Lefranc 1993; Farkas et al. 1997; Dinetti 1997; Morelli 2012). The main reason could be because, as recent studies have shown, road verges are used as network ecological corridors by various insects (Hobbs 1992; Vermeulen 1994; Vermeulen and Opdam 1995) that are potential prey for the Red-backed Shrike (carabids, butterfly, etc.). Preferring to take its prey on the ground, *Lanidae* can use an exposed road patch within its territory as an attractive place to do so. Furthermore, many roads are lined with power lines that are frequently used by birds as surveying and hunting posts (Bechet et al. 1998). However, the abundance of prey that *Lanius collurio* capture in these open spaces is certainly influenced by the state of surrounding habitats. Moreover, available suitable shrubs for nesting or perches were located in the vicinity of roads (34% of the total suitable shrubs were recorded as being less than 100m from the nearest road), perhaps due to a tendency encouraged by the long-standing local tradition of planting hedges and verges along country roads (these generally consist of *Crataegus* sp., *Prunus spinosa*, *Paliurus spina-christi*, *Ligustrum vulgare*, Morelli and Pandolfi 2011).

However, further research is needed to understand the real importance of each environmental variable in the selection of suitable shrubs by Red-backed Shrikes. This is mainly because many environmental variables could be strongly correlated, while others could be masked or hidden by other parameters (for example, the shape of the shrubs seems to be the same, whether close to or further away from the roads, but the shrubs nearest to the roads could also be pruned). Another important limitation of this work is due to the fact that only one landscape typology was sampled, meaning that the results are not really applicable to breeding habitat selection for the entire species, which is characterized by a relatively wide ecological plasticity in the choice of breeding habitat (Morelli 2012).

Furthermore, it would be important improve on our knowledge of the ecological offer of open spaces like countryside roads, which represent a low disturbance or low mortality risk to Shrikes, and may perhaps be good territory for hunting (Fernandez-Juricic et al. 2004). In this way, the results of this work could contribute to our understanding of the irregular distribution of the Red-backed Shrike in agricultural environments like those of central Italy. They could also provide useful indications for improving census techniques and planning conservation efforts for the species.

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# Changes in behavioural responses to infrastructure affect local and regional connectivity – a simulation study on pond breeding amphibians

Maj-Britt Pontoppidan<sup>1</sup>, Gösta Nachman<sup>1</sup>

<sup>1</sup> Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen

Corresponding author: *Maj-Britt Pontoppidan* ([mbp@bio.ku.dk](mailto:mbp@bio.ku.dk))

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## Abstract

An extensive and expanding infrastructural network destroys and fragments natural habitat and has detrimental effect on abundance and population viability of many amphibian species. Roads function as barriers in the landscape. They separate local populations from each other or prevent access to necessary resources. Therefore, road density and traffic intensity in a region may have severe impact on regional as well as local connectivity. Amphibians may be able to detect and avoid unsuitable habitat. Individuals' ability to avoid roads can reduce road mortality but at the same time road avoidance behaviour, can increase the barrier effect of the road and reduce connectivity. We use an individual based model to explore how changes in road mortality and road avoidance behaviour affect local and regional connectivity in a population of Moor frogs (*Rana arvalis*). The results indicate that road mortality has a strong negative effect on regional connectivity, but only a small effect on local connectivity. Regional connectivity is positively affected by road avoidance and the effect becomes more pronounced as road mortality decreases. Road avoidance also has a positive effect on local connectivity. When road avoidance is total and the road functions as a 100% barrier regional connectivity is close to zero, while local connectivity exhibit very elevated values. The results suggest that roads may affect not only regional or metapopulation dynamics but also have a direct effect on local population dynamics.

## Keywords

*Rana arvalis*, Individual based modelling, Road avoidance, Road mortality, Connectivity, Pond breeding amphibians

## Introduction

All over the world, amphibian populations are declining and many amphibian species are listed in the IUCN as threatened or vulnerable (IUCN 2012). The causes for the decline are hypothesized to be (combinations of) factors such as climate change, diseases, predation and UV-radiation. But the main factor, especially in the western world, is thought to be the increasing urbanisation (Alford and Richards 1999; Beebee and Griffiths 2005; Collins and Storfer 2003; Gardner et al. 2007). The negative effect of urbanisation is not only due to changes in land use and destruction of habitat. A huge infrastructural network functions as barriers to movement and causes the death of a huge number of amphibians every year (Andrews et al. 2008; Hamer and McDonnell 2008). Road density in an area as well as traffic density on individual roads have been shown to have a negative effect on amphibian populations (Eigenbrod et al. 2009; Fahrig and Rytwinski 2009; Hels and Buchwald 2001; Reh and Seitz 1990; Vos and Chardon 1998). Veysey et al. (2011) even found road density to have a stronger effect on population size than habitat availability, while Carr and Fahrig (2001) found more vagile species to be more vulnerable to road mortality.

Very little literature exists on amphibians' reactions to roads. The only study on this topic did not find any indication of road avoidance in *Rana pipiens* (Bouchard et al. 2009) and the large number of road kills (Elzanowski et al. 2009) suggests a low degree of road avoidance. However, amphibians are able to recognise and avoid unsuitable habitat. Although there are species specific variations, individuals tend to prefer more shady and moist habitat types (Mazerolle 2005; Mazerolle and Desrochers 2005; Popescu and Hunter 2011; Vos et al. 2007). In more open and dry habitats like fields and clear-cuts, water loss is bigger and survival lower resulting in avoidance of such habitats (Rothermel and Semlitsch 2002; Todd and Rothermel 2006). Individuals also tend to move more quickly in inhospitable habitats (Hartung 1991; Tramontano 1997). Traffic-associated stimuli as light and noise can affect amphibian behaviour (Mazerolle et al. 2005) and other species as snakes and salamanders exhibit road avoidance behaviour (Andrews and Whitfield Gibbons 2005; Madison and Farrand 1998). These observations suggest that amphibian movement and behaviour can be affected by roads.

Pond breeding amphibians require both terrestrial and aquatic habitat to complete their life cycle. Proximity between the required habitat types is important for the survival of the population. Loss of, or diminished access to, one or both habitats will affect population size and persistence probability (Dunning et al. 1992; Haynes et al. 2007; Johnson et al. 2007; Pope et al. 2000). Moreover, populations of pond-breeding amphibians are frequently considered to be structured as a regional network or a metapopulation, making dispersal between subpopulations essential to regional population persistence (Hels 2002; Marsh 2008; Marsh and Trenham 2001; Smith and Green 2005). Thus the barrier effect caused by roads may have severe consequences for populations of pond breeding amphibians.

We have developed an individual based model to assess the effects of infrastructure on landscape connectivity. The model is part of a larger study concerning road effects

on regional populations of Moor frogs (*Rana arvalis*). In this paper we present our model and explore how behavioural responses to infrastructure may affect local and regional connectivity. The ability to avoid roads may diminish the amount of road kills. This behaviour will prevent dispersal across the road but at the same time it may affect connectivity locally. Lower levels of road avoidance can reduce the road's barrier effect but this will probably depend on the level of road mortality. We hypothesize that

- Regional connectivity will be inhibited by high levels of road avoidance and high road mortality and will depend on interactions between the degree of road avoidance and road mortality.
- Local connectivity will be promoted by high levels of road avoidance but not be affected by road mortality.

We use a real Danish landscape with a population of Moor frogs (*Rana arvalis*) traversed by a large road to test how regional and local connectivity are affected by changes in road mortality and road avoidance.

## Methods

We use an individual based model to simulate the movements of juvenile Moor frogs and estimate immigration probabilities between habitat patches. The purpose of the model is to measure the connectivity of the landscape. In the following we use the terms dispersal and migration as defined by Semlitsch (2008), i.e. dispersal is “interpopulational, unidirectional movements from natal sites to other breeding sites” and migration is “intrapopulational, round-trip movements toward and away from aquatic breeding sites”. The habitat of pond breeding amphibians as the Moor frog includes terrestrial as well as aquatic habitat. Therefore we define the habitat patch of a subpopulation as a complementary habitat patch containing not only the breeding pond but also all accessible summer habitat within migration distance from the pond (Dunning et al. 1992; Pope et al. 2000).

## Model species

Moor frogs spend most of their life in terrestrial habitat; aquatic habitat is only used during the breeding season, which takes place in the early spring (Elmberg 2008; Glandt 2008; Hartung 1991). Soon after breeding, the frogs return to the summer habitat, which lies mostly within a 400 m radius from the breeding pond (Elmberg 2008; Hartung 1991; Kovar et al. 2009). Adult frogs show a high degree of site fidelity and often use the same breeding pond and summer habitat from year to year (Loman 1994). Long distance dispersal in Moor frogs takes place predominantly during the juvenile life-stage (Semlitsch 2008; Sinsch 1990; 2006). Shortly after metamorphosis, the young

frogs leave the natal pond and disperse into the surrounding landscape seeking out suitable summer habitat. Dispersal distances are between a few hundred meters up to 1–2 kilometres (Baker and Halliday 1999; Hartung 1991; Sinsch 2006; Vos and Chardon 1998). The juveniles stay in terrestrial habitat 2–3 years until they reach maturity, although some observations indicate that juvenile frogs follow the adults during the spring migration, without entering the breeding ponds (Hartung 1991; Sjögren-Gulve 1998).

## **Model overview**

Full model documentation following the ODD-template suggested by Grimm et al. (2006; 2010) as well as model parameterisation is provided in Appendix in the supplementary material. Netlogo v.4.1.3 (Wilensky 1999) is used as modelling environment (freely downloadable at <http://ccl.northwestern.edu/netlogo>).

The model considers a regional population of Moor frogs within a spatially explicit landscape matrix. The landscape is constructed from a 600 × 800 cell GIS raster map, each cell representing an area of 10 × 10 meters. A raster cell is characterised by a set of variables defining the habitat type and its value in regard to the different aspects of the life cycle and behaviour of the Moor frog (Table 1). Potential sites for subpopulations of Moor frogs are represented by a GIS point-data set of ponds surveyed during field work. Each pond is defined by an ID-number, a quality index and the summer habitat fragments located within migration distance from the pond (Table 1).

Immigration requires two events: 1) the successful dispersal of a juvenile frog to summer habitat outside its natal habitat patch and 2) subsequent successful migration from the new summer habitat to a nearby breeding pond. In real life dispersal starts just after metamorphosis in early summer and lasts until hibernation in the autumn. The second part of the immigration event, migration, takes place in the spring 2.5 years later. For simplicity, we simulate the dispersal and breeding migration, as if they take place in the same year.

The time step of the model is one day and the simulated period for dispersal as well as migration is 120 days each. At the start of a simulation, 500 frog agents are created at each pond. Each agent is assigned a random direction, which determines its preferred direction of movement. This direction does not change unless summer habitat is found. At each time step, a random daily travelling distance is chosen for each agent; the distance depending on the attractiveness of the current habitat. The distance is travelled one cell at a time. Depending on the relative attractiveness of the neighbouring cells, frog agents move to one of the cells, although backwards movement is not allowed. The movement rules generate a biased random walk away from the natal pond and in the preferred direction. During dispersal, frog agents encountering a cell with summer habitat will have a certain probability of settling in the habitat and stop dispersing. This probability will increase with time. At the end of the dispersal period all frog agents that have not settled in summer habitat are removed. Starting the migration phase, the remaining frog agents move toward the breeding pond associated



**Table 1.** List of variables characterizing the agents in the model.

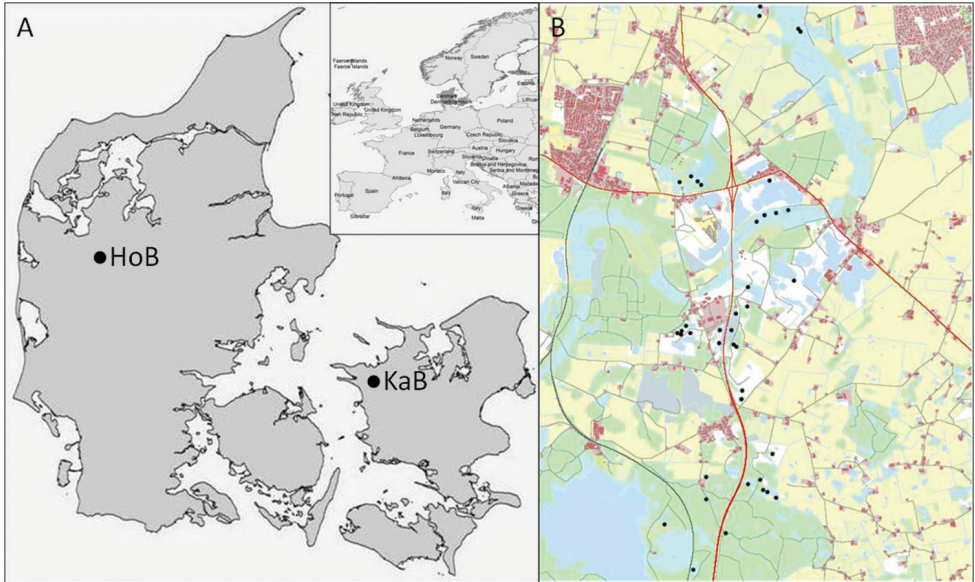
Variable	Notation	Value range	Agent type	Description
DailySurvival	$D_s$		Cell	Daily survival probability
HabitatAttraction	$H_a$	1–5	Cell	The cell's relative attraction to frogs during movement
HabitatCode	$H_c$		Cell	Cell code for habitat type
HabitatSurvival	$H_s$	1–5	Cell	The cell's relative survival index
SummerQuality	$H_q$	1–5	Cell	The cell's relative suitability as summer habitat
BreedingPond			Frog	Breeding pond of frog agent
NatalPond			Frog	Natal pond of frog agent
PondID			Pond	ID number
PondQuality	$Q$	0.1–1	Pond	Quality index of the pond
SummerHabitat	$A$		Pond	Summer habitat cells associated with the pond

with their summer habitat; in case several breeding ponds are available one is chosen randomly weighted by pond quality. After each time step, the survival probability of every frog agent is assessed, based on the daily survival rates associated with the habitat type traversed during the day.

### Input data

We use GIS data sets from a road project in Denmark, supplied by the Danish Road Directorate and Amphi Consult. The project concerns an area in north-western part of Zealand, 10 km east of the city of Kalundborg (55°40.14'N, 11°17.85'E) (Fig. 1). The area is characterised as semi-urban and agricultural landscapes, traversed by creeks and wetlands. A project data set contains a land cover map of the area and a point-data set of potential breeding ponds found during field surveys. The land cover maps are constructed following a protocol designed by amphibian experts (Hassingboe et al. 2012), in which a range of different habitat types are identified. Each habitat type has been assessed and ranked on a scale from 1-5, for the following three variables: the habitat's relative suitability as summer habitat ( $H_q$ ), its relative attraction to frogs during movement ( $H_a$ ) and the relative survival probability ( $H_s$ ) in the habitat. In the model the survival index ( $H_s$ ) is converted into a daily survival probability ( $D_s$ ) (see Appendix for details). Infrastructural elements like roads and railways are processed as any other habitat type and assigned values of habitat attraction and daily survival. However, in the literature the terms “road avoidance” and “road mortality” are more commonly used. To avoid confusion when discussing these effects, we therefore convert ( $H_a$ ) and ( $D_s$ ) to road avoidance ( $R_a$ ) and road mortality ( $R_d$ ), respectively, and invert the ranking, i.e.  $R_a = 6 - H_a$  and  $R_d = 1 - D_s$ .

The point-data set contains information on the location of the potential breeding pond, its ID-number as well as a quality index ( $Q$ ). Pond qualities ranges from 0.1 – 1 and relates to the suitability of the pond and the immediate surroundings in regard to



**Figure 1.** Study area. **A** Location of two study areas in Denmark. KaB is an area near Kalundborg on Zealand and HoB is near Holstebro in Jutland. Only KaB is used in the present analysis, but both areas are used for the parameterisation of the model **B** KaB map used in the analysis. Black dots are breeding ponds, test roads are marked with red.

egg and larval survival and are estimated by experts during field work. In this paper we have excluded low-quality ponds ( $Q < 0.6$ ), since they per definition have a low probability of maintaining a population on their own. The extent of the map is  $6 \times 8$  km and it contains 40 ponds.

## Scenarios

We create scenarios with increasing values of road avoidance,  $R_a = [1; 2; 3; 4; 5]$ , and road mortality,  $R_d = [0.1; 0.3; 0.5; 0.7; 0.9]$ , of the two major roads cutting through the map (Fig.1, roads shown in red). We run 25 simulations for every combination of the parameter values of  $R_a$  and  $R_d$ . As  $R_a$  increases the willingness of the frog agents to enter the road will decrease, while the probability of surviving will increase with decreasing values of  $R_d$ .

## Output

At the end of each simulation, the natal pond and the breeding pond of all frog agents are registered and immigration probability ( $p_{ij}$ ) between all pair-wise ponds is calculated. Landscape connectivity (S) is then found as

$$S = \sum_{i=1}^n \sum_{j=1}^n p_{ij}, \quad (i \neq j) \quad (\text{eq.1})$$

Local populations are identified by grouping ponds into clusters depending on their mutual connectivity, using the method of unweighted, arithmetic, average clustering as described by Legendre and Legendre (1998). Since, immigration probabilities between any two ponds are not necessarily symmetric, i.e.  $p_{ij} \neq p_{ji}$ , we use summed immigration probabilities as similarity measure ( $m$ ):  $m_{ij} = p_{ij} + p_{ji}$ . The threshold at which a given pond or cluster no longer can be added to another cluster is set to  $m_{ij} \leq 0.01$ . We define local connectivity as the connectivity within a cluster and regional connectivity is defined as the connectivity between all pair-wise combinations of clusters. Based on the clustering result we compute within-cluster connectivity ( $S_c$ ) for each cluster as

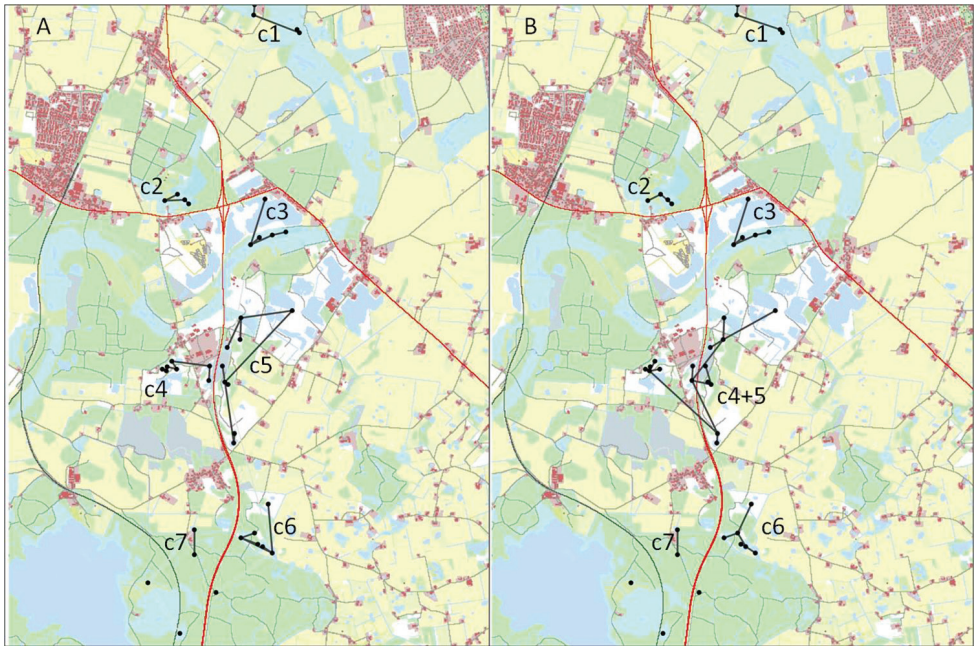
$$S_c = \sum_{i=1}^{n_c} \sum_{j=1}^{n_c} p_{ij}, \quad (i \neq j) \quad (\text{eq. 2})$$

where  $n_c$  is the number of ponds belonging to cluster  $c$ . Connectivity between clusters ( $S_b$ ) is then found as  $S_b = S - S_c$ . However, to be able to detect changes in local connectivity, the ponds constituting a cluster must be the same in all scenarios. Therefore, we use the cluster configuration found when  $R_a$  is set to 5 to define clusters, and use this in all calculations of within-cluster connectivity.

We use a multiple regression model, with the general form  $y = \beta_0 + \beta_1 R_a + \beta_2 R_a + \beta_3 R_a R_a + \varepsilon$ , to test for the effect of road avoidance ( $R_a$ ), road mortality ( $R_a$ ) and their interaction on landscape connectivity ( $S$ ), within-cluster connectivity ( $S_c$ ) and between-cluster connectivity ( $S_b$ ). Sequential Holm-Bonferroni correction is used to adjust p-values. When  $R_a$  is set to 5, frog agents do not enter the road, therefore the level of road mortality is inconsequential. Moreover, preliminary tests showed extreme connectivity values when the road is 100% blocked. Both of these factors risk masking the statistical effect of road mortality and road avoidance on connectivity at other levels of  $R_a$ . Consequently, the results from the scenarios with  $R_a = 5$  are excluded from the statistical testing.

## Results

Analyses of the scenarios with  $R_a = 5$  identify seven clusters (Fig. 2A, Table 2). Cluster c1 contains four ponds and is located rather remotely in the top of the map. Clusters c2 and c3 are found in areas close to where the two test roads cross and contains four, respectively, five ponds. Cluster c4 and cluster c5 contains seven and nine ponds, respectively. These are more widespread clusters situated on either side of the road in the middle of the map. The last two clusters c6 and c7 are placed near the bottom of the map and contain two and six ponds. As described in the method section we use this cluster configuration as a reference for all scenarios when calculating within-cluster connectiv-



**Figure 2.** Results from cluster analyses with two different parameter settings. **A**  $R_a = 5$ ,  $R_d = 0.1$  and **B**  $R_a = 4$ ,  $R_d = 0.1$ .

**Table 2.** Descriptive statistics of the identified clusters. The cluster's ID, number of ponds in the cluster, mean distance from the ponds to a road, the distance to the pond closest to the road and the number of pond members no more than 200 m from the road. Furthermore it is shown whether the cluster exhibits extreme connectivity values when  $R_a=5$ , its response to road avoidance and its response to road mortality.

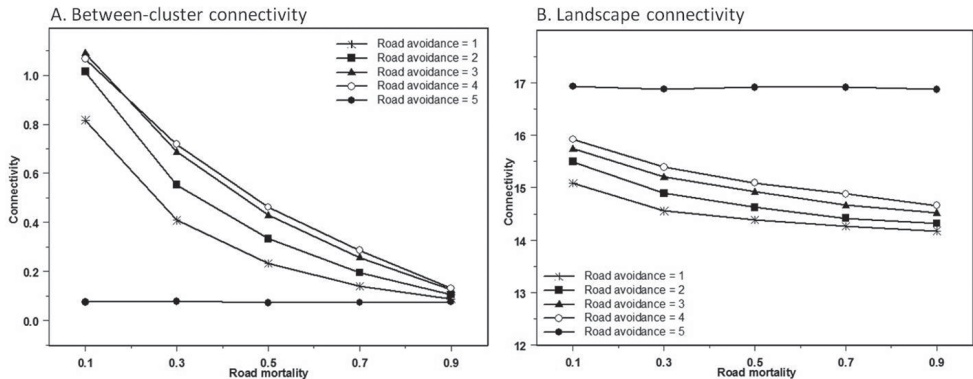
Cluster Id	Cluster characteristics				Respos patterns		
	Cluster size	Mean distance (m)	Min distance (m)	Ponds 200m	$R_a=5$	Avoidance	Mortality
c1	4	1322	1082	0	N	N	N
c2	4	184	110	3	Y	Y	N
c3	5	345	76	1	Y	Y	N
c4	7	431	61	2	Y	Y	Y
c5	9	223	71	6	Y	Y	Y
c6	6	323	98	1	Y	N	N
c7	2	385	318	0	N	N	N

ity. Nonetheless, the analyses show that cluster configurations do not change with the different scenarios except when road mortality is set to 0.1. In this case dispersal success is sufficiently high between cluster c4 and c5 and they fuse into one cluster (Fig. 2B).

When  $R_a \leq 4$ , road mortality has strong negative effect on the connectivity between clusters ( $S_j$ ) while road avoidance has a positive effect. Furthermore, there is an interaction effect; the effect of road avoidance becomes more pronounced as road

**Table 3.** Statistical results of multiple regression models. Statistical significance of variables and interactions in multiple regressions on landscape connectivity ( $S$ ), within-cluster connectivity ( $S_c$ ) of cluster  $c1 - c7$  and between-cluster connectivity ( $S_b$ ). Sequential Holm-Bonferroni correction is used to adjust  $p$ -values. Statistically significant values are shown in bold.

Dependent factor	df	Full model			Road mortality $R_d$		Road avoidance, $R_a$		Interaction $R_a * R_d$	
		$F$	$p$	$R^2$	Parameter	$p$	Parameter	$p$	Parameter	$p$
$S_{c1}$	496	0.30	0.82	0.002	-0.003	0.873	0.001	0.738	0.001	0.884
$S_{c2}$	496	7.20	<b>&lt;0.001</b>	0.042	0.018	0.281	0.012	<b>&lt;0.001</b>	-0.014	0.018
$S_{c3}$	496	39.31	<b>&lt;0.001</b>	0.192	-0.024	0.240	0.021	<b>&lt;0.001</b>	-0.020	<b>0.007</b>
$S_{c4}$	496	255.1	<b>&lt;0.001</b>	0.607	-0.053	0.014	0.064	<b>&lt;0.001</b>	-0.012	0.121
$S_{c5}$	496	487.9	<b>&lt;0.001</b>	0.747	-0.094	<b>&lt;0.001</b>	0.092	<b>&lt;0.001</b>	-0.006	0.522
$S_{c6}$	496	0.85	0.45	0.005	-0.014	0.496	0.002	0.739	0.002	0.775
$S_{c7}$	496	0.81	0.49	0.005	-0.005	0.584	0.001	0.676	0.0001	0.976
$S_b$	496	1814	<b>&lt;0.001</b>	0.917	-0.831	<b>&lt;0.001</b>	0.114	<b>&lt;0.001</b>	-0.096	<b>&lt;0.001</b>
$S$	496	1297	<b>&lt;0.001</b>	0.887	-1.005	<b>&lt;0.001</b>	0.307	<b>&lt;0.001</b>	-0.145	<b>&lt;0.001</b>

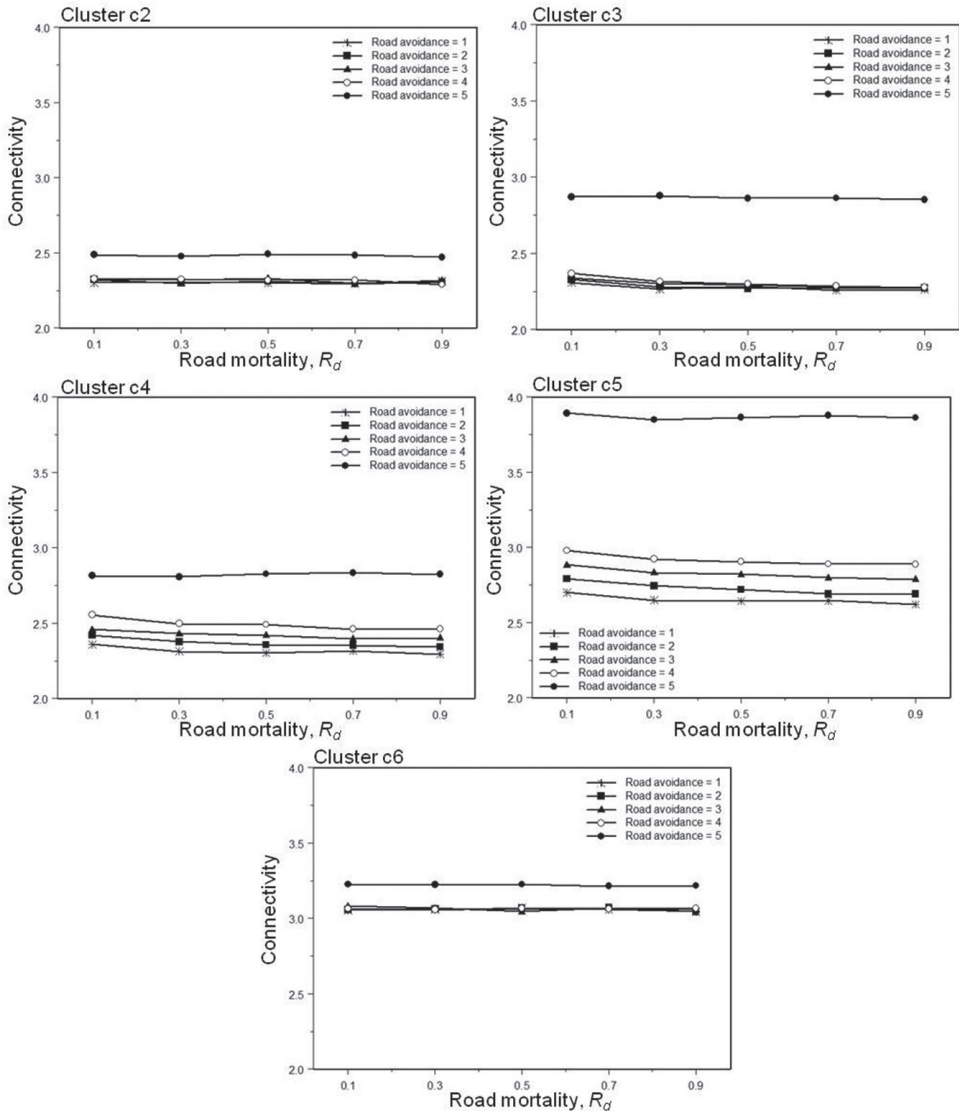


**Figure 3.** Effect of road avoidance ( $R_a$ ) and road mortality ( $R_d$ ) on **A** between-cluster connectivity ( $S_b$ ) and **B** landscape connectivity ( $S$ ).

mortality decreases (Table 3). These effects are all statistically significant ( $F_{3,496} = 1814$ ,  $p < 0.001$ ). When  $R_a = 5$ , between-cluster connectivity yields its lowest values (Fig. 3A). In these scenarios all dispersal across the road is impossible. Hence, the measured connectivity must represent the connectivity between clusters on the same side of the road.

Overall landscape connectivity ( $S$ ) exhibits very elevated values when road avoidance is total. Otherwise, landscape connectivity decreases with road mortality and increases with road avoidance, the effect of road avoidance being strongest at lower values of road mortality (Fig. 3B). All effects are statistically significant ( $F_{3,496} = 1297$ ,  $p < 0.001$ ) (Table 3).

In general, the same trends are found in within-cluster connectivity ( $S_c$ ) (Table 3). There are, however, some differences. Within-cluster connectivity of cluster  $c1$  and  $c7$  is affected neither by changes in road mortality nor road avoidance. These two clusters are also furthest away from the test roads (Table 2). Clusters  $c2$  through  $c6$  all exhibit



**Figure 4.** Effect of road avoidance ( $R_a$ ) and road mortality ( $R_d$ ) on within-cluster connectivity ( $S$ ) in cluster c2 – c6.

very elevated connectivity values when  $R_a = 5$ . Connectivity within these clusters also tend to increase with road avoidance and decrease with road mortality when  $R_a \leq 4$  (Fig. 4). However, the effect of road mortality is only statistically significant in clusters c4 and c5 (and after Bonferroni correction only c5). Both are large clusters with several pond members very close to the road (Table 2, Table 3). Clusters c2 - c5 are all significantly affected by road avoidance; in contrast to c6 in which the majority of member ponds are further away from the road (Table 2, Table 3).

## **Discussion**

As hypothesized road mortality has a negative effect on between-cluster connectivity. However, contrary to our expectation we find that road avoidance can promote connectivity across roads. An explanation could be that roads actually function as traps if road avoidance is low. In this model roads are not just lines to cross; they are considered the same way as other kinds of habitat. Hence, when habitat attraction of the roads is higher (and thus road avoidance low) than the surrounding habitat, the road may actually be the preferred habitat. Moreover, the survival probability on roads is always lower than in any other type of habitat. Thus, at high levels of road avoidance, frog agents only rarely enter the roads, but if they do they quickly leave it again and only suffer the high mortality for a short time. When road avoidance is low, frog agents enter the roads more willingly and will tend to stay there, suffering from the higher mortality for a longer time. The severity of the “trap” effect will depend on road mortality as, all else being equal, successful dispersal across the road depends on the survival probability. The results do in fact show a strong interaction; the positive effect of road avoidance on between-cluster connectivity getting more pronounced as road mortality increases.

In accordance with our second hypothesis, we find that road avoidance has a positive effect on local connectivity. In particular, when road avoidance is set to five, connectivity shows considerable elevated values. The strong effect on within-cluster connectivity of a 100 % barrier may seem surprising, but can be explained as a “deflection” effect. When the road is inaccessible road mortality is no longer an issue and a larger proportion of frog agents will survive. Moreover, the blockage forces the agents to move along the road instead of crossing. Taken together, this has the effect that a larger proportion of frog agents stays within the local area for a longer time, which increases the probability of an agent settling within the cluster, enhancing within-cluster connectivity. We did not expect road mortality to have an effect on within-cluster connectivity, but we do find a negative, although weak, response. This is probably because there will be a small proportion of frog agents entering the road and returning to the same side. The survival probability of these returnees will depend on road mortality.

The seven clusters identified in this study do not all respond in the same way to changes in road avoidance and road mortality. Two of the clusters, c1 and c7, are not affected at all; these are also the clusters furthest away from the road. Road mortality only significantly affects larger clusters with several pond members very close to the road; maybe because only these clusters have sufficient number of returnees for the effect to be detectable. Road avoidance, on the other hand, affects also clusters further away; only clusters with a minimum distance to road above 300 m are unaffected by road avoidance. The result suggests that if the road is within the summer habitat of some of the member ponds, then road avoidance will affect within-cluster connectivity.

In this study, scenarios with road avoidance set to five, correspond to real life situations where fencing along roads prevents access to the road. Our results suggest that fencing can result in highly increased local connectivity, even between ponds not in

immediate proximity to the road. Thus, fencing may not just mitigate road induced mortality but may actually enhance local population persistence. However, the results also show this to be at the cost of regional connectivity. Fencing separates a population into several smaller and more isolated groups of subpopulations, each of which may have a higher risk of extinction and a lower probability of recolonisation. In a simulation experiment with a local population of virtual animals Jaeger and Fahrig (2004) found that fencing could prolong persistence time but had little effect on persistence probability, and in most cases the population only survived on one side of the road. Moreover, studies have shown that gene flow between subpopulation and genetic diversity in a regional population can be reduced by the barrier effect of roads (Arens et al. 2007; Johansson et al. 2005; Reh and Seitz 1990). Thus, whether the positive effect of fencing on landscape connectivity translates into improved population persistence will depend on the number, quality and connectivity between subpopulation on the same side of the road (Hels and Nachman 2002).

The series of scenarios are hypothetical and all may not correspond to real life situations but road mortality can indeed range between very low and very high values, depending on traffic intensity. Extreme low values of road avoidance, to the point where the road becomes more attractive than the surrounding landscape, may seem very unrealistic. However, behavioural responses to traffic like immobilisation (Maze-rolle et al. 2005) can have similar effects; and after rain fall wet, dark roads may appear deceptively attractive to frogs (Andrews et al. 2008). Furthermore, the propensity of frogs to enter roads may depend on the property of the road or road verges. Thus, the level of road avoidance may, at least partly, be controlled by the design of the road.

Our study concerns a specific landscape and a specific species, but still it is possible to draw some general conclusion. First of all our results emphasize that connectivity is context dependent. The behaviour of the focal species, the structure of the landscape and their interaction are essential to how connectivity is realized. Furthermore, our simulations indicate that the barrier effect of roads not only affect dispersal across roads. Even between ponds located on the same side of the road, dispersal success can be highly susceptible to road avoidance and road mortality, depending on the distance to the road. This suggests that roads may affect not only regional or metapopulation dynamics but also have a direct effect on local population dynamics.

Very little is known about the effects of mitigation measures in general. Once mitigation measures are implemented, efforts are seldom put into discovering how well they work (Lesbarreres and Fahrig 2012; van der Grift et al. 2013). Simulation studies like the one presented here can provide a means to assess the effects of planned road designs and mitigation measures (van der Ree et al. 2009).

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## Appendix

Full model description following the ODD-template suggested by Grimm et al. (2006, 2010) and model parameterisation. (doi: 10.3897/natureconservation.5.4611.app). File format: Adobe PDF document (pdf).

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# Spatial Amphibian Impact Assessment – a management tool for assessment of road effects on regional populations of Moor frogs (*Rana arvalis*)

Maj-Britt Pontoppidan<sup>1</sup>, Gösta Nachman<sup>1</sup>

<sup>1</sup> Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

Corresponding author: *Maj-Britt Pontoppidan* ([mbp@bio.ku.dk](mailto:mbp@bio.ku.dk))

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## Abstract

An expanding network of roads and railways fragments natural habitat affecting the amount and quality of habitat and reducing connectivity between habitat patches with severe consequences for biodiversity and population persistence. To ensure an ecologically sustainable transportation system it is essential to find agreement between nature conservation and land use. However, sustainable road planning requires adequate tools for assessment, prevention and mitigation of the impacts of infrastructure. In this study, we present a spatially explicit model, SAIA (Spatial Amphibian Impact Assessment), to be used as a standardized and quantitative tool for assessing the impact of roads on pond-breeding amphibians. The model considers a landscape mosaic of breeding habitat, summer habitat and uninhabitable land. As input, we use a GIS-map of the landscape with information on land cover as well as data on observed frog populations in the survey area. The dispersal of juvenile frogs is simulated by means of individual-based modelling, while a population-based model is used for simulating population dynamics. In combination the two types of models generate output on landscape connectivity and population viability. Analyses of maps without the planned road constructions will constitute a “null-model” against which other scenarios can be compared, making it possible to assess the effect of road projects on landscape connectivity and population dynamics. Analyses and comparisons of several alternative road projects can identify the least harmful solution. The effect of mitigation measures, such as new breeding ponds and underpasses, can be evaluated by incorporating them in the maps, thereby enhancing the utility of the model as a management tool in Environmental Impact Assessments. We demonstrate how SAIA can be used to assess which management measures would be best to mitigate the effect of landscape fragmentation caused by road constructions by means of a case study dedicated to the Moor frog (*Rana arvalis*).

**Keywords**

*Rana arvalis*, Individual-based modelling, Fragmentation, Connectivity, Pond-breeding amphibians, Landscape planning, mitigation, management tool, population persistence

**Introduction**

Over the last decade a growing amount of literature has documented the severe impacts of transport infrastructure on biodiversity, population persistence and gene flow. An expanding network of roads and railways divides natural habitat into smaller and smaller fragments, affecting the amount and quality of habitat and reducing connectivity between habitat patches (Coffin 2007; Fahrig and Rytwinski 2009; Forman and Alexander 1998; Holderegger and Di Giulio 2010; Spellerberg 1998; Trombulak and Frissell 2000). To ensure an ecologically sustainable transportation system, it is essential to find agreement between nature conservation and land use. In Europe and the US, programs and policies have been developed to address this need in strategic and environmental impact assessments (Brown 2006; Iuell et al. 2003; Trocmé et al. 2003). However, sustainable road planning requires adequate tools for assessment, prevention and mitigation of the impacts of infrastructure (Beckmann 2010; Forman et al. 2003; Gontier et al. 2010).

Movement is vital to the survival of animal populations. The persistence of a population depends on the amount and accessibility of its required resources and, within a metapopulation framework, also on sufficient dispersal between subpopulations (Dunning et al. 1992; Wiens 1997). Taylor et al. (1993) defined connectivity as the degree to which the landscape facilitates or impedes movement among resource patches” and measures of connectivity are often used as indicators of a landscape’s capability to sustain a population. However, habitat requirements and behaviours differ between animal species and, thus, the connectivity of a landscape must in essence be species specific. Geographical information systems (GIS) have proved to be an important tool when assessing the impact of roads on landscape fragmentation and/or connectivity (Beckmann 2010; Brown 2006; Calabrese and Fagan 2004). Methods using least cost modelling (Adriaensen et al. 2003; Epps et al. 2007) or graph theoretical approaches (Bunn et al. 2000; Minor and Urban 2008; Zetterberg et al. 2010) usually combine GIS data with some species specific data such as dispersal distances or habitat suitability. However, none of these methods considers the particular dispersal, survival and establishment of the animals, which depend not only on the quality of the habitat but also on the behaviour of the animals, their responses to habitat conditions, landscape elements, interactions with other animals and many other factors. Individual based models (IBMs) have proved to be suitable for describing such processes (Grimm 1999; McLane et al. 2011) and recently there has been an increase in IBM case studies demonstrating the potential for analysing population dynamics emerging from the interactions between landscape settings and animal behaviour (e.g. Graf et al. 2007; Kramer-Schadt et al. 2004; Pe’er et al. 2011).

We have developed a strategic management tool to be used in assessment and mitigation of road effects on a regional population of pond-breeding amphibians. The model, called SAIA (Spatial Amphibian Impact Assessment), combines the use of GIS land cover maps with IBM and provides information on connectivity as well as estimates of population persistence. SAIA is to be used by the Danish road authorities when assessing how new road constructions may affect Moor frogs (*Rana arvalis*). In this paper we demonstrate how SAIA can be used for assessing which management measures would be best to mitigate the effect of landscape fragmentation caused by the construction of a road ca 90 km west of Copenhagen, Denmark. To achieve this goal the following specific research questions were addressed:

1. What is the structure of the regional habitat network before road construction?
2. How is the habitat network affected by the new road?
3. Which mitigation strategies are best suited to preserve the overall persistence of the regional population of Moor frogs?

## **Methods**

SAIA combines an individual based model with a population based model. The individual based model provides estimates of landscape connectivity and immigration probabilities between all pair wise ponds. The population based model provides estimates of population size and persistence probability.

We use the terms dispersal and migration as defined by Semlitsch (2008), i.e. dispersal is *interpopulational, unidirectional movements from natal sites to other breeding sites* and migration is *intrapopulational, round-trip movements toward and away from aquatic breeding sites*. The habitat of pond breeding amphibians, such as the Moor frog, includes terrestrial as well as aquatic habitat. Therefore, we define an adequate habitat patch of a subpopulation as containing not only the breeding pond but also all accessible summer habitat within migration distance from the pond (Dunning et al. 1992; Pope et al. 2000).

## **Model species**

Moor frogs spend most of their life in terrestrial habitat; aquatic habitat is only used during the breeding season in early spring (Elmberg 2008; Glandt 2008; Hartung 1991). Soon after breeding, the frogs return to their summer habitat, which lies mostly within a 400 m radius from the breeding pond (Elmberg 2008; Hartung 1991; Kovar et al. 2009). Adult frogs show strong site fidelity and often use the same breeding pond and summer habitat from year to year (Loman 1994). Long distance dispersal takes place predominantly during the juvenile life-stage (Semlitsch 2008; Sinsch 1990; 2006). Shortly after metamorphosis, the young frogs leave the natal pond and disperse into the surrounding landscape seeking suitable summer habitat. Dispersal distances

**Table 1.** List of variables characterizing the agents in SAIA.

Variable	Notation	Value range	Agent type	Description
Area Value	$W$	0.5; 1	Cell	Effective area of the cell
Daily Survival	$D_s$		Cell	Daily survival probability
Frog Density	$D$		Cell	Mean number of frogs in the cell
Habitat Attraction	$H_a$	1-5	Cell	The cell's relative attraction to frogs during movement
Habitat Code	$H_c$		Cell	The land cover category of the cell
Habitat Survival	$H_s$	1-5	Cell	The cell's relative survival index
Summer Quality	$H_q$	1-5	Cell	The cell's relative suitability as summer habitat
Breeding Pond			Frog	Breeding pond of frog agents
Natal Pond			Frog	Natal pond of frog agents
Pond ID			Pond	ID number
Pond Perimeter	$O$		Pond	Perimeter of the pond
Pond Quality	$Q$	0.1-1	Pond	Quality index of the pond
Population Size	$N_0$		Pond	Number of adult females (estimated as egg masses found in the pond during survey)
Summer Habitat	$A$		Pond	Summer habitat cells associated with the pond
Summer Habitat Area	$A'$		Pond	Effective area of associated summer habitat

are between a few hundred meters up to 1–2 kilometres (Baker and Halliday 1999; Hartung 1991; Sinsch 2006; Vos and Chardon 1998). The juveniles stay in terrestrial habitat 2–3 years until they reach maturity, although some observations indicate that juvenile frogs follow the adults during the spring migration, without entering the breeding ponds (Hartung 1991; Sjögren-Gulve 1998).

### Model overview

Full model description following the protocol suggested by Grimm et al. (2006, 2010) and model parameterisation are provided in Appendix. Table 1 shows a full list of model variables while a list of model parameters can be found in Table A3 in the Appendix. Netlogo v.4.1.3 (Wilensky 1999) was used as modelling environment (freely downloadable at <http://ccl.northwestern.edu/netlogo>).

### Map construction

To construct a model landscape in which our virtual frogs can move we use a GIS raster map of the study area with land cover data. Each raster cell contains information about the cell's land cover or habitat type ( $H_c$ ). Moreover, three variables are associated with each category of land cover/habitat (Table 2):  $H_q$ , the category's relative suitability as summer habitat;  $H_a$ , the category's relative attraction to frogs during movement and  $H_s$ , the category's relative survival index. For each cell, the assigned survival index is



**Table 2.** Land cover categories and the associated values of Habitat Survival, Habitat Attraction and Summer Quality.

Habitat Code ( $H_i$ )	Description	Habitat Attraction ( $H_a$ )	Habitat Survival ( $H_s$ )	Summer Quality ( $H_q$ )
2	4-lane motorway	2	N/A	1
3	2-lane motorway	2	N/A	1
4	Road, width > 6m	3	N/A	1
5	Road, width 3-6 m	3	N/A	1
6	Other roads	3	2	2
8	Pathway	4	4	3
10	Multiple surface	3	3	3
11	Railway	4	2	3
12	Building	1	N/A	N/A
15	Other made surface	2	3	2
18	Wetlands	5	5	5
20	Running water	4	4	3
22	Meadows	5	5	5
24	Grassland	4	4	4
25	Lakes	1	N/A	N/A
28	Hedgerow	4	4	4
29	Heath land	5	5	4
32	Woodland	4	4	4
34	Stand of trees	4	4	3
36	Bare surface	2	2	1
40	Fallow land	4	4	4
42	Field crops	2	2	2
50	Drift fence	1	N/A	N/A
60	Underpass	4	4	1

converted into a daily survival probability ( $D_i$ ). When concerning paved roads, the daily survival probabilities ranges between 0.1 and 0.8 depending on road category; all other land cover/habitat categories are assigned values between 0.9820 and 0.9995 (see Appendix in the supplementary material for details). Cells with structures or habitats which are assumed inaccessible to the frogs (e.g. buildings, fences or large water bodies) are given a habitat attraction of 1. This will prevent the frogs from entering the cell.

A point-data set containing information about potential breeding ponds found in the study area is used to create stationary pond agents. Each pond agent is characterized by an ID number, the perimeter of the pond ( $O$ ), initial population size (adult females) ( $N_o$ ) and a quality index ( $Q$ ) indicating the suitability of the pond and the immediate surroundings (20 m) in regard to egg and larval survival. In addition the pond variable  $A$  is updated with a list of summer habitat cells within migration distance. Summer habitat cells are identified as cells with SummerQuality ( $H_q$ ) > 3. Summer habitat cells can be completely surrounded by other summer habitat cells (core cells)

or have one or more neighbouring cells which are not summer habitat (edge cells). To account for edge effects, core cells are given an area value ( $W$ ) of 1 while  $W$  is 0.5 for edge cells (Watts and Handley 2010) and the effective area of the summer habitat ( $A$ ) is found as the sum of  $W$ -values of the summer habitat cells belonging to the pond. The individual based model only uses information about pond ID, quality, and summer habitat while all of the variables enter into the population based model.

### **Individual based model**

The IBM is largely identical to the model described in Pontoppidan and Nachman (2013). The model simulates the dispersal of juvenile frogs and estimates immigration probabilities between ponds. Immigration requires two events: 1) the successful dispersal of a juvenile frog to summer habitat outside its natal habitat patch and 2) subsequent successful migration from the new summer habitat to a nearby breeding pond. In real life dispersal starts just after metamorphosis in early summer and lasts until hibernation in autumn. The second part of the immigration event, migration, takes place in the spring 2.5 years later. For simplicity, we simulate the dispersal and breeding migration, as if they take place in the same year.

At the start of a simulation, 250 frog agents are created at each pond. The frogs then disperse through the landscape in random directions from the ponds until they find suitable summer habitat; the movement of the frogs depends on the attractiveness of neighbouring cells and the cells' suitabilities as summer habitat. Survival probabilities depend on the traversed habitat types. Unlike the former model, movement behaviour in SAIA also depends on weather conditions. A database containing data on daily precipitation (Cappelen 2009) is used to reflect natural weather patterns. At the start of a simulation, a random year is chosen from this database and at each time step, information on precipitation is drawn for the simulated day of the year. When daily precipitation exceeds a given threshold ( $a$ ), the variables `HabitatAttraction` and `DailySurvival` of all accessible cells are given the highest value. An exception is paved roads where only `HabitatAttraction`, but not `DailySurvival`, is changed. The simulation runs for 240 time steps, each time step representing one day. After each simulation, immigration probabilities between all pairs of ponds are calculated and an immigration matrix is constructed.

### **Population based model**

After the individual based simulation, a population based model simulates the population dynamics in each pond through 40 iterations of a life cycle model. The elements of the life cycle model are 1) Reproduction, 2) Survival and 3) Immigration. For simplicity, we only model the female part of the population. We assume a sex ratio of 1:1 and that females always become mated once in a season. Pond populations are grouped by age from 0 through 6 years, and survival and reproductive rates are based on life-table

**Table 3.** Life table for *Rana arvalis* constructed by amphibian experts.

Stage/Age	Survival probability	Fecundity ( eggs pr. female)
Egg/larvae	0.005	-
0	0.55	0
1	0.55	70
2	0.55	945
3	0.55	1190
4	0.50	1250
5	0.40	1300
6	0.20	1300

data constructed by amphibian experts (Fog and Hesselsøe 2009) (Table 3). The pond variable ( $N_p$ ) is set as the initial population size of the pond. Demographic but not environmental stochasticity is incorporated into the model.

Individuals can start reproducing in their third year. As in Hels and Nachman (2002), the expected egg production of a female is assumed to follow a negative binomial distribution with mean  $\bar{R}$  and clumping parameter  $k$ .  $\bar{R}$  is the mean number of eggs produced by a female of a given age. The number of two-weeks old frogs ready to disperse is considered as the reproductive output. This involves the survival of egg and larvae, as well as the survival of the young frogs the first two-weeks after metamorphosis. The overall probability that an egg develops into a frog that survives until dispersal time is assumed to be negatively affected by the density of eggs in the pond and positively affected by the quality of the pond. The conditional probability that a frog survives from age  $a$  to age  $a+1$  is assumed to depend on age. Furthermore, survival is assumed to depend on the frog density in the summer habitat. For simplicity, this is modelled as a “culling” process when frog density exceeds the carrying capacity of summer habitat. The carrying capacity is estimated as the mean initial frog density in summer habitat cells associated with the populated ponds. Immigration probabilities between all pairs of ponds are obtained from the immigration matrix constructed during the IBM. The actual number of immigrants a subpopulation receives depends on the reproductive output of each of the other ponds and the corresponding immigration probability. Emigration rates are not modelled explicitly.

**Output**

At the end of the individual based simulation, the following output was recorded:

the number of surviving frogs, the natal and breeding ponds of all frogs, and the immigration probabilities ( $p_{ij}$ ) between all pair-wise ponds. Landscape connectivity (S) is found as

$$S = \sum_{i=1}^n \sum_{j=1}^n p_{ij}, (i \neq j) \quad (\text{eq. 1})$$

At the end of the population based simulation, the estimated population size of each pond is recorded as the resulting numbers of frogs of ages 2 through 6. The model was run 50 times and mean connectivity with 95% confidence intervals (CI) was computed. For each pond, we computed mean population size with 95% confidence intervals (CI). Pond persistence probability was computed as the proportion of replicates where the estimated population size was positive. The regional population size was computed as the sum of all ponds. Mean number of populated ponds with 95% CI was also calculated. SAIA's connectivity measure is an index of the potential connectivity between all ponds, whether they are populated or not. The population based model links the potential connectivity with local population dynamics, and estimated abundances and persistence probabilities can be regarded as a result of the realised connectivity. The estimated landscape connectivity and population size are considered measures of the landscape's ecological performance in regard to the modelled species.

Cluster analysis was used to identify highly connected groups of ponds. Ponds were grouped into clusters depending on their mutual connectivity, using unweighted, arithmetic, average clustering as described by Legendre and Legendre (1998). Since immigration probabilities between ponds are not necessarily symmetric, i.e.  $p_{ij} \neq p_{ji}$ , we used summed immigrations probabilities as similarity measures ( $m$ ), i.e.  $m_{ij} = p_{ij} + p_{ji}$ . The threshold at which a given pond or cluster no longer can be added to another cluster was set to  $m_{ij} \leq 0.01$ . Connectivity between any pairs of clusters ( $S_{k,l}$ ) is found as

$$S_{k,l} = \sum_{i=1}^{n_k} \sum_{j=1}^{n_l} p_{ij}, \quad (i \neq j) \quad (\text{eq. 2})$$

where  $n_k$  and  $n_l$  are the number of ponds in clusters  $k$  and  $l$ , respectively. Cluster abundance is computed as the sum of the member ponds' estimated population size.

## Model validation

We have applied a bottom-up approach and used pattern oriented modelling (Grimm and Railsback 2005; Latombe et al. 2011) to parameterise and calibrate SAIA's sub-models controlling movement, dispersal and survival. This is documented in detail in Appendix in the supplementary material. However, lack of field data and the specificity of the model's emergent results to the modelled system complicate validation of the full model. Instead, we have used a heuristic approach, consulting amphibian experts during the whole modelling process to evaluate the plausibility of the emergent results. The population based model is based on expert data but is not validated against field data. Moreover, environmental stochasticity is not included in the population based model. Hence, the output should not be considered predictive, but rather as an index of the landscape's potential carrying capacity.

## **Case study**

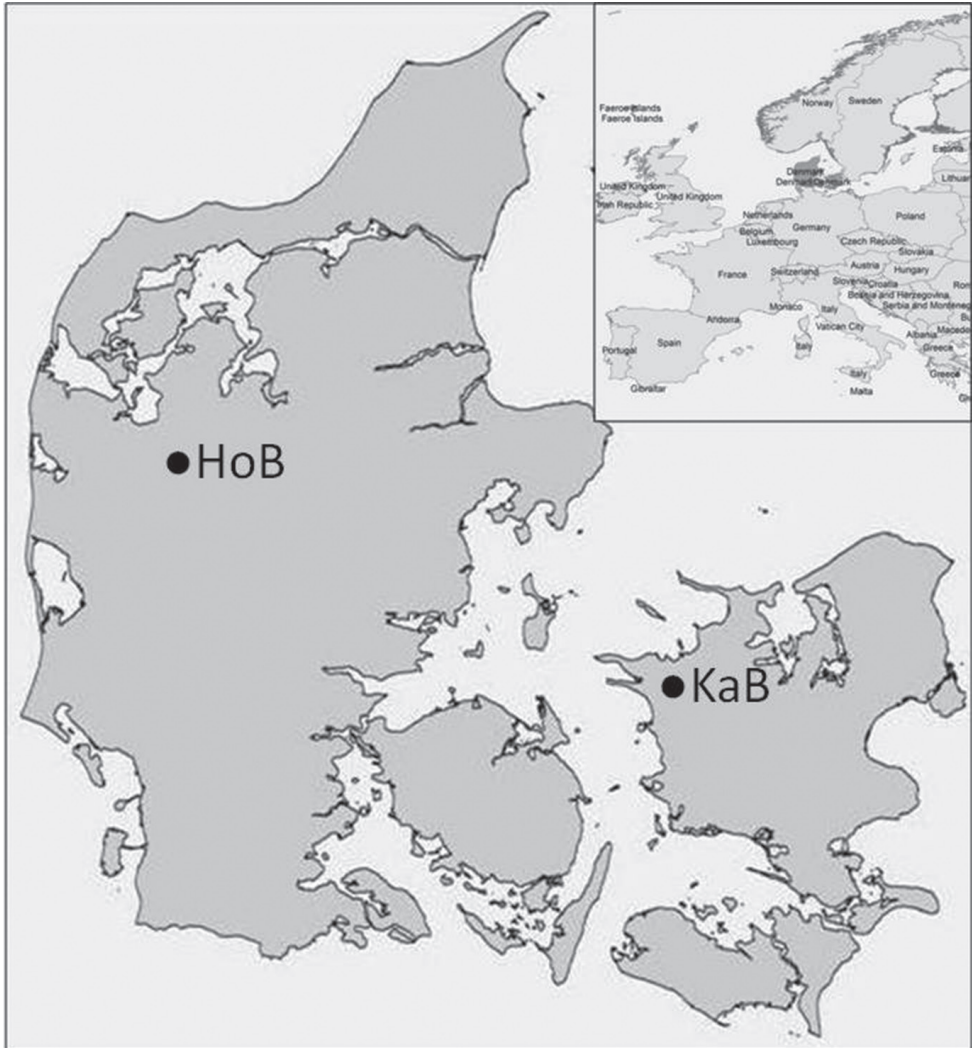
We apply SAIA to a road project in Denmark and demonstrate the workflow of an impact assessment. The project concerns an area in the north-western part of Zealand, 10 km east of the city of Kalundborg (55°40.14'N, 11°17.85'E) (Figure 1) and includes a broadening of an existing 2-lane motorway into a 4-lane motorway as well as an extension of the motorway. The assessment procedure can be divided into three parts – Initial analyses, Mitigation planning and Mitigation analysis.

## **Initial analyses**

This part involves the construction and analysis of two maps. The first map, Scenario 0, is a map of the landscape as it looks before the planned road project. This map serves as Null Scenario and the results of the analysis are considered the state of the landscape we wish to maintain. The second map, Scenario 1, is of the landscape as expected after road construction. Analysis of this map gives indications of the effects the planned road construction can have on the ecological performance of the landscape.

## **Scenario 0**

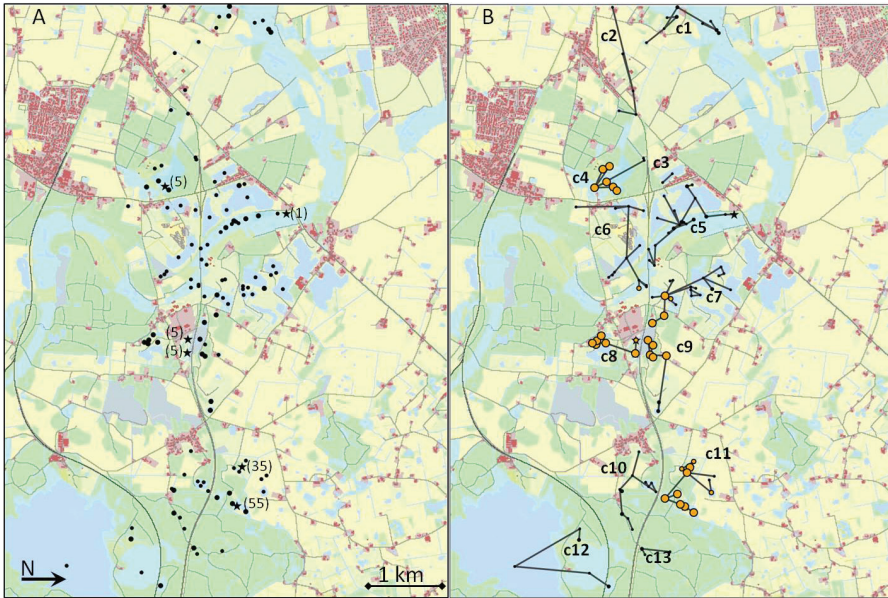
Construction of the map is based on a GIS data set from the road project, supplied by the Danish Road Directorate and an environmental consultancy firm, Amphi Consult. The extent of the land cover map is 600 × 800 cells, and each cell is 10 × 10 m. All cells are assigned values of  $H_a$ ,  $H_s$  and  $H_g$  depending on their land cover type, following a protocol designed by Amphi Consult (Hassingboe et al. 2012) (Table 2). A point data set contains information about potential breeding ponds found during a field survey of the area. The survey was conducted in spring 2012 by Amphi Consult in the initial phases of the road project following standard procedures (Fog and Hesselsøe 2009). The initial population ( $N_0$ ) was estimated as the number of egg masses found in the surveyed pond and is assumed to equal the number of breeding females in the pond. Pond quality ( $Q$ ) was assessed visually and includes factors such as the shape of the pond, degree of shading, vegetation in as well as around the pond and presence of predators (fish). The data set contains 121 ponds, of which 23 ponds are of high quality ( $Q > 0.6$ ). Six of the ponds are populated; population sizes ranging between 1 and 55 egg masses, in total 106 egg masses. The map with the location of the ponds is shown in Figure 2A, ponds containing egg masses are marked with a star shape and the number of egg masses found.



**Figure 1.** Location of two study areas in Denmark. KaB is an area near Kalundborg on Zealand and HoB is near Holstebro in Jutland. Only KaB is used in the present analysis, but both areas are used for the parameterisation of the model.

### Scenario 1

The map used in Scenario 0 is modified by changing the land cover category of the existing road section from a 2-lane motorway to a 4-lane motorway. The new section of the road is added as well and categorised as a 4-lane motorway (Figure 3A). As a consequence of the change in land cover category the daily survival probability ( $D_j$ ) of the road cells decreases from 0.20 to 0.10 (Table A5 in the Appendix). The road construction also involves removal of five unpopulated ponds along the road (Figure 3A).



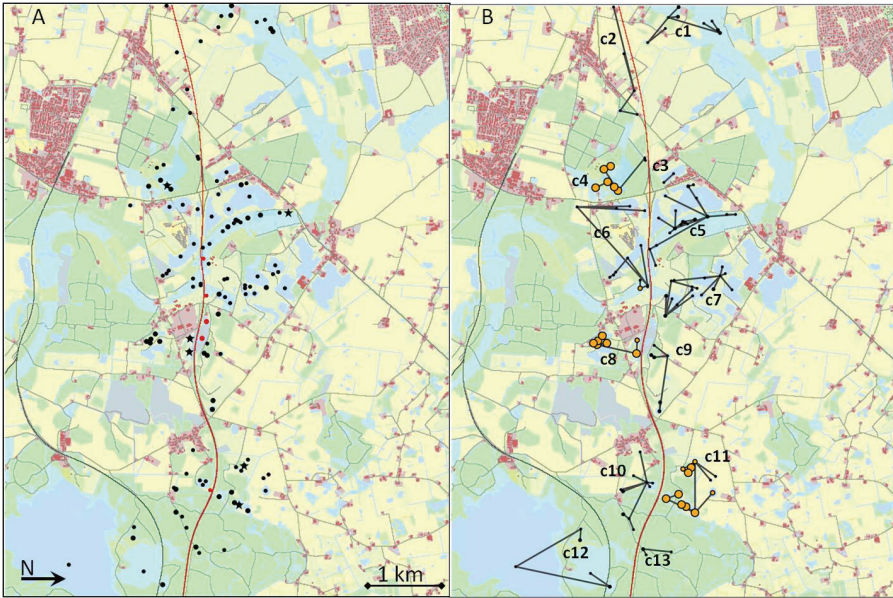
**Figure 2.** Scenario 0. **A** Map of the landscape before road constructions. Black dots represent potential breeding ponds. Small dots are ponds with pond quality ( $Q \leq 6$ ); large dots are ponds with  $Q \geq 7$ . Populated ponds are indicated with a star shape. The number of egg masses found in the pond is shown in parenthesis **B** Result of cluster analysis showing clusters c1–c13. Ponds linked with black lines belong to the same cluster. Pond size and colour indicate the result of the population based model. Yellow circles represent ponds with an estimated population size  $\geq 1$ . Ponds with larger yellow circles have a persistence probability  $> 0.75$ .

## Mitigation planning

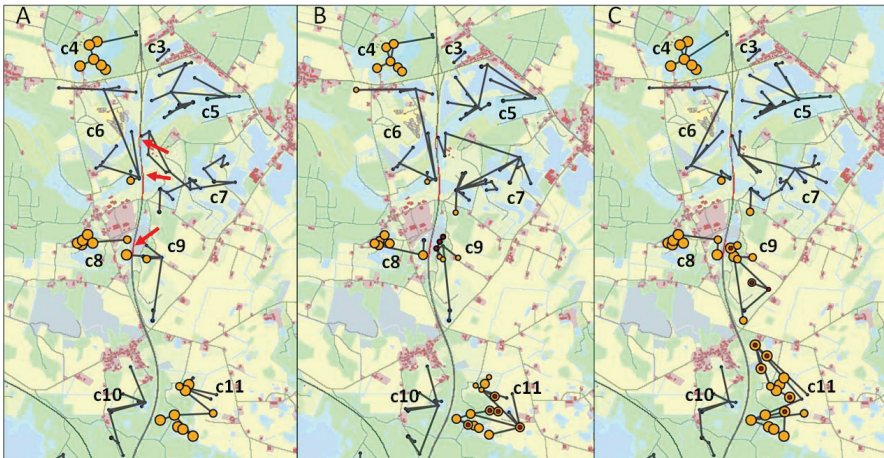
Once the analyses of Scenario 0 and Scenario 1 are done, planning of possible mitigation measures can start. The results from the initial analyses can give insights in the structure of the pond network and can locate areas or subpopulation where the road construction will have the strongest impact. Likely source populations and their colonisation potential may be identified and possible sink population may be recognised. Interpretation of the results provides a basis for considerations about which mitigation measures are needed and where to place them. A series of scenarios with different suggestions for mitigation measures can then be constructed and analysed.

## Mitigation analysis

In this case study we construct and analyse three alternative mitigation scenarios - Scenario 2, Scenario 3a and Scenario 3b. The choices of mitigation measures depend as just mentioned on the results of the initial analysis. Thus, the reasoning behind the different mitigation scenarios will be explained in the result section. However, the map construction of the three scenarios is briefly described below.



**Figure 3.** Scenario 1. **A** Map of the landscape after road constructions (red road). Black dots represent potential breeding ponds. Small dots are ponds with pond quality ( $Q \leq 6$ ); large dots are ponds with  $Q \geq 7$ . Populated ponds are indicated with a star shape. Pink ponds are ponds removed in connection with the constructions **B** Result of cluster analysis showing clusters c1–c13. Ponds linked with black lines belong to the same cluster. Pond size and colour indicate the result of the population based model. Yellow circles represent ponds with an estimated population size  $\geq 1$ . Ponds with larger yellow circles have a persistence probability  $> 0.75$ .



**Figure 4.** Analyses of mitigation measures. Result of cluster analyses showing clusters c3–c11. Ponds linked with black lines belong to the same cluster. Pond size and colour indicate the result of the population based model. Yellow circles represent populated ponds. Ponds with larger yellow circles have a persistence probability  $> 0.75$ . **A** Scenario 2 - Location of underpasses is shown with red arrows **B** Scenario 3a - Three new ponds in cluster c9 and five new ponds in c11 are shown with red dots **C** Scenario 3b - Eight new ponds connecting c9 and c11 are shown with red dots.



## **Scenario 2: Construction of underpasses and drift fences**

In this scenario we add three underpasses to the map used in Scenario 1. Drift fences are established along the road for 100 m on each side of the underpass, except for underpass 2 which has a 300 m drift fence to the east. The location of the underpasses is shown in Figure 4A. Underpasses are constructed by changing the habitat code and the associated values of habitat attraction ( $H_a$ ) and daily survival probability ( $D_j$ ) of the affected road cells. Drift fences are created by changing the habitat attraction of the affected road section to 1, thus preventing access to the cells.

## **Scenario 3a and 3b: Construction of artificial breeding ponds**

In these two scenarios eight artificial, high quality breeding ponds are added to the map used in Scenario 1. Scenario 3a and 3b represent two alternative locations of the eight ponds (Figure 4B and C). Each breeding pond is created as a pond agent and assigned a pond quality ( $Q$ ) of 0.7. The initial population size ( $N_o$ ) is set to 0. The pond perimeter ( $O$ ) is set to 79 m, corresponding to the average size of a standard artificial breeding pond.

## **Results**

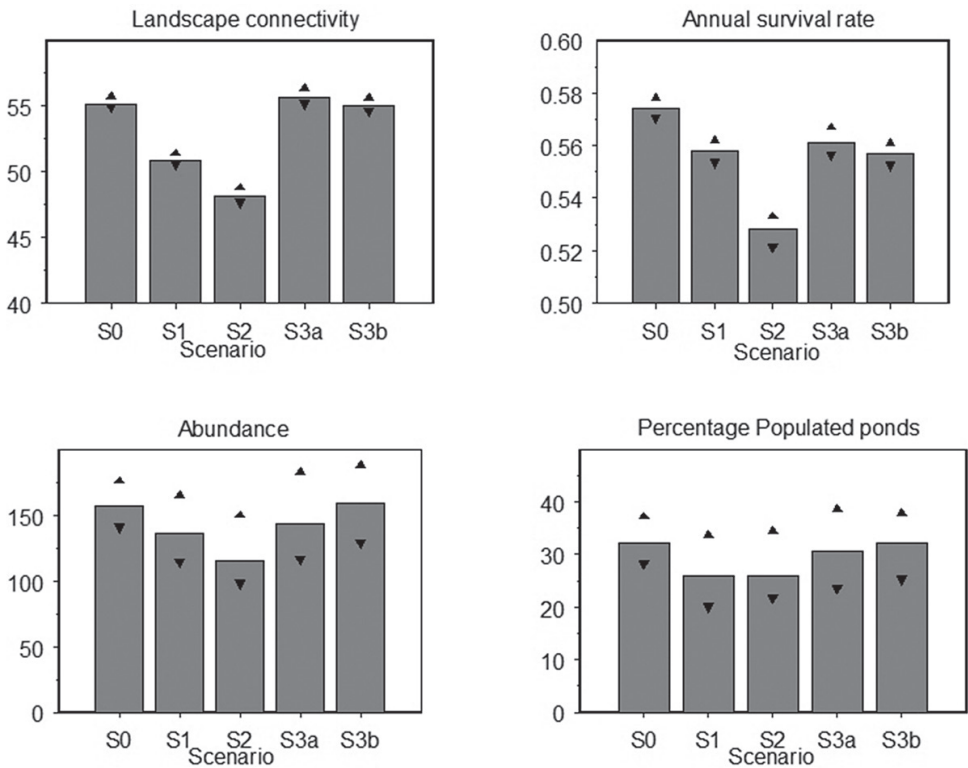
### **Initial analyses**

#### **Scenario 0**

The average percentage of ponds populated during a simulation is 32%, although only 22% of the ponds have a more permanent status (pond persistence probability > 0.75). The regional abundance of adult female frogs is estimated to be 157; the percentage of frogs surviving during dispersal is 57 %, and landscape connectivity is 55 (Figure 5). The cluster analysis groups the 121 ponds into 13 clusters, cluster sizes ranging from 2-20 ponds (Figure 2B, Table 4). The six populated ponds found during field surveys are distributed on four different clusters. One pond with only one adult female is found in cluster c5. Another pond, with an initial population of five, belongs to cluster c4 and two other ponds, also with a  $N_o$  of five, are found in cluster c8. Cluster c11 contains the remaining two populated ponds with an initial total population of 90 adult females. Apart from cluster c5, all of these initially populated clusters exhibit high viability. Clusters c4, c8 and c11 have mean pond persistence probabilities between 77% - 93% and estimated cluster abundances from 23–51 adult females. Cluster c9 also shows high values of abundance and persistence. Although initially unpopulated, c9 contains several high quality ponds and is connected with c8 and c11 which may promote colonisation and establishment. In cluster c6 and c7, the mean

**Table 4.** Results from analysis of Scenario 0 (before road construction).

Cluster ID	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11	c12	c13
Number of ponds in cluster	9	5	2	8	20	13	19	7	7	11	12	5	3
Number of high quality ponds (Q > 0.6)	2	0	0	4	2	0	1	7	3	0	3	1	0
Connectivity to other clusters	0.45	0.54	0.30	0.57	2.19	1.13	2.94	0.36	1.20	0.07	0.10	0.05	0.06
Estimated cluster abundance	0	0	0	49	0	3	11	23	14	0	51	0	0
Mean pond persistence probability	0	0	0	0.82	0.03	0.29	0.35	0.93	0.73	0.01	0.77	0	0.13
Connectivity to c4	0	0.09	0.04	-	0.01	0.44	0	0	0	0	0	0	0
Connectivity to c8	0	0	0	0	0	0.23	0.04	-	0.10	0	0	0	0
Connectivity to c11	0	0	0	0	0	0.00	0	0	0.02	0.02	-	0	0.06



**Figure 5.** Key results from analysis of the five scenarios. Upper and lower 95% confidence limits are indicated with black triangles.

pond persistence probability is considerably lower (29–35%) as is the estimated cluster abundance. While the two clusters, especially c6, are connected with other populated clusters, they lack high-quality ponds and the clusters may function as sinks. In the remaining clusters the estimated abundance is less than one individual.

### **Scenario 1**

After construction of the road, the percentage of populated ponds is reduced to 26% and the number of ponds with a persistence probability > 0.75 is now down to 16%. Survival rate of dispersing frogs is 56% and estimated regional abundance is 136 adult females. Landscape connectivity decreases to 51 (Figure 5). The number of clusters is unchanged but connectivity between clusters is reduced (Table 5). Connectivity from c7 and c9 to their primary source (c8) decreases more than 80%. Moreover, three ponds are lost in c7 and c9 due to the road construction. Estimated abundance and mean pond persistence probability decreases in c7 and c9 and these clusters are no longer able to uphold viable populations (Figure 3B). However, the initially populated clusters c4, c8 and c11 are not affected by the road construction.

### **Mitigation planning**

The initial analyses reveal that the landscape contains three viable populations (c4, c8 & c11) centred on the initially populated ponds. These populations appear not to be affected by the road construction and in the simulations the clusters seem to function as sources enabling colonisation and establishment of populations in c9 and c7. Cluster c4 has a large and viable population, but even though it is well connected with the neighbouring clusters their qualities are not high enough to enable establishment of new populations. Since c4 is not connected with c7 and c9, its potential as source cluster is low. Cluster c8 seems to be the primary source cluster to c9 and c7; however, expansion of the road heavily reduces its value as a source. Furthermore, the removal of three ponds between c9 and c7 may diminish the connectivity between these clusters. Cluster c11 has a viable population and although situated somewhat remotely there is still some connectivity to c7 and c9.

The results indicate that, in order to compensate or mitigate the effect of the road project, the best strategies will be either to re-establish connectivity across the road between cluster c8 and clusters c7/c9 and between cluster c7 and c9 or to take advantage of the viability of cluster c11 and its source potential. Based on this, we create and analyse the following scenarios:

*Scenario 2:* Connectivity across the road is re-established by constructing three underpasses and drift fences along the middle section of the motorway (Figure 4A). Two of the underpasses (including drift fences) were placed between cluster c6 and c7; the

**Table 5.** Results from analysis of Scenario 1 (after road construction).

Cluster ID	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11	c12	c13
Number of ponds in cluster	9	5	2	8	19	13	17	7	6	9	12	5	3
Number of high quality ponds (Q > 0.6)	2	0	0	4	2	0	1	7	2	0	3	1	0
Connectivity to other clusters	0.02	0.10	0.27	0.52	1.69	0.67	1.92	0.23	0.55	0.06	0.09	0.05	0.06
Estimated cluster abundance	0	0	0	50	2	2	1	24	5	0	49	0	0
Mean pond persistence probability	0	0	0.03	0.84	0.05	0.24	0.08	0.93	0.26	0	0.78	0	0.15
Connectivity to c4	0	0.08	0	-	0	0.44	0	0	0	0	0	0	0
Connectivity to c8	0	0	0	0	0	0.20	0.01	-	0.02	0	0	0	0
Connectivity to c11	0	0	0	0	0	0	0	0	0.03	0	-	0	0.06

third between cluster c8 and c9. The expectation is that connectivity between cluster c8 and c9/c7 will improve and enable establishment of populations in cluster c9.

*Scenario 3a:* The quality of cluster c9 and c11 is improved by establishing three, and then five, new high quality ponds within the range of the clusters (Figure 4B). The three new ponds in cluster c9 are expected to improve the probability of successful establishment of immigrants as well as reconnect c9 with c7. We expect an increase in abundance in cluster c11, and hence increased immigration to and colonisation of cluster c9.

*Scenario 3b:* In this modification of scenario 3a the quality of cluster c9 and c11 is still improved but with only one and two ponds, respectively. The remaining five ponds are used to create a dispersal corridor between cluster c11 and c9 (Figure 4C). This strategy is expected to enhance the abundance in cluster c11 and to improve connectivity to c9, thereby increasing the probability of colonisation.

## Mitigation analyses

### Scenario 2

Quite unexpectedly, the creation of drift fences and underpasses do not improve the condition of the landscape. The mean percentage of populated ponds is 26% and the percentage of ponds with persistence probability > 0.75 is 16% as in Scenario 1. However, the estimated regional abundance of female adults decreases to 115, landscape connectivity is 48 and dispersal survival rate 53% (Figure 5). As expected, connectivity between c8 and c9 is greatly improved. Cluster c9 now spans the road and has annexed one of the ponds in the periphery of c8 (Figure 4A). Abundance and mean pond persistence probability of cluster c9 increase; this, however, is due to the inclusion of a pond from cluster c8. Persistence and abundance do not improve on the original con-

**Table 6.** Results from analysis of mitigation measures. Scenario 2: Drift fences and underpasses; Scenario 3a: Implementing new ponds in clusters c9 and c11; Scenario 3b: Implementing new ponds as corridor between c9 and c11.

Cluster ID	Estimated cluster abundance			Mean pond persistence probability			Connectivity to c8			Connectivity to c11		
	S2*	S3a	S3b	S2*	S3a	S3b	S2*	S3a	S3b	S2	S3a	S3b
c4	40	48	49	0.82	0.82	0.82	0	0	0	0	0	0
c7	1	3	4	0.08	0.11	0.11	0.002 (0.004)	0	0	0	0	0
c8	17 (21)	23	23	0.90 (0.95)	0.90	0.92	-	-	-	0	0	0
c9	6 (2)	11	10	0.38 (0.27)	0.44	0.58	0.19 (0.29)	0.02	0.02	0.025	0.03	0.22
c11	40	50	61	0.74	0.80	0.85	0	0	0	-	-	-

\* In scenario 2 one pond originally belonging to c8 is annexed by c9. Entries in parentheses are values based on the original cluster configurations.

figuration of cluster c9 (Table 6). Apart from cluster c9, connectivity between initially populated clusters and other clusters does not improve. Connectivity to cluster c4 and c11 is unchanged, while connectivity to cluster c8 actually decreases. Finally, the abundance of frogs in cluster c4 and c11 decreases to 20% even though connectivity both within the cluster and to other clusters is unchanged.

### Scenario 3a

Establishment of eight new ponds has a positive effect on landscape condition. The estimated number of adult females in the region increases to 143, percentage of populated ponds is 31% and 19% of the ponds are permanently populated. Landscape connectivity is 56 and dispersal survival rate 56% (Figure 5). The five new ponds in cluster c11 perform well and contain permanent populations. However, the performance of the cluster does not improve, apart from a slightly higher persistence probability (Table 6). Cluster c9 seems to benefit from the additional ponds, although none of the new ponds contain permanent populations. Cluster abundance and connectivity are nearly restored to their original conditions although mean pond persistence probability is still below 50%. Connectivity from cluster c7 to other ponds improves somewhat, but not enough to restore the cluster to its former performance (Figure 4B).

### Scenarios 3b

With this strategy we succeed in restoring the landscape to its original ecological performance. The number of adult female frogs in the region is 159. Mean percentage of

populated ponds is 32% and 22% are populated permanently. Dispersal survival rate is 56% and landscape connectivity is 55 (Figure 5). Three of the new ponds are now part of cluster c9 while the remaining five new ponds belong to cluster c11. Connectivity between cluster c9 and c11 is strong and six of the new ponds contain permanent populations (Figure 4C). The abundance and mean persistence probability of cluster c11 increase and are now better than before the road construction. Conditions in cluster c9 also improve, compared to Scenario 1, but its original performance is not quite restored. The performance of cluster c7 does not change and is still at the same level as found in Scenario 1 (Table 6).

## Discussion

This study demonstrates how initial analyses of the landscape before and after the planned road constructions can help to identify which areas will be most affected by the construction. The analyses enable the user to recognise the colonisation potential of the clusters and to identify source or sink clusters and to use this knowledge for planning mitigation measures. In the present case study, the simulations indicated that the six populations recorded during the field survey will be largely unaffected by the road construction. Nevertheless, the road construction will severely impair the colonisation potential of cluster c8, thereby reducing the ecological performance of the landscape. Of the three mitigation strategies tested, the analysis showed that Scenario 3b is the best solution. This strategy of connecting clusters c9 and c11 restores the landscape to its former ecological performance. Even though not all individual ponds or clusters will be in the same condition as before, the strategy promotes viable populations on both sides of the road. The strategy is not strictly aimed at mitigating the impaired connectivity across the road, but rather tries to compensate for the effects of road construction by improving other areas. Still, the populations on either side of the road are not totally isolated from each other; some dispersal does take place making genetic exchange possible.

Comparing the results from the analyses of Scenarios 3a and 3b suggests that the location of compensating new ponds is not trivial. In both scenarios cluster c11 gets five new ponds, all of high quality. Nevertheless, the results differ quite a lot. Scenario 3a places the new ponds within the cluster sharing the summer habitat of other ponds. Even though the new ponds are colonized and support viable populations, the abundance of frogs within the cluster does not improve. In Scenario 3b, where the abundance of frogs within cluster c11 increases, the new ponds were placed between c9 and c11 and only partly share summer habitat with other ponds. This result emphasizes that for the Moor frog the carrying capacity of an area is not improved by adding new ponds, only new or better summer habitat can achieve this. Hence, we may improve cluster performance by creating new ponds in unutilized summer habitat within dispersal distance.

In Scenarios 3a and 3b, cluster c9 is also enlarged with three new ponds. In these cases there was no difference in frog abundance in the cluster whether the new ponds were placed in unused summer habitat or not. In both scenarios, though, mean pond persis-

tence probability greatly improved compared to Scenario 1. So, while adding ponds to a cluster did not improve carrying capacity, it ensured a more viable cluster population.

The analysis of Scenario 2 showed that drift fences and underpasses have negative effects on the ecological performance of this landscape. This result is highly surprising as well as controversial since fences and underpasses are standard mitigation measures used in many road projects (Iuell et al. 2003). Even though fences and underpasses are supposed to prevent road mortality and promote connectivity, the overall annual survival rate, as well as connectivity, decreased. These effects are probably mostly due to the fences. Underpasses per se do not change movement patterns, but fences do. Moreover, we did see increased connectivity locally across the road between c8 and c9. Fences may force individuals to move along the road, exposing them to low quality habitat for a longer time. Furthermore, the mitigation measures may be counterproductive if the combination of fences and underpasses lead individuals into low quality habitat or areas without ponds to colonize. The population dynamics in the ponds is an emergent property, dependent on local conditions as well as regional dynamics. The change in connectivity and movement patterns caused by the mitigation measures, therefore, seems to be able to affect abundances even in clusters farther away.

Very little is known about the effects of mitigation measures on connectivity and local and regional population persistence. Once mitigation measures are implemented, efforts are seldom put into discovering how well they work. Recordings of animals using wild life passages reveal nothing about effects on local and regional persistence (Lesbarreres and Fahrig 2012; van der Grift et al. 2013). In a simulation study on a generic species, Jaeger and Fahrig (2004) found that fencing, while preventing road mortality, did not necessarily improve population persistence and they recommended fencing only when road mortality is 100 %. In a study on moose (*Alces alces*), Olsson and Widen (2008) found that fences resulted in decreased use of wildlife passages. Our simulation results underscore the need for a better understanding of how mitigation measures affect animal behaviour and population dynamics.

## **Conclusion**

When planning road constructions, it is important to integrate mitigation measures right from the start. Often there are economic constraints on which measures are possible, certain structures as viaducts or bridges may already be in place or land available for compensation measures is restricted. SAIA offers a tool to evaluate different scenarios to find the best combination of mitigation measures for a given set of conditions. The model is meant to be used by non-specialists – all that is needed are GIS maps of the different scenarios. We attempted to find a balance between detailed and yet intuitive and easy interpretable output. Even though SAIA was developed for the Danish Road Directorate, its use is not restricted to road constructions but can be applied to other structures affecting the landscape and their potential impacts on wildlife.

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## Appendix

Full model description following the protocol suggested by Grimm et al. (2006, 2010) and model parameterisation. (doi: 10.3897/natureconservation.5.4612.app). File format: Adobe PDF document (pdf).

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# Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network

Kevin Morelle<sup>1</sup>, François Lehaire<sup>1</sup>, Philippe Lejeune<sup>1</sup>

<sup>1</sup> Department of Forest, Nature and Landscape, Gembloux Agro Bio-Tech, University of Liege, 5030 Gembloux, Belgium

Corresponding author: *Kevin Morelle* ([kevin.morelle@ulg.ac.be](mailto:kevin.morelle@ulg.ac.be))

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## Abstract

This paper is the first to report data on wildlife-vehicle collisions (WVC) in Wallonia, southern Belgium, characterised by one of the densest road network worldwide. With the collaboration of police we identified 3965 accidents involving “free ranging animal” between 2003 and 2011. We observed that these accidents with free ranging animals result in 13% of cases in injuries for the drivers or passengers, and in less than 1% of cases in fatalities (death). 78% of these casualties involve wild animals, among which wild boar take the largest part (39%). During the covered period we observed an annual increase of WVC of 21%. For wild boar and red deer, this increase was significantly correlated with hunting statistics, used as an index of population density. The temporal analysis demonstrated an increase of WVC during night time with peak of accidents at dusk and dawn. Monthly distribution revealed the role of breeding, dispersal and hunting in shaping temporal patterns of accidents. Spatial analysis, focusing on wild boar, roe deer, red deer and red fox demonstrated clustering of accidents for all these species, until scale between 20 to 70 km. Mapping of accidents via Kernel density analysis permitted us to highlight areas with high risk of WVC risk. Our study suggests that the problem of car accidents due to wildlife is an increasing concern in Wallonia but results on spatial and temporal patterns should help for setting up mitigation measures in the most sensible areas. Moreover we suggest that police data source should be used for nationwide analysis and for comparison between countries.

## Keywords

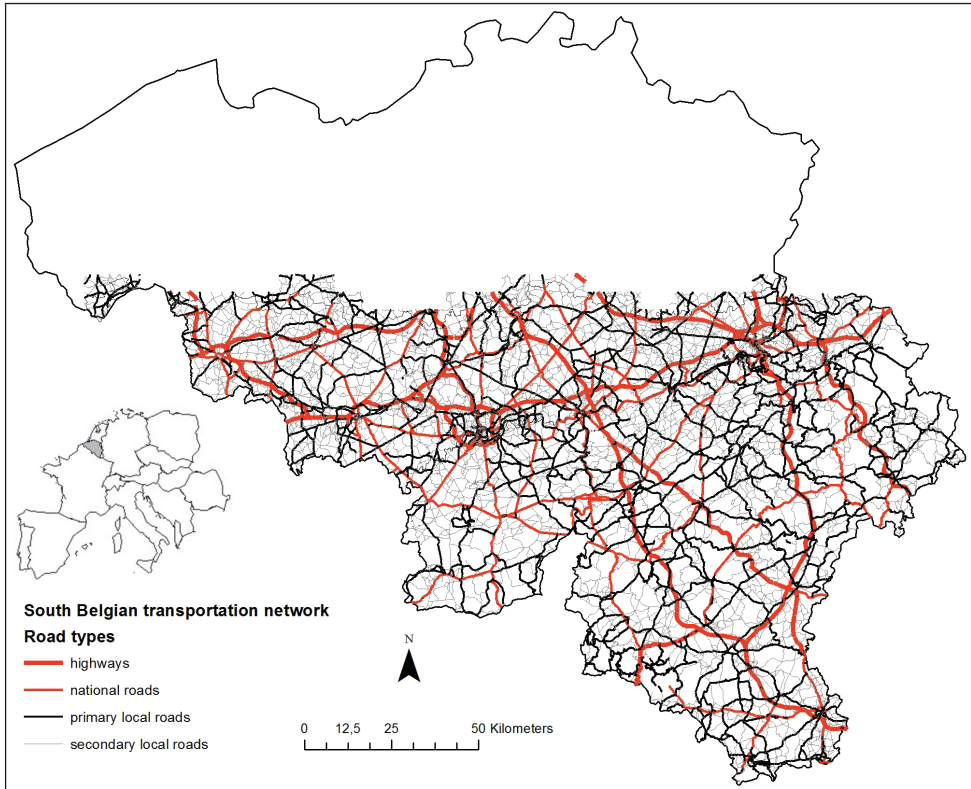
Wildlife-Vehicle Collisions (WVC), roads, spatio-temporal distribution, Wallonia

## Introduction

These last decades, simultaneous increase in infrastructure networks and ungulates populations (Burbaité and Csányi 2010; Milner et al. 2006; Saez-Royuela and Telleria 1986) has led to an increase in the number of wildlife vehicle collisions (Groot Bruinderink and Hazebroek 1996; Romin and Bissonette 1996; Seiler 2004). WVC have important social, economic and ecological consequences. Socially, WVC threaten traffic and human safety and cause injuries, trauma and in some cases death of car drivers or passengers (Williams and Wells 2005). Although WVC involve any size of species, car damage, injuries or fatalities are mostly caused by collision with larger species (> 30kg) (Barthelmess and Brooks 2010; Ford and Fahrig 2007). Economically, these accidents have also high impact through vehicle damage. Hence, in France this cost has been evaluated to 200 million euros for the year 2003, five times more than the cost of damage to agriculture by wildlife for the same year (Vignon and Barbarreau 2008). Ecologically, WVC induce population reduction (Lodé 2000) and can impact differently animal populations (Bissonette and Adair 2008). It can affect weakly animal population when accounting for a small part only of the population mortality (Groot Bruinderink and Hazebroek 1996), moderately when reaching mortality level equal to hunting activities (Forman and Alexander 1998; Gosselink et al. 2007) or greatly in some cases when population viability is threaten (Huijser and Bergers 2000; Kramer-Schadt et al. 2004). Roads also act as barriers to animal movement within the landscape causing local population disappearance (Shepard et al. 2008) and isolating animal population on several unconnected subpopulations under higher risk of extinction (Lodé 2000). Transport infrastructures also induce habitat modifications and landscape fragmentation (Forman and Alexander 1998).

To develop effective mitigation measures, knowledge about location and time of road casualties involving wildlife is required. It is important that every country undertakes road ecology researches because any situation is specific and can bring new relevant information on patterns of WVC. Moreover standardised data collection at national scale could help facilitating meta-analysis (Knapp 2005), understanding effect of density and configuration of transport infrastructure on ecosystems functioning at broader scale (van der Ree et al. 2011) and facing the problem of time and space extrapolation (Roedenbeck et al. 2007). Road ecology requires thus now more collaboration between countries to develop adapted mitigation strategies and improve road planning in areas where transport network is still under development.

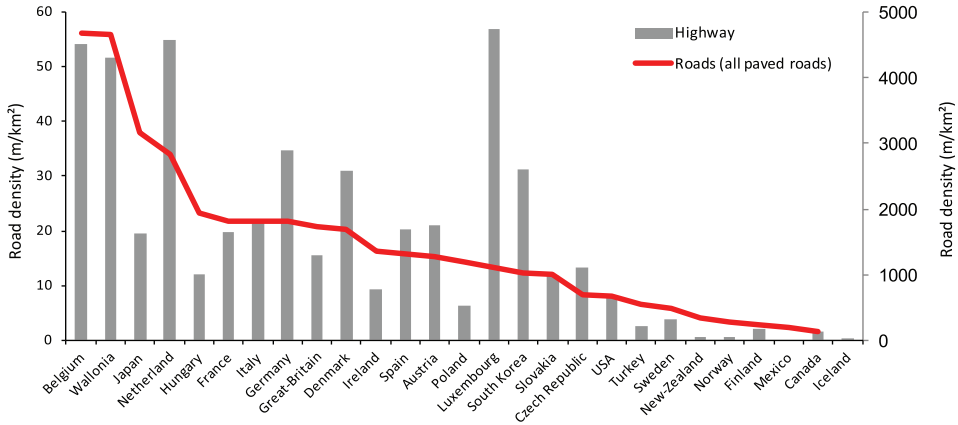
Literature about factors explaining wildlife-vehicle collisions is abundant, demonstrating the importance of this topic. During these last years many studies have brought up results on WVC for numerous countries, e.g. Spain (Colino-Rabanal et al. 2012; Diaz-Varela et al. 2011; Lagos et al. 2012; Rodríguez-Morales et al. 2013), Hungary (Cserkés et al. 2013; Markolt et al. 2012), Sweden (Neumann et al. 2012), Poland (Tajchman et al. 2010), USA (Danks and Porter 2010), Ireland (Haigh 2012).



**Figure 1.** South Belgian (Wallonia) and its road network within Europe and Belgium.

Road characteristics, traffic volume, drivers visibility and intersection of roads are important causes of WVC (Colino–Rabanal et al. 2012; Gunson et al. 2011; Madsen et al. 2002; Seiler 2004). Temporal trends in number WVC are known to match animal behavior and biology, with WVC occurring mainly during breeding and dispersal period at a seasonal scale, or to daily foraging and resting requirement of animal (Groot Bruinderink and Hazebroek 1996; Haigh 2012; Diaz-Varela et al. 2011).

However, in Wallonia, southern part of Belgium (Figure 1), no published data on accidents involving large species has been published so far. Contrary to Flanders (northern part of Belgium), Wallonia was not part of the COST 341-project ‘Habitat Fragmentation due to linear Transportation infrastructure’ (Damarad and Bekker 2003). Regionalisation of competency such as road and environment management in Belgium creates such reared situation where one part of the country might be involved in a project but not the other one. Currently, the only published data on WVC in Belgium is from Holsbeek et al. (1999) who showed how Belgian road network affects small to medium size mammals and birds. Particularly, this study showed the importance of hedgehog and red foxes in WVC, accounting for



**Figure 2.** OECD countries classified according to their roads and highways density (OECD Factbook 2008: Economic, Environmental and Social Statistics, SPF Mobility and Transport).

60% of total animals found killed. Holsbeek et al. (1999) estimated the number of animal roadkills in Belgium to 4 000 000. The absence of more published results on road ecology in Belgium can also be explained by the scattered information between insurance companies, forest state, local authorities, police, hunters and environmentalists (personal observation).

With its 4.8km/km<sup>2</sup> of public roads, Southern Belgium (Wallonia) has one of the densest road networks of Western Europe combined to high human population density of 209 inhabitants per km<sup>2</sup> (SPW 2012). Although, the Belgian road network is already developed since decades and has not seen great changes lately, the car fleet number has hugely increased between 1977 (3 315 071 vehicles) and 2011 (6 861 777 vehicles). Due to a particularly dense road network (Figure 2), an increasing game species populations (red deer, roe deer and wild boar) and the current lack of available statistics, Wallonia is an interesting region to study the patterns of animal road accidents.

The aim of our research is to provide the first results of spatial and temporal patterns of WVC for southern Belgium. In particular we analysed casualties regarding their specific composition (percentage of involved species), and for main game species (red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa* and red fox *Vulpes vulpes*) causing most important social and economic damages, we analysed temporal (annually, monthly, daily and hourly) and spatial distribution patterns.

## Methods

Our study area is the Walloon region, southern part of Belgium (50°30N, 4°45E, Figure 1). Climate is sub-oceanic temperate with a mean annual temperature of 8°C and a mean monthly temperature varying between 2 to 16°C. The mean annual



rainfall is 900mm, and the mean annual length of snow cover is over 25 days. Roe deer, red deer and wild boar are the most abundant wild ungulates.

Data sources used to investigate accidents involving animals are manifold: insurance companies (Inbar et al. 2002; Vignon and Barbarreau 2008), local management authorities (Baker et al. 2004), traffic safety authorities (Colino-Rabanal et al. 2012; Diaz-Varela et al. 2011), systematic road monitoring (Hell et al. 2005) or police database (Balčiauskas and Balčiauskienė 2008). Apart from systematic observations on road sections, most of these methods cannot be considered as exhaustive since they are dependent on many factors (e.g. casualties' record by police/insurance or volunteer participation in data retrieval) preventing collection of all WVC cases (personal observation). In our study, we opted for data from the police considering its availability and its relatively standardised collection protocol. Indeed, although the method is likely to underestimate the total number of accidents, as police is not called in every casualties cases, we assumed that impact with large mammals (wild boar, roe deer, red deer and red fox) have higher chance to end into important car damage requiring police intervention and report. We thus hypothesized that for the species of interest information from police provide the most representative dataset of the number of animal-related accidents.

We investigated police database to search for traffic accident involving any domestic or wild animal species. Information's on accidents resulting in injuries or fatalities were directly available from the central police database, while for accidents resulting in car damages each paper statement had to be checked out individually. In total, the collected data cover the period between 2003 and 2011, and consist of 3965 accidents. For each event we recorded date, time, species involved, and information about the location when available. From the 3965 accidents, 51% could be georeferenced by their milestone reference or by a detailed description of the location with an accuracy of 100m. Milestone references or detailed location were then exported into X Y value by using the corresponding value from the Wallonia road agency.

Exploratory analysis aimed at identifying species involved by calculating absolute and relative frequency of WVC occurrence for each category of species. Types of roads on which accidents occurred were also identified. For the temporal and spatial patterns analysis we only considered the following main game species: red and roe deer, wild boar and red fox. The reason for this choice is twofold. Firstly, they are the main species involved in WVC with social and economic consequences for which mitigation measures are required. Secondly, data available in police database contain only cases where at least car damages occur, preventing exhaustive information on WVC with small mammals to be analysed.

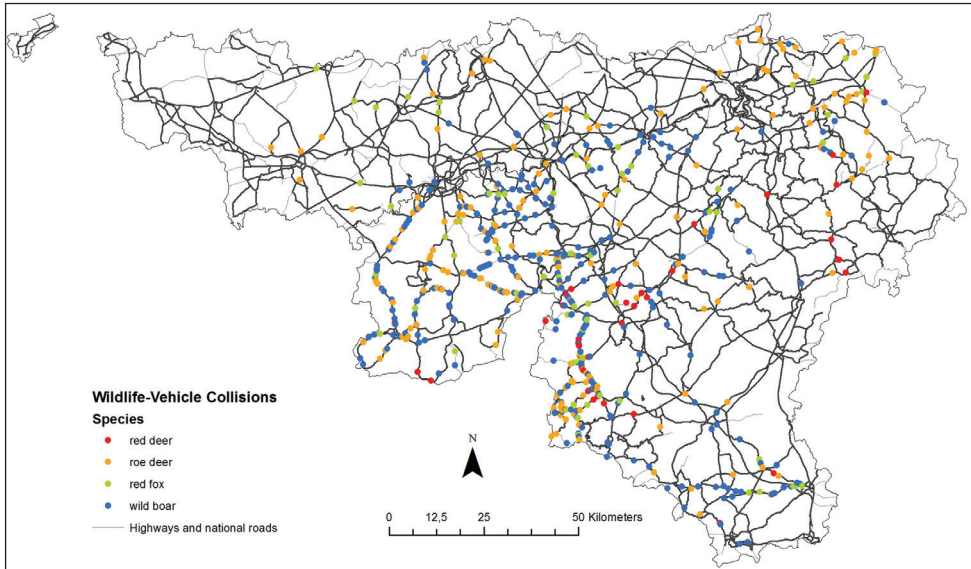
Temporal analysis focused on annual, monthly, weekly and daily distribution patterns of WVC. For each of these timescale, we looked for differences in roadkills relative frequency by using chi-square goodness-of-fit test (Greenwood and Nikulin 1996). Using radar charts in Excel (Microsoft Corp. 1985–2007), we compared hourly distribution of accidents involving wild and domestic species (Lagos et al. 2012). We considered all the WVC from the study period together as we did not observe year effect on the temporal patterns.

For the spatial analysis we only consider accidents that occur along highways and national roads, due to the high complexity of the local road network and the relative low number of WVC compared to the total length of the road network. In total, we had thus a dataset composed of 840 casualties (Figure 3). Spatial pattern of WVC was assessed in three steps.

In a first step, we used nearest neighbour distance (NND) to assess the distribution of animal-related casualties along the road network (Gonser et al. 2009). For each species, we compared the observed mean distance of each accident to its nearest neighbour with the expected mean distance if accidents were randomly distributed along road (CRS, complete spatial randomness). NND analysis allows to determine whether WVC are aggregated or not along the road network. We compared observed value to 100 Monte Carlo simulations of a random distribution that allows estimating mean and confidence intervals at 5% for expected value. If the observed value is higher than the upper confident interval, points are aggregated, otherwise under the lower confidence interval, points are dispersed (Okabe et al. 2013). Departure from a random distribution was confirmed by calculating the Clark-Evans index which is the ratio of observed and expected mean distance, values  $>1$  indicating points are aggregated, otherwise points are dispersed (Clark and Evans 1954).

In a second step, we identified hot spot of collisions for each species by means of a kernel density analysis (Bailey and Gatrell 1995; Okabe et al. 2009). Kernel density expresses the number of collision per kilometer of roads for all the of species of interest. Mapping kernel density allows identifying hotspot zones where mitigation measures should be set up. We used a bandwidth of 500m as the search radius for calculating the number of accidents, to estimate a density value. This value of 500m is reasonable to discriminate priority areas on which implement mitigation measures should be developed (Conruyt-Rogeon and Girardet 2012). Estimated densities were then classified using the Jenks methods, based on minimization and maximization of variance respectively, within and between density classes (Jenks and Caspall 1971).

In a third step, we examined spatial structure of WVC at various spatial scales using the Ripley K function describing distribution patterns of points in space at different scales (Mountrakis and Gunson 2009; Ripley 1976). Originally this function is used for 2-D applications. Here to consider 1-D issue of point distributed along a line, we used the Global auto K function provided by the SANET tools under ArcGIS 10 (Okabe and Yamada 2001). For each WVC cases, the number of neighbors WVC is calculated at spatial scales multiple of 500m along the road network. For detecting deviations from spatial homogeneity, we used the L-function, a variant of the Ripley's K for testing range of spatial structure (Bailey and Gatrell 1995). This L-function is the difference between the observed and expected K-values at each spatial scale  $r$  (Clevenger et al. 2003; Langen et al. 2012) and presents the advantage compared to the K-function to be normalized at 0 (representing random distribution). Expected values (mean and 95% CI) were calculated using 100



**Figure 3.** Distribution of WVC along highways and national roads.

Monte-Carlo simulations of random points distributed along the road network. Observed  $L(r)$  values were then plotted against the expected values. At each scaled distance  $r$ , the value of  $L(r)$  above or under the 95%CI revealed respectively an aggregated or a dispersed distribution of WVC along the road network. Due to the small number of WVC relative to full Walloon road network, we perform this third analysis on a sub-region that contains the highest density of WVC as indicated by the kernel density map.

All the spatial analyses were performed with the use of the extension SANET<sup>®</sup> 4.1. Beta for ArcGIS 10 which provides tools adapted to perform spatial analysis along linear features (Okabe et al. 2006).

## Results

### Species composition

In total 14 different species were identified: 5 domestic species representing 13% of accidents cases and 9 wild species representing 78% of accidents, the rest was undetermined species (Table 1). For the domestic species, dogs take the largest part of accidents with close to 10%, while wild boar and roe deer are together responsible of 45% of accidents with wild animals. 13% of accidents resulted in human injuries or death and the rest resulted in car damages. 7% of casualties occur on highways, 50% on national roads and 43% on regional or local roads.

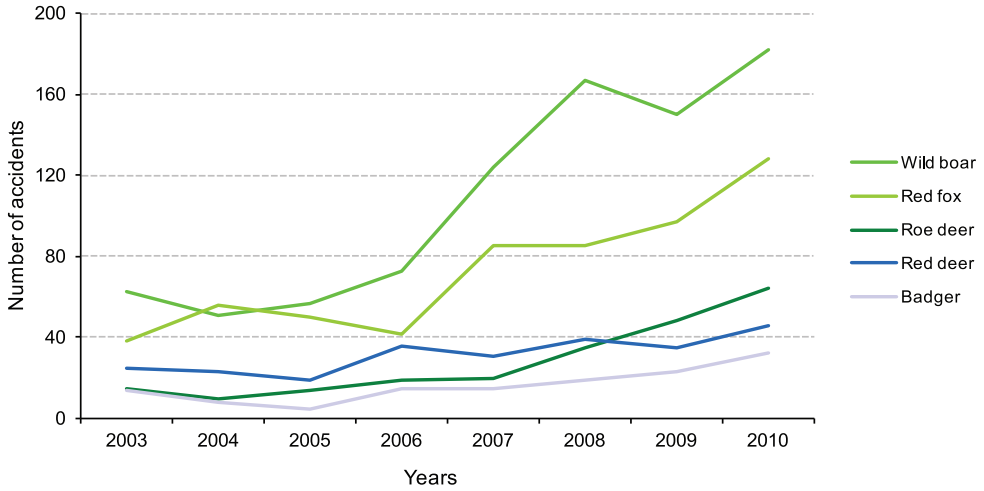
**Table 1.** Species involved in road accidents in Wallonia between 2003 and 2011.

	No human injuries		Human injuries		Total	
	Number	Percentage	Number	Percentage	Number	Percentage
<b>Domestic species</b>						
Dog	262	6.61	120	3.03	<b>382</b>	<b>9.63</b>
Horse	24	0.61	24	0.61	<b>48</b>	<b>1.21</b>
Cow	28	0.71	19	0.48	<b>47</b>	<b>1.19</b>
Cat	26	0.66	11	0.28	<b>37</b>	<b>0.93</b>
Pig	0	0.00	1	0.03	<b>1</b>	<b>0.03</b>
Total domestic species	340	8.58	175	4.41	515	12.99
<b>Wild species</b>						
Wild boar	975	24.59	81	2.04	<b>1056</b>	<b>26.63</b>
Roe deer	682	17.20	30	0.76	<b>712</b>	<b>17.96</b>
Fox	279	7.04	14	0.35	<b>293</b>	<b>7.39</b>
Red deer	244	6.15	28	0.71	<b>272</b>	<b>6.86</b>
Badger	147	3.71	5	0.13	<b>152</b>	<b>3.83</b>
Pheasant	89	2.24	2	0.05	<b>91</b>	<b>2.30</b>
Hare	59	1.49	1	0.03	<b>60</b>	<b>1.51</b>
Bird	53	1.34	4	0.10	<b>57</b>	<b>1.44</b>
Rabbit	15	0.38	0	0.00	<b>15</b>	<b>0.38</b>
Fallow deer	6	0.15	1	0.03	<b>7</b>	<b>0.18</b>
Bighorn	4	0.10	2	0.05	<b>6</b>	<b>0.15</b>
Weasel	2	0.05	0	0.00	<b>2</b>	<b>0.05</b>
Red squirrel	1	0.03	0	0.00	<b>1</b>	<b>0.03</b>
Raccoon	1	0.03	0	0.00	<b>1</b>	<b>0.03</b>
Unspecified ungulates	361	9.10	24	0.61	<b>385</b>	<b>9.71</b>
Total wild species	2557	64.49	192	4.84	3110	78.44
Undetermined	199	5.02	141	3.56	<b>340</b>	<b>8.58</b>
<b>Total</b>	<b>3457</b>	<b>87.19</b>	<b>508</b>	<b>12.81</b>	<b>3965</b>	<b>100.00</b>

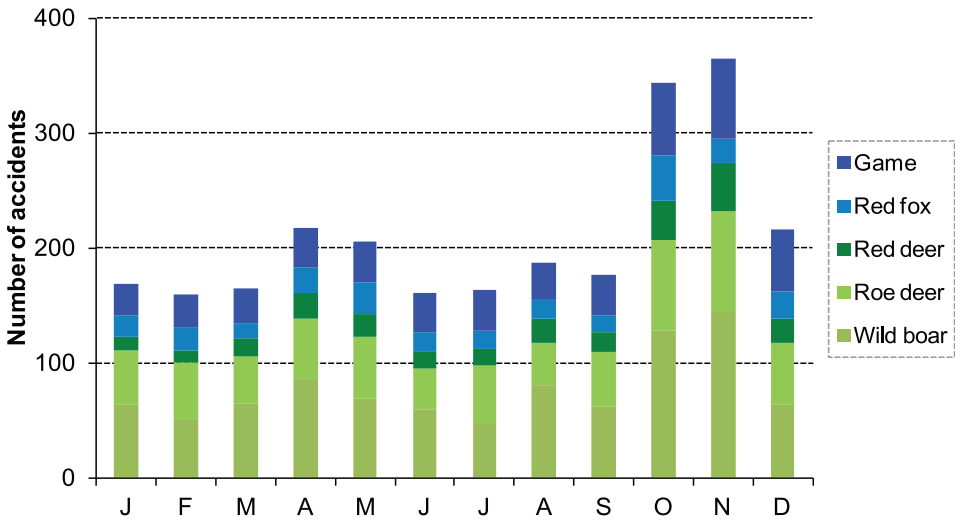
### Temporal distribution

WVC increased by 117% during the study period. Specifically roadkills increased by 50% for badger, by 193% for red deer, 242% for roe deer, 194% for wild boar and 52% for red fox (Figure 4). Abundance indexes coming from hunting bag records (annual number of shot animal) were highly (0.89 for wild boar and 0.67 for red deer) to poorly (-0.07 for roe deer) related to number of accidents.

All the game species investigated showed not uniform monthly distribution of accidents (Figure 5). Casualties with red deer ( $\chi^2 = 41.6$ ,  $df = 11$ ,  $p < 0.001$ ) increase in April-May and then from September to November. For roe deer ( $\chi^2 = 70.4$ ,  $df = 11$ ,  $p < 0.001$ ) accidents peak also in April-May and then in October-November. Wild boar ( $\chi^2 = 456.9$ ,  $df = 11$ ,  $p < 0.001$ ) have their maximum from October to December, while red fox ( $\chi^2 = 32.6$ ,  $df = 11$ ,  $p < 0.001$ ) accidents are more evenly distributed with peaks in January, May and October-November.



**Figure 4.** Annual variation of the number of accidents involving badger, red fox, roe deer, red deer and wild boar.



**Figure 5.** Monthly distribution of road casualties for red fox, red deer, roe deer, wild boar, and others undetermined game species.

Although we could visually observe an increase in the number of accident occurrences during weekend for wild boar, we did not observe significant differences with other days of the week (Figure 6).

Hourly distribution for both wild ( $\chi^2 = 959.2$ ,  $df = 23$ ,  $p < 0.001$ ) and domestic ( $\chi^2 = 87.2$ ,  $df = 23$ ,  $p < 0.001$ ) species was not uniformly distributed. WVC show tendency towards night and morning distribution while collisions with domestic species are more evenly distributed during daytime with peak between 5 and 7 pm (Figure 7).

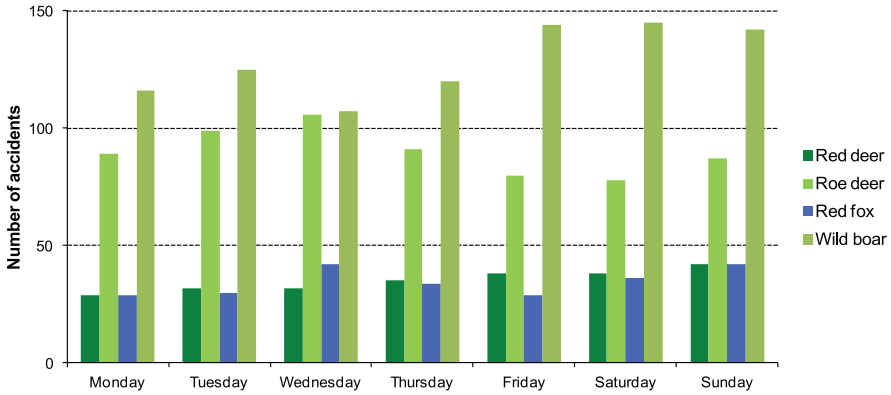


Figure 6. Daily distribution of road casualties for red fox, red deer, roe deer and wild boar.

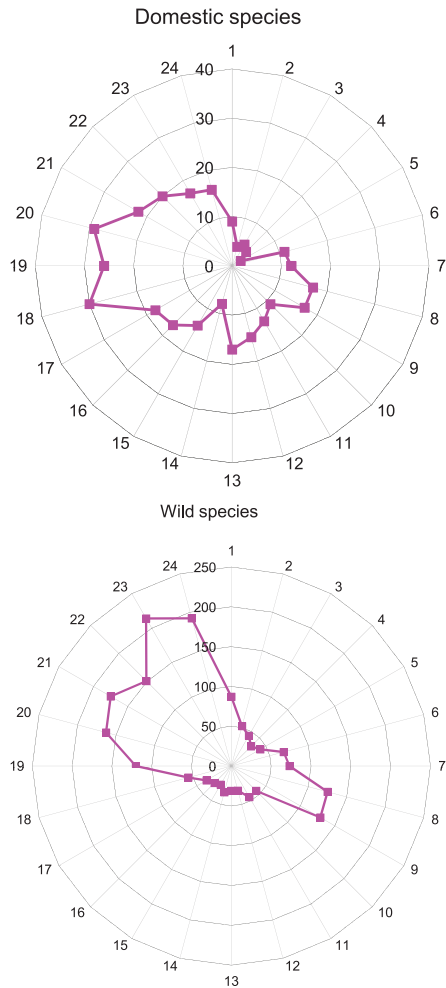


Figure 7. Hourly distribution patterns of road accidents for wild and domestic species.

**Spatial patterns**

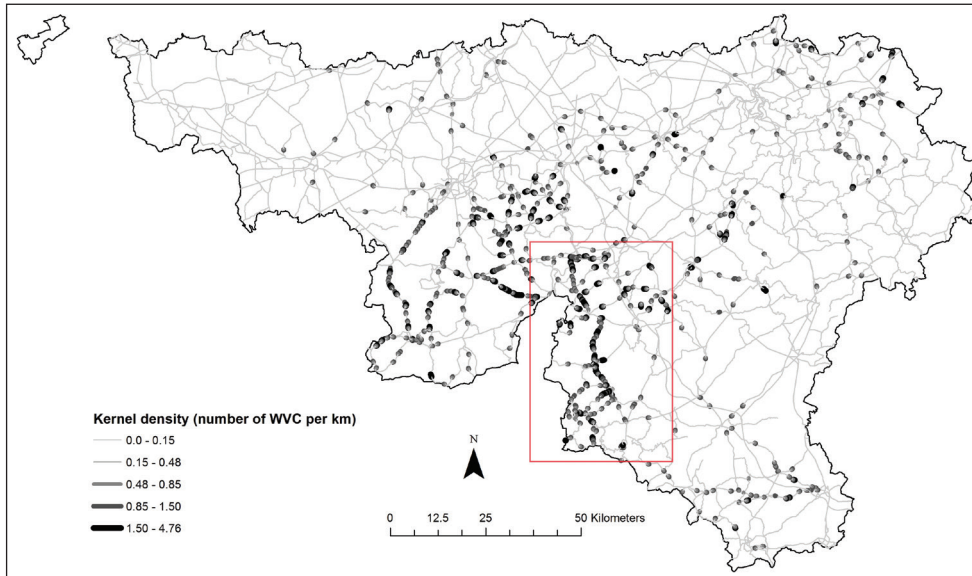
We observed that all game species were not randomly distributed along highways and national road network (Table 2, nearest neighbour distance and Clark-Evans index).

Kernel density analysis revealed heterogeneous distribution WVC along the road network (Figure 8). Concentration of accidents for all species is observed in the centre-south of Wallonia.

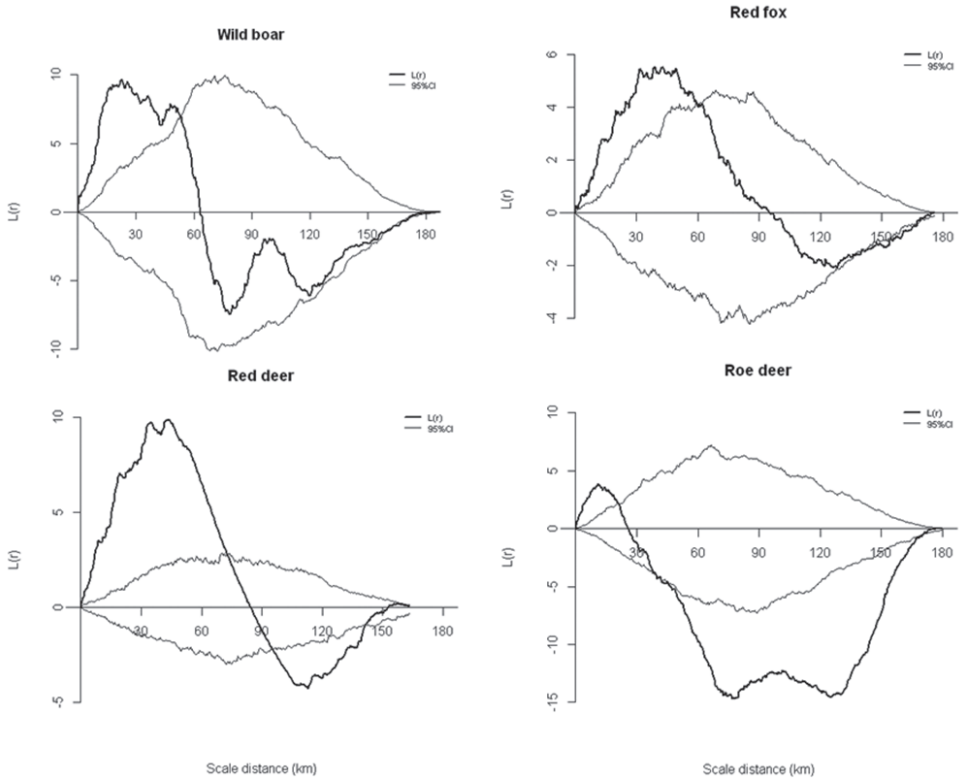
For all the species but roe deer, distribution of roadkills followed the same patterns, with significant clustering at scale ranging from one to more than fifty kilometres (Figure 9). While wild boar and red fox accidents become randomly distributed at large scale (> 60 km), red and roe deer accidents, quickly switch from a clustered to a dispersed distribution. For roe deer, clustering of accidents occurred until a scale of twenty kilometres and at scale higher than forty kilometres distribution becomes dispersed (Figure 9).

**Table 2.** Results of the spatial distribution patterns analysis with the Clark-Evans index (value > 1 for aggregated distribution) and P-value for Nearest Neighbour Distance analysis.

Species	n	Clark-Evans index	CRS (NND)
All	840	0.52	p < 0.05
Red deer	56	0.41	p < 0.05
Roe deer	260	0.63	p < 0.05
Wild boar	421	0.46	p < 0.05
Red fox	103	0.51	p < 0.05



**Figure 8.** Kernel density estimation for WVC considering all species across the whole area and study period (2003–2011). Bandwidth used was 500m and cell size was 50m. In red, the delimited area concentrating high risk areas where the spatial structure analysis (K and L-function) was performed.



**Figure 9.** Plot of the L-statistic as a function of scale for distribution of the four main game species road-kills on the selected area of Wallonia. Solid lines represent the observed number of neighbors per roadkill event along the road minus the expected number of neighbors if the roadkills were randomly distributed. Roadkills are significantly clustered ( $P < 0.05$ ), dispersed or randomly distributed at scale  $r$  when, respectively,  $L(r)$  is above, under or within the 95% confidence interval.

## Discussion

We observed that 87% of accidents with animals result in car damages, which is in accordance with a study by Williams and Wells (2005) who found a value of 80%. Most of these accidents are caused by wild animals which are in accordance with what has been observed in Europe and North American. Large mammals (over 30kg), usually ungulates, are indeed known to be more frequently involved in collisions with vehicles (Conover et al. 1995; Putman 1997). We didn't achieve in deep review of the causal factors of accidents with domestic animal, however we might suspect escapement of cattle and dog as the main reason for impact with these animal on the roads. Appropriate fencing (preventing access of cattle, horses to the roads) as well as good handling of dogs could help decreasing casualties with domestic animals. Although large species are the main reasons for car accident, non-negligible part (7% of total accidents) is due to small species, and this percentage even reaches 17% when including dogs.



In Sweden wildlife-related accidents is suspected to cause an average annual loss of 1–12% of the estimated population of common mammal species (Seiler et al. 2004). On average, for the studied period, the proportion between accidents and hunting bag was 0.5% for wild boar, 0.22% for roe deer and 0.27% for red deer. If we assume hunting bag as an index of population number and the estimation from Seiler et al. (2004) to be similar in Wallonia, we can say that police data for these three species includes between 4–50% for the wild boar, 2–20% for roe deer and 2.5–27% for red deer of the total annual casualties with these wild species.

### **Temporal patterns**

During the study period, the number of WVC has increased constantly and sharply for most of the species, particularly for wild boar and red deer. This annual increase seems to be related to population increase if we assume hunting statistics and number of car accidents reflect well animal population size (Inbar et al. 2002). In the case of wild boar the strong correlation between hunting bag and WVC seems however to reflect direct relationship between population density and car-accidents (Rosell et al. 2010).

Monthly distribution of WVC demonstrated effects of breeding, dispersal and external factors on increase of movement and consecutively on risk of accidents. These results are in accordance with Hell et al. (2005) with higher frequency of road kills in spring and summer. In autumn, increase in WVC is likely to denote the impact of hunting activities on movement of game species (Sforzi and Lovari 2000). Among these, wild boar is importantly implied in roads accident during the autumn. This may be related to the effect of hunting activities on the increase movement of wild boar, and consequently the chance of road crossing during this period (Keuling et al. 2008). In Wallonia, driven hunt is the most used hunting practice and this kind of control method can affect greatly wild boar movement (Maillard and Fournier 1995). Autumn peak in red fox is likely to be attributed to dispersal occurring at this period of the year, when sub adults that did not find space in their natal social groups disperse (Rushton et al. 2006), and have higher chance to be killed when crossing roads. Rutting activities during these period also increase movement of males and the risk of WVC (Doncaster and Macdonald 1997). However in urban areas, red fox can develop movement strategies to account for the particularly dense road network (Baker et al. 2007). Peak of WVC for roe deer in Spring can also be related to natal dispersal of subadults (Wahlström and Liberg 1995) and confirmed results obtained in others studies (Lagos et al. 2012; Markolt et al. 2012).

Peak of accident events at dusk and night reflects the nocturnal behaviour of mammals living in human-disturbed areas, forcing them to switch most of their foraging activities during night when risk of being seen or disturbed by human is lowered (Cahill et al. 2003; Danilkin and Hewison 1996; Doncaster and Macdonald 1997). At dusk and dawn car traffic is also higher due to people driving back home from or towards their working place. Visual conditions at these hours are not really good either (dark-

ness, presence of fog) and can also partly explain higher number of accident events. In the middle of the night, number of accidents decreases, resulting of the reduced activity of animal as well as a lowered traffic.

### **Spatial distribution**

Although national and highways account for 14.6% of the total length of the road network in Wallonia, we observed that more than a half of the WVC occur on these roads. This disproportionate number of accidents on major roads is in accordance with results reviewed in Langbein et al. (2011). Difference in traffic volume can explain partly this difference with twice as much traffic volume observed on highways and national roads (15 billion vehicle-kilometer/year) compared to local and regional road system (8.4 billion vehicle-kilometer/year) (SPW 2012). The lower traffic on these local roads is likely to be compensated by higher density of this type of roads, and thus higher number of crossing events of these roads by wild animals.

Spatial analyses of accidents showed that for all species, the distribution along the road network was not random. We indeed observed that WVC were highly clustered along highways and national roads in Wallonia, Southern Belgium. Spatial structure demonstrated a clustered patterns, also observed for roe deer in Denmark (Madsen et al. 2002) and for roe deer and wild boar in Spain (Diaz-Varela et al. 2011).

We decided to concentrate our effort for analyzing spatial structure at various scales by means of the Ripley K and the L-function on a smaller size area because when including the whole network we observed clustering patterns at all scales because the number of WVC was too low regarding the total length of the road network (Langen et al. 2012). This subarea was select based on the result of the kernel density estimation that allows us to select the most suitable area in term of number of accident and road length. We observed peak of clustering at scales ranging from 10km for roe deer to 40km for red fox. In the literature, we did not find results for the same species as we investigated, but the results are in accordance with the moose which has clustering value ranging from 2.5 to 30km (Mountrakis and Gunson 2009) and for a guild of mammalian species in Brazil ranging from 15 to 30km (Coelho et al. 2008).

Kernel density mapping showed areas with higher risk of WVC. Road density and land cover are likely to explain this non-random pattern (Gonser et al. 2009). A more thorough analysis on the factors associated with these areas is currently undergoing and will help understanding what elements of the landscape and the road characteristics affect the likelihood of accidents with animals. A common belief is that wildlife casualties are likely to occur in highly forested area, but recent papers have demonstrated the role of agricultural land on risk of casualties with deer (Gonser et al. 2009) and wild boar (Colino-Rabanal et al. 2012) particularly. These habitats are indeed particularly interesting for both species, providing both cover and food resources.

## **Mitigation measures**

The Wallonian road network is almost completely developed since decades now. Implementing wildlife passage on already built highways is more expensive than when it is included from the beginning in road construction plan. However mitigation measures should locally be set up in most risky areas to decrease the number of casualties. Indeed, as we have seen, accidents with wild mammals show strong temporal and spatial patterns, and the peaks identified could help to set up measures that increase the awareness of drivers during more sensible period of the year or the day. Informative signs on potential animal crossing along the road have been demonstrated to increase the alertness of drivers (Stout et al. 1993) and to decrease the car speed which positively affect number of collisions (Sullivan et al. 2004). Signs however are also known to be often ignored by drivers. In Belgium, crossing signs already exist on most of the road network. We aim in further analysis to put in relation the distribution of the signs with the areas of high concentration of accidents (“hotspots”), to see if they overlap well (Krisp and Durot 2007). Most of these signs have been installed in potential risky areas but the accuracy of their positioning (regarding WVC hotspots) has never been controlled so far. Now with the northern expansion of wild boar an update of the caution signs should be carried out on the Belgium road network. It seems thus urgent to propose localised measures during some period of the year/day to prevent casualties, by lowering speed limitation in these riskier areas and focusing on an adapted management plan (increase culling) in the neighborhood of these road segments. This last measure could also be temporally counterproductive, hunting activities being known to increase animal movement and thus risk of crossing roads (Keuling et al. 2008; McIlroy and Saillard 1989). However we think that, applied with caution, management of species causing problem is an unavoidable task to include in a mitigation plan.

Next to roadkills, road network have others negative effects on large mammals. They can indeed act as barriers for animal movement, subdividing species into sub-population, although this might depend of the effect of the road type and the species. Hence, in Belgium a recent study by Frantz et al. (2012) showed how highways might impact differently wild boar and red deer, this latter being affected more by the barrier effect of roads. Transport planning should thus do something for mitigate effect on red deer as probably building up passage over main identified crossing points.

## **Conclusion**

Our study is the first to bring results in Wallonia about WVC. We brought insights into species involved and in the spatio-temporal patterns of these accidents. Wild boar and roe deer constitute the major part of the accidents. Temporal analysis showed the role of animal biology in explaining monthly and daily patterns of WVC occurrences. Multi-scale spatial analysis demonstrated the clustering patterns

of accidents in Wallonia for the main game species. These results highlight the need to take both spatial and temporal components into account for building predictive model. The next step of our research will indeed be dedicated to joining the results of this research together with landscape and road factors to build a predictive model of WVC hotspots and to propose mitigation strategies that could enhance both human and animal safety. GPS data collected on wild boar and red deer will be used to determine the road effect for these two species behaviour. This will bring us new understanding on the real effect of road network on animal behaviour. However many WVC are still not reported, because of the absence of police statement, but would be required to measure more precisely long-term effects of roads on main game species. We thus hope these first results will be helpful in convincing stakeholders (police, local authorities, insurance companies, forest administration, naturalists, drivers) to collaborate so that better data collection could be achieved in the near future.

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# Potential impact of sea level rise on French islands worldwide

Celine Bellard<sup>1</sup>, Camille Leclerc<sup>1</sup>, Franck Courchamp<sup>1</sup>

<sup>1</sup> *Ecologie, Systématique & Evolution, UMR CNRS 8079, Univ. Paris-Sud, F-91405 Orsay Cedex, France*

Corresponding author: *Celine Bellard* ([celine.bellard@u-psud.fr](mailto:celine.bellard@u-psud.fr))

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## Abstract

Although sea level rise is one of the most certain consequences of global warming, yet it remains one of the least studied. Several studies strongly suggested that sea level rise will accelerate in the future with a potentially rise from 0.5 to 2 m at the end of the century. However, currently island conservation programs do not take into account the potential effects of sea level rise. Therefore, we investigated the potential consequences of sea level rise for 1,269 French islands worldwide, by assessing the total number of island that will be totally submerged for three different scenarios (1, 2 and 3 m). Under the worst scenario, up to 12% of all islands could be entirely submerged. Two regions displayed the most significant loss of island: New Caledonia and French Polynesia. Focusing on New Caledonia, we highlighted that endemic plant species that are already classified as critically endangered by the IUCN will be the most vulnerable to sea level rise. Losses of insular habitats will thus be important in the next decades for the French islands. Given that French islands covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean, our results suggested that the implications for the 180 000 islands around the world should be considerable. Therefore, decision makers are required to define island conservation priorities that will suffer of the future sea level rise.

## Keywords

French islands, sea level rise, insular biodiversity, climate change

## Introduction

Despite considerable attention to global change effects, few studies focused on the consequences of sea level rise (Menon et al. 2010; Wetzel et al. 2012; Schmidt et al. 2012). Many studies showed that global warming will be one of the biggest threat to future biodiversity, and predictions could play an important role in alerting scientists and decision makers to support the development of proactive strategies to reduce climate change impacts on biodiversity (Bellard et al. 2012). Potential effects of sea level rise are of considerable interest because of its potential impact on biodiversity and society. By 2030, 50% of the world population will live within 100 km of the coast (Small and Nicholls 2003; Bindoff et al. 2007). The two major causes of global sea level rise are thermal expansion of the oceans (water expands as it warms) and the loss of land-based ice due to increased melting. During recent years, for which the observing system is much better, thermal expansion and melting of land ice each account for about half of the observed sea level rise (Solomon et al. 2007). Several recent studies strongly suggest that sea level rise will increase by 0.5 to 2.3 m at the end of the century (Rahmstorf 2007; Pfeffer et al. 2008; Grinsted et al. 2009; Jevrejeva et al. 2010; Nicholls and Cazenave 2010; Traill et al. 2011). Most dramatic scenarios of ice sheet melting and sliding lead to potential sea level rise of 4 to 6 m (Overpeck et al. 2006). Sea level increases could lead to the total immersion of many low-lying islands, associated with potential important consequences for biodiversity. Surprisingly, few studies have focused on consequences of sea level rise on islands and their biodiversity, only specific archipelagos that represent very limited subsets of existing islands (Baker et al. 2006; Webb and Kench 2010; Wetzel et al. 2012; Bellard et al. 2013), or on continental coastlines (Menon et al. 2010; Hinkel et al. 2010; Traill et al. 2011) have been studied. Yet, islands are generally considered as important hotspots of biodiversity due to very high endemism richness, about 70,000 vascular plant species are endemic to islands (Kier et al. 2009). In particular, among French territories, four of them are present in biodiversity hotspots. Although French islands only represent 0.08% of Earth land surface, they contain 1.4% of the plants, 3% of the molluscs, 2% of fishes, 1% of reptiles and 0.6% of birds of the world. Therefore, one could expect significant loss of insular biodiversity due to sea level rise. For example, the endangered Lower Keys Marsh rabbit (*Sylvilagus palustris hefneri*) already lost 64% of its habitat, the majority due to sea level rise (>48%) (Schmidt et al. 2012). While actions to mitigate climate change and its consequences in islands are being debated, few studies regard the potential impact of an increase of sea level on insular habitats.

Here, we assessed impacts of sea level rise on islands ( $n=1269$ ) under French jurisdiction. This sample includes islands of various sizes, geological types and elevations, and covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean. We investigated three scenarios of projected sea level rise on these islands, to provide estimations of loss of entire islands. First, we considered a global sea level rise by 1 m that is slightly below the average of six recent projections of sea level rise for 2100 (Overpeck et al. 2006; Rahmstorf 2007; Pfeffer et al. 2008; Grinsted et al. 2009; Jevrejeva et al. 2010; Nicholls and Cazenave 2010). We also explored another

realistic upper bound of 2 m sea level rise (Nicholls and Cazenave 2010) and an extreme scenarios of 3 m (Hansen 2007). In addition, we studied sea level rise of two different types: a uniform increase over the globe or a recent projection that considers the regional variability of sea level rise based on a synthesis of 16 sea level rise models (see Figure 2B for details). The latter projection is more realistic because heterogeneous ocean warming will lead to non-uniform thermal expansion (Cazenave and Llovel 2010) and leads to average rises of 1.05, 2.10 and 3.15 m, hereafter termed  $\sim 1$  m,  $\sim 2$  m and  $\sim 3$  m in order to compare with homogeneous rises.

For each scenario, we assessed the number of islands that would be entirely submerged, which was estimated by overlying maximal island elevation with local sea level projections. These must be considered very conservative estimates of biodiversity impacts of sea level rise on islands because we only consider losses on islands that are totally submerged. Finally, we also highlighted a case study of New Caledonia taking into account partial habitat losses of islands and potential loss of endemic plant species area distribution due to sea level rise.

## Materials and methods

### French islands

In order to be exhaustive, we defined both islands and islets as “islands”, the only difference being the size (islet have a smaller area). The majority of islands represent single landmasses, but in some cases, mostly for atolls like Tuamotu, islands may consist of numerous islets sharing a common geological origin. France possesses around 2,000 islands across the world, but many are located in rivers or lakes. Among oceanic islands, topographic data are available for 1,269 islands that encompass all latitudes and geologic types of island ecosystems. Moreover, French islands are present in 4 of the 25 hotspots of global biodiversity including the Caribbean islands, Indian Ocean islands, Polynesia Micronesia islands, and New Caledonia islands (Myers et al. 2000). Furthermore, the French maritime domain encompasses 10% of the coral reefs and 20% of the atolls of the planet.

### Elevation data

Island coordinates were derived mostly from the Geonames database (<http://www.geonames.org/>) and inspection of satellite imagery on Google earth. To obtain data on maximal elevation (*i.e.*, the difference in meters between sea level and the highest point) of each island, we used two different databases: IGN map (National Institute of Geographic information) where maximum elevation is provided for most of the studied islands (<http://www.geoportail.fr/>) and elevation data from Google Earth for the few remaining islands. For those few islands, Google Earth was used to check that at least one point in elevation was higher than the considered sea level rise.

## Assessing impacts of sea level rise on islands

### Sea level rise scenarios

Islands are identified as submerged if their highest elevation is below the considered sea level rise projection. We used two different scenarios of sea level rise. First, we used a homogeneous scenario, where sea level rise is equal at all latitudes and longitudes. Then, we used a heterogeneous projection of sea level, where we considered spatial variability of the rates of sea level rise, which is mostly due to non-uniform changes in temperature and salinity, and related to changes in the ocean circulation. For the homogeneous scenario, we used an uniform increase of sea level by 1, 2 and 3 meters over the globe. For the heterogeneous scenario, we used the IPCC map that represents an ensemble mean of 16 Atmosphere-Ocean General Circulation Models, under the scenario A1B, which considered regional variability. Using ArcGIS, we determined the location of each island and we attributed the sea level value of increase by 2100 that varied from 0.05 m to 0.65 m for each island according to the projected local sea level rise. Because it is impossible to obtain island elevation data in decimeter units, we rounded off to the full next meter, always making a conservative estimate when doing so (e.g., 1.8 m to 2.7 m was considered as 2 m, see Fig. 2B for details). As mean sea level rise based on the IPCC scenarios (0.35 m) is now considered too conservative (Nicholls and Cazenave 2010), we have considered three different heterogeneous projections: a mean rise of 1.05 m, 2.10 m 3.15 m to match with the homogeneous scenarios of 1, 2 and 3 m. In the main text, these are notated as ~1 m, ~2 m and ~3 m, respectively. We assumed that all Mediterranean islands will be subject to an increase in sea level from 0.35 to 0.45 m (like the Atlantic zone) because data produced for 2021–50 mean projected an increase of sea level that ranges between +7 and +12 cm (Gualdi et al. 2013).

### Number of island submerged

We used total island submersion as a metric because accurate digital elevation models (DEM) are not publicly available for all these islands, especially low-lying islands that are expected to be the most vulnerable to sea level rise. Additionally, assessing sea level rise impacts on low-lying islands is impossible without high resolution because most of the current satellite-based DEMs contain biases that greatly exceed the precision required for a study of low lying island submersion (Hinkel et al. 2010).

## Case study of New Caledonia

### Elevation data

In order to consider partial habitat losses, we used the Digital Elevation Model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008), we did not consider connectivity of cells or lateral erosion. We also calculated the sum of the number of pixels under the 3 different sea level rise projections by island and for the entire region using R.15 version.

## Endemic plant species

We obtained endemic species area distribution polygons provided by the IUCN database for each of the 64 plants (IUCN 2012). Then, we calculated the species area distribution that will be submerged under an increase of sea level by 1, 2 and 3 meters for each endemic plant species within New Caledonia according to their spatial distribution.

## Results

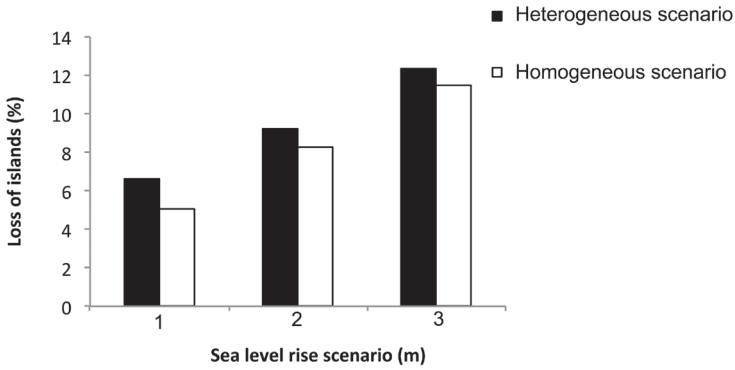
### Potential island losses

We calculated the number of islands entirely submerged under three different scenarios of sea level rise ( $\sim 1$ ,  $\sim 2$  and  $\sim 3$  m) and two projections homogeneous and heterogeneous. Our results indicated that about 5% of islands would be entirely submerged with a globally uniform sea level rise of 1 m (Figure 1). This corresponds potentially to 64 French islands that will be vulnerable to an increase of sea level by 1 meter. The uniform increase of sea level by 3 m increased this estimate to about 11% (*i.e.*, 145 islands). Using a spatially heterogeneous sea level rise scenario, we showed greater losses ranging from 6% to 12% of submerged islands for scenarios of  $\sim 1$  and  $\sim 3$  m, respectively (see Figure 1 and Material and methods). This last result corresponds potentially to 83 and 156 islands that will be at risk of submersion in the future. Globally, the number of islands potentially vulnerable to sea level rise was slightly more important for heterogeneous scenarios, whereas results using homogeneous scenarios were lower. However, for all projections considered, the regions with the most important number of islands potentially threatened were New Caledonia (>30% of the total islands entirely submerged were located in New Caledonia), French Polynesia (>30%) and the Mediterranean (10%), although many islands will also be submerged in other regions such as Caribbean islands, Madagascar and Guyana (Figure 2A and Figure 3).

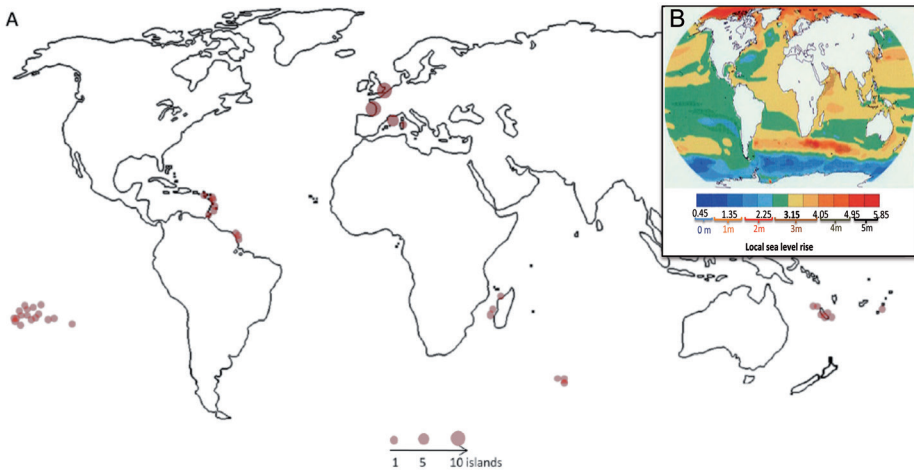
Consequently, rising sea would potentially threaten a considerable part of French insular biodiversity, especially in New Caledonian region. Considering that at least 5% of the number of islands will be entirely submerged under an increase of sea level by 1 meter, many plants will be endangered by an increase of sea level as well as other species located in these islands. In addition, other islands that are not under French jurisdiction but that are located in these regions could be highly vulnerable to sea level rise, and the potential losses of insular habitat could be very similar at the world scale.

### New Caledonia case study

Because our results showed that New Caledonia region is particularly sensitive to sea level rise, we decided to study the potential partial losses in this region. Overall, our results showed that between 1.7 and 2% of New Caledonian area will be permanently



**Figure 1.** Percentage of islands entirely submerged under three scenarios (lower ≈1 m, middle ≈2 m and upper ≈3 meters) and two projections (homogeneous rise and heterogeneous rise).

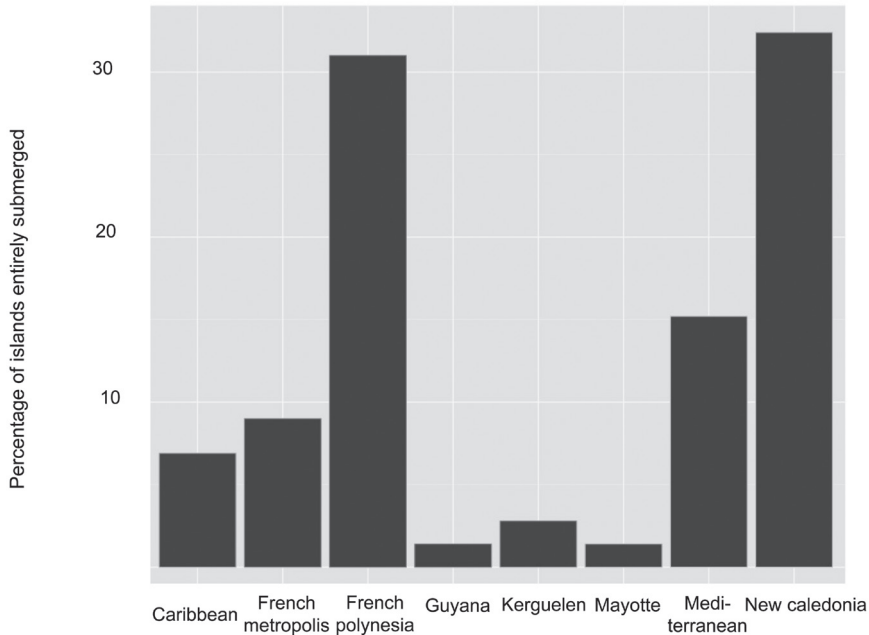


**Figure 2. A** Spatial distribution of submerged French islands following the pessimistic scenario (~3 m rise) **B** Local sea level change (m) due to ocean density and circulation change relative to the global average during the 21<sup>st</sup> century under SRES A1B scenario.

submerged under an increase of sea level rise by 1 to 3 meters, respectively (Figure 4AB). Taking into account partial losses of New Caledonian islands, we estimated that between 2.3% and 6.8% of islands will have more than half of their area entirely submerged. With an increase of sea level by 1 meter, 29.5% of New-Caledonian islands will have between 1 and 25% of their area inundated. Based on our results, more than 50% of islands will be safe from permanent inundation because of their high elevation profile (Figure 4C) although we recognized that indirect effects of sea level rise such as lateral erosion could lead to significant effects for these islands.

Using the endemic plant species distribution, we estimated the species area distribution that will be submerged under an increase of sea level by 1, 2 and 3 meters. We then calculated the potential area losses for each endemic plant species under the different scenario of



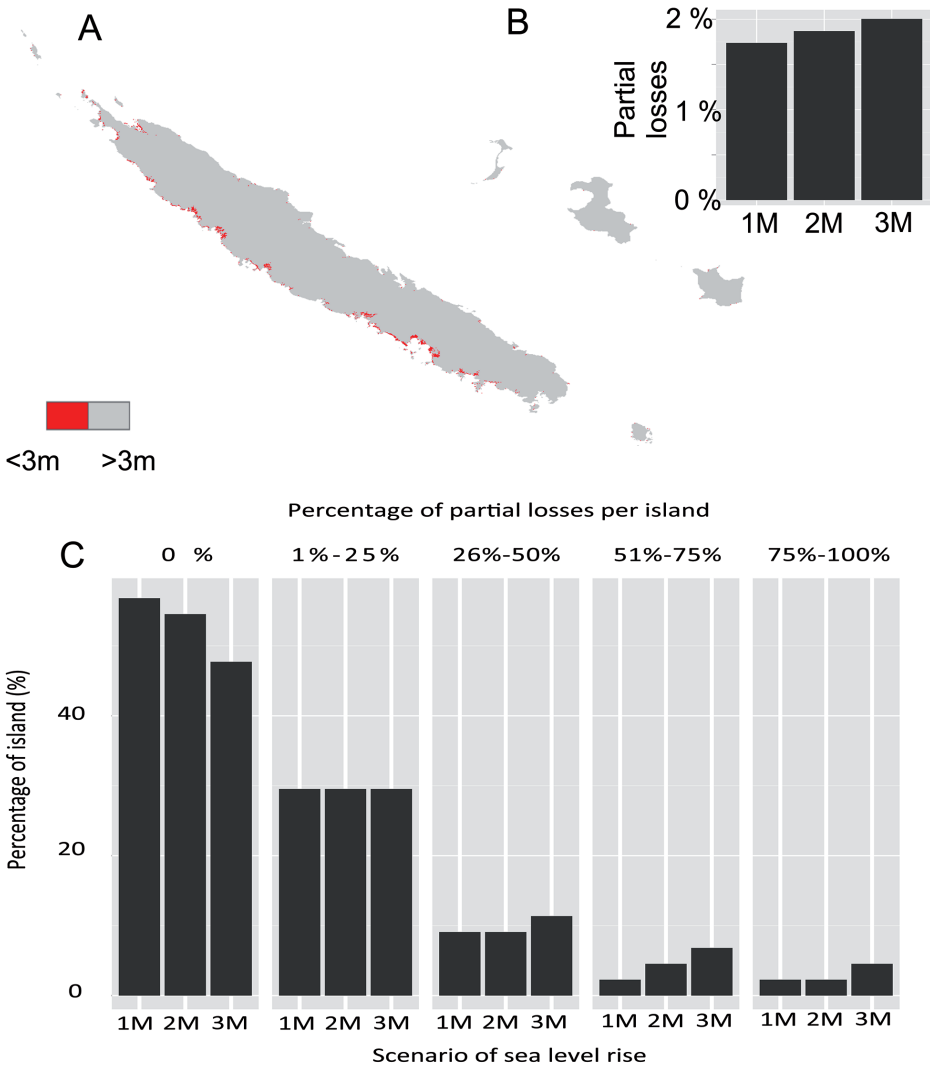


**Figure 3.** Spatial distribution of the entirely submerged islands for the different French regions under an increase of sea level by 3 meters.

sea level rise and we averaged according to the IUCN status. Overall, our results showed that endemic plant species will lose between 1.25% and 3.98% of their area distribution under an increase of sea level by 1 and 3 meters, respectively (Figure 5). With an increase of sea level of 3 meters, the habitat loss of the species that are classified as “least concern” by the IUCN was 1.16%, while it reached 6.88% for the “critically endangered” plant species. These results highlighted that the vast majority of endemic plant species vulnerable to an increase of sea level, are already at a high risk of extinction. Consequently, species that already are at higher risk of extinction will lose the largest habitat following sea level rise.

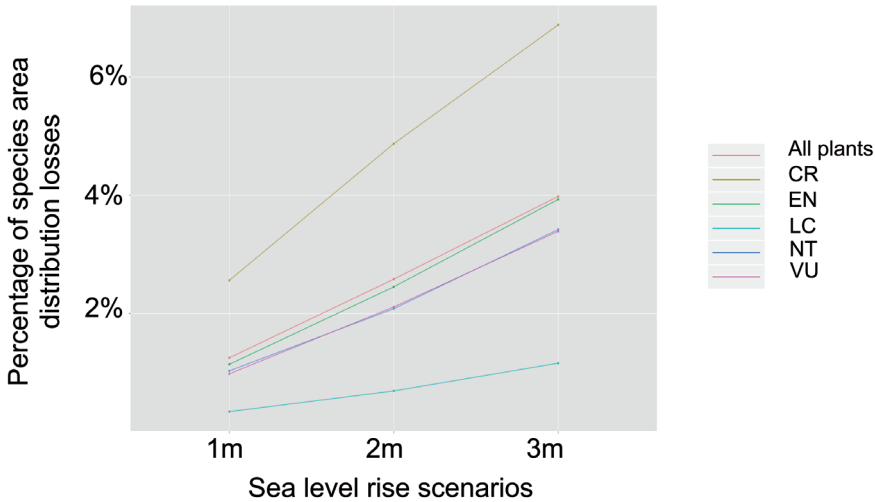
## Discussion

Over the next 60 years, sea level rise and higher storm frequency, together with natural and human-induced subsidence, population growth and urbanization, will cost roughly 9% of global GDP (Hanson et al. 2010). However, little attention has been paid to island vulnerability directly caused by sea level rise (Menon et al. 2010; Wetzel et al. 2012). It is clear that sea level rise will be the largest driver of habitat loss for insular habitats (Wetzel et al. 2012). Sea level rise is a particularly critical consideration for preserving coastal biodiversity, yet many approaches for prioritizing conservation networks do not take this into account (Runting et al. 2013). Our results predicted that impacts of sea level rise on insular French habitats are likely to be important, especially for two regions: New Caledonia and French



**Figure 4.** **A** Map representing the partial habitat losses of New Caledonia region with an increase of sea level by 3 meters **B** Percentage of areas partially submerged in New Caledonia region under an increase of sea level by 3 meters **C** Percentage of island that are partially submerged for different classes of submersion.

Polynesia. Under an increase of sea level by 1 m, at least 5% of islands will be potentially entirely submerged. Our pessimistic scenario projected a loss of up to 11% of French islands. Globally, we did not observe important differences between homogeneous and heterogeneous projections results. Other studies that attempted to study the potential impacts of sea level rise in terrestrial eco-regions (Menon et al. 2010) and on Indo-Malaysian islands (Wetzel et al. 2012) showed results of the same order of magnitude. We do regret our inability to work with a greater precision of elevation data and to take into account partial



**Figure 5.** Percentage of species area distribution submerged under 3 different scenario of sea level rise for 64 endemic plants. We grouped the different species according to their IUCN status. CR : Critically endangered, EN : endangered, VU : vulnerable, NT : Near threatened and LC : least concern.

habitat losses due to marine intrusion for all the French islands. However taking into account partial losses of New Caledonia, we showed that this region will also suffer from significant partial losses of insular habitat. Therefore, neglecting partial loss of islands means that the impact of sea level rise will cause probably more dramatic land losses than projected by the study for the other regions. Actually, several factors may underestimate habitat loss estimations, especially: lateral erosion, tidal range, centennial tides or floods and increased salinity on new shorelines. For instance, beach erosion along the United States East Coast due to sea level rise was about two orders of magnitude greater than the rate of sea level rise (Zhang et al. 2004). This means that, for example, a 1 meter rise of sea level would create habitat loss of about 100 meters inland along the coasts due to lateral erosion. Therefore, results are conservative and they give evidence that sea level rise represents an important threat on insular biodiversity over the next decades. We did not either consider the indirect habitat losses following displacement of human population from inundated areas and the potential important ecological consequences if urban and intensive agricultural areas in the coastal zones of islands are relocated to the hinterland (Wetzel et al. 2012), though these effects have been shown to be sometimes greater than the losses directly due to sea level rise.

Then, regarding endemic species distributions over New Caledonia, we showed that species that are already at risk of extinction were the most vulnerable to sea level rise. This result is particularly important, because it means that endemic plants that are at risk of extinction are mainly located on the coastal areas. Although we focused on endemic plant species, rising seas will also flood other populations of different taxonomic groups including invertebrates and vertebrates. In addition, the two most important regions that are susceptible to be threatened by sea level rise are part of biodiversity hotspots. For instance, French Polynesia contains 85 of the 425 atolls of the world that shelter nearly 19,000

vascular plant species including 3,450 endemic species. These species may also have to face many threats such as salinity intrusion, submersion, soil erosion and climate changes.

We attempt a first approximation of the potential impact of sea level rise on French biodiversity following marine intrusion. In our study, most of islands that showed important vulnerability to sea level rise were atolls. Their remoteness from mainland, flat topography and great susceptibility to natural disturbances (e.g., hurricanes) might lead to a low biodiversity present in these islands. Thus, the biodiversity on small islands and other low-lying coastal regions appeared to be highly vulnerable to sea level rise, but it is unclear how many species could be lost under existing sea level rise projections. To conclude, some patterns emerging from this study provided useful information for conservation planning. As our climate continues to change at a faster rate than previous century, sea level rise will create further challenges for the conservation of insular ecosystem in French territories, and in low lying areas worldwide. Given that French islands covers all latitudes in the Pacific, Indian and Atlantic oceans and in the Mediterranean, with the French maritime domain being ranked as the second largest in the world, our results suggested that the implications for the 180 000 world islands around the world should be considerable. Assuming that French islands are representative of worldwide islands, roughly 10,800 islands could be entirely lost with the 1 meter scenario. Consequently, new prioritizations programs for islands have to be established in order to mitigate the impacts of sea level rise. For example, in order to anticipate threats and prepare adequate conservation actions (e.g., local protection, identification of refuges or translocation programs), conservation managers have to target specific islands that have high risk of being permanently inundated within the next decades. Our results suggested that the effects of sea level rise will be particularly dangerous for New Caledonia, and French Polynesia. Considering their important contribution to global biodiversity and the threat of sea level rise for future biodiversity of some of these islands, there is an urgent need that islands feature prominently in global and regional conservation prioritization schemes. In addition, with accepted projections of sea level rise now exceeding one meter, the improvement of estimates of the associated loss of insular habitat and biodiversity becomes essential. In addition, it would be advantageous for decision makers to have more certainty about future sea level rise, the nonlinearity of ice-sheet melt makes accurately predicting the change in sea level at a particular date unattainable at present (Hansen 2007). We hope that this study will provide a first valuable attempt for new research efforts in this direction.

## **Acknowledgements**

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# Generation length for mammals

Michela Pacifici<sup>1</sup>, Luca Santini<sup>1</sup>, Moreno Di Marco<sup>1</sup>, Daniele Baisero<sup>1</sup>,  
Lucilla Francucci<sup>1</sup>, Gabriele Grottole Marasini<sup>1</sup>, Piero Visconti<sup>1</sup>, Carlo Rondinini<sup>1</sup>

<sup>1</sup>Global Mammal Assessment program, Department of Biology and Biotechnologies, Sapienza Università di Roma, Viale dell'Università 32, I-00185 Rome, Italy

Corresponding author: *Moreno Di Marco* ([moreno.dimarco@uniroma1.it](mailto:moreno.dimarco@uniroma1.it))

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## Abstract

Generation length (GL) is defined as the average age of parents of the current cohort, reflecting the turnover rate of breeding individuals in a population. GL is a fundamental piece of information for population ecology as well as for measuring species threat status (e.g. in the IUCN Red List). Here we present a dataset including GL records for all extant mammal species (n=5427). We first reviewed all data on GL published in the IUCN Red List database. We then calculated a value for species with available reproductive parameters (reproductive life span and age at first reproduction). We assigned to missing-data species a mean GL value from congeneric or confamilial species (depending on data availability). Finally, for a few remaining species, we assigned mean GL values from species with similar body mass and belonging to the same order. Our work provides the first attempt to complete a database of GL for mammals; it will be an essential reference point for all conservation-related studies that need pragmatic information on species GL, such as population dynamics and applications of the IUCN Red List assessment.

## Keywords

Age at first reproduction, conservation assessment, IUCN Red List, longevity, reproductive life span

## Introduction

Generation length (GL) has been defined in a number of ways and has been approximated with a number of different formulas (IUCN 2013). The two most common definitions of GL are: 1) “the average age of parents of the current cohort” (IUCN 2001, 2012b), 2) “the age at which half of total reproductive output is achieved by an individual” (IUCN 2004). GL is a key vital statistic of animal populations and is used in a multitude of ecological analyses (Gaillard et al. 2005, Perry et al. 2005, Jiguet et al. 2007). In IUCN Red List assessments, GL is used as a reference time-frame to assess a species extinction risk due to population reduction (criterion A), continuing decline of small populations over a definite time period (criterion C1; IUCN 2012b), calculated extinction probability (criterion E; Mace et al. 2008). Nonetheless, such an important variable is often hard to calculate due to the paucity of detailed reproductive data. Therefore it is missing for most species, even among relatively well-studied groups such as mammals. Methods to fill missing-data gaps in biological datasets, such as multiple imputation, have been applied in mammals (e.g. Di Marco et al. 2012). However, such methods depend largely on data availability and assume that missing data are distributed randomly (e.g. among orders). We address this gap and provide the first attempt to complete a database of GL for mammals based on recently published datasets, using published metrics as well as taxonomic and allometric species relationships.

## Taxonomic coverage

This database covers all 5427 extant species in the class Mammalia. The taxonomy follows the IUCN Red List of Threatened Species version 2012.2.

## Methods

For 439 species, we used stated GL in years available from published IUCN Red List assessments (IUCN 2012a); for 822 additional species we derived GLs from data on species' reproductive life span and age at first reproduction (see Generation Length model, below). We obtained life-history traits from PanTHERIA (Jones et al. 2009) and AnAge (Tacutu et al. 2013). Moreover, for carnivores and ungulates, we applied a multiple imputation procedure to estimate missing values of life history variables (see below for a detailed description). We compiled the GL values of 3722 remaining species by assigning them the mean GL value of congeneric or confamilial species (when expert-based GL values of congeneric species were not available) in the same bin of log body mass.

For the mammal body masses, we used PanTHERIA (Jones et al. 2009) as our main reference, and complemented the missing data with numerous other sources, including books and primary literature (see Appendix). For species that lacked body mass data (1047), we calculated the average body mass of congeneric or confamilial species.



For 315 species, lacking a congeneric or confamilial species in the same bin of log body mass, we assigned the mean GL value of congenics or confamilials, irrespective of their body mass. For the remaining species (n=116, 2.1 % of the total), where no information was available for congeneric or confamilial species, we assigned the mean GL value of species in the same bin of log body mass, belonging to the same order, or simply the mean GL values of the order (2 species, *Ptilocercus lowii* and *Cyclopes didactylus*). We made an exception for the two species of Dermoptera and 9 species of small mammals (body mass < 100 g); since they were the only representatives of their orders, we estimated mean GLs from species belonging to the same bin of log body mass. In this way, we obtained a GL value for all existing 5427 mammals.

### Generation length model

We estimated GL for mammals from information on species age at first reproduction and reproductive life span, by applying the methodology described in the IUCN Red List Guidelines (IUCN 2013):

$$GL = R_{span} * z + AFR \quad (\text{eq. 1})$$

where  $R_{span}$  is the species reproductive life span, calculated as the difference between the age at last reproduction and the age at first reproduction (AFR), and  $z$  is a constant “depending on survivorship and relative fecundity of young vs. old individuals in the population” (IUCN 2013). Generation length values in the Red List are typically provided for threatened species (Vulnerable to Critically Endangered) assessed under criteria A and C1 (IUCN 2001). As largely discussed (e.g. Purvis et al. 2000; Cardillo et al. 2005), threatened species are generally characterised by relatively slow life histories respect to non-threatened species (e.g. they are generally larger, have longer gestation times, smaller litter sizes etc.). This has a potential to bias the fitting of GL model parameter toward long-living species respect to short-living ones. Nonetheless, a moderate change in the  $z$  parameter, e.g.  $z=0.29$  in our model (calculated as the slope of the linear regression between GL and  $R_{span}$  for 221 species) vs the theoretical threshold of 0.5 proposed in IUCN guidelines, will have little influence on the calculation of a GL value for short-living species (such as most of rodents), e.g. their modelled GL will remain below 3.3 years in any case (i.e. the arbitrary threshold adopted for short-generation species in the Red List). For those 221 species with GL data reported in IUCN Red List assessments, we modelled the linear relationship between expert-based GL values and calculated GL values (from reproductive life span and age at first reproduction). We found a good fit ( $R^2=0.84$ ) and a high correlation ( $\text{cor}=0.92$ , p-value of the Pearson’s test <  $2.2e-16$ ), which indicate a good correspondence between reported and calculated GL values, and we are confident that this is a good validation of the overall validity of the GL data reported in the IUCN Red List for mammals. Discrepancies between the calculated GLs and the GLs IUCN might

be a mix of process uncertainty (errors in the model) and observation uncertainty (errors in expert-based GL estimates), which are impossible to tease apart.

Since age at last reproduction is generally related to longevity in the wild (IUCN 2013), we assumed it to be equal to the maximum known longevity of the species. Even if published data on maximum longevity often refer to captive individuals, which might cause biases in Rspan estimates, we believe that these biases will probably influence only a limited number of large-bodied species. Moreover, since data on GL stated from experts were available for the majority of large-body species, we reduced the risk of using inaccurate data. We assumed AFR to be equal to age at first birth following IUCN guidelines (IUCN 2013). When information on age at first reproduction for a species was not available, we estimated it by summing gestation length and age at female sexual maturity. For species without empirical data on age at first reproduction for females, we used age at sexual maturity for males.

For carnivore and ungulate species, we completed missing data on maximum longevity and age at sexual maturity through a multiple imputation procedure (Rubin 1987). Carnivores and ungulates are generally characterized by lower levels of missing life-history data respect to other mammal groups (e.g. see Jones et al. 2009). Reproductive parameters used in our analyses were available for over 50% of species among Carnivora, Cetartiodactyla and Perissodactyla. Missing life-history traits were imputed, separately for carnivores and ungulates, following the procedure described in Di Marco et al. (2012). In both datasets, all missing data were imputed 10 times in order to obtain 10 complete datasets for each group. Finally, a median value was calculated for all imputed data for maximum longevity and sexual maturity for each species. Multiple imputation analyses were conducted in R using the package MICE (van Buuren and Groothuis-Oudshoorn 2010).

## Dataset description

The dataset includes generation lengths for 5427 mammal species. Fields given are:

1. TaxID: identification number of species;
2. Order;
3. Family;
4. Genus;
5. ScientificName;
6. AdultBodyMass\_g: body mass of species in grams;
7. Sources\_AdultBodyMass: AnAge, Animal Diversity, Encyclopedia of Life (eol.org/), Nowak and Paradiso 1999, PanTHERIA, Smith et al. 2003, Verde Arregoitia et al. 2013, Mean congenetics, Mean\_confamilials;
8. Max\_longevity\_d: maximum longevity (days) mediated from PanTHERIA, AnAge and Carn\_Ung (multiple imputation for carnivores and ungulates);

9. Sources\_Max\_longevity: AnAge, Carn\_ung (multiple imputation for ungulates and carnivores) and PanTHERIA;
10. CalculatedRspan\_d: reproductive life span (days) calculated from maximum longevity and age at first reproduction;
11. AFR\_d; age at first reproduction (days);
12. Data\_AFR: calculated or published data;
13. CalculatedGL\_d: GL (days) calculated from reproductive life span and age at first reproduction;
14. GenerationLength\_d: best known estimate of GL (days), including information taken from IUCN database, calculated data and mean estimates;
15. Sources\_GL:
  - GMA (IUCN Red List data);
  - Rspan-AFB (GL calculated as the difference between reproductive life span and age at first birth);
    - Rspan-AFR(SM+Gest) (when data on age at first reproduction were not available, we calculated this parameter as the sum between age at female sexual maturity and gestation length);
    - Rspan-ASMmales (GL calculated with age at sexual maturity for males, when data on age at first reproduction for females were not available);
    - Mean\_congenerics\_same\_body\_mass (mean GL calculated from congeneric species in the same bin of log body mass);
    - Mean\_congenerics (mean GL calculated from congeneric species, irrespective of body mass);
    - Mean\_family\_same\_body\_mass (mean GL calculated from confamilial species in the same bin of log body mass);
    - Mean\_family (mean GL calculated from confamilial species, irrespective of body mass);
    - Mean\_order\_same\_mass (for species with unknown parameter estimates, we assigned the mean GL value of species in the same bin of log body mass and belonging to the same order);
    - Mean\_order (mean GL calculated from species belonging to the same order, irrespective of body mass);
    - Mean\_all\_orders\_same\_body\_mass (species for which we estimated mean GL from species belonging to the same bin of log body mass).

## Data sources

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at <http://doi.org/10.5061/dryad.gd0m3>

## Original source

Pacifici M, Santini L, Di Marco M, Baisero D, Francucci L, Grottole Marasini G, Visconti P, Rondinini C (2013) Generation length for mammals. *Nature Conservation* 5: 87–94. doi: 10.3897/natureconservation.5.5734

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## Appendix

Database on generation length of mammals. (doi: 10.3897/natureconservation.5.5734.app). File format: Microsoft Excel file (xls).

**Explanation note:** Database on generation length of all extant mammals, with 5427 records.

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Database on generation length of mammals. doi: 10.3897/zookeys.5.5734.app

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