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Flavio Zanini, Anna Klingemann, Rodolphe Schlaepfer, and Benedikt R. Schmidt

Abstract: Species movement and occupancy of habitat patches are dependent on landscape permeability. Some land-use types (e.g., roads) may be barriers to animal movement. Analyses of the effect of landscape structure on patch occupancy usually use circular buffers around focal patches. The main assumption of this methodological approach is that species are affected by a particular landscape element equally in every direction from a given patch. This assumption is likely not to hold if animal movement is restricted by barriers because barriers reduce movement patterns and reshape the ideal circular buffer into a noncircular buffer. We developed a method to determine the effect of landscape variables on the distribution of two amphibian species that explicitly takes dispersal barriers into account. We extracted landscape variables within (*i*) circular buffers (CB) and (*ii*) barrier-based buffers (BBB). BBB were produced by reducing the boundaries of CB according to major impassable barriers. The BBB approach almost doubled the explained deviance of multiple regression models in comparison with the CB approach. Moreover, CB and BBB models included different predictor variables. We suggest that the BBB approach is more useful than the traditional CB analyses of species–habitat relationships because ecological barriers are explicitly taken into account.

Résumé : Le déplacement des espèces et leur utilisation des parcelles d'habitat dépendent de la perméabilité du paysage. Certaines utilisations des terres (par ex., routes) peuvent devenir des barrières pour le déplacement des animaux. Les analyses des effets de la structure du paysage sur l'utilisation des parcelles utilisent généralement des zones tampons circulaires autour des parcelles ciblées. La présupposition principale de cette approche méthodologique est que les espèces sont affectées de façon égale dans toutes les directions autour de la parcelle par un élément donné du paysage. Cette présupposition risque de ne pas tenir lorsque le déplacement des animaux est restreint par des barrières, parce que les barrières limitent les patrons de déplacement et transforment la zone tampon idéale de circulaire en non circulaire. Nous avons mis au point une méthode qui détermine les effets de variables du paysage sur la répartition de deux espèces d'amphibiens et qui tient compte de façon explicite des barrières à la dispersion. Nous avons extrait les variables du paysage au sein (*i*) de « zones tampons circulaires » (CB) et (*ii*) de « zones tampons basées sur les barrières » (BBB). Nous avons produit les BBB en réduisant les CB en fonction des principales barrières infranchissables. Par rapport à l'approche CB, l'utilisation de BBB double presque l'explication des écarts à la moyenne dans les modèles de régression multiple. De plus, les modèles CB et BBB incluent plusieurs variables prédictives. Nous croyons que la méthode BBB est plus utile que les analyses traditionnelles CB des relations espèce–habitat, car elle tient compte explicitement des barrières écologiques.

[Traduit par la Rédaction]

Introduction

The structure and human use of the landscape several kilometres away from a wetland may affect the structure of the biological community within the wetland (Findlay and Houlahan 1997; Mazerolle and Villard 1999; Joly et al. 2001). Therefore, knowledge of the effects of landscape variables on the distribution of species will be useful for conservation and landscape planning, for example, by assisting managers in identifying suitable sites for the creation of new ponds and wetlands (Pellet et al. 2004). However, whereas it is well known that ecological barriers affect the colonization of a particular site, the role of barriers has not yet been adequately studied (Ray et al. 2002). We addressed

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this issue in a study on amphibians, the most highly threatened group of vertebrates (Houlahan et al. 2000; Stuart et al. 2004).

The composition of the landscape surrounding ponds has been shown to be important for pond-breeding amphibian species. Many previous studies are based on landscape variables extracted within circular buffers centred on ponds (Knutson et al. 1999; Rubbo and Kiesecker 2005; Van Buskirk 2005; Denoël and Lehmann 2006). Other studies used circular buffers of different radii to estimate the spatial scale of landscape effects on pond occupancy (Findlay and Houlahan 1997; Vos and Chardon 1998; Johnson et al. 2002; Houlahan and Findlay 2003; Knutson et al. 2004; Pellet et al. 2004; Price et al. 2005).

The use of circular buffers assumes that the landscape has an isotropic effect on the species occurrence so that species are affected by a particular landscape element equally in every direction from a given pond. This is not a realistic assumption because ecological barriers that reduce dispersal can alter movement patterns (Gibbs 1998; Stevens et al. 2004; Marsh et al. 2005) and thereby reshape the ideal circular area into a noncircular form, which better reflects the real use of the landscape by amphibians (e.g., as shown by radio-tracking studies; Schabetsberger et al. 2004). Ray et al. (2002) explicitly modeled landscape use by amphibians and convincingly showed the effect of matrix permeability on the shape of accessible area around a pond. Ray et al. (2002) also demonstrated that land-use variables computed in these buffers based on landscape permeability improved the prediction of toad presence when compared with the ideal circular buffers. Therefore, in spite of being simple to compute, the use of circular buffers might lead to erroneous conclusions regarding the the effects of landscape variables on pond occupancy and species distribution. This may lead to errors in conservation planning.

Quantifying the effect of barriers and landscape permeability is a daunting task because of the lack of information about the effect of habitat types on species movement and the difficulty of ascribing a resistance coefficient to each habitat type (Pither and Taylor 1998; Adriaensen et al. 2003; Stevens et al. 2004). Such information is time- and cost-demanding and difficult to generalize across species and space, because it requires intensive fieldwork, expensive radio-tracking equipment, and specific experimental design (Pither and Taylor 1998; Adriaensen et al. 2003; Stevens et al. 2004). However, it is sometimes possible to rapidly identify the major impassable barriers in a landscape. This allows obtaining an approximation of the real landscape resistance. For example, highways or canalized rivers can safely be expected to be a completely impassable barrier for amphibians.

The goal of our study was to assess the effect of landscape variables on the occurrence of two amphibian species when major barriers in the landscape are considered. We tested whether species occurrence is predicted better by landscape variables extracted within traditional circular buffers (hereafter CB) or barrier-based buffers (hereafter BBB). We called these latter types of buffers BBB because they were computed by removing from CB those areas that were not accessible from ponds owing to (putative) insurmountable barriers. We predict that landscape variables within BBB better explain species distribution than CB.

Materials and methods

Study area and species

The study area is the Rhone plain below 1000 m above sea level in southwestern Switzerland (Fig. 1). The plain has a mean width of 2–3 km and is bordered to the south and to the north by the Swiss Alps. Apart from villages and small cities, agriculture (essentially orchards and vineyards) is the predominant land use in the plain (76.6%) (Zanini et al. 2006). The heavily canalized Rhone river and a highway divide the study area lengthwise (Fig. 1).

We studied two amphibian species: (1) the European common toad (*Bufo bufo* (L., 1758)), which used to be widely distributed all over Switzerland but is now in decline (red-list status VU; Schmidt and Zumbach 2005), and (2) the European common frog (*Rana temporaria* L., 1758), which is wide-spread in Switzerland and currently not threatened (status LC). Data on presence or absence of the species in 88 ponds (Fig. 1) was provided by the Swiss Amphibian and Reptile Conservation Program (http://karch.ch/; accessed 24 October 2006) and by Paul Marchesi (Drosera SA), who intensively surveyed the study area so that non-detection is not an issue. In the survey of Schmidt and Zumbach (2005), per-visit detection probabilities of *R. temporaria* and *B. bufo* were 70.5% and 57.7%, respectively. Hence, absence can be inferred with 95% confidence after only three and four visits, respectively (Pellet and Schmidt 2005). We considered a species present in ponds if adults, tadpoles, or juveniles were detected at least once between 1997 and 2003. This approach avoids effects of short-term fluctuations in pond occupancy that tend to be independent of habitat characteristics (Schmidt and Pellet 2005). *Bufo bufo* was found in 42% (37/88) of the sites, while *R. temporaria* occurred in 56% (49/88) of the sites.

Landscape variables in circular (CB) and barrier-based (BBB) buffers

We measured landscape variables in the surroundings of the breeding sites using MapBasic version 7.5 and MapInfo version 7.5 GIS software (MapInfo Corporation © 1985–2003, Pitney Bowes MapInfo EMEA, Windsor, Berkshire, UK). We derived land-use data from VECTOR25, the vector format of the 1:25000 topographical maps of Switzerland provided by the Swiss Federal Office of Topography (Swisstopo). Precision of maps is approximately 3–8 m. Maps are revised at intervals of 6 years; we used the most recent maps from 2002 to 2003.

We measured landscape variables (i.e., the area of agricultural land, forest, lake, urban, vineyard, marsh, bush, and gravel pits, as well as the total length of rivers, first-class roads (at least 6 m wide), second-class roads (at least 4 m wide), rail roads, and hedgerows) both in BBB around the ponds and in the commonly used CB.

BBB and CB represent an approximation of the potential amphibian movement area around the breeding sites. To estimate this potential amphibian movement area, we first computed 17 CB of different radii centred on each breeding pond (radii = 100, 200, 300, . . . , 900, 1000, 1200, 1400, 1600, 1800, 2000, 2500, and 3000 m). The largest discs were chosen according to potential amphibian mobility and

Fig. 1. Study area and 88 study ponds in the Rhone plain, Central Valais, Switzerland, where European common toads (*Bufo bufo*) and European common frogs (*Rana temporaria*) were surveyed. We show, with the example of one pond, the 17 barrier-based buffers (see text). The radii of buffers vary from 100 m up to 3 km. To not overload the map, land-use types are not shown. The shading shows the topography. The map was reproduced by permission of the Swiss Federal Office of Topography (Swisstopo no. BA081153).
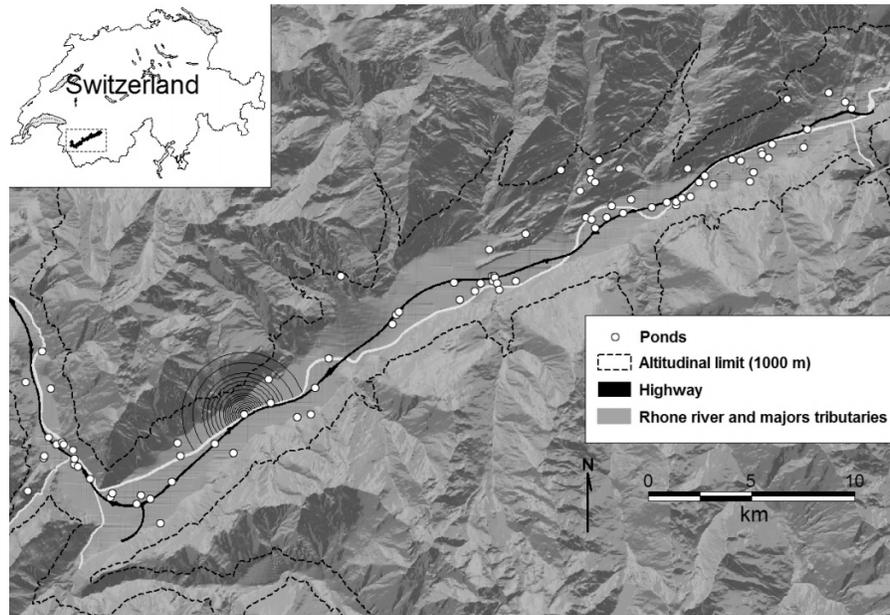
are based on recent studies suggesting that landscape variables within 2000 m and beyond could affect amphibian species occurrence (Houlahan and Findlay 2003). Second, to create BBB, we removed the surfaces in each CB inaccessible to *B. bufo* and *R. temporaria*. To do so, we removed the area separated from the breeding site by barriers that we considered a priori to be insurmountable for both species. In our study, we considered three major linear topographical elements as insurmountable barriers: the Rhone river, three canalized tributaries of the Rhone river, and the main highway (Fig. 1). The Rhone river is more than 40 m wide, has man-made banks, and a mean annual discharge of 187 m^3·s^{-1} (Loizeau and Dominik 2000). The river was canalized many decades ago. Highways are known to be barriers to amphibian movement and may even lead to genetic substructuring of populations (Reh and Seitz 1990). In our study area, highway construction began in the early 1970s. The highway is 40 m wide and has four lanes. The railway was built in 1865 and its track is about 10 m wide. Thus, sufficient time has elapsed for barrier effects to have occurred (Findlay and Bourdages 2000.).

The 14 landscape variables represent different land uses that may potentially affect amphibian distribution in Switzerland (Pellet et al. 2004), and which cover together 100% of the surface in the buffers. The analysis of land use at various buffer radii around the breeding sites (multi-scale sampling) allowed us to estimate the distance at which landscape variables affect the amphibian use of ponds and whether the effect depended on the type of buffer (Pellet et al. 2004).

Statistical analysis

To verify that the ponds can be considered independently distributed over our landscape and not located in clusters of

occupied and empty ponds (i.e., no spatial autocorrelation), we used the "ncf" package of R version 2.1.0 (Bjørnstad 2001–2004) to calculate Moran's *I* (Legendre 1993; Kühn 2007) and the associated statistics for distance classes of 1 km. We calculated 1000 permutations to determine if spatial autocorrelation was significantly different from zero ($p < 0.05$) for all distance classes.

We tested associations between amphibian pond occupancy and landscape variables with logistic regression models (Sokal and Rohlf 1995). We used landscape variables as explanatory variables (predictors) and the presence or absence of a species as the binary response. We used the same statistical procedures for CB and BBB.

We built a multiple logistic model for each 1 of the 17 buffer radii considering together all the landscape predictors from the same-sized buffer. Then, we carried out a stepwise regression to identify the best model for each buffer radius. The best model has the lowest AIC value (Akaike's information criterion; Burnham and Anderson 2002; Mazerolle 2006). The procedure was accomplished by the stepAIC function from the package MASS of the program R version 2.1.0 (R Development Core Team 2004). stepAIC does both forward and backward selections and selects models with lower AIC scores. This analysis was carried out twice, once for CB and once for BBB.

After having found the best model for each buffer radius, we wanted to know which BBB or CB model at which radius overall described the distribution of the data best. We used the differences in AIC (ΔAIC) and Akaike weights (*w*; Burnham and Anderson 2002; Mazerolle 2006) to compare the relative performance of the 17 CB models (1 for each radius) and the 17 BBB models that were selected using stepwise regression in the previous step. Models having ΔAIC < 2 have substantial support, those in which 4 <

Fig. 2. Mean (SD) area of buffers surrounding the ponds at different radii for barrier-based buffers (BBB) and circular buffers (CB). BBB correspond to CB reshaped according to major impassable barriers for movement of European common toads (*Bufo bufo*) and European common frogs (*Rana temporaria*) in the study area (highways and canalized rivers).
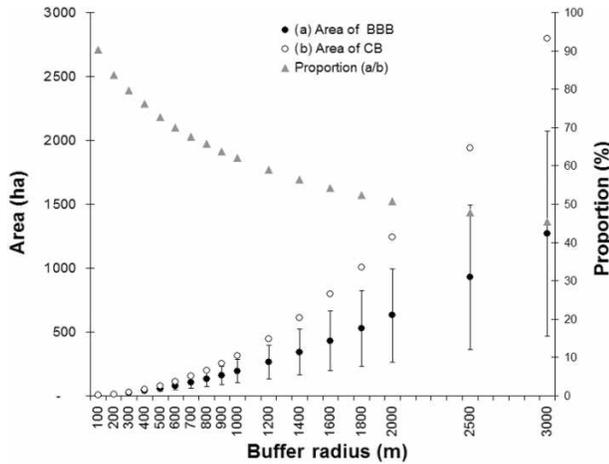
ΔAIC < 7 have considerably less support, and models having ΔAIC > 10 have essentially no support. The support refers to the relative capacity of a model to describe the information present in the data. Akaike weights (w) can be interpreted as the probability that model i is the best model for the observed data given the candidate set of models. The sum of all Akaike weights is 1.

The explained deviance of the models was adjusted (adj. D^2) for the number of observations and the number of parameters in the model (Guisan and Zimmermann 2000).

Results

Moran's I statistics indicated that there was no spatial autocorrelation in response variables. Therefore, the observations of species in ponds can be considered independently distributed, validating the species–habitat statistical tests.

As expected, the selected insurmountable barriers considerably reduced the amount of terrestrial habitat around ponds that is available for species. Indeed, compared with CB, the reduction of BBB area increased as the buffer radii increased (Fig. 2). For example, at 1000 m, the mean value of the BBB corresponded to 62% of the CB area with the same radius. The proportion was lowest at 3000 m radius (45%).

The comparison of the relative performance of BBB and CB models clearly showed that BBB models explained the data substantially better than CB models (Table 1). BBB models were generally well supported by the data where Akaike weights for CB models were all ≤0.01. BBB models were better supported by the data because they had higher D^2 values. These general results were true for both species. No single BBB model was found that was clearly the best description of the data (Table 1). For *B. bufo*, we observed substantial support (ΔAIC < 2) for models with landscape variables measured at a radius of 600, 700, and 200 m. In the case of *R. temporaria*, the substantial support was found for five models (800, 900, 1000, 1200, and 2500 m).

Table 1. Model selection by buffer radius and buffer type (BBB, barrier-based buffers; CB, circular buffers) for European common toads (*Bufo bufo*) and European common frogs (*Rana temporaria*).
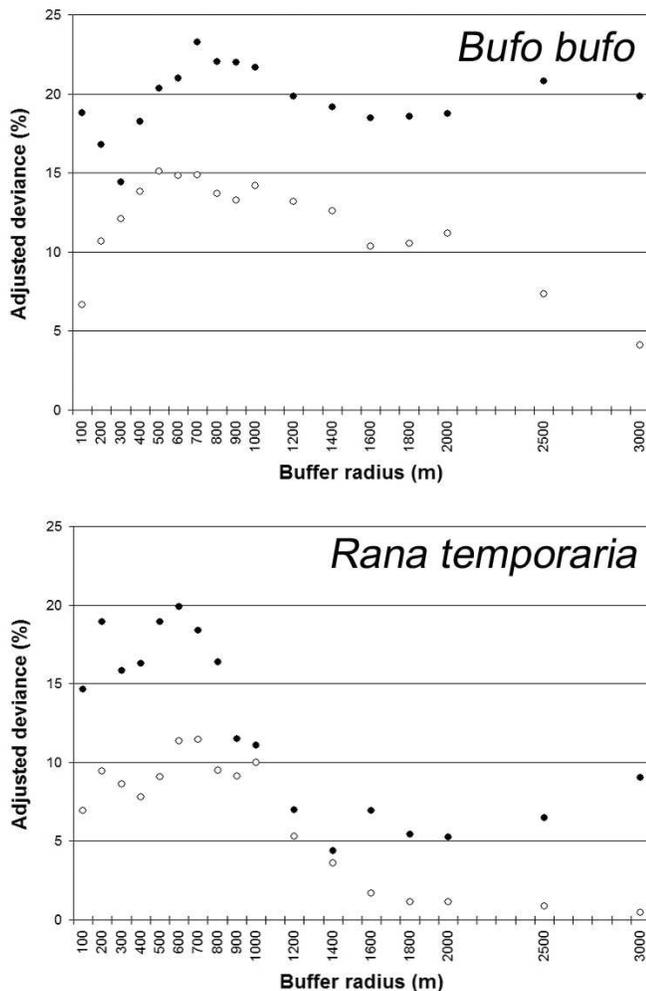
Buffer	Radius (m)	K	D^2 (%)	Adj. D^2 (%)	ΔAIC	w
Bufo bufo						
BBB	600*	7	25	20	0.00	0.36
BBB	700	6	23	18	0.81	0.24
BBB	200	8	25	19	1.98	0.13
BBB	500	9	26	19	2.85	0.09
BBB	800	6	21	16	3.08	0.08
BBB	400	9	24	16	5.73	0.02
BBB	900	3	14	12	6.22	0.02
BBB	1000	3	13	11	6.71	0.01
BBB	300	10	25	16	7.08	0.01
CB	600*	4	14	11	7.17	0.01
CB	700	5	16	11	7.87	0.01
CB	200	2	10	9	7.91	0.01
BBB	100	11	24	15	9.16	0.00
CB	800	4	13	9	9.34	0.00
CB	1000	5	14	10	9.52	0.00
CB	900	4	12	9	9.78	0.00
CB	500	4	12	9	9.81	0.00
Rana temporaria						
BBB	800*	4	25	22	0.00	0.18
BBB	900	4	25	22	0.06	0.18
BBB	1000	4	24	22	0.43	0.15
BBB	2500	4	24	21	1.43	0.09
BBB	1200	3	22	20	1.64	0.08
BBB	2000	2	20	19	2.07	0.06
BBB	1400	3	21	19	2.45	0.05
BBB	600	6	26	21	3.04	0.04
BBB	700	9	30	23	3.22	0.04
BBB	1600	3	20	18	3.27	0.04
BBB	3000	5	24	20	3.43	0.03
BBB	500	6	25	20	3.76	0.03
BBB	1800	5	22	19	4.94	0.02
BBB	100	9	26	19	8.16	0.00
BBB	400	9	26	18	8.76	0.00
BBB	200	8	24	17	9.48	0.00
CB	500*	6	20	15	9.72	0.00

Note: Models are ranked by increasing order of Akaike's information criterion (AIC) scores. Only models with ΔAIC < 10 are shown. K is the number of model parameters. D^2 and adj. D^2 are the explained and adjusted deviances, respectively (Guisan and Zimmermann 2000). ΔAIC is the difference between the AIC of the model and the minimum AIC among models. w is the Akaike weight of the model.

*Denotes models whose parameter estimates are shown in Table 2.

By comparing the adjusted deviance by buffer radius we found that patterns are similar, but BBB perform better than CB at all buffer radii (Fig. 3). In general, the difference in the relative performance of the two approaches depended on the buffer radius. For *B. bufo*, the major discrepancies were found at <900 m and at >1600 (Fig. 3). The maximum discrepancy (10%) was at 500 m. For *R. temporaria*, the discrepancy was important at all buffer radii except at 300 m. The maximum discrepancy (16%) was measured at 3000 m. On average, the adjusted deviance is approximately two times higher in BBB than in CB (12% and 6% for

Fig. 3. Proportion of adjusted explained deviance for multiple models built up within the radii of each buffer. ●, adjusted deviance for barrier-based buffers (BBB); ○, adjusted deviance for circular buffers (CB).

Table 2. Estimates of slopes of predictor variables (on the logit scale) retained in the best circular buffer (CB) and barrier-based buffer (BBB) models (marked with an asterisk in Table 1) for (*a*) European common toads (*Bufo bufo*) and (*b*) European common frogs (*Rana temporaria*).

(*a*) *Bufo bufo* (best model buffer radii of 600 m (CB) and 600 m (BBB)).

Predictor	CB (slope (SE))	BBB (slope (SE))
Intercept	–11420.0 (5895.0)	–15570.0 (4706.0)*
Railroad	— (—)	21.8 (14.1)*
Forest	0.04 (0.02)*	— (—)
Second-class road	7.22 (3.06)*	8.00 (3.83)*
First-class road	–7.18 (3.81)	31.85 (13.43)*
Bush	–0.82(0.36)*	–2.28 (0.75)*
Vine	— (—)	0.04 (0.02)
Mineral	— (—)	0.18 (0.09)
Hedge	— (—)	4.97 (2.65)

(*b*) *Rana temporaria* (best model buffer radii of 500 m (CB) and 800 m (BBB)).

Predictor	CB (slope (SE))	BBB (slope (SE))
Intercept	8292.0 (5340.0)	–17410.0 (5778.0)*
Marsh	0.35 (0.25)	0.28 (0.36)
Forest	— (—)	0.034 (0.01)*
Second-class road	— (—)	3.48 (2.21)
Hedge	— (—)	9.99 (4.75)*
Orchard	–0.05 (0.02)*	— (—)
Railroad	8.76 (5.25)	— (—)
Bush	0.87 (0.44)*	— (—)
Lake	–0.22 (0.097)*	— (—)
Mineral	0.17 (0.10)	— (—)

Note: Slopes and standard errors (SE) were originally estimated on a meter or meter^2 scale; hence, they were very small. For better readability, the estimates were scaled up to represent the slopes and SE on a hectare scale. A dash indicates that a predictor variable was not retained in a model.

*Confidence interval does not include zero.

B. bufo, respectively, and 20% and 12% for *R. temporaria*, respectively).

The best CB and BBB differed in various ways. For *B. bufo*, the same "best" buffer radius was selected for both CB and BBB models, but this was not the case for *R. temporaria* (Table 1). Different predictor variables were included in the CB and BBB models for both species (Table 2). The stepAIC function in the program R retained some predictor variables in the final model even though the confidence interval of the slope included zero; these predictor variables are not discussed further. CB and BBB models had only about half of the predictor variables in common. If the same predictor variables were included in the CB and BBB models, then slope estimates were mostly similar. There were, however, cases of strong differences. For example, the estimated slope for the effect of first-class roads on the pond occupancy in *B. bufo* differed between CB and BBB models: CB models predicted a positive effect, whereas BBB models predicted a negative effect. From a biological point of view, predictor variables in the best models included variables that describe availability of habitat (e.g., presence of hedges) and variables that are suspected to be partial barriers to animal movement (e.g, roads; interestingly, slopes of these variables were positive rather than negative as expected).

Discussion

We present a new method to determine the effect of landscape variables on the distribution of two anurans that takes barriers to movement explicitly into account. Our results showed that the proposed BBB analysis increases the explanatory power of the models representing the effect of landscape variables at various distances from ponds and out performs the traditional CB analysis (Table 1). This result is consistent with the only study that explicitly modeled the effects of barriers on the shape of the area that can be used by amphibians as terrestrial habitat (Ray et al. 2002). We therefore suggest that the BBB approach appears to be ecologically more appropriate than traditional CB analysis. Below we also explain how our novel method can be used to identify major ecological barriers to animal movement.

Increasing urbanization and habitat alterations make it particularly important to find ways to assess the impact of

land-cover changes on the distribution of natural populations. We proposed a relatively simple approach that includes the effect of ecological insurmountable barriers in amphibian distribution models. Our results clearly showed the important improvement of the explanatory power of the models and then the increased ecological adequacy of the landscape variables computed within the BBB.

More complex and more realistic simulations of species movement in the area surrounding a breeding site can and should be made (e.g., Ray et al. 2002; Joly et al. 2003), but the gaps in knowledge regarding permeability of landscape elements to amphibian movement considerably limits those approaches. The validation of such models is difficult because field studies or experiments on the terrestrial movement of amphibians in relation to land-use types are still rare (Rothermel and Semlitsch 2002; Stevens et al. 2004; Mazerolle and Desrochers 2005) and are likely to be limited to some species and type of landscapes. Therefore, in the absence of adequate ecological information for more precise definition of the area used by a species during their life cycle, methods such as ours may constitute a valuable alternative in predictive distribution studies.

The fact that the effect of landscape variables in the BBB better explained species occurrence than traditional CB implies that the species distribution is affected by the barriers we used in our analysis. This, however, is not the only use of the BBB approach. We used well-known barriers to improve the prediction of amphibian pond occupancy. If the BBB method is used the other way round, then it may be used as a tool to assess whether putative barriers indeed are barriers. One might test whether BBB based on such putative buffers improve the prediction of pond occupancy in comparison with CB. If such BBB indeed improve prediction of animal patch occupancy, then we suggest that this constitutes first evidence of a barrier effect of these putative barriers. An open question is whether the BBB method is sufficiently sensitive to detect barriers that only partly restrict animal movement.

Our analysis also showed that landscape structure far away from the wetlands affect their use as breeding sites by both *B. bufo* and *R. temporaria*. This is not surprising because both species are known to be vagile and migrate several kilometres away from the breeding ponds. Distances >3 km have been observed for *B. bufo* (Heusser 1968) and Baker and Halliday (1999) showed that *R. temporaria* was able to colonize new ponds at distances up to 950 m from existing ponds. Best CB and BBB models had the same or different radii for *B. bufo* and *R. temporaria*, respectively. Although the difference for *R. temporaria* was not great, CB models appeared to underestimate the spatial scale of landscape effects on pond occupancy.

The best CB and BB models shared only about half of the predictor variables, whereas the other half was unique to either CB or BBB model. Interestingly, although BBB a priori exclude barriers to dispersal, variables that represent transportation infrastructure were included in the final model. In contrast to the general expectation (Fahrig et al. 1995; Vos and Chardon 1998; Findlay and Bourdages 2000; Schmidt and Zumbach 2008), the effects of roads and railway lines was positive rather than negative. An explanation for this surprising result might be that the presence of roads

covaries with an unmeasured landscape element that has positive effects on amphibians (e.g., ditches and fallow strips along roads). Forest cover and hedge density had positive effects on pond occupancy as expected. These landscape elements create landscape diversity that is overall suitable for amphibians. In addition, it should be noted that hedges are often found along roads.

The radius of a buffer can be interpreted as the distance away from a breeding pond that is used as terrestrial habitat by amphibians (Vos and Chardon 1998; Houlahan and Findlay 2003; Pellet et al. 2004). When using the CB approach, the radius of buffers is directly interpretable as the distance from ponds at which the landscape is used by species. With BBB, this relation is not direct because the radius does not correspond to a circular area. However, the result from BBB can be used for mapping the area around ponds where the landscape is the most strongly associated with the occurrence of species (e.g., the area within 600 m for *B. bufo*, w = 0.36; Table 1). This landscape is likely of main concern in terms of habitat and environmental stressors for species persistence, and needs particular attention when landscape projects are planned.

The proposed BBB approach is potentially applicable to any species functioning on a spatially defined patch basis (e.g., spiders inhabiting arable land; Schmidt et al. 2008), as well as to various applications in conservation biology. We envision at least three uses of our method. First, it allows a better assessment of the effects of landscape variables on the distribution of species. Second, it allows testing hypotheses regarding the effects of putative barriers on the distribution of species. Third, in systems where ecological barriers have already been identified and where the ages of the barriers are known (e.g., the year when a highway was constructed), it can be used to assess whether a response of the species to habitat fragmentation has already occurred or whether the response occurs in a time-lagged fashion (Findlay and Bourdages 2000). In conclusion, we suggest that species distribution studies considering ecological barriers are essential for the development of valuable conservation strategies, especially when the fragmentation of the study area suggests an important reduction of the movement possibilities of the species.

Acknowledgements

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