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HABITAT COMPLEMENTATION IN A HIGH ELEVATION MIDWIFE TOAD (*ALYTES OBSTETRICANS*) METAPOPULATION: MANAGEMENT IMPLICATIONS

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Résumé

Les amphibiens font partie de la classe des vertébrés les plus menacés et leur nombre est globalement en baisse partout dans le monde. Une des menaces les plus importantes constitue la destruction de leurs habitats, étant donné que la plupart des amphibiens doivent atteindre différents habitats non interchangeables pour compléter leur cycle de vie, à travers un processus appelé complémentation d'habitats. Ce processus est particulièrement intéressant chez le crapaud accoucheur (*Alytes obstetricans*) qui est une espèce menacée qui peut coloniser des milieux de haute altitude, où la survie hivernale pourrait être un facteur limitant de la croissance de la population. Dans notre étude, nous avons évalué l'effet de 13 facteurs à l'échelle locale et du paysage pouvant affecter la distribution des populations et leur occupation du territoire. Nous avons mené un suivi qui comprenait trois visites par site au cours d'une saison de reproduction sur 84 plans d'eau situés dans des pâturages de haute altitude en Suisse. Nous avons ensuite utilisé des techniques de modélisation d'occupation avec une méthode basée sur la probabilité d'estimation des taux d'occupation des sites à partir de détection/non-détection des têtards et/ou des adultes, afin d'éviter des erreurs de mesure importantes comme les fausses absences. Le meilleur modèle résultant indique que la proportion de forêt autour des plans d'eau a une influence négative sur l'occupation du crapaud accoucheur alors que les murs de pierres sèches (un de leurs habitats terrestres principaux) ont un effet positif. En effet, à haute altitude, cette espèce resterait toujours dans les murs de pierres sèches à proximité des plans d'eau et n'aurait pas besoin de grandes surfaces de forêt pour la complémentation d'habitats, car les sites d'hivernage et d'estivage seraient vraisemblablement les mêmes, contrairement à la plupart des autres espèces d'amphibiens. Nos résultats ont permis d'identifier des habitats potentiellement de haute qualité et permettraient d'encourager les gestionnaires des pâturages dans le but de protéger les plans d'eau et leurs habitats terrestres ainsi que de créer des sites plus favorables pour conserver et augmenter la taille de la population de cette espèce.

Mots-clés

Paysage, amphibien menacé, modélisation d'occupation des sites, altitude, murs de pierres sèches, proportion de forêt.

Habitat complementation in a high elevation midwife toad (*Alytes obstetricans*) metapopulation: management implications

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Running title

Alytes obstetricans habitat complementation in high elevation

Abstract

Amphibians are the most threatened vertebrate class and are declining across the globe. One of the major threats is habitat destruction, given that most amphibians need to link different non-substitutable habitats to complete their life cycle, a process called landscape complementation. Habitat complementation is particularly interesting in the threatened midwife toad (*Alytes obstetricans*) that can colonize high altitude environments, where winter survival might be an overlooked limiting factor of population growth. In our study, we evaluated the effect of 13 local and landscape-scale factors affecting population distribution and occupancy. We conducted a monitoring survey of 84 water bodies, including three visits per site during one breeding season, located in high elevation pastures in Switzerland. We then used occupancy modeling techniques with likelihood-based method for estimating site occupancy rates from detection/non-detection of *A. obstetricans* tadpoles and/or adults, avoiding important measurement errors such as false absences. The best resulting model indicated that forest cover had a negative influence and dry stone walls (one of their preferred terrestrial habitats) had a positive effect on *A. obstetricans* occupancy. Indeed, this species in high altitude would always stay in dry stone walls close to breeding water bodies. This species did not need surrounding areas of large forestation for landscape complementation, since their wintering and summering sites are likely to be identical – a feature unlike most other amphibian species. Our findings enable identification of potential high-quality habitat, in turn enabling both the encouragement of pasture managers to protect those water bodies and terrestrial habitats and the creation of more favorable sites to conserve and increase this species population size.

Keywords

Landscape, threatened amphibian, site-occupancy modeling, altitude, dry stone walls, forest cover.

Introduction

Amphibians are very important in biodiversity, as they are part of a significant proportion of vertebrate biomass in several ecosystems, and they are important in the food web as prey and predator species (Hamer and McDonnell, 2008). However, this class has been declining across the globe for several decades (Houlahan et al., 2000). Their decline is the most rapid among vertebrates. With 30 % of all species listed as threatened, they may be the only group considered to be globally at risk (Stuart et al., 2004; Wake and Vredenburg, 2008). This decline is likely to accelerate during this century, due primarily to human activities (Beebee and Griffiths, 2005; Hof et al., 2011). Indeed, the major threats identified are habitat destruction, land-use and climate change, the spread of the pathogenic fungal disease chytridiomycosis, and water pollution (Dudgeon et al., 2006; Hof et al., 2011).

Several studies have investigated the environmental variables that could influence amphibian distribution, occupancy and abundance, as assessed on three different scales: pond level, biotic interactions level and on the landscape level. At the pond level, parameters known to affect amphibian occupancy and abundance include: area and perimeter, the latter being related to the length of the shores, which are the direct link between aquatic and terrestrial environments and both area and perimeter have shown a positive correlation with amphibian larvae density and richness (Gagné and Fahrig, 2007; Oertli et al., 2000; Saunders, 2004); depth, which can on the one hand reduce aquatic vegetation (tadpoles refuges) and increase predators density if ponds are too deep and on the other hand increase probability of drying if ponds are not deep enough (Suislepp et al., 2011); solar exposition, which depends on canopy closure (Jennings et al., 1999), increasing species richness and diversity as heat from sunlight enhances tadpoles development (Blaustein and Kats, 2003; Lesbarrères et al., 2010); and finally water conductivity, which is important for osmoregulation and amphibian development and also indicate more time for mineral leaching (Bradford et al., 2003; Klaver et al., 2013). At the biotic interactions level, tadpole predators have been shown to impact amphibian populations by foraging effectively in prey refugia. Indeed, high predator density may negatively affect tadpoles abundance (Baber and Babbitt, 2004; Caldwell et al., 1980). Finally at the landscape level, important variables for amphibian occupancy and abundance include: altitude, which is negatively correlated with species distribution and richness (Soares and Brito, 2007); pond connectivity, which could be important for metapopulation structures (Marsh and Trenham, 2001); forest cover, an important landscape characteristic that could be positively or negatively correlated with amphibian occurrence depending on the species (Buskirk, 2005); and finally terrestrial habitats where amphibians spend the majority of their lives, perhaps better explaining their abundance and occupancy than the quality of breeding ponds (Marsh and Trenham, 2001).

This last variable is particularly important, given that most amphibians need to link different habitat types to complete their life cycle, a process called landscape complementation (Dunning et al., 1992). Most amphibians need different non-substitutable resources and cannot fulfill their lifecycle if they cannot reach resources, such as summer foraging patches, overwintering sites and breeding ponds (Dunning et al., 1992; Stebbins and Cohen, 1995). Suitable aquatic compartments are primordial as they are used to meet and breed for most species (Stebbins and Cohen, 1995; Zug et al., 2001). However, terrestrial habitats are generally less well defined. It is believed that the proximity between aquatic and terrestrial habitats and the area of the latter may play a key role in the occupancy of a patch (Pope et al., 2000). Indeed, as amphibians usually have limited dispersal capabilities (Sinsch, 1990) and are small and slow-moving (Stebbins and Cohen, 1995), both habitats have to be near. The distance constraint manifests at a local scale to possibly alter habitat complementation (Guerry and Hunter Jr, 2002). Additionally, at a larger scale of metapopulations, it can reduce exchanges between population individuals to threaten re-colonization and gene flow possibilities (Hanski and Gaggiotti, 2004; Marsh and Trenham, 2001).

The midwife toad *Alytes obstetricans* (LAURENTI, 1768)*,* listed as endangered in Switzerland (EN according to the IUCN criteria) (Schmidt and Zumbach, 2005), inhabits terrestrial habitats, such as dry stone walls, dead wood heaps and sunny scree, throughout the year in immediate proximity of breeding water bodies (Schlüpmann, 2009). After terrestrial mating, males have the peculiarity of providing care to its spawn by carrying them during their early development (Böll et al., 2012; Uthleb, 2012). Midwife toads can colonize high altitude valleys (Meyer et al., 2009) in extreme environments, where winter survival might be an overlooked limiting factor of population growth. Therefore, with the present study we aim to improve our understanding of landscape and habitat complementation in high altitude with a threatened amphibian species. Ultimately, by identifying the local and landscape-scale factors affecting population density and reproductive success, we desire to better target conservation measures and to provide clear advice to pasture managers.

Methods

Study area

The study area is located in high pastures of a natural park in the Jura Mountains located in the Swiss Canton of Vaud (study area center: 46.52° N, 6.14° E), an area with calcareous soils and semi-continental to mountain climate (Hugger, 1975). It covers about 54 km^2 with elevation ranging from 1120 to 1510 m a.s.l. The landscape is mainly composed of pasture (*Cynosurion*) and spruce-fir forest (*Abieti-Piceion*) (Delarze et al., 2015). The pastures are characterized by the presence of cows in summer only (from May to September) for grazing purposes.

Alytes obstetricans survey

Water bodies in the study area have been located with 1:25’000 maps, orthophotos on QGIS v. 2.12 (QGIS Development Team, 2015) and with documents attesting water presence loaned by the Parc naturel régional Jura Vaudois. Three types of water bodies (n = 84) have been surveyed. The first type are called agricultural pools (n = 16), an artificial hole surrounded by barriers, covered with plastic sheeting that is used to accumulate rainwater to supply to cows (Supplementary material Figure 1A). They are cleaned every 3-4 years and there is no fixed vegetation, usually only algae. The second type are cisterns (n = 22), which is an old version of the first type. They are dug in the soil with the edges covered with stones and used to have the same function (some are still used to supply water to cows) (Supplementary material Figure 1B). The third type are ponds (n = 46), which can be naturally or artificially dug in the soil (Supplementary material Figure 1C). Each was visited once by day between June 1st and June 25th 2015 and three times at night between June 2nd and August 21st 2015. Daily visits consisted of characterizing water bodies and their environment by measuring conductivity, depth, solar exposition and quantifying *A. obstetricans* tadpoles with a dip net, tadpole predators and terrestrial habitat (see *Environmental predictors* section). Night visits occurred in the first part of the night and consisted of call surveys during 15 minutes at each site and light surveys by walking along water body shores to look for *A. obstetricans* tadpoles and tadpole predators. The combination of the three methods (netting, calling, searching) considerably increases *A. obstetricans* detection probability (Petitot et al., 2014).

Environmental predictors

We selected 6 environmental variables that could affect detectability and a set of 13 different environmental variables that could affect occupancy, classified into 3 categories (Table 1) in order to investigate *A. obstetricans* occupancy in the study area.

Detectability variables:

During the amphibian survey, several factors can influence detectability of the target species. We have to take them into account to avoid incorrect assessment of occupancy. The detectability variables selected are (1) date of the survey, (2) time of the site-survey, (3) percentage of moon surface visibility provided by timeanddate.com (http://www.timeanddate.com/moon/switzerland/lausanne), (4) amount of rainfall per hour, (5) air temperature per hour, (6) average relative air humidity rate at 2 m above the ground per hour. Rain, temperature and humidity have been provided by *Météo Suisse* from either Les Charbonnières or La Dôle weather station depending on water body location.

Occupancy variables:

Aquatic habitats have characteristics that could be determinant for *A. obstetricans* tadpole presence, such as water quality, that are linked to water body properties. Thus, we considered the following five variables associated with pond characteristics: (1) water body perimeter, (2) water body area; both of them computed on QGIS (QGIS Development Team, 2015), (3) water body depth approximated by measuring 4 times around, at 1 m from the shore, (4) water conductivity averaged by measuring 4 times around with an electrical conductivity meter (Model WTW LF 315 / KLE 315), 25 cm under the surface and (5) solar exposition by computing canopy closure proportion above water bodies with a convex spherical densiometer (Model A – Robert E. Lemmon) (Werner, 2009).

Adults *A. obstetricans* are directly in contact with the environment surrounding water bodies, since they must go through it to reach the water to release the eggs. Understandably, they choose terrestrial habitats close to water (Schlüpmann, 2009). Thus, we measured five variables associated with water body environment, including two variables characterizing terrestrial habitat within 50 m around the target water body: (1) dry stone wall total length and (2) stone heaps total area. Three other variables representing the landscape environment have been measured: (3) water body elevation, (4) proportion of forested area within 1000 m around target water body and (5) water body connectivity. All those factors were computed with QGIS and R v3.2.2 (R Core Team, 2015). We measured connectivity with simplified distance-weighted area of occupied habitats (incidence function model) (Prugh, 2009) that resulted in the following formula: $S_i = \sum_{j \neq i} \exp(-\alpha d_{ij})$, where S_i is the source patch, α equals 1/average migration distance of the species and d_{ij} represents the distance between focal patch i and patch j. We fixed average migration distance to 1 km given that it has been shown that *A. obstetricans* could travel up to 1.5 km to colonize new ponds, but they usually run through approximately 1 km (Ryser et al., 2003).

Finally, biotic interactions could happen in the water with *A. obstetricans* tadpoles, so we considered the three following supposed predators: (1) maximum number of alpine newt larvae observed, (2) maximum number of alpine newts observed and (3) maximum number of dragonfly larvae (*Aeschnidae* family) more than 3 cm long observed.

Modeling techniques and statistical analysis

First of all, as variable ranges are quite different, every variable has been normalized to guarantee stable convergence. During fieldwork, detection probability of calling males was low, which means that not detecting *A. obstetricans* males at a site does not imply that the species is absent. The detection and non-detection history for each visit in each site permit estimation of detection probabilities and proportion of occupied sites (MacKenzie et al., 2002). Consequently, to avoid important measurement errors and biasing our conclusions, we used modeling techniques with likelihood-based methods for estimating site occupancy rates from detection/non-detection of *A. obstetricans* tadpoles and/or adults (Fiske and Chandler, 2011). It provides a flexible framework where covariate information can be included and that allows missing observations in order to supply good estimates of the occupancy rates (MacKenzie et al., 2002). We built every model with the help of *occu* function in package *unmarked* (Fiske and Chandler, 2011) in R. The first step was to build a null model designed to produce a pattern that would be expected in the absence of a particular ecological mechanism (Gotelli and Graves, 1996), without implementing habitat or meteorological co-variables. Then, the second step was to analyze *A. obstetricans* detection probabilities by including only detectability variables in the models. We then used the variables from the best detection model to explore habitat factors influencing occupancy. Consequently, the third step was to analyze occupancy probabilities by adding habitat variables to the models based on six hypotheses (Table 2) that could influence *A. obstetricans* occupancy (abiotic aquatic features, abiotic + biotic aquatic features (total aquatic), water body environment, landscape, tadpoles predators, terrestrial habitats). Each of those six models have been selected following minimum Akaike information criterion (AIC) criteria in order to identify the model that is the best supported by the data among the other models (Johnson and Omland, 2004). ∆AIC have been computed in order to visualize the difference between AIC scores of each model and AIC score of the best fitting model. In order to better estimate detectability and occupancy, we indicated in every model 5 sites that were reported to be occupied since 2012 to the Centre Suisse de Cartographie de la Faune (CSCF), but without detection of the species during survey (*knowOcc* argument in *occu* function). Results of this analysis have then been used to model habitat quality, thus to predict *A.obstetricans* occupancy, in order to target conservation measures of the species with help of QGIS, ArcGIS v10.2.2 (ESRI, 2015) and predict function in R. Finally, threshold values of significant variables at which there is 50 % occupancy probability have been computed with predict function in R.

Results

Alytes obstetricans survey

During the field survey, we detected 42 *A. obstetricans* tadpoles and 21 calling males on 13 sites (15 % species site-occupancy). Species distribution varied between 0 and 10 for tadpole abundance (mean = 0.5 $\pm$ 0.9) and between 0 and 6 for calling male abundance (mean = 0.28 $\pm$ 0.5).

Modeling techniques and statistical analysis

First of all, computed *A. obstetricans* detection probability from the null model was 27.2 % and 32.6 % for occupancy probability in the study area, which could represent an important risk of false absences. We tested whether date, humidity, moon, rain, temperature and time influenced detectability by comparing selected models (Table 3). Every model has a ΔAIC less than 6, thus they can be considered as equal (Burnham and Anderson, 2002; Richards, 2005; Symonds and Moussalli, 2011). As no clear model is better than another, none of the six factors listed above has an influence on species detectability. We therefore performed occupancy models with the null model for detection (meaning no detectability covariates). In the set of occupancy models, full and total aquatic did not converge, surely because of the higher number of co-variables implemented and of the dataset size, so we removed them from the outcome set (Table 4). The best resulting model is the total environment that has a ΔAIC = 3 compared to the second one, and the evidence ratio, computed with AIC weights, equals $\frac{0.6347}{0.1477} = 4.3$ which means that it is approximately 4 times more likely that the first model is the best model in terms of the Kullback–Leibler discrepancy than is the next-best model (Burnham and Anderson, 2002; Wagenmakers and Farrell, 2004). However, this model does not fit the data very well (R^2 = 0.214) but does have the highest R squared of the set. This total environment model identifies forest cover as having a negative significant influence on occupancy (*P* = 0.02), altitude and dry stone wall length as having a positive marginally significant effect (respectively *P* = 0.09 and *P* = 0.06) and finally, connectivity and stone heaps not presenting significant influence (respectively *P* = 0.31 and *P* = 0.17) (Table 5). We computed threshold values based on this model, at which there is 50 % occupancy probability for forest cover and dry stone wall, the latter because it is the closest to being significant. The resulting threshold for forest total cover of 1000 m around water bodies is 49 %, and for dry stone wall total length of 50 m around water bodies is 100 m (Figure 1). Assuming that under 49 % of forest cover and more than 100 m of dry stone wall is an optimal habitat, we built a projection for the whole study area of the expected *A. obstetricans* occupancy (Figure 2). With this projection we can locate the most suitable areas for new water body creation, emphasizing the importance of habitat complementation for *A. obstetricans* distribution.

Discussion

Despite the high number of night sessions in the field survey, the proportion of occupied sites (0.15) is low. *A. obstetricans* is known to be difficult to detect, but detection probability (0.272 in our study) is usually higher in lower altitude studies (0.57 in Pellet and Schmidt, 2005). However, small colonies that we found (up to 6 calling males) are quite usual. Indeed it is rare to find more than about ten calling males in a population (Jacob et al., 2007). It is therefore difficult to estimate population size (Yoccoz et al., 2001), as not all males may call at the same time

(Jacob et al., 2007) and since cryptic females are hardly detectable. Moreover, it was difficult to estimate real tadpoles abundance given that they can lie low and typically shun torchlight by hiding at the bottom of the ponds. Given the small populations detected, it was not appropriate to analyze *A. obstetricans* abundance, thus we probed site-occupancy modeling. However, nondetection of *A. obstetricans* calling at a site does not imply that the species is absent. Thus to avoid false absence bias, we estimated site-occupancy rates with methods taking into account detection probability (MacKenzie et al., 2002). The resulting estimated occupancy in the study area (0.326) is also low and is likely to be biased downwards as we obtained a low detection probability (Kéry and Royle, 2008).

In terms of detectability, none of the numerous survey-specific variables had an influence. However, precipitations and date appear in the first three best models, so they probably are more important factors than others. On the other hand, it seems there is no favorable date or time of the night during the breeding season to detect *A. obstetricans*. Then, humidity and air temperature have negligible effect on sound propagation (Llusia et al., 2013a). Indeed, air temperature did not seem to have an influence on detectability, as air climate has already shown that males could call under a wide range of temperature (Heinzmann, 1968) and even more for those living in higher altitude, where it is usually colder (Llusia et al., 2013b). Concerning precipitation, it does not seem to affect species detectability, just as Márquez (1992) did not observe any correlation between rainfall and *A. obstetricans* activity. Finally, moon phases do not seem to influence *A. obstetricans* calling either, even if several studies have shown an activity decrease in different anuran species during full moon, explained by nocturnal predator attack risk and by decrease of food availability (Church, 1960; FitzGerald and Bider, 1974). Therefore, if none of the tested variables influences detectability, it may be affected by a combination of several non-tested variables. However, those results have to be taken lightly as detectability probability was low and led to low statistical power.

In terms of occupancy, the best resulting model seems to be far more likely than the second best model while considering AIC weight, even though they have a small difference in AIC and neither fit the data well (low Rsq). The high number of absences during the survey, as well as low detectability and occupancy probabilities certainly justify the low statistical power. Therefore we have to be careful while interpreting results stemming from the total environment model.

Forest cover appeared to have a positive influence on occupancy only when less than half of the surface was forested. *A.obstetricans* is known to prefer non-forested open environments in several countries at the local scale (Grossenbacher, 1988; Jacob et al., 2007). However, at the landscape scale it might serve as a barrier to migration for emerging toadlets that disperse. Indeed, toadlets might not want to cross large forested area as it will be less probable to find sunny places with sparse vegetation like adults are known to prefer (Meyer et al., 2009; Uthleb, 2012). Moreover, high forest cover might be detrimental to tadpoles, known to have the capacity to overwinter in colder environments (Böll et al., 2012), because it might result in less oxygenated water as Oertli et al. (2000) showed a negative correlation between dissolved oxygen concentration in water bodies and proportion of forested area in the environment due to degradation of an important contribution of organic matter that consumes oxygen. Furthermore, large forested area proportion can reduce wind impact that promotes oxygenation of the water (Oertli et al., 2000).

Following the nearly significant variable of the total environment model is just as interesting. Indeed, dry stone wall appeared to have a positive effect on *A.*

obstetricans occupancy, which makes sense as it is described as one of their habitats (Böll et al., 2012; Mermod et al., 2010; Uthleb, 2012). *A. obstetricans,* like all amphibians, are ectothermic. Dry stones are thus suitable as they accumulate heat all day long and release it during the night (Jacob et al., 2007), when the species needs energy to sing and forage for instance. Moreover, in those high pastures, dry stone walls are more or less the only possible terrestrial habitats (Supplementary material Figure 2), as no shallow landslides with mineral or loose substrate exist, nor do the talus or scree as that would be characteristic of other areas where they live (Grossenbacher, 1988). However, stone heaps that are supposed to be used as terrestrial habitats had no effect on occupancy. This might be explained by the usually small footprint of the heaps whereas *A. obstetricans* might need terrestrial habitats that extend over longer surface (like dry stone walls). Those dry stone walls in high pastures also extend below the ground (Bloesch et al., 1994), an essential element to ensure that terrestrial habitats are frost-free and therefore usable as wintering site (Meisterhans, 1969).

The third variable is only marginally significant and has a questionable influence. Indeed, altitude seems to have a positive effect. The altitudinal limit of the species in Switzerland is around 1500 m (Grossenbacher, 1988), which corresponded to the maximum elevation of our study area (the highest occupied site was at 1430 m). Indeed, at higher altitude the environments were well preserved, probably because the sites are less accessible to anyone, implying likely better quality as human might negatively impact the natural environments (Goudie, 2013). Thus, a possible explanation of this positive influence would be a local effect due to the topography of this particular area that cannot be extrapolated in other areas.

In brief, forest cover proportion is favorable for amphibian species richness

(Herrmann et al., 2005), because most species need forest in habitat complementation as a suitable wintering site, which is different than summering sites. Additionally, most amphibian species also need forest to border the breeding pond, as distinct from *A. obstetricans* which often uses the same habitat in summer and winter (Böll et al., 2012; Münch, 2004). This means that midwife toads in high altitude would always stay in their terrestrial habitats, most likely dry stone walls, and could winter under ground level still within the same walls. Thus, they would not need forest to border breeding ponds and would not find such an environment a suitable habitat (Buskirk, 2005). Apparently, landscape complementation in those high populations would consist of water bodies that are near a given length of dry stone wall (or other possible terrestrial habitats) and not surrounded by too large a forest (projected habitat quality map on Figure 2). Concerning the projected hypothetical habitat quality map, the majority of occupied sites are in the green (favorable) areas or at least close to it. However, some sites are in the red (low quality) areas and some are unoccupied in the green areas. The high number of absences that led to low correspondence between the model and the data could explain this statistical model-based map.

Management implications

Despite the fact that the study was conducted on a restricted area and during only one breeding season, we obtained important results concerning management and conservation of high pastures for *A. obstetricans*. Here we provide evidence that variables at local and landscape levels affect the species distribution. This highlights the importance of considering those aspects in the management of a high natural park to correctly identify and protect the most suitable areas in order to target species conservation measures. Thus, in keeping with our results, we strongly recommend that forest, pasture and natural park managers protect breeding ponds having at least 100 m of dry stone wall within 50 m, and less than 50 % forest cover within 1000 m, in order to favorably influence *A. obstetricans* occupancy. Moreover, we additionally advocate either adding or restoring dry stone walls where the length is too small, reducing forest surface around water bodies near existing populations, and building new water bodies in places where both terrestrial habitats and forest cover are suitable. Practically, occupied sites in the green areas of the habitat quality map (Figure 2) should be protected, whereas unoccupied sites in the green areas should be targeted for restoration and protection. Green areas where there is no existing site should be targeted for any new water body creation projects, whereas occupied sites in the yellow and red areas should be improved in quality depending on what elements of high habitat quality are missing. We showed that terrestrial habitats such as dry stone walls are very important for this species, serving as likely habitat all year long. Thus it is of crucial importance to protect such dry stone walls and restore them if needed. At a larger scale, it is important to increase the number of favorable water bodies especially around isolated populations. Both in consideration of the metapopulations and given that *A. obstetricans* is a very low disperser, lack of favorable water bodies could have serious negative impacts. In conclusion, our findings shed light on specific conservation methods that should be used for this endangered species. By better understanding their unfamiliar environment, we can protect and create suitable habitats, thus increasing population size.

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Figure legend

Figure 1: *A. obstetricans* predicted occupancy probability in function of (A) dry stone wall length [m] within 50 m around water bodies and (B) forest cover [%] within 1000 m. Dotted lines represent confidence intervals from the model and dashes on the x-axis represent the observed data.

Figure 2: Study area located in the Jura Mountains in Western Switzerland (black area on the Swiss map). Dots represent surveyed site; black ones indicate *A. obstetricans* presence and white ones indicate *A.obstetricans* absence. Colored areas display the expected occupancy according to the projected habitat quality (green, optimal habitat; yellow, potential habitat; red, low quality habitat).

Table 1: Summary of the meteorological and environmental variables collected related to *A.obstetricans* detectability and occupancy. The buffer stands for the scale at which the variables have been measured (radius centered on the pond).

Table 2: Summary of the variables contained in the four simple models based on hypothesis (left column) and in the three combined models (upper line). Combined models contain variables from simple models with crosses.

Table 3: Summary from fitting seventeen detectability models. ∆AIC is the relative difference between its Akaike information criterion score and the AIC of the most probable model (lowest AIC). AICwt is the AIC model weight and Rsq is the R-squared index (Nagelkerke, 1991).

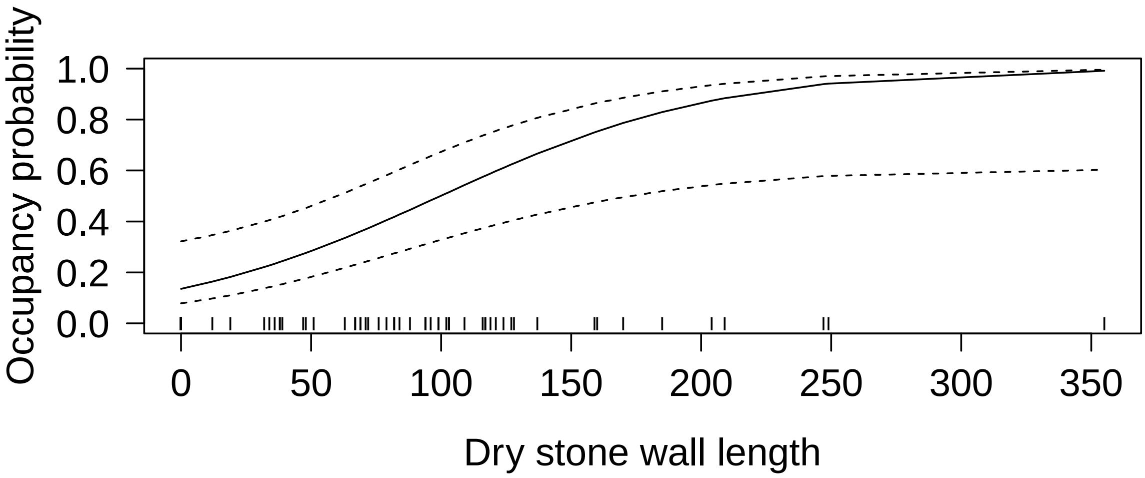
Table 4: Summary from fitting six occupancy models (full and total aquatic are not shown because they did not converge). ∆AIC is the relative difference between its Akaike information criterion score and the AIC of the most probable model (lowest AIC). AICwt is the AIC model weight and Rsq is the R-squared index (Nagelkerke, 1991).

Table 5: Outcome of the most parsimonious model (total environment). Significant terms (or nearly: $P < 0.06$) are in bold.

Figures

Figure 1

A



B

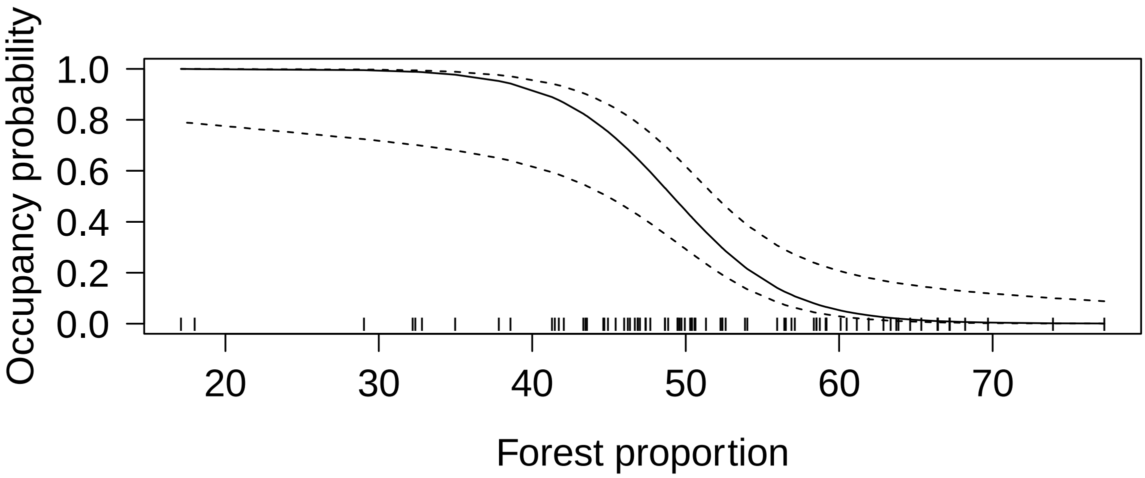


Figure 2

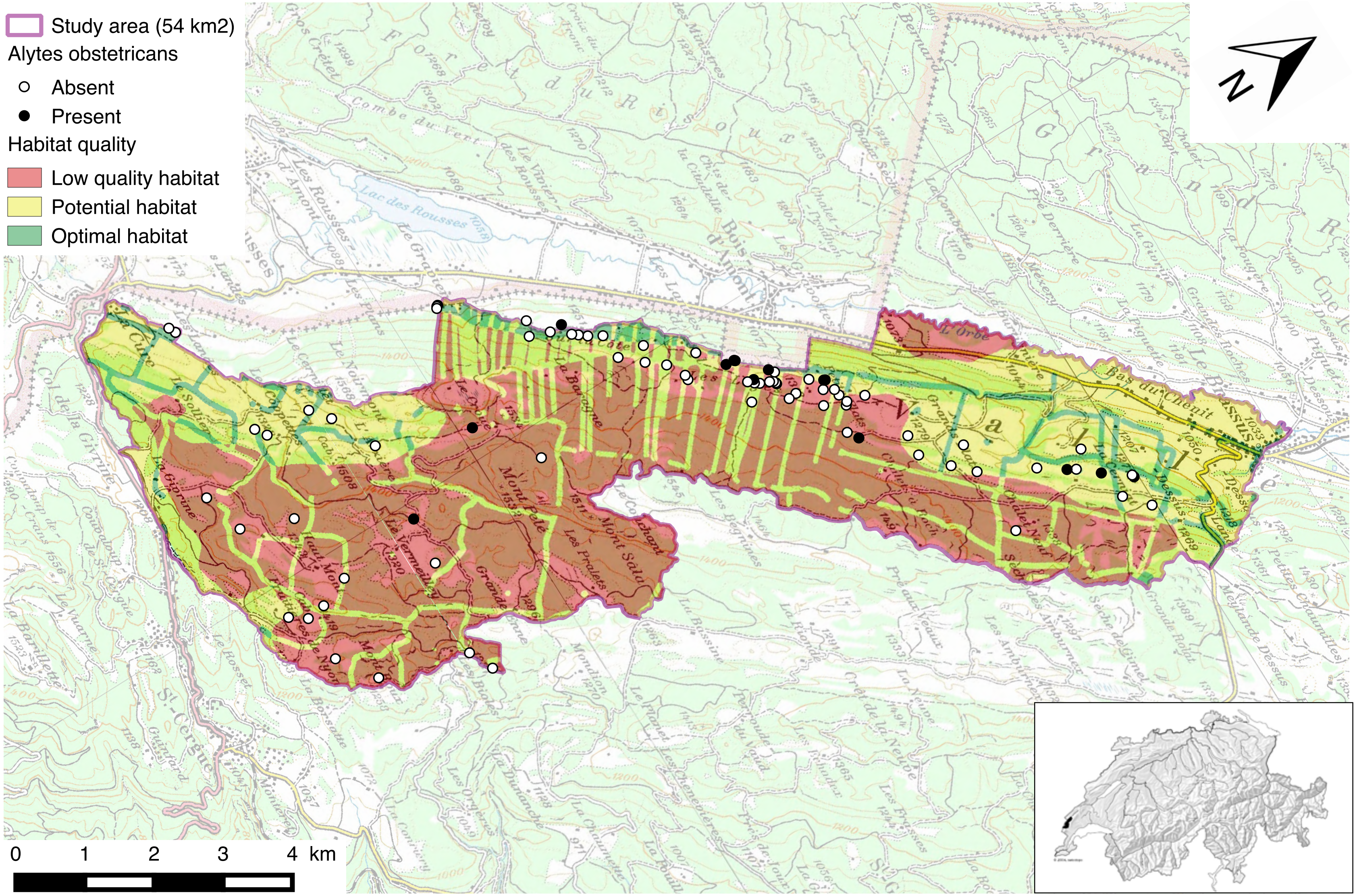

Study area (54 km2)
Alytes obstetricans
Absent
Present
Habitat quality
Low quality habitat
Potential habitat
Optimal habitat
N
0 1 2 3 4 km

Table 1

Variable	Description	Mean (range)	Buffer	Data source
Detectability variables				
Date	date of night survey	10.07.2015 (02.06.2015 - 21.08.2015)		
Humidity	average relative air humidity rate at 2 m above the ground [%]	79.35 (50.7 - 99.5)		Météo Suisse
Moon	moon visible surface [%]	48.85 (0.4 - 99.8)		timeanddate.com
Rain	amount of precipitation per hour [mm]	0.054 (0 - 1.6)		Météo Suisse
Temperature	air temperature per hour [°C]	14.8 (6 - 23)		Météo Suisse
Time	time at site during night survey [min]	21 (1315 - 177) = 00:21 (21:55 - 02:57) [h]		
Occupancy variables				
Aquatic variables				
Area	Water body area [m^2]	63.77 (1 - 448)	Pond	GIS
Conductivity	Mean water conductivity [µS/cm]	244.59 (3 - 599)	Pond	Field
Depth	Mean water body depth [m]	0.72 (0.085 - 2)	Pond	Field
Perimeter	Water body perimeter [m]	24.98 (5 - 87)	Pond	GIS
Solar exposition	Mean solar exposition on the water body [%]	86.62 (0.52 - 99.84)	Pond	Field
Environmental variables				
Altitude	Altitude of the water body [m]	1293.72 (1118.1 - 1511.8)	Pond	GIS
Connectivity	Distance-weigthed connectivity index	9.76 (1.68 - 18.79)	Pond	R
Dry stone wall	Dry stone wall total length [m]	67.5 (0 - 355)	50 m	GIS
Forest proportion	Proportion of forest surface [%]	51.4 (17.11 - 77.27)	1000 m	GIS
Stone heaps	Stone heaps area [m^2]	45.24 (0 - 574)	50 m	GIS
Biotic variables				
Alpine newt larvae	Maximum number of alpine newt larvae observed	15.29 (0 - 200)	Pond	Field
Alpine newts	Maximum number of adult alpine newts observed	23.012 (0 - 254)	Pond	Field
Dragonfly larvae	Maximum number of dragonfly larvae observed	1.69 (0 - 26)	Pond	Field

Table 2

	Variables	psi(total aquatic)p(.)	psi(total environment)p(.)	psi(full)p(.)	psi(.)p(.)
psi(aquatic)p(.)	Area, Conductivity, Depth, Perimeter, Solar exposition	×		×	
psi(landscape)p(.)	Altitude, Connectivity, Forest proportion		×	×	
psi(predators)p(.)	Alpine newts, Alpine newt larvae, Dragonfly larvae	×		×	
psi(terrestrial habitats)p(.)	Dry stone wall, Stone heaps		×	×	

Table 3

Models	AIC	ΔAIC	AICwt	Rsq
psi(.)p(rain+date)	145.62	0.00	0.37	0.12
psi(.)p(date)	148.40	2.78	0.09	0.05
psi(.)p(rain)	148.98	3.36	0.07	0.04
psi(.)p(.)	149.79	4.16	0.05	0.00
psi(.)p(date+time)	149.96	4.34	0.04	0.06
psi(.)p(moon+date)	149.99	4.36	0.04	0.06
psi(.)p(temperature+date)	150.19	4.57	0.04	0.05
psi(.)p(humidity+rain)	150.25	4.63	0.04	0.05
psi(.)p(humidity+date)	150.40	4.78	0.03	0.05
psi(.)p(moon+rain)	150.52	4.90	0.03	0.05
psi(.)p(rain+time)	150.82	5.20	0.03	0.04
psi(.)p(temperature+rain)	150.98	5.36	0.03	0.04
psi(.)p(moon)	151.16	5.54	0.02	0.01
psi(.)p(humidity)	151.57	5.95	0.02	0.00
psi(.)p(time)	151.66	6.04	0.02	0.00
psi(.)p(temperature)	151.72	6.09	0.02	0.00
psi(.)p(full)	152.08	6.46	0.01	0.14

Table 4

Models	AIC	ΔAIC	AICwt	Rsq
psi(total environment)p(.)	143.97	0.00	0.63	0.21
psi(landscape)p(.)	146.89	2.92	0.15	0.13
psi(predators)p(.)	146.98	3.01	0.14	0.12
psi(terrestrial habitat)p(.)	149.74	5.77	0.04	0.06
psi(.)p(.)	149.79	5.82	0.03	0.00
psi(aquatic)p(.)	153.05	9.08	0.01	0.10

Table 5

Term	Estimate	Std error	z value	*P* value
(Intercept)	-0.60	0.74	-0.81	0.42
Altitude	2.31	1.35	1.71	0.09
Connectivity	0.70	0.69	1.01	0.31
Dry stone wall	**1.33**	**0.72**	**1.86**	**0.06**
Forest proportion	**-3.00**	**1.32**	**-2.28**	**0.02**
Stone heaps	2.33	1.69	1.38	0.17