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HABITAT PREFERENCES OF BREEDING AMPHIBIANS IN EASTERN SPAIN

ÁNGEL GÁLVEZ[1,3], DONALD T. MCKNIGHT[2], AND JUAN S. MONRÓS[1]

[1]*Institute Cavanilles of Biodiversity and Evolutionary Biology, University of Valencia, c/ Catedrático José Beltrán Martínez 2, 46980 Paterna, Valencia, Spain*
[2]*College of Science and Engineering, James Cook University, Townsville, Queensland, Australia*
[3]*Corresponding author, e-mail: angel.galvez@uv.es*

***Abstract*.—The aim of this research was to determine the reproductive habitat preferences of several species of amphibians in eastern Spain. We recorded amphibian presence/absence and measured biotic and abiotic variables at 67 ponds in a 43.5 km^2 area representing a wide variety of aquatic ecosystems, such as temporary and semi-permanent cisterns, drinking troughs, and natural and artificial ponds, all of various sizes and depths. We used this information to predict occupancy using Generalized Linear Models. We built models for the Iberian Ribbed Newt (*Pleurodeles waltl*), Iberian Green Frog (*Pelophylax perezi*), Common Midwife Toad (*Alytes obstetricans*), Natterjack Toad (*Epidalea calamita*), and Mediterranean Parsley Frog (*Pelodytes hespericus*). We also found Common Toad (*Bufo spinosus*) and Spadefoot Toad (*Pelobates cultripes*) but did not build models for them. The variables that explained occupancy were species specific, with depth and, especially, the type of substratum playing key roles in most of them. Type of substratum reflected pond age and was represented by hard substratum (associated with new artificial ponds and structures), hard substratum covered by soft sediment (associated with old artificial ponds and structures), and soft substratum (associated with old natural ponds). The differences among the species in occupancy models indicate that species-specific management actions may be necessary to preserve the amphibian community in the long term.**

Key Words.—Alytes obstetricans; breeding habitat; *Epidalea calamita*, generalized linear model; occupancy; *Pelodytes hespericus*; *Pelophylax perezi*; *Pleurodeles waltl*

INTRODUCTION

Almost a third of all amphibian species are currently endangered (International Union for Conservation of Nature [IUCN]. 2004. Evaluación global de los anfibios. International Union for Conservation of Nature and Natural Resources, Conservation International and NatureServe. Available from www.globalamphibians.org [Accessed 11 July 2018]). Moreover, many species are suffering declines that are leading to local extinctions (Beebee and Griffiths 2005). The main threats that are causing this worldwide decline are related to anthropogenic activity, including habitat loss and degradation, introduction of exotic species, diseases, and global climate change (Cushman 2006; Bosch et al. 2009; Preston et al. 2012; Harper et al. 2015; Patar et al. 2016). Efforts to reverse these negative effects need to take into account the ecological needs (including habitat preferences) of each species (Boyd et al. 2008). Region-specific studies are crucial in this respect because habitat-use models constructed for a given region may have limited transferability to other regions (Zanini et al. 2009).

The documented bias in ecological research towards birds and mammals relative to amphibians and reptiles is evident in Spain (Martín-López et al. 2011), which has a high biodiversity in the European context (IUCN. 2013. Spain's diversity at risk. A call for action. International Union for Conservation of Nature and Natural Resources. Available from cmsdata.iucn.org/downloads/spain_s_biodiversity_at_risk__fact_sheet_may_2013.pdf [Accessed 11 July 2018]). Only a few studies about breeding habitat preferences of amphibians have been carried out in Spain, mostly in protected areas (Bosch and Martínez-Solano 2003; Orizaola and Braña 2006; Gómez-Rodríguez et al. 2009; Benítez et al. 2017). Here we have focused on an area that has not been previously studied in detail, in inland eastern Spain. This region is a dry, mountainous area, with few permanent ponds and streams, where the only breeding aquatic habitats available for amphibians are temporary and semi-permanent ponds. The amphibian community includes a relatively low number of species compared to the rest of the Iberian Peninsula, some of which are locally threatened due to habitat loss and fragmentation (Beja et al. 2009). Human activity, particularly farming and hunting, has created new artificial ponds and transformed natural ones extending their hydroperiod. These habitats are potentially valuable for amphibians, and it is important to investigate the factors that determine patterns of amphibian occupancy among them.

We investigated patterns of breeding site occupancy in an amphibian community of seven species in a network of 67 ponds in the municipality of Alcublas (eastern Spain). We measured biotic and abiotic variables at each pond and used generalized linear models to identify the factors best explaining the presence/absence of each species. Thus, we obtained useful information to facilitate the development of management actions.

Due to the absence of streams in our study area, we focused variable selection on aspects like hydrogeomorphology, connectivity, and past or present cultural use. We also took into account some physical and chemical variables. In particular, we hypothesized that the type of substratum (with three categories: hard substratum, soft substratum and hard substratum covered by soft substratum) would be the most influential variable, because it is a proxy of pond age. Artificial or transformed ponds usually present a hard (concrete) substratum, while natural ponds almost always have a soft substratum. Ponds with a hard substratum covered by soft substratum represent old artificial ponds whose hard substratum has been covered by sediment. We expected that these differences may be associated with differences in the structure of the community, with older ponds harboring more species than newer (artificial) ones.

MATERIALS AND METHODS

We carried out this study in the municipality of Alcublas, Spain (Fig. 1). The area is characterized by a Mediterranean macrobioclimate, with unpredictable precipitation, and a general deficit of water during the times of the year when the temperature is more favorable to the development of amphibians (Rivas-Martínez 1987). We surveyed amphibians in 67 ponds in a study area of low mountains, 43.5 km^2 in area, at an average elevation of 800 m above sea level. The landscape is dominated by rainfed almond orchards and regenerating forests that followed a wildfire in 2012. The distance between the closest ponds was 1 m, whereas the distance between the furthest ponds was 9 km (Fig. 1). The selected ponds included all types of available aquatic habitats, including water cisterns, drinking troughs, and temporary ponds. Rivers and streams are absent in the study area. According to the best of our knowledge, our pond sample includes virtually every pond in the study area, excluding three ponds that were difficult to access due to poor road conditions. We based the selection of these ponds on our previous knowledge of the area and information from local people who provided exact pond locations.

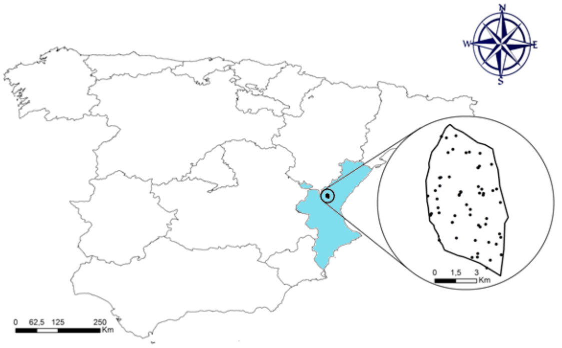

FIGURE 1. Location of the study area (polygon containing dots) in the municipality of Alcublas, within the Valencian Community (blue), Spain. Dots indicate the location of each of the 67 ponds included in the study.

We visited each pond once every two weeks from the beginning of March to the end of May 2015 (total: six diurnal visits per pond), covering the breeding season of all species present and part of their larval periods (Sewell et al. 2013). We determined the presence of species visually and by dip-netting, including adult stage, larval stage, and eggs. Also, each time we visited the pond, we measured 17 habitat variables that we believed to be important determinants of habitat occupancy by amphibians.

We transformed continuous variables into averages of the total of the six measurements for later analysis (Table 1). We included the presence of other amphibian species as covariates in the models for each species to account for possible predation (especially the effect of *P. waltl* on larvae and eggs) or competition effects. We assessed most of the variables visually or with the help of Google Earth (Google Inc., Mountain View, California, USA), but we used instruments to measure pH and temperature (Hanna Instruments, Woonsocket, Rhode Island, USA; model HI 98127), conductivity (Hanna Instruments; model HI 98311), and oxygen concentration (BTW, Weilheim, Germany; model C/Oxi315i; Table 1). Due to the absence of large aquatic predators such as fish, crayfish, or aquatic birds in the studied ponds, we did not include any variables related to predation.

We used Generalized Linear Models (GLM) with binomial error distribution to model the occurrence of each species with respect to the average of the ecological variables measured. To reduce the number of explanatory variables, we ran binomial regressions for species presence/absence with each variable (Hosmer and Lemeshow 2000) and used only those variables with $P \leq 0.15$. Then, we tested for multi-collinearity between predictors with Spearman correlations and removed one of the correlated variables when the rs score was at least 0.6. We introduced all the possible combinations of the final set of explanatory variables in GLM to select the models which best fit the data under the Akaike

Table 1. Variables measured in each pond, the method used, and explanation of some aspects of variables for amphibians in the municipality of Alcublas, Spain. Data for continuous variables are averages of measurements on six visits.

Variable	Measurement	Explanation
Landscape structure		
Type of dominant terrestrial habitat surrounding the pond (< 50 m) (Terrestrial habitat)	Visually	Categorical variable with the following levels: crops, regenerating pine forest, regenerating holm-oak forest, scrub, urban
Light exposure of the pond (Light)	Visually	Categorical variable with the following levels: Total absence of sunlight, shadow in any moment of the day, sunlight all day
Minimum distance to closest road [m]	Google Earth	Related with mortality, and possibly a dispersal barrier
Minimum distance to closest human crop field [m]	Google Earth	Related to nutrient pollution
Minimum distance to the closest pond [m]	Google Earth	Related to habitat connectivity
Livestock use	Visually	Categorical variable with the following levels: Not used by livestock, used by livestock
Hydrogeomorphology		
Average pond surface area ("Surface") [m^2]	Google Earth or measuring tape	
Average maximum pond depth ("Depth") [m]	Measuring tape	
Average availability of structures to attach eggs ("Egg support")	Visually	Percentage of surface with presence of branches, rocks or vegetation
Type of substratum ("Substratum")	Visually	Three levels: soft, hard, hard substratum covered by soft sediment.
Pond duration ("Hydroperiod ")	Visually	Categorical variable with the following levels: one to three months, more than three months
Accessibility	Visually	Categorical variable with the following levels: non accessible (presence of vertical structures that prevent amphibians from entering or leaving the pond), accessible
Biotic and abiotic variables		
Average algal coverage	Visually	Percentage of surface of the water film where light cannot pass through because of algae
Average water temperature [ºC]	Instrument (see text)	
Average pH [H+]	Instrument (see text)	
Average conductivity [µS/cm]	Instrument (see text)	
Average oxygen concentration [mg/l]	Instrument (see text)	
Presences of amphibian species	Visually; dip-netting	Related to predation and competition

information criterion (AIC; Akaike 1973; Burnham and Anderson 2002; Johnson and Omland 2004). Given that the number of sampled sites was large enough (> 40), we did not implement any correction for small sample size (AICc; Burnham and Anderson 2002; Johnson and Omland 2004).

To evaluate model performance, we calculated a Receiver Operating Characteristic (ROC) curve for each model (Hanley and McNeil 1982). These curves are calculated by comparing observed and expected values according to the model. The curve delimits an area (AUC, or area under the curve) that determines the predictive ability of the model. This AUC ranges from 0.5 to 1 (where AUC = 1 is perfect predictive ability, and AUC = 0.5 corresponds to no discriminant ability). Finally, we tested for spatial autocorrelation in the presence of each species with Moran's I test to verify if there was any spatial effect in our models, with a significance level of 95% ($P \leq 0.05$; Moran 1953). We selected variables and calculated ROC curves with software IBM SPSS Statistics 22.0 (IBM Corporation 2013). We constructed GLMs with software R 3.2.0 (R Core Team 2015), and we tested for spatial autocorrelation with software Past3 (Hammer et al. 2001).

Results

We found seven amphibian species: the Iberian Ribbed Newt (*Pleurodeles waltl* Michahelles, 1830); Iberian Green Frog *Pelophylax perezi* (López-Seoane,

Table 2. Summary of the variables characterizing the 67 ponds in the study area in the municipality of Alcublas, Spain. Data for continuous variables are average ± standard error, and range, for six measurements. Data for categorical variables are the percentage of the levels of each category. Levels for each variable are: Terrestrial habitat (1: crops; 2: regenerating pine forest; 3: regenerating holm-oak forest; 4: scrub; 5: urban), Light (1: total absence; 2: partial exposure; 3: total exposure), Livestock use (1: Not; 2: Yes), Substratum (1: soft; 2: hard; 3: hard covered by soft substratum), Hydroperiod (1: one to three months; 2: more than three months), and Accessibility (1: non accessible; 2: accessible).

	Average ± SE	Range	% Level 1	% Level 2	% Level 3	% Level 4	% Level 5
Terrestrial habitat	-	-	32.84%	16.42%	16.42%	29.85%	4.48%
Light	-	-	19.4%	28.4%	52.2%	-	-
Distance to roads (m)	60.7 ± 6.3	0.5–787	-	-	-	-	-
Distance to crops (m)	86.7 ± 7.5	1–593	-	-	-	-	-
Distance to ponds (m)	355.7 ± 39.9	1–1,890	-	-	-	-	-
Livestock use	-	-	34.3%	65.7%	-	-	-
Surface area (m^2)	317.4 ± 192.7	0.1–60,000	-	-	-	-	-
Depth (m)	0.55 ± 0.02	0.06–1.92	-	-	-	-	-
Egg support (%)	28.5 ± 1.8	0–100	-	-	-	-	-
Substratum	-	-	19.4%	52.2%	28.4%	-	-
Hydroperiod	-	-	17.9%	82.1%	-	-	-
Accessibility	-	-	80.6%	19.4%	-	-	-
Algal coverage (%)	9.9 ± 1.8	0–61.67	-	-	-	-	-
pH	8.46 ± 0.03	7.1–10.8	-	-	-	-	-
Temperature (° C)	19.3 ± 0.3	1.6–29.5	-	-	-	-	-
Conductivity (µS/cm)	431.4 ± 21.01	49.4–2,870	-	-	-	-	-
Oxygen (mg/l)	7.3 ± 0.12	0.71–15.7	-	-	-	-	-

1885); Common Midwife Toad (*Alytes obstetricans* Laurenti, 1768); Natterjack Toad (*Epidalea calamita* Laurenti, 1768); Mediterranean Parsley Frog (*Pelodytes hespericus* Diaz-Rodríguez et al., 2017); Common Toad (*Bufo spinosus* Daudin, 1803); and Iberian Spadefoot Toad (*Pelobates cultripes* Cuvier, 1829). We did not find any amphibian species in 10 ponds (15% of the ponds surveyed) whereas we found amphibian species in 57 ponds (85% of the ponds surveyed). *Alytes obstetricans* was the most widely distributed, being found in 68.7% of the ponds. *Epidalea calamita*, which was present in 56.7% of the ponds, was clearly the most abundant species. *Pelodytes hespericus*, *Pelophylax perezi*, and *Pleurodeles waltl* were found in 29.9%, 11.9%, and 7.5% of the sites, respectively. Finally, we found *Bufo spinosus* or *Pelobates cultripes* each in only one pond, and we did not include them in the modelling due to their very low occurrence.

In general, the surveyed ponds were small, with an average surface area of 317.3 m^2, and shallow, with an average depth of 0.55 m (Table 2). Nevertheless, we found a maximum surface area of 60,000 m^2 and a maximum depth of 2 m (Table 2). Except for nine human structures such as cisterns or drinking troughs, all ponds were temporary or semi-permanent ponds. As for type of substratum, natural soft substratum was the least frequent level (19.4%; Table 2). Hard substratum appeared in 28.4% of cases, and hard substratum covered by soft sediment in 52.2% of cases (Table 2). We did not find any significant results in the spatial autocorrelation tests for presence of each species (Moran's I = 0.001–0.058, P = 0.061–0.282).

Six variables were represented among the models for the five species, with type of substratum represented for four of the species (Table 3). The best model for *P. waltl* had an AIC score of eight and no model had a difference in AIC score lower than two units (Table 3). Pond depth and type of substratum explain pond occupancy by this species. This model had an excellent predictive ability (AUC = 0.932).

For *P. perezi*, we obtained a single candidate model (Table 3) with a good predictive ability (AUC = 0.712). There was no model with a difference in AIC score smaller than two units with respect to the best model (Table 3). Both temperature and pond depth were positively correlated with pond occupancy, whereas the type of substratum was not a significant factor.

We obtained four possible models explaining patterns of pond occupancy in *A. obstetricans* (Table 3). The only variable in common across models was the type of substratum, with hard substratum covered by soft sediment the most significant level. Two additional variables (depth and algal coverage) appeared in two models each, but depth had a negative coefficient

Table 3. Models obtained for each amphibian species. *P*-value and coefficients of each parameter are shown, as well as the AIC and AUC values. Multiple models are provided when the highest AIC values differed by < 2.

Model	AUC	AIC	Variable	*P*-value	Coefficient	Standard Error
Pleurodeles waltl						
1	0.932	8	Intercept	0.992	-847.5	89,377.5
			Depth	0.992	1,278.58	135,249.03
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.993	-1,629.4	174,154.4
			Type of substratum (Soft over hard)	0.999	45.9	31,719.4
Pelophylax perezi						
1	0.874	44.91	Intercept	0.036	-7.3	3.5
			Depth	0.224	2.1	0.9
			Temperature	0.026	0.3	0.2
Alytes obstetricans						
1	0.695	79.05	Intercept	0.022	-2.1	0.9
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.010	2.4	0.9
			Type of substratum (Soft over hard)	0.001	3.37	1.06
			Algal coverage	0.096	0.04	0.02
2	0.710	79.92	Intercept	0.208	-1.38	1.09
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.016	2.2	0.9
			Type of substratum (Soft over hard)	0.003	3.09	1.06
			Depth	0.301	-0.9	0.8
			Algal coverage	0.155	0.04	0.3
3	0.693	80.26	Intercept	0.444	-0.7	0.9
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.025	1.9	0.8
			Type of substratum (Soft over hard)	0.003	2.96	1.02
			Depth	0.159	-1.2	0.9
4	0.671	80.43	Intercept	0.054	-1.5	0.8
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.015	2.1	0.9
			Type of substratum (Soft over hard)	0.001	3.2	1.0
Epidalea calamita						
1	0.859	56.37	Intercept	0.908	-0.2	1.5
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.267	-1.5	1.4
			Type of substratum (Soft over hard)	0.215	2.1	1.7
			Egg support	0.020	0.04	0.01
Pelodytes hespericus						
1	0.785	59.78	Intercept	0.993	-16.9	2,242.4
			Type of substratum (Soft)	-	0	-
			Type of substratum (Hard)	0.008	-2.69	1.02
			Type of substratum (Soft over hard)	0.226	-1.0	0.8
			Livestock use (No)	-	0	-
			Livestock use (Yes)	0.993	17.9	2,242.4

whereas coverage had a positive one (Table 3). The predictive ability of these models was acceptable, with an AUC value around 0.70.

For *E. calamita*, there was only one candidate model (Table 3) and it had good predictive ability (AUC = 0.814). According to the respective coefficients, only hard substratum contributed negatively. The other variables (proportion of structures where eggs can be attached and soft substratum over a hard one) were positively associated with pond occupancy. Finally, we obtained a single model for *P. hespericus*. In this species, hard substrates (both by itself and when covered with a soft substratrum) were negatively associated with pond occupancy, whereas livestock use had a positive effect (Table 3). The model had a good predictive ability (AUC = 0.749).

Discussion

We found important differences across species in breeding habitat selection. Moreover, we found that the type of substratum was a significant factor in the models for all species except *P. perezi*. Therefore, this variable appears to play a key role in the reproductive habitat selection of most species. However, this variable, in addition to the other significant variables, influenced the preferences of each species in different ways.

In the model for *P. waltl*, soft sediment and the depth of the pond were positive predictors of presence of the species. Soft substrata and great depth are often associated with long-lasting ponds, like semi-permanent or permanent ponds, which are necessary for the long larval development of this species (Shi and Boucaut 1995). Also, if the pond begins to dry, soft substrata, or hard substrata covered by sediment, allows these animals to bury themselves and wait for the next inundation (Valverde 1960). Finally, soft sediment allows submerged vegetation to become established, which is important because these animals use the vegetation as egg attachment points and as refuge (Álvarez et al. 1988). The advantages of a soft sediment are absent in ponds with a hard substratum, such as concrete or rock, in line with the negative weight of the latter variable in the model. According to this model, a hard substratum covered by a soft one would be more suitable than a soft one. However, most of the surveyed artificial ponds were not very deep (and their hydroperiod was shorter than the ponds with soft substratum, which were deeper). In ponds with a hard substratum covered by soft sediment, deeper ones, with longer hydroperiod, would be appropriate for this species, according to our model.

For *P. perezi*, the most significant variable in the model was pond temperature, which may be related to the species phenology. *Pelophylax perezi* is a late breeder, usually starting its activity in early spring and breeding through late spring and summer (Salvador and Carrascal 1990). In addition, their larvae can survive in conditions of high temperature and low oxygen concentration (Díaz-Paniagua 1983, 1988). Previous studies have reported that *P. perezi* seems to avoid cold water bodies (Malkmus 1997). Additionally, there was a positive influence of depth, presumably because it is related with pond hydroperiod (Brooks 2002), and this species requires fairly permanent aquatic habitats because of their long larval period (Diaz-Paniagua 1983; García-París 1989). It was found frequently in large ponds with great surface area and depth, where it shared habitat with *P. waltl*, but it was also found in a couple of small ponds with vertical walls, small area, and great depth.

We obtained four possible models for *A. obstetricans*. The probability of *A. obstetricans* presence tended to decrease with pond depth and increase with hard substratum and hard substratum covered by soft sediment. It is possible that this result could be related to the breeding behavior of the species because, unlike *P. waltl*, they do not need structures to attach their eggs (Arnold and Overden 2002), so they can exploit habitats with absence of macrophytes. They also have a longer larval stage than other native species, like *E. calamita* and *P. hespericus* (Crespo 1982), so they need ponds with longer hydroperiod; however, natural, long-lasting ponds that keep their original hydrogeomorphology are usually occupied by *P. waltl*, which are important predators of the community (Rodríguez-Jiménez 1985). Therefore, because *A. obstetricans* does not require vegetation but still need ponds with long hydroperiod, it can avoid predation by breeding in artificial ponds that lack *P. waltl*. Thus, human constructions are very suitable habitats, and in fact *A. obstetricans* frequently appears in shallow, artificial ponds with a hard substratum, such as cisterns and drinking troughs (Bosch, J. 2003. Sapo partero común – *Alytes obstetricans*. *In* Enciclopedia Virtual de los Vertebrados Españoles. Carrascal, L.M., and A. Salvador (Eds.). Museo Nacional de Ciencias Naturales, Madrid, Spain. http://www.vertebradosibericos.org/ [Accessed 2 July 2007]). Among those variables contributing significantly, algal coverage was the least important, but it had a positive coefficient. This may be related to the fact that algal coverage is an important food source for tadpoles (Peterson and Boulton 1999).

For *E. calamita*, both egg support and type of substratum had important effects in the occupancy model. This could be explained because long egg cords are attached to subaquatic structures, such as vegetation, stones, or branches (López-Jurado 1983). Therefore, a pond with a hard and bare substratum would in principle not represent an optimal habitat for the species, but the presence of structures like branches, stones, or land roughness might promote its occupancy. In addition, *E. calamita* is a habitat specialist, breeding in ephemeral ponds (Banks and Beebee 1987), like the small, shallow, unnatural ponds of the study area, with a soft substratum over concrete (Ruhi et al. 2012). Thus, the best local habitat, according to our model, would be a pond with soft over hard substratum allowing some vegetation to grow.

Finally, soft substratum was the only non-negative level for *P. hespericus*, according to our model. This may be also related with the oviposition behavior of the species, in which egg masses are attached to structures like branches of aquatic or semi-aquatic vegetation (Escoriza, D. 2015. Sapillo moteado – *Pelodytes hespericus*. *In* Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., and I. Martínez-Solano. (Eds.). Museo Nacional de Ciencias Naturales, Madrid, Spain. http://www.vertebradosibericos.org/ [Accessed 2 July 2018]), which are present in ponds with a soft substratum. Livestock use was also a strong predictor of pond occupancy, with a positive effect, perhaps attributable to the selection of ponds with longer hydroperiod by shepherds.

In comparison to a previous study carried out in Andalucia, southern Spain, by Benítez et al. (2017), we found some differences, but not incompatibilities. For example, surface area was a significant variable in their model for *E. calamita*, and connectivity (comparable with variables in our study such as minimum distance to the closest pond or minimum proximity to roads) was a significant predictor for *P. perezi*. These variables were not significant in our models for these species. These differences are probably due to the higher diversity of habitats and larger study area in the Benítez et al. (2017) study, and the absence of lotic ecosystems in our study. However, there are some similarities between the two studies. First, pond depth and the presence of natural ponds with soft substrata were important for *P. waltl* in both studies. Similarly, for *P. perezi* both studies showed a positive effect of water temperature. Finally, for *E. calamita*, Benítez et al. (2017) showed a preference for temporary ponds, but in our study most ponds were temporary. Thus, our models add information about the preferences of each species in a different region, broadening our knowledge on interpopulation variability in patterns of pond occupancy.

Our results can inform land managers and help design new breeding habitats, improving regional connectivity and abundance. It is important to understand the ecological needs of each species prior to population declines, and our study helps to fill that need by providing important information about breeding habitat requirements of these species. Importantly, we have shown that patterns of breeding site occupancy are different among species, which calls for species-specific actions to ensure their conservation. Our models can be applied in habitat restoration, reintroduction, and population reinforcement projects aimed at the long-term preservation of viable amphibian communities.

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Ángel Gálvez obtained his Bachelor of Biology at University of Valencia, Spain, in 2015. He obtained a Master's degree in Biodiversity, Conservation and Evolution at University of Valencia in 2016. At present, he is pursuing a Ph.D. degree in Biodiversity and Evolutionary Biology at University of Valencia, studying metacommunities of temporary ponds. He has worked at Valencian Albufera Natural Park radio-tracking reintroduced Hermann's Tortoise (*Testudo hermanni*) and geolocating exotic plant species. (Photographed by Antonio Gómez).

Donald McKnight (holding two Diamond-backed Watersnakes, *Nerodia rhombifer*) is currently a Ph.D. student at James Cook University, Townsville, Queensland, Australia, where he is studying the effects of chytridiomycosis on frog population genetics. He received his Bachelor's degree in Biology from Messiah College in Grantham, Pennsylvania, USA, where he conducted research on the movements, microhabitat selection, and population ecology of Eastern Box Turtles (*Terrapene carolina carolina*). He completed his M.S. in Biology at Missouri State University, Springfield, Missouri, USA, in May 2014. For his Master's research, he studied herpetological communities, with a focus on turtle communities and the ecology of Western Chicken Turtles (*Deirochelys reticularia miaria*). (Photographed by Jennifer McKnight).

Juan S. Monós is an Associate Professor of Ecology at the University of Valencia (Spain) and Director of the Cavanilles Institute of Biodiversity and Evolutionary Biology. He received his B.A. in Biology and his Ph.D. in Biology from the University of Valencia, studying ecological aspects from the Montpellier Snake (*Malpolon monspessulanus*) in the Eastern Iberian Peninsula. Currently, his studies are about population ecology of terrestrial vertebrates, mainly birds, focused on the conservation of small populations. He also works on the ecology of other vertebrates such as mammals (bats), amphibians living in temporal ponds, and reptiles in the Albufera de Valencia Natural Park. (Photographed by Juan S. Monrós).

Appendix. Data, introduced in the models, of the variables characterizing ponds in the study area, including average of the 67 ponds, standard error, minimum and maximum values for continuous variables (Distance to roads, DR; Distance to crops, DC; Distance to ponds, DP; Surface, Sr; Depth, D; Egg support, ES; Algal coverage, AC; Temperature, T; Conductivity, C, and Oxygen, O, saturation) and the percentage of the levels of each categorical variable (Terrestrial habitat, TH: 1: crops; 2: regenerating pine forest; 3: regenerating holm-oak forest; 4: scrub; 5: urban; Light, L; 1: total absence; 2: partial exposure; 3: total exposure; Livestock use, LU; 1: Not; 2: Yes; Substratum, S; 1: soft; 2: hard; 3: hard covered by soft substratum; Hydroperiod, H; 1: one to three months; 2: more than three months; and Accessibility, A; 1: non accessible; 2: accessible). The abbreviation SR = species richness.

Site	SR	TH	L	DR (m)	DC (m)	DP (m)	LU	Sr (m^2)	D (m)	ES (%)	S	H	A	AC (%)	pH	T (ºC)	C (µS/cm)	O (mg/l)
ALC01	2	4	2	91	204	210	0	3.9	0.2	40	2	2	0	30.83	8.1	19.0	453.2	7.4
ALC02	1	4	3	62	27	275	0	7.4	0.3	20	2	2	1	0	8.2	14.7	448.3	8.4
ALC03	1	5	2	3	27	43	1	5.4	0.3	0.8	2	2	0	0	7.7	12.1	923.6	7.5
ALC04	1	5	2	2	50	60	0	17.1	0.4	10	2	2	0	30	8.3	12.1	642.3	7.7
ALC05	1	4	2	33	30	275	1	2	0.1	80	2	2	1	23.3	8.8	15.4	433.3	9.9
ALC06	1	1	3	13	7	186	1	7.6	0.5	0	2	2	0	0	8	15.3	1149.3	7.6
ALC07	1	1	3	6	25	606	0	3.3	0.2	0	2	2	0	0	8.3	14.2	498.5	5.8
ALC08	1	1	3	1	3	8	1	9.3	0.4	20	2	2	0	3.3	8.1	11.4	885.8	7.6
ALC09	1	2	3	45	106	283	0	7.7	0.4	30	2	2	1	0	8.4	16.1	571	9.9
ALC10	2	1	2	11	18	1	0	0.8	0.06	5	2	2	1	41.7	8.7	15.6	289.1	8.5
ALC11	0	4	3	25	65	16	0	3.6	0.2	20	2	2	0	20	9.2	15.2	283.8	7.7
ALC12	0	1	1	11	13	216	0	6.6	0.5	0	2	2	0	0	8.2	13.4	160.7	6.4
ALC14	1	1	1	1	1	228	0	0.3	0.7	0	2	2	0	0	8.2	12.2	399.8	4.7
ALC15	0	1	1	7	12	250	0	0.4	0.9	0	2	2	0	0	8.4	13.1	170.3	6.5
ALC16	1	3	1	36	145	375	0	0.3	0.7	0	2	2	0	0	8.4	12.9	279.7	8.3
ALC17	1	1	1	4	10	458	0	0.2	0.7	0	2	2	0	0	8.1	11.6	318.2	6.0
ALC18	0	1	1	8	20	547	0	2.3	1.1	0	2	2	0	0	8.6	12.6	232	8.1
ALC19	0	1	1	5	8	756	0	0.3	1.9	0	2	2	0	0	8.5	12.9	198.7	7.2
ALC20	3	1	2	0.5	48	1	1	2.5	0.3	0	2	1	1	0	7.8	16.8	298.7	6.7
ALC21	2	1	3	2	43	1	0	24.8	1	0	2	2	0	0	8.8	14.9	240.8	8.4
ALC22	1	3	1	106	98	436	0	0.1	0.5	0	2	2	0	0	8.3	13.1	283	7.5
ALC23	1	1	1	1	6	231	0	0.2	1.3	0	2	2	0	0	8.6	13.3	134.3	7.5
ALC24	0	3	1	133	177	231	0	0.3	0.7	0	2	2	0	0	8.2	13.4	497.8	4.8
ALC25	0	4	1	1	35	16	0	45	0.6	0	2	2	0	0	8.5	11.6	261.7	7.4
ALC26	2	1	2	10	38	1890	1	186.4	0.8	0	3	2	0	0	8.5	12.5	362.3	7.5
ALC27	2	1	3	4.45	12	4	1	3.8	0.3	100	1	1	0	0	7.5	18.1	600	4.7
ALC28	3	4	3	23	22	691	1	118.4	0.9	56.7	1	2	1	0	7.8	15.6	363.2	12
ALC29	4	2	3	27	11	551	1	279.4	1.5	63.3	1	2	0	0	8.4	14.6	229	8.1
ALC30	2	4	3	23	15	602	1	70.4	0.6	20	3	2	1	5	8.4	16.9	156.5	7.3
ALC31	4	4	3	7	13	44	1	557.2	1.7	85	1	2	1	19.2	8.8	16.1	422.8	8.1
ALC32	2	4	2	243	26	93	1	65.1	0.6	73.3	1	1	0	26.7	7.6	15.6	1548.7	3.6
ALC33	1	4	2	243	26	93	1	6	0.7	50	1	2	0	40	7.5	18.2	2426	1.9
ALC34	4	4	3	4	13	24	1	713.1	0.7	88	1	1	1	34	7.9	18.2	334.2	5.5
ALC35	1	4	3	26	16	17	1	8.5	0.09	80	1	2	0	0	8	13.7	258	6.4
ALC36	3	1	3	10	12	8	0	60.8	0.5	10	2	2	0	14.2	8.2	13.3	818.8	8.2

Site	SR	TH	L	DR (m)	DC (m)	DP (m)	LU	Sr (m²)	D (m)	ES (%)	S	H	A	AC (%)	pH	T (ºC)	C (µS/cm)	O (mg/l)
ALC37	0	4	1	1	16	1	1	0.1	0.2	0	2	2	0	0	8.1	11.7	357.8	6.8
ALC38	1	1	2	26	39	382	0	4	0.1	0	2	2	0	41.7	7.9	12.8	1402.7	5.9
ALC39	3	1	2	4.5	5.5	238	1	1.7	0.5	15	2	1	0	8.3	8.1	10.5	369	3.3
ALC40	1	2	2	148	14	138	1	0.5	0.2	20	2	2	0	0	8.05	8.95	287.5	6.1
ALC41	1	2	3	91	9	455	1	1.9	0.5	83.3	2	1	0	33.3	9.8	15.5	136.8	12.2
ALC42	2	4	2	252	23	964	1	1.8	0.1	0	2	2	0	0	8.2	10.4	594.2	4.7
ALC43	2	1	3	2	5	163	1	2.9	0.7	15	2	2	0	3.3	9.1	15.9	231.8	10.6
ALC44	1	4	3	1.5	18	606	0	1.6	0.5	0	2	1	0	0	8.5	13.6	309.5	7.6
ALC45	3	3	3	9	4.12	983	1	40.5	0.6	81.7	3	2	0	30	9.2	17.8	173.8	8.5
ALC46	2	3	3	8	593	471	1	60.7	0.6	90	3	2	0	26.7	9.2	17.8	158	8.4
ALC47	2	2	3	51	109	455	1	48.9	0.4	91.7	3	2	1	29.1	9.4	16.4	113.3	10.1
ALC48	3	4	3	91	388	805	1	49.3	0.2	20	3	2	0	0	8.7	17.3	315.4	7.4
ALC49	4	3	2	5	481	805	1	66.5	0.6	43.3	3	2	0	4.2	8.6	19.1	184.8	7.1
ALC50	2	3	3	30	54	236	1	85.3	0.6	66.7	3	2	0	0	8.3	16.8	1340.3	7.3
ALC51	2	3	3	787	529	696	1	100.4	0.2	25	3	2	0	15	8.8	14.6	310.5	7.6
ALC52	3	3	3	136	77	696	1	66.6	0.5	48	3	2	0	13	8.9	15.9	153.4	7.8
ALC53	2	2	3	265	109	373	1	39.2	0.3	70	3	2	0	61.7	8.9	13	136.7	5.3
ALC54	2	3	2	298	234	302	1	60.2	0.6	5	3	2	0	3.3	8.7	16.6	306.3	7.7
ALC55	2	4	3	80	36	381	1	63.9	0.3	0	3	2	0	8.3	9.9	15.9	1192.1	2.7
ALC56	3	4	3	8	29	460	1	28.7	0.3	50	3	2	1	0	8.8	16.8	188.5	7.6
ALC57	2	2	3	21	49	138	1	107.6	0.4	92	3	2	0	35	9.3	17.1	112.6	8.9
ALC58	2	2	3	8	295	697	1	39	0.2	5	3	1	0	0	8.2	15.1	399.3	7.1
ALC59	2	4	2	231	31	241	1	164.5	0.6	30	1	1	1	0	8.05	14.3	249.5	6.5
ALC60	3	2	3	497	164	697	1	20.8	0.1	50	3	2	0	50	8.4	12.6	448.2	7.1
ALC61	3	3	3	19	457	302	1	81.8	0.6	0	3	2	0	0	8.9	17.9	582.2	7.1
ALC62	3	2	3	20	25	147	1	55.8	0.2	80	3	1	1	15	8.7	14.5	185.8	8.1
ALC63	2	2	2	192	543	257	1	51	0.3	30	3	2	0	0	8.1	18.2	418	7.4
ALC64	3	1	3	14	6	113	1	96.6	0.6	86	1	1	0	0	7.8	13.8	330.8	5.4
ALC64	3	1	3	14	6	113	1	96.6	0.6	86	2	2	0	1.9	7.5	14.1	914.2	12.2
ALC65	0	5	2	1.69	17	46	1	11.8	0.9	20	2	2	0	0	7.9	12.3	430.3	5.9
ALC66	2	1	2	3.39	7.77	4	1	6.6	0.9	80	1	1	0	0	8.05	16.9	157	7.6
ALC67	2	4	3	1.1	45	58	1	47,130	0.5	80	-	-	0	0.00	7.46	8.95	112.6	1.92
Minimum	0	-	-	0.50	1.00	1.00	-	0.10	0.06	0.00	-	-	0	0.00	7.46	8.95	112.6	1.92
Maximum	4	-	-	787.0	593.0	1,890.0	-	47,130	1.92	100.0	-	-	1	61.67	9.88	19.05	2,426.0	12.23
Average ± SE	1.7 ± 1.1	-	-	68.5 ± 15.8	86.7 ± 7.5	355.7 ± 39.9	-	756.9 ± 702.8	0.53 ± 0.04	31.8 ± 4.2	-	-	-	9.9 ± 1.8	8.46 ± 0.06	14.6 ± 0.3	454.9 ± 49.3	7.2 ± 0.2
% Level 1		32.84	19.40	-	-	-	34.30	-	-	-	16.4	17.9	80.6	-	-	-	-	-
% Level 2		16.42	28.40	-	-	-	65.70	-	-	-	53.70	82.10	19.40	-	-	-	-	-
% Level 3		16.42	52.20	-	-	-	-	-	-	-	29.90	-	-	-	-	-	-	-
% Level 4		29.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
% Level 5		4.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-