High-resolution remote-sensing data in amphibian studies: identification of breeding sites and contribution to habitat models

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Remote sensing can provide an alternative to field data sampling in many species-habitat studies. However, its usefulness may depend on the species, habitat studied, spatial resolution and extent. We used a high spatial and spectral remote-sensing image to locate and delineate small amphibian breeding sites in a Mediterranean ecosystem (Doñana National Park). We also evaluated its usefulness in detecting habitat heterogeneity (number and evenness of different radiometric zones) within ponds and its relationship to amphibian species richness. Furthermore, Generalized Linear Models (GLMs) were used to evaluate the usefulness of high-resolution remote-sensing data to model amphibian distribution at species level (presence/absence data), both when used alone or as a complement to field data. Amphibian species richness correlated positively with habitat heterogeneity when we discriminated a low number of potential different zones within ponds (four vs nine). For most species, remote-sensing data improved on amphibian distribution models built from field data but were of limited utility when used alone. In consequence, although remote-sensing data could be used for the preliminary identification of ponds supporting high species richness, we recommend initial assessment of its utility for identifying species-specific breeding sites before conducting survey programmes based on it.

Key words: habitat heterogeneity, hyperspectral data, Mediterranean temporary ponds, wetlands

INTRODUCTION

Freshwater ponds support more species, more unique species and more scarce species than other water-body types, such as streams or rivers (Williams et al., 2004). In particular, freshwater ponds with a recurrent dry phase (temporary ponds) constitute the main breeding habitat of many invertebrate (Williams, 1997; Grillas et al., 2004; Williams, 2006) and amphibian species (Díaz-Paniagua, 1990; Griffiths, 1997; Semlitsch, 2003). Nevertheless, and despite its conservation value, pond ecosystems are threatened worldwide by their drastic diminution in number (Oertli et al., 2005). In order to protect such valuable and vulnerable ecosystems, Mediterranean temporary ponds are considered a priority habitat under the European Union Habitats Directive (European Commission, 2007), deserving specific conservation programmes. Conservation programmes require from ecosystem monitoring, which is difficult in Mediterranean temporary ponds due to their unpredictability, temporal fluctuations and frequently small size. Besides, cost-efficiency precludes unlimited sample sizes. For this reason, ponds expected to support rare, endangered or a large number of species should be identified and prioritized in monitoring programmes.

Remote sensing may provide data from broad spatial extents that would be prohibitively expensive if collected using field-based methods (Kerr & Ostrovsky, 2003). The usefulness of remote-sensing data to predict species distributions constitutes an important research topic (Kerr & Ostrovsky, 2003; Turner et al., 2003; Gottschalk et al., 2005). Previous studies have explored the contribution of remote-sensing data, in comparison to climatic variables, to predictive species modelling at large scales (Venier et al., 2004; Zimmermann et al., 2007; Buermann et al., 2008). However, similar approaches have rarely been conducted for vertebrates at smaller scales. To be useful at landscape scale, remote sensing should at least be able to delineate potential habitats for the species of interest. The application of remote sensing to map potential habitats will provide a highly valuable tool for the management and conservation of species associated with spatially discrete habitat patches, such as pond-breeding amphibians. Despite remote-sensing data being regarded as a useful tool for the delineation and monitoring of freshwater ecosystems (Revenga et al., 2005), it has rarely been applied to amphibian research, with only a few studies focusing on global (Carey et al., 2001; Middleton et al., 2001) and landscape scales (Scribner et al., 2001). Most previous remote-sensing studies of aquatic ecosystems have focused on the delineation of large water bodies (see Ozesmi & Bauer, 2002, for a review), in particular in the Mediterranean region (Alphan & Yilmaz, 2005; Castañeda et al., 2005; Papastergiadou et al., 2007). Small freshwater ponds, an important breeding habitat for amphibians, have frequently been disregarded because of the spatial resolution constraints of satellite remote sensing. However, recent technology (i.e. airborne sensors)

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produces high-resolution spatial and spectral images, enabling the detection of small ponds (Weiers et al., 2004; Lacaux et al., 2007). From a biotic perspective, high-resolution images might also enable the identification of habitat characteristics that condition the distribution of associated species (see Lacaux et al., 2007, for an example of the application of high spatial resolution satellite imagery to monitor mosquito habitat) and, in consequence, facilitate the identification of habitats holding rare, endangered or a large number of species. These theoretical potentials of high-resolution remote-sensing data should be evaluated prior to the undertaking of survey, conservation or monitoring programmes based on it. Doñana National Park, where a large number of temporary ponds are protected (Díaz-Paniagua et al., 2006), can provide a model system to assess the contribution of remote sensing to habitat models of amphibians breeding in small temporary ponds.

The existence of specific microhabitats within water bodies is especially important for some amphibian species (Díaz-Paniagua, 1987; McAlpine & Dilworth, 1989). Both depth and aquatic vegetation cover were previously observed to influence amphibian species-specific preferences for particular zones within ponds in Doñana National Park (Díaz-Paniagua, 1987). Moreover, the great diversity of ponds in the area and, therefore, differences in microhabitat presence and extension, result in differential usage of ponds as breeding habitats, with some species being restricted to a particular kind of water body (Díaz-Paniagua, 1990). Observed spatial segregation due to abiotic characteristics of ponds, both at local (pond) and microhabitat scales, enables the differentiation of pond types and, furthermore, of zones within larger ponds favourable for particular species.

On the other hand, number, spatial structure and extent of microhabitats are factors determining habitat heterogeneity within a water body. Habitat heterogeneity positively correlates with species diversity since complex habitats usually provide more niches and diverse ways of exploiting the environmental resources (see Tews et al., 2004, for a review). Therefore, the assessment of habitat heterogeneity can be used to identify breeding habitats favouring amphibian diversity.

In this study, we expected remote sensing to be useful in delineating different zones within ponds reflecting microhabitat differences. The underlying rationale is that, in the study area, pond microhabitat zonation can be established based on differences in aquatic vegetation distribution, related to differences in depth (Díaz-Paniagua, 1987). On the other hand, hyperspectral remote-sensing data have been used to identify differences in vegetation (Hirano et al., 2003; Schmidt & Skidmore, 2003) and depth (Marcus et al., 2003) and have also allowed delimitation of different zones within different water bodies (Marcus, 2002; Marcus et al., 2003). We therefore used remote-sensing data to identify different radiometric zones, i.e. zones with different radiometric reflectance, presumably caused by differences in depth and vegetation, within larger ponds. Radiometric zones were expected to be useful in predicting habitat availability and suitability for particular amphibian species as well as ponds supporting high amphibian richness in Doñana National Park.

With this study, we make an initial assessment of the contribution of remote-sensing data to amphibian distribution studies, both at community and species level. We hypothesize that high-resolution remote sensing will identify amphibian breeding sites that have been missed in previous cartographies built by photointerpretation (Bravo & Montes, 1993). We also hypothesize that remote sensing data will be a useful predictor in habitat models, as reported at larger scales (Venier et al., 2004; Zimmermann et al., 2007; Buermann et al., 2008), although the best models will be those built from remote-sensing and field data. In particular, in this study, we evaluate the potential of remote-sensing to: 1) map a system of small temporary ponds; 2) identify different radiometric zones within the ponds, as a surrogate for habitat heterogeneity; 3) explore the potential of radiometric zones for explaining species distribution and species richness; and 4) explore the potential of radiometric zones for enhancing habitat distribution models based on field-measured pond characteristics. This study is not designed to model amphibian habitat requirements, which will be analysed in further studies conducted in the entire national park, including a larger number of amphibian breeding sites.

MATERIALS AND METHODS

Doñana National Park (54,252 hectares; see Siljeström et al., 1994, for a general description), located in south-western Spain (Fig. 1), is considered to be one of the largest and most important wetlands in southern Europe. Our study area comprises approximately 7,500 hectares of sandy soils in the national park (Fig. 1), where a large number of ponds are usually formed during the rainy season (Díaz-Paniagua et al., 2006; Serrano et al., 2006). These water bodies vary widely in size, from rain puddles (several square metres) to large temporary ponds (>1 hectare). Most water bodies in this area are temporary ponds that dry out during the summer. Only two shallow lakes, larger than 10 hectares, are permanent water bodies, although they have been reported to dry out sporadically. Temporary ponds are also subject to a wide range in the duration of flooding. Water-table depth determines the onset and duration of inundation, with flooding occurring when the water table rises above the topographical surface (Serrano et al., 2006). Water-table depth also determines the presence of hygrophyte vegetation in the immediate surroundings of many ponds (dense vegetation mainly composed of *Erica scoparia* L., *Erica ciliaris* L., *Calluna vulgaris* (L.) Hull and *Ulex minor* Roth.). As a consequence, many pond basins are completely or partially enclosed by a fringe of hygrophyte vegetation that may be occasionally flooded. In addition, these water bodies differ in depth (Díaz-Paniagua, 1990), vegetation (Rivas-Martínez et al., 1980; García Murillo et al., 2006) and water chemistry (Serrano & Toja, 1995; Serrano et al., 2006; Gómez-Rodríguez et al., in prep.).

For this study, we collected field data (pond characteristics and amphibian presence) from 63 ponds. Because of logistic limitations, we only selected 51 water bodies, not

Fig. 1. Location of Doñana National Park Park in southwestern Spain and orthophotography of the study area. The solid line represents the Doñana Biological Reserve, where most of the study ponds are located. The dotted line represents the study area.

necessarily the same as those previously surveyed, to develop the classification of pixels into different radiometric zones using remote-sensing techniques. We applied this classification to all pixels within the 63 field-monitored ponds.

Pond characteristics

In this study we considered the following characteristics of 63 ponds: hydroperiod (duration of flooding), water depth, percentage of surrounding vegetation, temporal surface connection to adjacent ponds and presence within ponds of deeper anthropogenic zones (hereafter referred to as *zacallones*, the local name), which prolong the hydroperiod and are used to water cattle or wild mammals during the dry season (Serrano et al., 2006). In addition, we also considered pond coordinates and size, both extracted from the water-body cartography mapped with remote-sensing analyses (see below).

Hydroperiod was categorized into five groups according to data obtained in 2003: 1) ephemeral ponds (flooded for 1–2 months), 2) intermediate temporary ponds (3–6 months), 3) long-duration temporary ponds (7–11 months), 4) permanent water bodies (12 months) of natural origin (size >10 hectares) and 5) permanent water bodies (12 months) of anthropogenic origin, locally named isolated *zacallones* (size 20–30 m^2). Although most ponds were regularly visited in various monitoring programmes during that year, the exact date of desiccation could not be assessed for several water bodies. In these cases, hydroperiod category was inferred from control ponds (n=21) that were visited on a weekly basis and represented the same pond typologies. Pond typologies were based on characteristics related to flooding duration, such as aquatic vegetation associations (Rivas-Martínez et al., 1980), basin topography and past recordings of hydroperiod in those ponds in wet years (Díaz-Paniagua, unpubl. data). Depth ranged from several centimetres in small puddles to more than 2.5 m in the largest ponds, and was grouped into three relatively broad categories: shallow (maximum depth approximately 40 cm), medium (maximum depth approximately 40–80 cm) and deep (approximate maximum depth >80 cm). Proportion of the pond shore surrounded by adjacent hygrophyte vegetation, estimated from aerial photography, fell into five categories: 1) hygrophyte vegetation surrounding more than 75% of the pond; 2) hygrophyte vegetation surrounding 25–50% of the pond; 3) hygrophyte vegetation surrounding less than 25% of the pond; 4) no hygrophyte vegetation, but trees in the immediate surroundings of the pond, and 5) no hygrophyte vegetation nor trees in the immediate surroundings of the pond. We also distinguished between isolated ponds and ponds showing temporal surface connection to other water bodies, by visual inspection of the water-body cartography (see below) and field verification. Temporal surface connection to a larger water body was determined if the pond was identified as part of a bigger mass of water. In those cases, limits between ponds had to be manually delineated, based on aerial orthophotography (Junta de Andalucía, 2003). Presence or absence of *zacallones* within the pond was assessed during amphibian field surveys.

Amphibian sampling

Although remote-sensing data were taken in 2004, amphibian data were collected during a four-year survey (2001–2004), to avoid overlooking the presence of any species as a result of inter-annual turnover in community composition (Skelly et al., 1999; Trenham et al., 2003). We assessed amphibian reproductive success in 63 ponds using dipnetting techniques to detect species larvae (Heyer et al., 1994). Depending on different monitoring programmes, 31 ponds were sampled repeatedly (2–18 surveys), while the rest were surveyed only once in the four years of the study (mean number of surveys = 4.37±1.35 S.D.). The total number of species detected in a pond during the period 2001–2004, not accounting for the fact that there was a different sampling frequency, represented the cumulative species richness in the pond ("species richness"). The correlation between species richness and the number of visits yielded a low value of shared variation (Spearman correlation, r=0.380, P<0.05). This low correlation suggests that differences in sampling effort are not a relevant bias for richness values.

Amphibian sampling consisted of the capture of larvae using a dipnet along two perpendicular transects in each pond. We identified in situ the individuals captured in each sampling unit (three consecutive sweeps on a stretch of approximately 1.5 m length) and then released them into the pond. Sampling effort was proportional to pond size, except when not logistically achievable due to the large size of the water body (long-duration and perma-

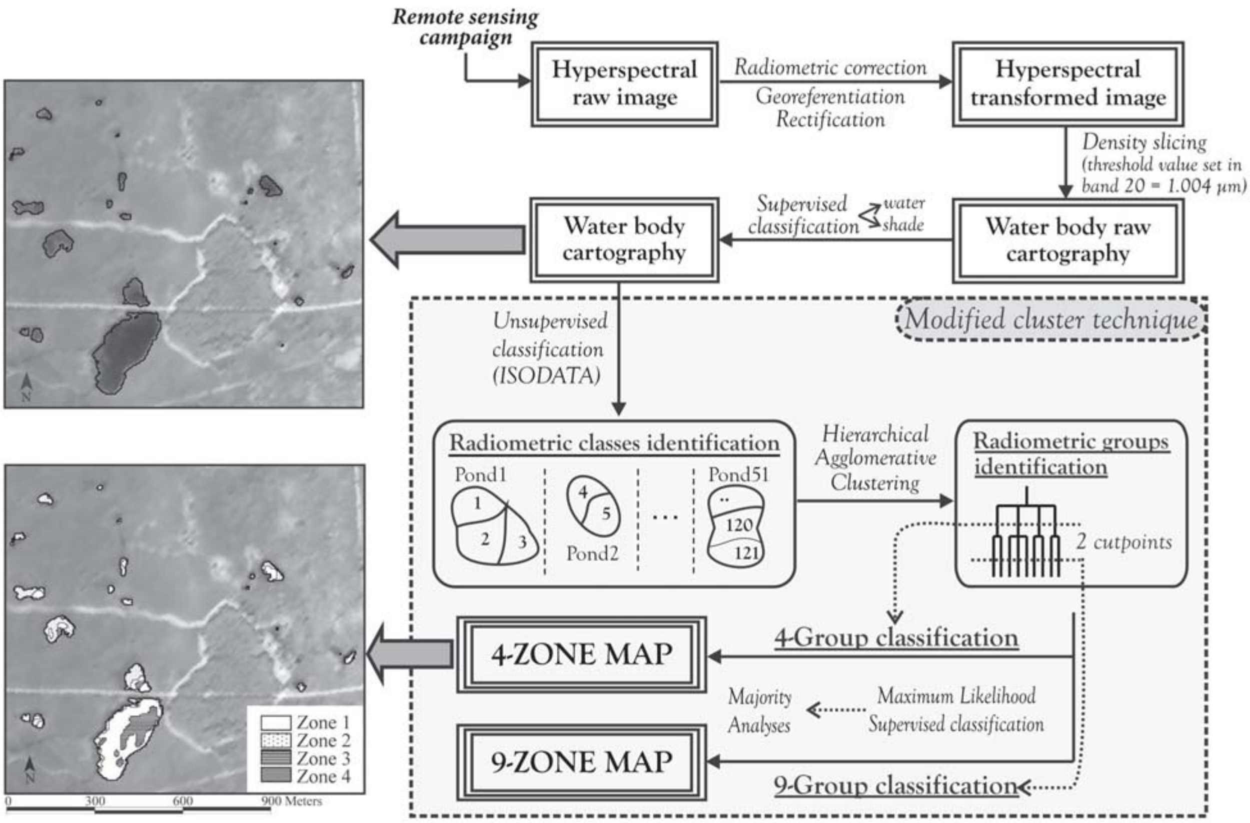

Fig. 2. Scheme of the methodology applied. Remote sensing and classification analyses were conducted to obtain two cartographies representing different types of spectral classes (radiometric zones) within ponds. Cartographies differed in number of radiometric zones considered: nine (9-ZONE MAP) or four (4-ZONE MAP). A subsample of the study area is used to illustrate the water body cartography and the 4-ZONE MAP cartography.

nent water bodies), in which case we tried to sample all different pond microhabitats. Sampling units were separated by a minimum of five metres to avoid interference between surveys.

Remote-sensing analysis of high-resolution spectral and spatial data

The study area was overflown during a remote-sensing campaign conducted by the Remote Sensing Laboratory of the Instituto Nacional de Técnica Aeroespacial (INTA) in a period of maximum inundation, April 2004. An airborne hyperspectral spectrometer (AHS) (Sobrino et al., 2006) was used to obtain a cloud-free image with a spatial resolution of 5 × 5 m. We chose a remote-sensing image taken in a period of maximum flooding to map all potentially distinguishable radiometric zones, i.e. zones with different radiometric reflectance within ponds, presumably caused by differences in depth and vegetation. This cartography was considered a reference characterization of maximum pond heterogeneity and zonation.

We radiometrically corrected the image, converting digital numbers (DNs) to absolute radiance values based on the instrument's calibration coefficients. We geo-referenced the image applying second order polynomial transformation and nearest-neighbour resampling. Afterwards, we applied remote-sensing techniques to delineate water bodies and to map different zones within (Fig. 2). All analyses, except where otherwise noted, were conducted using ENVI 4.0.

We delineated water bodies by applying a density slicing (Richards & Jia, 1999) in an infrared spectral band (λcentre = 1.004 μm; λwidth = 0.030 μm), based on land and water differences in absorption of radiation in the near-infrared part of the spectrum (Lillesand & Kiefer, 1994). This technique consists of applying a threshold value that discriminates potential water bodies (pixel values below the threshold) from land (pixel values above the threshold), the latter being masked as zero values. We applied a supervised classification (Lillesand & Kiefer, 1994; Richards & Jia, 1999) to the resulting image (only potential water bodies), a procedure that clusters pixels into user-defined classes, in order to separate shaded areas from water, using field surveys and visual inspection of orthophotography (Junta de Andalucía, 2003) as input data.

We mapped different radiometric zones within water bodies by applying a technique derived from the modified cluster technique first described by Fleming et al. (1975), to bands in the visible and infrared part of the spectrum (21 bands; λ=0.453–1.622 μm). Our application of the modified cluster technique basically consisted of initially applying an ISODATA unsupervised classification (Lillesand & Kiefer, 1994; Richards & Jia, 1999) to aggregate similar pixels into spectral classes in 51 water bodies. Since we conducted an independent ISODATA classification in each water body, we had to group similar spectral classes, identified in different ponds, using hierarchical agglomerative clustering (Statistica 6.0). Hierarchical agglomerative clustering groups spectral classes based on similarity of spectral values, starting with individual classes until all classes are linked in different clusters. The number of groups is not known *a priori* and has to be determined from visual inspection of the results (dendrogram). Two different linkage-distance cut points were established, based on dendrogram branch length (representing the degree of dissimilarity). The first linkage-distance cut point was set to differentiate the maximum number of major (largely dissimilar) types of spectral classes, yielding a 4-GROUP classification. The second linkage-distance cut point was set to differentiate the maximum number of distinguishable groupings that had a similar number of spectral classes (ten spectral class types). However, two of these latter types of spectral classes presented low statistical differences in their response patterns, as evidenced by their low separability index (Jeffries-Matusita and Transformed Divergence; Richards & Jia, 1999), and had to be merged, yielding a 9-GROUP classification. For each classification, we performed a maximum likelihood supervised classification (Lillesand & Kiefer, 1994; Richards & Jia, 1999) on the 63 field-sampled ponds and applied majority analysis to smooth the final image through elimination of spurious pixels by means of changing their class identity to the dominant one in the adjacent pixels. This smoothing is necessary in order to preserve the integrity of polygons (i.e. we delineate homogeneous zones expected to correspond to different habitats).

We produced two different maps, one distinguishing four different types of spectral classes (hereafter called radiometric zones) that may be present within water bodies (4-ZONE MAP) and the other distinguishing nine (9-ZONE MAP).

Statistical analyses

We calculated the number and evenness of radiometric zones for each water body and each cartography (4-ZONE MAP and 9-ZONE MAP). Evenness of radiometric zones constitutes an index of structural diversity, representing habitat heterogeneity (Tews et al., 2004), and was computed as the Shannon diversity index using vegan package (Oksanen et al., 2007) in R (R Development Core Team, 2006). Differences in zone number and evenness (habitat heterogeneity within pond) among depth and hydroperiod categories were tested with ANOVA analyses. We squared the Shannon index in the 9-ZONE MAP to achieve normality in model residuals. Relationship between species richness and number and evenness of radiometric zones was computed as a Spearman correlation for each cartography.

We built generalized linear models (GLMs; McCullagh & Nelder, 1989) to evaluate the predictive ability of radiometric zones for amphibian species occurrence. Models were not built for species present in less than 20% of ponds, due to their low prevalence. Additionally, we reduced potential biases caused by differences in species phenology in the area (Díaz-Paniagua, 1988) by means of reducing each species dataset to the data recorded when the species was available to be detected in the field. Thus, for each species and sampling season, we considered only the surveys conducted between the dates of first and last detection of the species in any pond in the entire study area. We built GLMs using binomial errors and logit link. The response variable was a bound vector (number of presences/number of absences). Bound vectors weighted cases in proportion to the number of surveys conducted in the pond (number of presences + number of absences). Model development and variable selection was based on Akaike's selection criterion (AIC), using an automatic forward–backward stepwise procedure (step.glm, S-Plus 2000).

The same analyses were applied to model species richness, using the number of species detected in a pond as a response variable with Gaussian errors and identity link. Each case was weighted by the number of surveys conducted in the pond.

We built five different models for each species and for species richness:

One POND model. Characteristics of ponds assessed during field visits, as well as pond area and latitude and longitude of the centre of water body, to evaluate spatial dependence, were tested as potential predictors.

Two RADIOMETRIC models. We built two models; one considered four radiometric zones (RM4) and the other nine (RM9) as potential predictors. Predictors consisted of the percentage of each radiometric zone in the pond as well as the number of different radiometric zones and surface area of the whole pond. All Pearson correlation coefficients calculated between predictors were lower than 0.75, so all variables were tested as potential predictors.

Two SEQUENTIAL models. Models built from pond variables were tested for improvement by including radiometric predictors: one model was built for four radiometric zones (SEQ4) and another for nine (SEQ9). We fixed the predictor variables from the final explanatory POND model as the initial and minimum model for each species. Then, we allowed the inclusion of radiometric variables: percentage of each radiometric zone and number of different radiometric zones.

Models were evaluated based on discrimination ability, with the same dataset used for model building. This will overestimate their accuracy but will not affect model comparisons (Seoane et al., 2004). Goodness-of-fit was assessed by calculating Spearman correlation coefficients, considered an effective accuracy measure for probabilistic models (Miller et al., 1991), between the ratio of number of presences/number of visits and the predicted probability of occurrence. Model type differences were tested with a repeated measures ANOVA and post-hoc Tukey's pairwise comparisons of correlation coefficients.

Table 1. Mean number and standard deviation (S.D.) of the number and evenness of radiometric zones per pond, specified for the whole study area (TOTAL) and also differentiating among ponds with different relative depth categories and different hydroperiod categories. Two cartographies of radiometric zones are considered, one differentiating four zones (4-ZONE MAP) and the other nine (9-ZONE MAP).

		4-ZONE MAP				9-ZONE MAP			
		Number		Evenness		Number		Evenness	
	N	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
TOTAL	63	2.57	0.78	0.702	0.266	4.08	1.60	0.987	0.416
Relative depth									
Low	26	2.19	0.75	0.565	0.304	3.46	1.48	0.842	0.468
Medium	29	2.69	0.66	0.776	0.191	4.21	1.45	1.049	0.346
High	8	3.38	0.52	0.880	0.148	5.63	1.51	1.232	0.333
Hydroperiod									
Ephemeral	7	2.86	0.90	0.745	0.282	4.29	1.89	1.001	0.489
Intermediate	36	2.44	0.73	0.671	0.263	3.92	1.50	0.983	0.424
Long duration	16	2.63	0.81	0.751	0.295	4.06	1.61	0.985	0.398
Permanent	2	3.50	0.71	0.732	0.188	6.50	2.12	0.968	0.399
Zacallon	2	2.50	0.70	0.701	0.197	4.00	1.41	1.046	0.720

RESULTS

We mapped a total of 1106 ponds, with a minimum pond size of 5 × 5 m. Remote-sensing analyses showed that most ponds contained several radiometric zones, whose mean number was 2.57 (±0.78 S.D.) in the 4-ZONE MAP and 4.08 (±1.60 S.D.) in the 9-ZONE MAP. The number of radiometric zones registered varied significantly with depth (ANOVA, $F_{2,60}$=9.930, P=0.002 in the 4-ZONE MAP and $F_{2,60}$=6.857, P=0.002 in the 9-ZONE MAP), being higher in relatively deeper ponds (Table 1). The number of radiometric zones was not related to differences in hydroperiod (ANOVA, $F_{4,58}$=1.232, P=0.307 in the 4-ZONE MAP and $F_{4,58}$=1.293, P=0.283 in the 9-ZONE MAP) (Table 1). We also found significant differences, according to depth, in radiometric zone evenness, measured as an index of habitat heterogeneity (ANOVA, $F_{2,60}$=7.722, P=0.001 in the 4-ZONE MAP and $F_{2,60}$=3.560, P=0.035 in the 9-ZONE MAP). Habitat heterogeneity increased with relative water depth (Table 1). No differences were found among hydroperiod categories (ANOVA, $F_{4,58}$=0.498, P=0.737 in the 4-ZONE MAP and $F_{4,58}$=0.077, P=0.989 in the 9-ZONE MAP).

Amphibian surveys revealed the presence of 10 species: *Bufo bufo* (Linnaeus, 1758), *Bufo calamita* Laurenti, 1768, *Pelodytes ibericus* Sánchez-Herráiz, Barbadillo, Machordom & Sanchiz, 2000, *Pelobates cultripes* (Cuvier, 1829), *Discoglossus galganoi* Capula, Nascetti, Lanza, Bullini & Crespo, 1985, *Pelophylax perezi* (Seoane, 1885), *Hyla meridionalis* Boettger, 1874, *Pleurodeles*

Table 2. Discrimination ability of amphibian occurrence models, presented as Spearman's correlation coefficients between predicted probability of occurrence and percentage of presences (number of presences/number of surveys). Discrimination ability in cumulative species richness models is presented as Spearman's correlation coefficients between the observed number of species and the predicted number of amphibian species. Nomenclature corresponds to GLM model type: POND = models built from field-assessed characteristics; RM = RADIOMETRIC model = models built from radiometric zones; SEQ = SEQUENTIAL models = model built from field-assessed characteristics and radiometric zones; and maximum number of different radiometric zones considered (4 vs 9).

	Spearman's correlation coefficient				
Response variable	POND	RM4	RM9	SEQ4	SEQ9
Species richness	0.500	0.349	0.199	0.500	0.527
Species occurrence					
Bufo calamita	0.498	0.273	0.146	0.498	0.515
Pelobates cultripes	0.543	0.388	0.261	0.543	0.644
Discoglossus galganoi	0.468	0.230	0.353	0.499	0.440
Hyla meridionalis	0.331	0.250	0.300	0.381	0.449
Pleurodeles waltl	0.430	0.416	0.327	0.430	0.488
Triturus pygmaeus	0.294	0.215	0.360	0.391	0.339
Lissotriton boscai	0.383	0.205	0.060	0.443	0.451

waltl Michahelles, 1830, *Triturus pygmaeus* (Wolterstorff, 1905) and *Lissotriton boscai* (Lataste, 1879). Pond species richness correlated significantly with the number of radiometric zones (Spearman correlation, r=0.476, P<0.001) and habitat heterogeneity (Spearman correlation, r=0.400, P=0.001) in the case of four types of radiometric zones (4-ZONE MAP), but not in the case of the 9-ZONE MAP (number of radiometric zones: Spearman correlation, r=0.249, P=0.051; habitat heterogeneity: Spearman correlation, r=0.191, P=0.136). Habitat use was modelled for seven species. *Pelophylax perezi*, *P. ibericus* and *B. bufo*, present in fewer than 20% of the ponds (12, five and five respectively), were excluded from the analysis due to their low prevalence.

Models of amphibian occurrence based on pond characteristics or exclusively on radiometric zones were not highly predictive (Table 2). Models built only from radiometric variables as predictors (RADIOMETRIC models) produced results of a lower explanatory ability than did models from pond characteristics (POND models) (Fig. 3, Table 3). Sequential models discriminated better than POND models (Fig. 3), although significance was not high (Table 3). Post-hoc Tukey tests did not differentiate sequential models built from radiometric predictors calculated from 4-ZONE MAP from sequential models built from radiometric predictors calculated from the 9-ZONE MAP (SEQ4 and SEQ9), but did differentiate the latter from models only built from pond characteristics (Table 3). Thus, SEQUENTIAL models built from a cartography representing nine radiometric zones significantly improved on POND model discrimination.

A similar pattern was observed when considering species richness as the response variable (Table 2). SEQUENTIAL model discrimination of the nine-radiometric-zone model (SEQ9) was superior to that of more simple models.

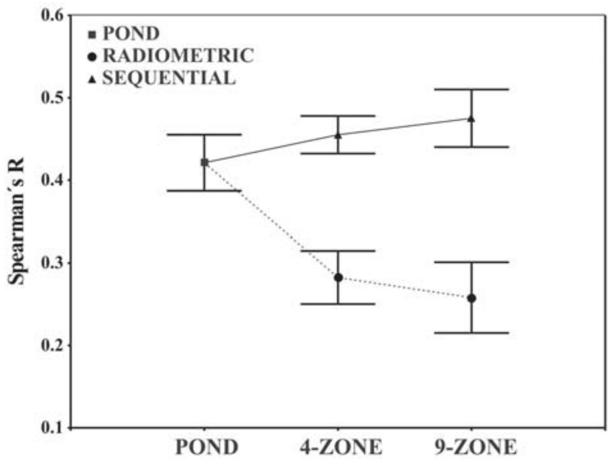

Fig. 3. Mean and standard error of Spearman's correlation coefficients between the predicted probability of occurrence and percentage of presences (number of presences/number of surveys) of seven amphibian species. Three modelling approaches with different sets of predictor candidates were evaluated. Models built from radiometric zones (RADIOMETRIC) were compared with models built from pond characteristics (POND) and with models allowing the inclusion of potential radiometric predictors once explanatory variables of pond characteristics were fixed (SEQUENTIAL). Two cartographies, one representing nine radiometric zones (9-ZONE MAP) and another representing four (4-ZONE MAP), were considered as potential predictors in radiometric and sequential models.

DISCUSSION

The spatial distribution of freshwater habitats should be considered in conservation strategies since it determines the distribution and dynamics of associated species, such as amphibians (Semlitsch & Brodie, 1998; Semlitsch, 2003). We have applied remote-sensing techniques to a high spectral and high spatial resolution image to locate and delineate temporary ponds in an area within the boundaries of Doñana National Park. As recommended by Frazier & Page (2000) with Landsat data, our methodology was mainly based on applying density slicing in a band from the near-infrared part of the spectrum, due to land and water differences in absorption (Lillesand & Kiefer, 1994). We identified 1106 water bodies in an area in which a previous inventory had delineated 84 ponds, with a minimum pond basin of 100 m^2, using visual photointerpretation of orthophotography (Bravo & Montes, 1993). Due to the high spatial resolution of the AHS image, we detected ponds with a smaller size (25 m^2). Since previous studies have reported a mean size of

Table 3. Results from the repeated measures ANOVA analysis comparing the discrimination ability of POND models with that of RADIOMETRIC and SEQUENTIAL models. *F* statistics, degrees of freedom and *P*-values are shown. *P*-values of pairwise posthoc Tukey comparisons are also shown.

	POND models	Posthoc Tukey
RADIOMETRIC models	$F_{2,12}$ = 6.743, P=0.011	POND vs RM4 (P=0.034)
		POND vs RM9 (P=0.014)
		RM4 vs RM9 (n.s.)
SEQUENTIAL models	$F_{2,12}$ = 4.180, P=0.042	POND vs SEQ4 (n.s)
		POND vs SEQ9 (P=0.036)
		SEQ4 vs SEQ9 (n.s)

0.53 ha for amphibian breeding sites in the study area (Gómez-Rodríguez et al., in prep.), we think that the spatial resolution of the AHS image was adequate for the detection of most amphibian breeding ponds. The most important advantage of using remote sensing data in wetland studies is that it can produce spatially explicit information about large areas that may not be achievable using field sampling techniques (Shuman & Ambrose, 2003). In our study area, the field-assessed mapping of such a large amount of temporary ponds would have been prohibited by cost.

Remote sensing also enables the detection of environmental parameters influencing species' habitat selection or indirect predictors of their distribution (Turner et al., 2003). The successful prediction of species distribution with the use of land cover data depends on the characteristics of the species (Kerr & Ostrovsky, 2003; Arntzen, 2006), as some species' habitat requirements may not be identified by remote-sensing techniques. In the present study, the utility of remote-sensing data as an alternative tool to field data differed depending on the level of organization (community-level vs species-level). At community level, it could be used to identify ponds with high species richness by identifying those presenting high habitat heterogeneity. However, at species level, remote-sensing data presented limited utility as a predictor of species distributions when used alone and hardly improved on amphibian distribution models built from field data. In consequence, high-resolution remote-sensing data are not robust enough to identify potential breeding sites for particular species. Nevertheless, the results of our study, carried out in Mediterranean temporary ponds surrounded by sparse vegetation and with inter-annual variation in abiotic characteristics such as size, depth or hydroperiod, should only be extrapolated with caution to other types of water bodies or landscapes. This fact does not diminish the relevance of our results, since monitoring and conservation of Mediterranean temporary ponds is considered a priority (Zacharias et al., 2007).

Our results show that species richness is positively correlated with the number of radiometric zones and with habitat heterogeneity for pond zonation based on coarse identification of radiometric zones (4-ZONE MAP). However, an increase in the number of radiometric zones differentiated within ponds (9-ZONE MAP) yielded non-significant correlations with cumulative species richness. Therefore, amphibian species richness is related to zone numbers and habitat heterogeneity for general classes of microhabitats, but no further specialization is detected with more sensitivity in zone differentiation. So, this result suggests that a broad classification of microhabitats (that are assumed to reflect broad categories, i.e. "*Juncus* spp.", "bare soil", "aquatic macrophytes") works better than a more detailed classification in which such microhabitats are subdivided (i.e. "shallower *Juncus* spp.", "deeper *Juncus* spp."). Using remote sensing, there is no difference in the cost of conducting a 4-ZONE or 9-ZONE classification. However, a broad classification is easier and less costly than a more detailed one if microhabitat zonation is done from field surveys. On the other hand, we tested for differences in the number of zones and habitat heterogeneity among hydroperiod and depth categories. We found significant differences among depth categories, indicating that radiometric zonation probably reflects pond depth zonation , because deeper ponds had a larger depth gradient, and therefore comprised a larger number of radiometric zones and radiometric zone evenness. On the contrary, we did not find differences in either habitat heterogeneity or zone number among hydroperiod categories.

We also studied the relevance of radiometric zones in modelling the distribution of particular amphibian species. Our study shows that radiometric zones were not good predictors of amphibian occurrence *per se* and therefore could not be used for the preliminary identification of species-specific potential breeding sites of interest before field surveys. This result suggests that important habitat characteristics for particular species may not be identified by remote-sensing techniques. On the other hand, for most species, radiometric zones contributed, and were complementary, to general pond characteristics in predicting amphibian occurrence. Hence, at landscape scale, high-resolution remotely-sensed variables are useful additional predictors for the spatial distribution of pond-breeding amphibian species. Analogous results have been reported at larger scales when assessing the contribution of satellite data to topo-climate variables for predictive modelling of trees (Zimmermann et al., 2007; Buermann et al., 2008), mammals (Buermann et al., 2008) and birds (Venier et al., 2004; Buermann et al., 2008). However, these studies show that remote-sensing data were also useful predictors when used alone due to the fact that land cover patterns, obtained with satellite data, are highly correlated with bioclimatic gradients at large scales. Our result agrees with Saveraid et al. (2001), who state that habitat mapping with remote sensing should be complemented with landscape and habitat data collected in the field to predict species occurrences. Although an exhaustive habitat model would require a larger sample size, we think that our sample size was large enough for an initial assessment of the predictive ability of remote-sensing data in amphibian species modelling. Simultaneous field data collection was not possible in this study, so we did not relate radiometric categories to specific amphibian habitats, but rather assessed the predictive ability of remote-sensing data. Nevertheless, we think that our approach is of interest because remote-sensing campaigns performed with other aims (and thus lacking adequate ground-validation data of pond habitats) can provide radiometric information useful for amphibian distribution in similar temporary water systems. Potentially valuable information could be lost if such data were not examined for the purposes of this study.

Studies relating amphibian presence and abiotic characteristics might be biased by the temporal dynamics of amphibian populations (Skelly et al., 1999; Trenham et al., 2003) or their habitats (Skelly, 2001). In these cases, many studies reduced potential errors by considering cumulative fauna of several subsequent breeding seasons rather than annual fauna (Hecnar & M'Closkey, 1996; Houlahan & Findlay, 2003) or by consideration of reference values of temporally variable characteristics (Hecnar & M'Closkey, 1996; Houlahan & Findlay, 2003). Our modelling approach is based on similar assumptions, since we related maximum potential heterogeneity and zonation with the maximum number of species recorded. Nevertheless, we think that an increase in temporal resolution (i.e. seasonal or annual) of the AHS imagery to represent habitat temporal dynamics might model cumulative fauna better than a "static" cartography does, for the latter represents a snapshot of a highly dynamic and stochastic system, as the pond network in Doñana National Park is (Fortuna et al., 2006). We also consider that the study of remote-sensing images from different years would facilitate the assessment of inter-annual variation in habitat extent and condition, which might be related to temporal variation in amphibian communities (Skelly et al., 1999; Trenham et al., 2003). This would be of special relevance in Mediterranean ecosystems, which are characterized by their unpredictability and fluctuations (Blondel & Aronson, 1999; Allen, 2001).

Finally, our models could have been improved with the inclusion of additional explanatory variables that potentially influence amphibian habitat selection at different scales, such as landscape characteristics (Burne & Griffin, 2005; Van Buskirk, 2005; Denoël & Lehmann, 2006). Similarly, an increase in spatial resolution would enable the delineation of very small water bodies, such as rain puddles. This might have improved models of species reported to breed in highly ephemeral water bodies in the study area, such as *B. calamita* or *D. galganoi* (Díaz-Paniagua, 1990).

We conclude that, although remote sensing provided a powerful tool in many species–habitat relationship studies (Gottschalk et al., 2005), it was not useful in pre-identifying species-specific breeding habitats of interest. However, its application to the assessment of habitat heterogeneity could be used as a proxy to identify, prior to field surveys, ponds supporting high species richness, which should be preserved and monitored. The remote assessment of potential habitats of interest has special relevance in large areas with a high density of water bodies, such as Doñana National Park (Díaz-Paniagua et al., 2006), where exhaustive survey and monitoring programmes cannot be conducted and sampling effort has to be optimized. On the other hand, the inclusion of remote-sensing data in medium-term conservation programmes could provide valuable information to assess changes in habitat heterogeneity over time that might even be associated with habitat degradation. Finally, we also acknowledge the potential of high-resolution remote-sensing data for the assessment of the spatial distribution of breeding habitats, which is of special relevance for amphibian dynamics at regional scales, and should be considered in conservation strategies (Semlitsch & Brodie, 1998).

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