

Reproductive dynamics of three amphibian species in Mediterranean wetlands: the role of local precipitation and hydrological regimes

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SUMMARY

1. Although the influence of water availability and precipitation regimes on amphibians has been studied at large scales, whether and how interannual rainfall and hydrological variations affect amphibians dynamics at a local scale have rarely been addressed. In this respect, accounting for variations in species detectability in space and time has also been overlooked.
2. We assessed the effects of rainfall and hydrological variations on the breeding dynamics of three amphibian taxa: *Pelodytes punctatus*, *Hyla meridionalis* and *Pelophylax* spp. in 20 ponds of the Camargue region (southern France) over a 7-year study period.
3. We used multiple season occupancy models to test the effect of winter–spring rainfall and interannual variations in hydroperiod, mean water depth and drought events on tadpole presence in spring (March–June), a proxy for breeding dynamics.
4. We used an independent survey with spatial replicates (dipnet sweeps) to disentangle the relative contributions of phenology and detectability to the absence of records in a given month. For the three taxa considered, the probability of missing a species when that species was actually present in a pond was most often negligible. Hence, we could consider that multiseason models properly tracked changes in species phenology.
5. *Pelodytes punctatus* was first detected in March, while the two other taxa appeared later in April. *Hyla meridionalis* appeared as a mid-season species with much more synchronous pond occupancy than *Pelodytes punctatus*. The detection peak of *Pelophylax* spp. was short and unexpectedly early for this taxon.
6. Seasonal winter–spring rainfall was associated with a decrease in extinction rates and even more strongly with an increase in colonisation rates at individual ponds.
7. Colonisation rate increased following an annual drought and was best modelled as a negative quadratic effect of the variance of pond hydroperiod. Extinction probability was best modelled by a negative quadratic effect of mean water level. Hence, breeding was more stochastic (i) in unpredictable and shallow ponds because of yearly drying up and (ii) in highly predictable and deep ponds, possibly due to the presence of predators such as fish and crayfish.
8. Overall, we show that ponds with intermediate rather than extreme variations in environmental conditions currently correspond to optimal breeding sites. Our study demonstrates that amphibian monitoring coupled with fine-scale analysis of environmental conditions is necessary to understand species dynamics in the long run and to inform conservation efforts for these species.

Keywords: habitat unpredictability, Mediterranean, occupancy models, ponds, tadpoles, turnover

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Introduction

Environmental predictability is known to affect species life-history traits (Southwood, 1977; Switzer, 1993; Braby, 2002). In particular, in unpredictable environment, species must adopt specific breeding strategies (e.g. diapause, skipping) because of the risk of reproductive failure (Simeone *et al.*, 2002; Lehikoinen, Kilpi & Öst, 2006). In such environments, variable conditions typically generate spatially and temporally heterogeneous patterns of reproduction that may be described as local colonisation and extinction dynamics (Peltonen & Hanski, 1991). Modelling those two processes from long-term data is a key to better understanding of how environmental unpredictability shapes reproductive strategies of species.

In this respect, studying the reproduction of pond-breeding amphibians is particularly straightforward. These species typically thrive in widely varying environments (Joly & Morand, 1994; Morand & Joly, 1995). To reduce predation pressure at the larval stage, many amphibian species breed in fish-free habitats that exhibit large fluctuations of their flooding conditions (Hecnar & M'closkey, 1997; Smith *et al.*, 1999). However, such a strategy is also risky as the drying up of those habitats before larval metamorphosis can lead to a seasonal failure of reproduction (Newman, 1992). Because reproductive effort and success of amphibians directly depend on the availability of fresh water (Rowe & Dunson, 1993; Jakob *et al.*, 2003), we expect both rainfall and hydrological regimes to have a major impact on breeding dynamics. This may be even more important in dry climates such as the Mediterranean one under which pond flooding strongly varies at intra- and interannual scales (Gomez-Rodriguez, Bustamante & Diaz-Paniagua, 2010a). Such a heterogeneous and unpredictable system leads to large variation in the yearly composition of amphibian communities (Gomez-Rodriguez *et al.*, 2010b,c).

Most studies dealing with the impacts of water availability on the structure of amphibian communities have been based on restricted study periods. However, assessing such effects from a short-time scale is unsatisfactory when the studied animals are expected to experience repeated breeding failures during their lifetime. In this paper, we evaluate the impacts of winter–spring rainfall and hydrological variations on the breeding dynamics of amphibians at the time horizon of at least one generation of breeders. To address this question, we analysed the breeding dynamics of three amphibian taxa – *Pelodytes punctatus*, *Hyla meridionalis* and *Pelophylax* spp. – in a Mediterranean wetland system, the Camargue (southern France) over a 7-year study period (2004–2010). The 7-year

sampling period covers at least one generation of breeders as suggested by the life span of the three target species or of closely related taxa (c. 4–7 years; Pellet, Helfer & Yannic, 2007; Erişmiş *et al.*, 2010; Serkan *et al.*, 2011). Since amphibian breeding patterns vary over space and time (Fortuna, Gomez-Rodriguez & Bascompte, 2006; Werner *et al.*, 2007), their reproductive dynamic can be modelled in terms of turnover rate (local colonisation and extinction) that reflects variations in pond occupancy (used or not used for reproduction) among breeding seasons. We used multiple season occupancy models (Mackenzie *et al.*, 2003) to estimate the probability of tadpole presence while accounting for imperfect detection in space and time.

We specifically tested the following predictions. (i) Because rainfall influences amphibian population trends at a large scale (Alford & Richards, 1999), we expected tadpole presence to vary with annual rainfall at the local scale. Therefore, we tested the effect of winter–spring rainfall on breeding occurrence. (ii) Classically, stability and predictability of flooding conditions impact the structure of amphibian communities (Babbitt, 2005; Baber, Babbitt & Tarr, 2003). We thus expected breeding dynamics to be affected by mean water level and predictability of flooding duration at the time scale of a breeder generation. Therefore, we tested the effect of mean water level and variance of hydroperiod (a proxy for predictability of the flooding duration). (iii) We expected *Pelodytes punctatus* to be more sensitive to rainfall and to prefer ponds with shorter hydroperiod (Beja & Alcazar, 2003; Richter-Boix, Llorente & Montori, 2007), than the *Pelophylax* spp. complex which is more dependent on permanent ponds (Diaz-Paniagua, 1990; Richter-Boix *et al.*, 2007; Gomez-Rodriguez *et al.*, 2009). *Hyla meridionalis* should be moderately affected and fall between these other two taxa in terms of sensitivity to rainfall and hydroperiod (Richter-Boix, Llorente & Montori, 2006).

Methods

Study area and sampling

The study was conducted at the Tour du Valat nature reserve (Lat. 43°29'N, Long. 4.39'E) in the Camargue, southern France (Fig. 1). The reserve covers 2600 ha of salt steppes, Mediterranean lawns and forested patches and includes 118 ponds with various hydroperiod regimes (detailed below). Ponds can also differ according to their size, origin (natural or artificial) and management (managed or not). In 2004, we randomly selected 20 ponds representative of the diversity of the 118 ponds regarding these major characteristics. There was no difference

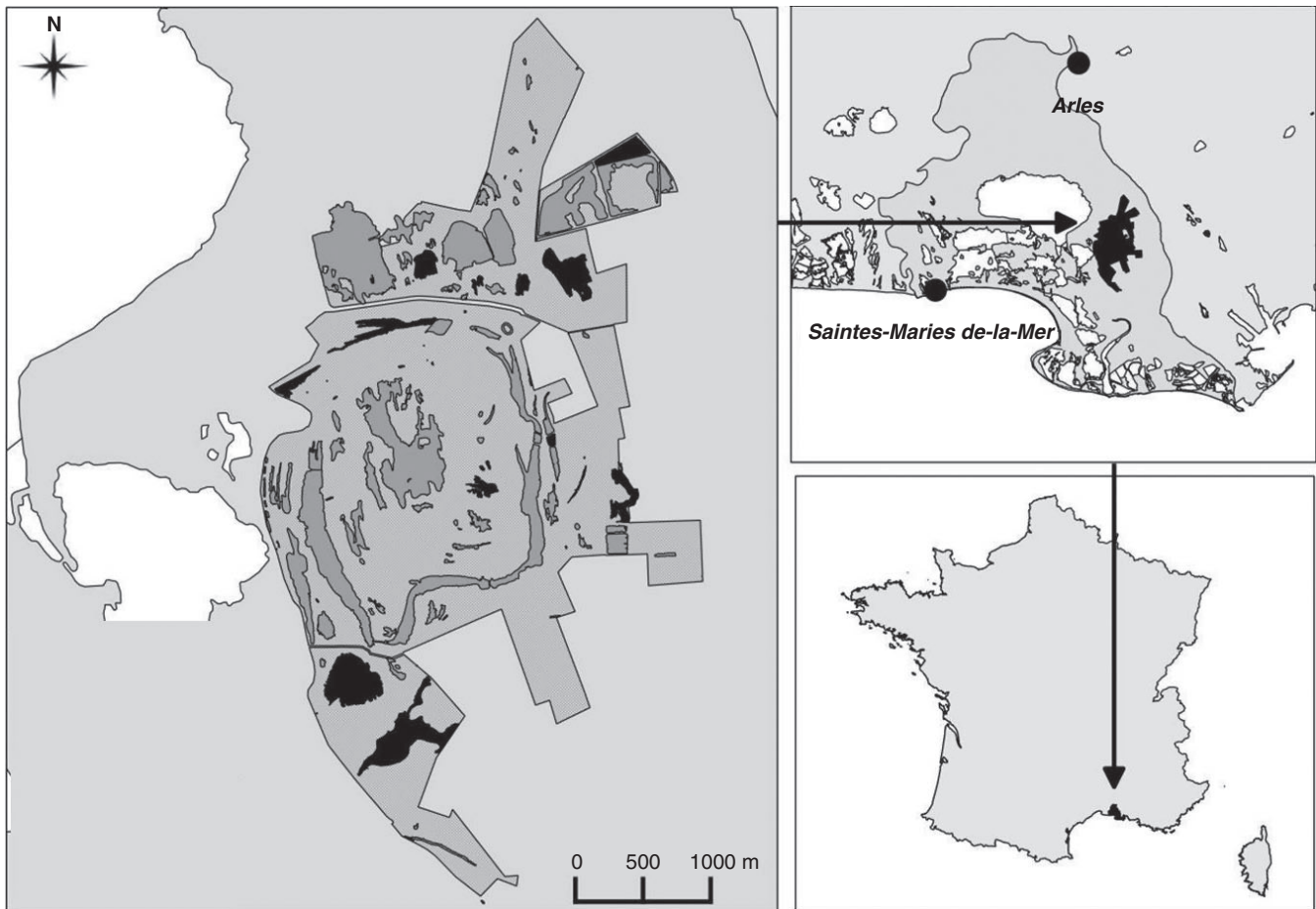


Fig. 1 Location of Tour du Valat estate in the Camargue (southern France) with its network of ponds (in dark grey) shown in the left-hand panel of the figure. The 20 ponds sampled are shaded in black.

between the 20 sampled ponds and the 118 ponds regarding their maximal flooding area ($\chi^2 = 1.15$, d.f. = 2, $P = 0.5$), origin (two modalities: artificial and natural ponds; $\chi^2 = 0.19$, d.f. = 1, $P = 0.65$) or management (two modalities: artificial or natural flooding; $\chi^2 = 2.3$, d.f. = 1, $P = 0.12$). The area (surface area at the maximum of flooding) of the 20 ponds considered varied from 0.08 to 33.5 ha (Fig. 1). Rainfall, proportion of pond drying up, mean pond water level and hydroperiod varied widely across years (Fig. 2).

Amphibian breeding surveys were conducted from 2004 to 2010 by the same observer. The twenty ponds were sampled five times per year (March, April, May, June and November) to track the phenology of the whole amphibian community in the study area. During each visit to a given pond, 15 consecutive dipnet sweeps were performed on a fixed line transect, from the edge of the pond towards its centre. The distance between dipnet sweeps was standardised to 1.5 m. All captured tadpoles were identified, counted and then released at the end of

the sampling visit. The numbers of individuals for each species were pooled within each visit. To assess finer seasonal variation in detection probability that could result from phenology, individuals of each species were separately counted for each single dipnet sweep in 2009 (see Data analyses). Eight taxa were captured: *Lissotriton helveticus*, *Pelodytes punctatus*, *Hyla meridionalis*, *Pelobates cultripes*, *Bufo calamita* and Ranid species. The three Ranid species *Pelophylax perezi*, *Pelophylax kl. grafi* and *Pelophylax ridibundus* were pooled into a generic genus (*Pelophylax* spp.) since these species cannot be discriminated at the tadpole stage. Only samples from March to May for *Pelodytes punctatus* and from April to June for *Hyla* and *Pelophylax* spp. were sufficiently large to be used for the subsequent analyses.

At each visit, the presence or absence of water in the pond was noted and the maximum water level of the ponds was recorded using a tape measure. The annual hydroperiod was estimated by the number of months during which the pond was flooded.

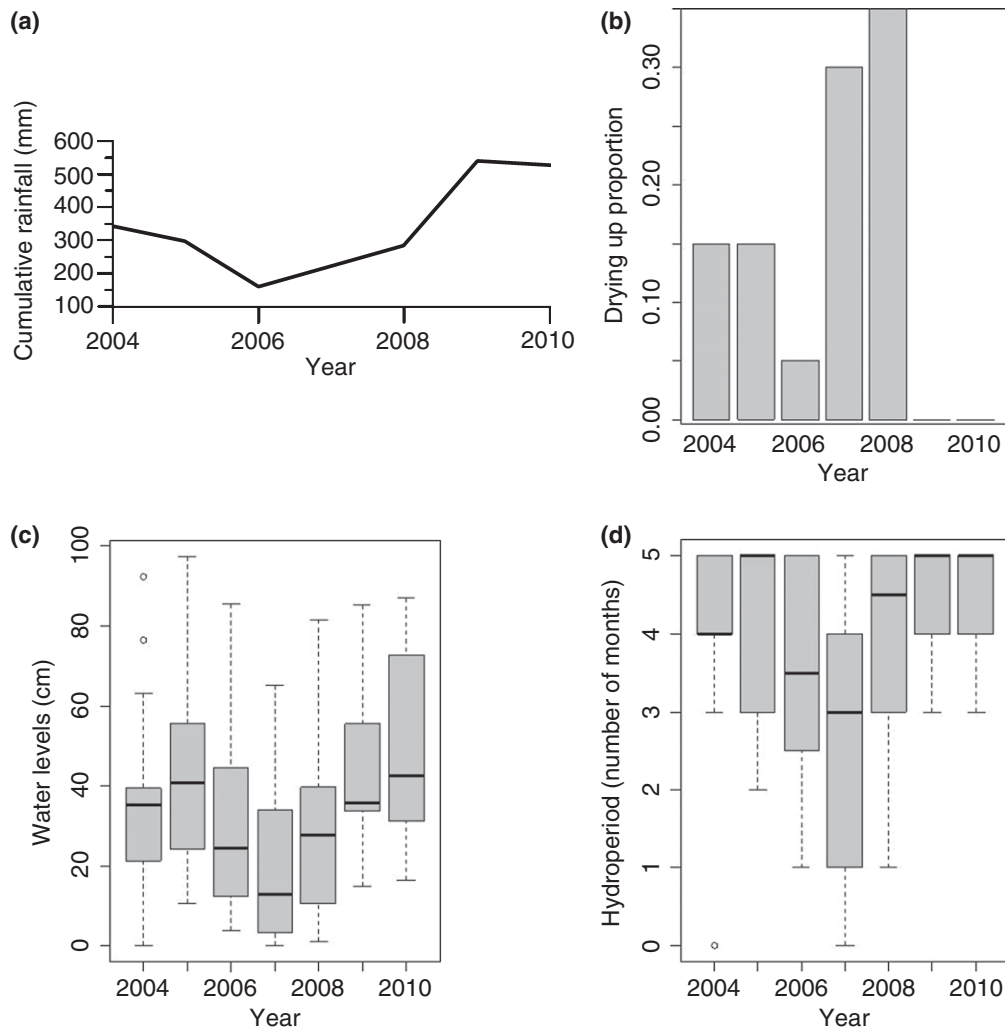


Fig. 2 (a) Winter–spring rainfall accumulation, (b) proportion of ponds drying up, (c) mean pond water level and (d) mean pond hydroperiod recorded during the 7-year study period (2004–2010) of the occupancy of three amphibian species in the Camargue (France). Pond hydroperiod is the number of months a pond was flooded during the February–June period (corresponding to the breeding phenology of the amphibians in the study area).

Data analyses

Several studies have shown that amphibian detection is usually < 1 and varies according to space and time (Mazerolle *et al.*, 2007; Curtis & Paton, 2010; Gomez-Rodriguez *et al.*, 2012). This imperfect detectability is generally due to habitat characteristics (Mazerolle *et al.*, 2007), phenology of the species of interest or sampling design properties (Heyer *et al.*, 1994; Bailey, Simons & Pollock, 2004). Hence, during a given sampling visit, we had to account for the possibility that a given species could be present but not detected. We used multiseason occupancy models (Mackenzie *et al.*, 2003) that take into account such imperfect detection of the targeted species and provide a useful approach for studying meta-population or patchy population dynamics. This model

structure is equivalent to the Pollock's Robust Design classically used in capture–mark–recapture models (Pollock, 1982). The survey consists of replicates of N primary sampling sessions between which changes in occupancy through local extinction (ϵ) and colonisation (γ) may occur (Mackenzie *et al.*, 2003). Each primary period includes several secondary sampling sessions during which the sites are considered to be closed (i.e. no changes in occupancy should occur among these secondary sampling sessions). In our sampling design, the secondary sampling sessions are the three visits made in spring each year which allow the estimation of yearly detection probability, while the primary sampling sessions are the annual surveys, which allow the estimation of occupancy, local extinction and colonisation probabilities from 1 year to another. Note that in our case, local extinction and colonisation rates do

not represent population vital rates but the interannual dynamics of pond occupancy for breeding.

In multiseason occupancy modelling, one of the most important statistical assumptions is that the sites are closed to changes in occupancy during a given primary sampling session (Mackenzie *et al.*, 2002). This assumption is essential since in a typical capture history containing at least one encounter, the 0 (if any) must result from detection failures (and not true absences) in order properly to estimate detection probability. Our survey clearly does not fulfil this condition since reproduction and larval phenology induce intraseasonal variations in pond occupancy. In other words, the absence of a species in a given month in a pond which is known to have been occupied over the breeding season may result either from the species having been missed by the observer while it was present, or from its true absence because breeding has not started or is already finished. Acknowledging this potential issue, recent studies of amphibian pond occupancy have used the multiseason approach (Hossack & Corn, 2007) assuming that modelling time-specific detection probabilities for each secondary session overcome the restriction to assume the 'closed-site' hypothesis. However, this strategy may still provide biased estimates of detection when availability and detectability are not constant through time.

In fact, the monthly detection probability modelled using time-specific models is a mixture of the probability to be available for detection (so-called *availability* in the robust design context) and of detection given that the species is actually available for detection (so-called *detectability*). Availability and detectability probabilities can be separately estimated only when using robust design approaches or if these two probabilities can be assessed independently in a period of time short enough for local extinction and colonisation to be negligible. In our situation, this would necessitate a two-level robust design, that is, yearly open primary sessions, monthly open secondary sessions and for instance daily closed tertiary sessions. Unfortunately, as is often the case in amphibian studies, we do not have repeated detection events over very short periods such as days to build such models. However, in 2009, the presence of each species was recorded separately for each dipnet sweep instead of being pooled and recorded for each secondary session. This data set allowed modelling detection probability given that the species is available for detection, that is, detectability. If detectability is close to 1, then monthly detection probability estimated in the multiseason models will reflect the variations in availability. In such situation, monthly detection and occupancy probabilities are unbiased.

We thus first constructed single-season occupancy models using the 2009 data set for each target species (*Pelodytes punctatus*, *Hyla meridionalis*, *Pelophylax* spp.) and each monthly visit (Table S1). We used each of the 15 consecutive dipnet sweeps of a single visit as distinct spatial replicates. Each sweep was considered as a secondary sampling unit within a given pond and a substitute for a temporal subset (e.g. Kendall & White, 2009). This design is equivalent to a sampling without replacement in that a sampled location (here a point on the line transect) cannot be resampled a second time within a visit. As shown by Guillera-Arroita (2011), sampling without replacement does not induce bias in the estimator of site occupancy when each spatial subunit has a constant probability of occupancy, regardless of the occupancy status of other subunits within the same sampling site. All sweeps were separated by 1.5 m, but randomly regarding pond vegetation for instance. Moreover, we did perform 15 dipnet sweeps, which means that the dipnet sweeps are spread over 22.5 m across the ponds. It is highly unlikely that tadpole captures and occupancy would be correlated over such a long distance. We then used single-season modelling (Mackenzie *et al.*, 2002) to estimate tadpoles' detectability from this 2009 data set.

After having ascertained the closed-site assumption, we then ran multiseason occupancy modelling using the global data set (7-year, 20 ponds and monthly records) including the three species as a group effect so that parameters that would not be species-specific could be modelled across species with higher statistical power. This also permitted us to test possible species-specific differences within a single-model selection process.

All models were run using the Unmarked library (Fiske *et al.*, 2010) in R 2.12 statistical software (R Development Core Team, 2011). Four parameters were estimated directly: (i) (ψ) the probability that amphibian reproduction occurs in a site during the 1st year of the survey (2004), (ii) (ε) the probability that a breeding site is abandoned from year t to $t+1$, (iii) (γ) the probability that an unoccupied site becomes a breeding site from year t to $t+1$ and (iv) (P) the probability to detect at least one tadpole a given year. Annual pond occupancy was iteratively computed using the initial occupancy (ψ) and the transition parameters (extinction and colonisation rates, respectively), following Mackenzie *et al.* (2003):

$$\Psi_{(t+1)} = \Psi_{(t)} (1 - \varepsilon_{(t)}) + (1 - \Psi_{(t)}) \gamma_{(t)}$$

Parameters were estimated through three successive steps. In a first step, we modelled detection probability by

comparing five candidate models (see Table S2 step 1 for each model and their justifications). For this step (ψ), (γ) and (ϵ) parameters were held constant. In a second step, starting from the best structure selected for detection probability, we modelled initial occupancy (Table S2 step 2) while holding (γ) and (ϵ) constant. In a third step, we tested several scenarios on transition rates using the parameters (p) and (ψ) of the best-selected model (Table S2 step 3). Model comparisons were performed using AIC_c (Burnham & Anderson, 2002). The relative support for each of the models was assessed using Akaike weight (w ; Burnham & Anderson, 2002).

Finally, we evaluated whether the modelling of amphibian breeding dynamics could be improved by including the effects of several environmental covariates. We first evaluated the effects of hydroperiod (H04) and water level (WL04) in 2004 on the initial occupancy (ψ). We also evaluated whether initial occupancy (ψ) was species-specific (SP04). Colonisation (γ) and extinction (ϵ) were then modelled as a function of (i) winter–spring cumulative rainfall (R) calculated from the monthly values (from November to June) recorded at the Tour du Valat meteorological station, (ii) the mean water level of the pond over the 7-year period (WL), (iii) the hydroperiod variance over the 7-year period var(H) and (iv) a dummy variable for pond drying up over a breeding season (D); a null value of pond drying up ($D = 0$) indicated that the site was unavailable for spawning because of the lack of water. As species may exhibit nonlinear response to environmental variations, we tested for quadratic and logarithmic effects of these variables on both occupancy and transition parameters.

Potential correlation of pond covariates was explored to avoid entering combinations of correlated covariates in

models. Water level and hydroperiod were highly correlated (Pearson's correlation tests, $r = 0.71$, $t = 7.61$, d.f. = 58, $P < 0.001$). Semi-variograms plotted for each variable (Ord and Getis, 1995) did not indicate the presence of spatial autocorrelation. We therefore considered that sites were spatially independent in all analyses.

Results

Overall, 6939 tadpoles were captured over the 7-year study. The total number of captured tadpoles varied widely among years (mean per year and SD = 694 ± 770), between and within species. In *Hyla meridionalis* (total number = 4324, mean per year and SD = 618 ± 618), which is the most abundant species in our sample, the number of tadpoles captured ranged from 149 in 2006 to 2503 in 2010. *Pelophylax* spp. (total number = 448, mean per year and SD = 64 ± 601) and *Pelodytes punctatus* (total number = 222, mean per year and SD = 32 ± 35) were less well represented. The number of *Pelophylax* spp. tadpoles captured ranged from 3 in 2007 to 96 in 2010, while the number of *Pelodytes punctatus* tadpoles ranged from 4 in 2007 to 206 in 2010. Breeding events may occur in November in *Pelodytes punctatus* and *Pelophylax* spp, but they have not been included in our analyses since we only recorded such events in 2004 (*Pelodytes punctatus*, 74 tadpoles; *Pelophylax* spp, 2 tadpoles).

Single-season modelling in 2009

For the three taxa considered, the probability of missing a species given it is present after 15 dipnet sweeps ($(1-p)^{15}$) was systematically < 0.05 and often < 0.001 except for *Pelophylax* spp. in May, when it was 0.40 (Table S1; Fig. 3).

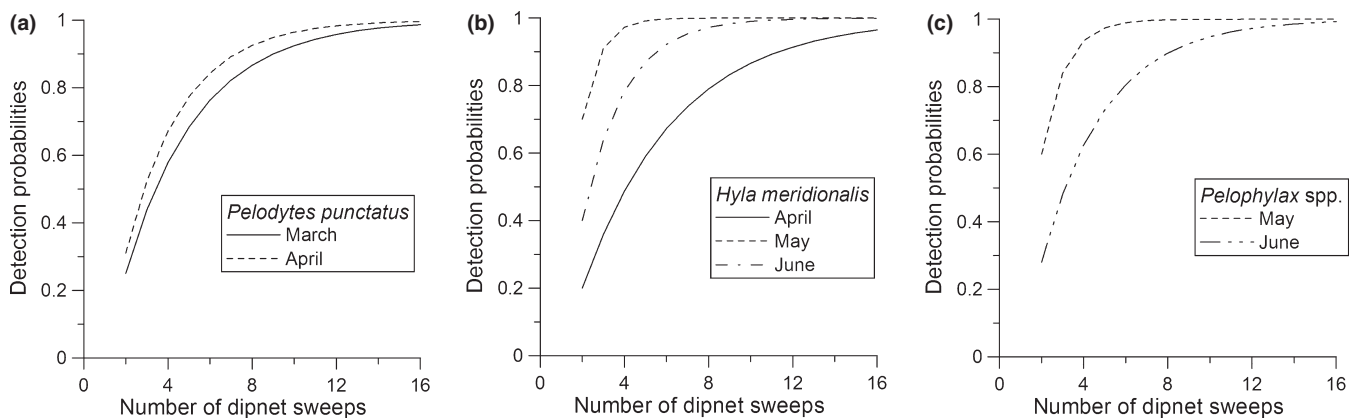


Fig. 3 Detection rates of the three target amphibian species (a, b, c) according to the number of dipnet sweeps as estimated by the single-season model run for the 2009 data set.

In this case, the low detection rate was caused by an extremely low abundance. Hence, the sampling protocol successfully detects a species given it is present in a pond almost all the time. In turn, we can consider that the 0s of our data set correspond to real absences (unavailability for detection) and that the monthly detection probabilities estimated by the multiseason approach directly reflect the changes in species availability due to phenology.

Multiseason modelling

As expected, pond occupancy rate varied widely over the 7-year study period with a marked decline down to 0.29 and a subsequent increase up to 0.71 (Fig. 4). Availability (P , as modelled by detection probability in the multiseason model) varied between species and across the 3 monthly visits (Table S2, Step 1, Model 1: $AIC_c = 951.15$, $w = 1.00$). The model including the interaction between species and month was much better than the additive model ($\Delta AIC_c = 57.3$). This is consistent with field observations and the result of single occupancy modelling for the individual species. Availability of *Pelodytes punctatus*, the first species to colonise breeding ponds, increased throughout the season from 0.14 (C.I. 95% = 0.07–0.25) in March to 0.45 (0.33–0.59) in April and 0.50 (0.37–0.63) in May. *Hyla meridionalis* is a mid-season species and was more available than *Pelodytes punctatus*. Its availability was estimated as 0.14 (0.08–0.24) in April, 0.95 (0.89–0.98) in May and 0.79 (0.61–0.90) in June. Finally, the availability of the *Pelophylax* complex was 0.32 (0.27–0.45) in April, 0.82 (0.65–0.92) in May and 0.14 (0.03–0.45) in June.

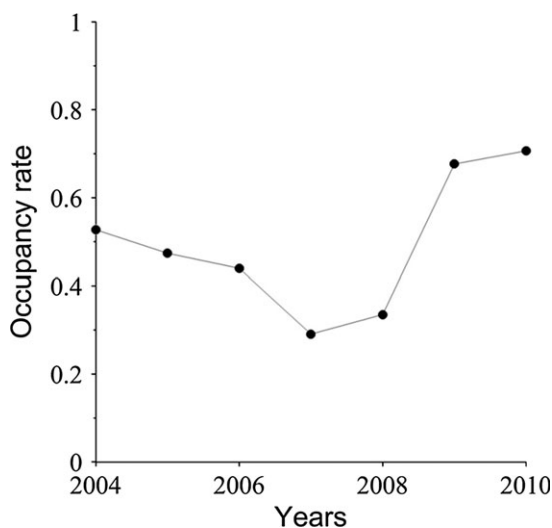


Fig. 4 Changes in pond occupancy rates by three amphibian taxa (*Hyla meridionalis*, *Pelodytes Punctatus* and *Pelophylax* spp.) from 2004 to 2010 in the 20 ponds studied in the Camargue (France).

There was no evidence of any covariate influencing initial occupancy (Table S2, Step 2, Model 1: $AIC_c = 951.15$, $w = 0.27$). Thus, covariate effects on initial occupancy were small or not significant. In addition, the species-dependent model did not receive a high degree of support ($\Delta AIC_c = 4.85$), suggesting that the initial occupancy probabilities of ponds were identical for the three taxa. Additional species-specific multiseason occupancy models run to ascertain this result confirmed the absence of significant difference among species (see Fig. S1). Thus, we retained the (ψ) constant model for the following step.

Transition rates were not species-specific, and the best model included several additional covariates. Quadratic effects of hydroperiod variance and depth on γ and ϵ , respectively (Table S2, Step 3, Model 1: $AIC_c = 934.84$, $w = 0.61$), and a logarithmic effect of the cumulative rainfall on both transition parameters provided a better fit for the data (Table S2, Fig. 5a,b). As expected, important rainfall events during the winter–spring period (November–June) positively influenced the colonisation probabilities of breeding sites and decreased extinction probability. Furthermore, drying up of a breeding site in 1 year positively affected its colonisation rate the following year (γ). Water levels and the variance of pond hydroperiod also affected turnover rates (i.e. colonisation and local extinction), although differently for each transition parameter. Indeed, a quadratic effect of the average water level improved the modelling of extinction probability, suggesting that ϵ was higher for sites with extreme values of water levels (low and high) than for sites with intermediate water levels (Fig. 5c). Likewise, colonisation was best modelled by a quadratic relationship with the variance of pond hydroperiod (Fig. 5d), suggesting the existence of an optimal hydroperiod maximising colonisation.

To ascertain that these effects were not generated by a single species driving the result of the models, we artificially inflated the species-specific data set by bootstrapping 1000 times the original data sets to generate virtual data sets of 20, 40, 60 and 80 ponds. This approach allowed the evaluation of the power to detect the effect of a covariate on each species separately. For each virtual data set generated, we calculated the number of times the covariates was significant. Whereas the power to detect the effects was low in species-specific data sets, the covariates were significant in 80–90% of the bootstraps when the virtual data set included 60 ponds (see Table S3). This number of ponds remains small confirming that the effects were present for the three species. Species-specific responses to these effects also confirm a similar response of the three species (see Fig. S2).

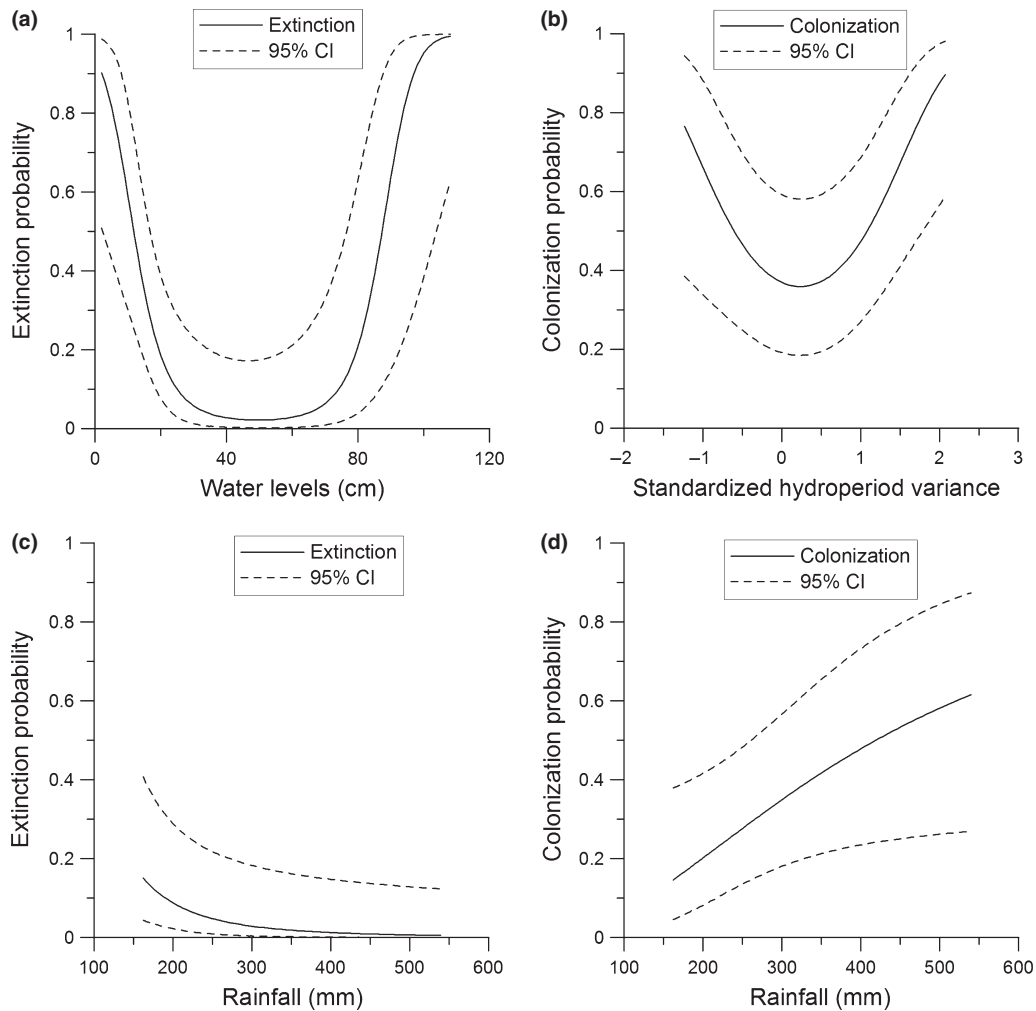


Fig. 5 Turnover probabilities according to winter–spring rainfall: (a) extinction probability and (b) colonisation probability. Turnover probabilities according to the standardised variance of pond hydroperiod and water level: (c) extinction probability and (d) colonisation probability (continuous line) and 95% confidence intervals (broken line). Continuous lines indicate probabilities, and broken lines show 95% confidence intervals.

Discussion

Our results show that precipitations, hydroperiod variations and water levels affect the local breeding colonisation and extinction of three amphibian species in the Camargue, southern France. These results take into account possible bias resulting from imperfect detection, one of the most important issues in ecology and conservation (Mackenzie *et al.*, 2002; Defos Du Rau, Barbraud & Mondain-Monval, 2005). This was carried out using multiseason occupancy models that represent an increasingly popular approach for this kind of data (Mackenzie *et al.*, 2003; Hossack & Corn, 2007). However, separating the probability of being available for detection (*availability*) and the probability of detection given availability (*detectability*) is not usually examined. By using an independent survey with spatial

replicates (dipnet sweeps), we ascertained that the zeros in our multiseason data set truly corresponded to unavailability for detection and not to the lack of detection given that all the species were detectable. This complementary analysis allowed us to show that the detection probability of the species given it is present was close to 1 for a given month within an annual survey. We could therefore be confident that the detection probability modelled in the multiseason models directly reflected the phenology of the species, a hypothesis rarely tested in previous studies.

Over the 7-year study, *Pelodytes punctatus* was the earliest detected species (in March), while the two other groups appeared later (in April). *Pelodytes punctatus* is known to exhibit high plasticity in terms of reproductive phenology (Guyétant, Temmermans & Avriillier, 1999; Jakob *et al.*, 2003; Richter-Boix *et al.*, 2006), which is

possibly reflected here by its low detection rate at the activity peak of tadpoles ($P = 0.45$, $P = 0.50$, in April and May, respectively). While a secondary peak of reproduction is usually registered in November (Jakob *et al.*, 2003), in the Camargue such late breeding activity appears to be facultative (during the study period only in 2004 and 2005) and less productive than in spring (total number of tadpoles captured during the 7-year period = 90, which represents only 20% of the overall production). In the study area, *Hyla meridionalis* appeared as a mid-season species with a much more temporally limited pond occupancy period than *Pelodytes punctatus* as shown by the very high values of detection at the activity peak of tadpoles in May ($P = 0.95$). Indeed, this species is expected to be more thermophilic than *P. punctatus* (Richter-Boix *et al.*, 2006). While it has been shown that *Hyla meridionalis* tadpoles sometimes occur in March in southern France (Jakob *et al.*, 2003), we did not find any evidence that this species was active at larval stage during this period in the Camargue (tadpoles were never captured in March over the 7-year study). In our case, the peak of *Pelophylax* spp. tadpoles was in May ($P = 0.82$), which is congruent with Richter-Boix *et al.* (2007). However, the peak appears to be surprisingly short; the species is known to breed from spring to summer in other Mediterranean ponds (Jakob *et al.*, 2003). The number of captured tadpoles was always very low for this species (< 260 captured during the complete study period), although it is known to produce high numbers of eggs (in *Pelophylax ridibundus*, from 1199 to 13252 eggs for the absolute fecundity of females, see Ivanova & Zhigal'ski, 2011). This discrepancy may result from the *Pelophylax* assemblage being at the edge (suboptimal habitat) of its habitat preference as these species require long hydroperiods (Richter-Boix *et al.*, 2007).

Low cumulative winter–spring rainfall may result in spatial contraction of breeding activity, which is then restricted to a few ponds. In turn, high rainfall events permit spatial expansions as reflected by the increase in occupancy rate in the last years of our study. This pattern is widespread in amphibians (Salvador & Carrascal, 1990; Donnelly & Crump, 1998; Gomez-Rodriguez *et al.*, 2010b,c). In dry years, adults may limit their investment in reproduction or even skip reproduction (Pechmann *et al.*, 1991; Diaz-Paniagua, 1998). Lack of precipitation is also expected to reduce the dispersal ability of amphibians (Spieler & Linsenmair, 1998), especially when they have to cross unsuitable terrestrial habitats like salt steppes or dry lawns in order to reach breeding sites. Here, colonisation increased with winter–spring rainfall. Indeed, extinction probabilities increased from 0 to 0.15

(95% CI 0.04–0.41) when cumulative rainfall decreased from 543 to 169 mm, while colonisation probabilities increased from 0.15 (0.04–0.38) to 0.61 (0.29–0.87) when cumulative rainfall increased from 169 to 543 mm. This unbalanced response to rainfall explains why the study area supported more occupied breeding sites in 2010 than it did 6 years before in 2004.

We also found that the turnover (i.e. both the extinction and colonisation rates) was high in predictable-deep ponds (low hydroperiod variance and high mean water level) and unpredictable-shallow ponds (high hydroperiod variance and low mean water level). In unpredictable-shallow ponds, such changes are linked to frequent drying up that makes reproduction more uneven. In the predictable-deep ponds, breeding presence is more irregular, presumably due to the presence of unfavourable hydrophytic vegetation (Grillas & Battedou, 1998) and predators, such as fish (Petranka *et al.*, 1987; Brönmark & Edenhamn, 1994; Hecnar & M'closkey, 1997) and crayfish (Gherardi, Renai & Corti, 2001; Cruz, Rebelo & Crespo, 2006) that are known to affect amphibian richness and distribution. It is also confirmed by the small number of tadpoles captured in those ponds (< 20 tadpoles ever recorded during the 7-year period). It consequently suggests that reproduction of the three target species is more constant at sites corresponding to an intermediate position on the gradient of stability and predictability of flooding conditions. In this respect, our results are in accordance with many studies that have shown that flooding duration has a wide-ranging impact on amphibian communities (Pechmann *et al.*, 1989; Snodgrass *et al.*, 2000; Baber *et al.*, 2003). For instance, Heyer, Mcdiarmid & Weigmann (1975), Wilbur (1984) and Werner *et al.* (2007) demonstrated that amphibian species richness may exhibit a unimodal curve which peaks at intermediate hydroperiod.

In our study, we did not find any evidence for species-specific differences in initial occupancy rate nor in local colonisation/extinction probabilities. Concerning initial occupancy, we suspect that such an effect was not detected because (i) *Pelodytes punctatus* and *Hyla meridionalis* occupied the sites in the same proportion in 2004 (between 50 and 60%; see Fig. S1) and ii) the occupancy rate of *Pelophylax* spp. marginally differed from the occupancy of the two other taxa (0.36). Our results also suggest that the three taxa responded similarly to water availability and hydrological variation in the combined analysis (i.e. multiple occupancy model including the three target species). This is confirmed by the species-specific analysis (see Fig. S2). If the different species dynamics were influenced by different covariates, we may not have been able to detect any covariate effect on

dynamic. Indeed, the combination of different species together would have inflated the heterogeneity in the data set and thus reduced our power to detect any relationship.

To conclude, analysing the variations in site occupancy status provides an interesting and relevant approach to assess the underlying mechanisms involved in the organisation of animal communities within space and time. In species that breed in fluctuating environments, and especially amphibians, such studies are crucial to understand better how random variations in several environmental components are expected to influence reproductive dynamics. It is also a key point to help conservation of these species through an adequate management of breeding sites facing anthropogenic disturbances and the expected impacts of global changes.

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References

- Alford R.A. & Richards S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics*, **30**, 133–165.
- Babbitt K.J. (2005) The relative importance of wetland size and hydroperiod for amphibians in southern New Hampshire, USA. *Wetlands Ecology and Management*, **13**, 269–279.
- Baber M.J., Babbitt K.J. & Tarr T.L. (2003) Patterns of larval amphibian distribution along a wetland hydroperiod gradient. *Canadian Journal of Zoology*, **81**, 1539–1552.
- Bailey L.L., Simons T.R. & Pollock K.H. (2004) Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*, **14**, 692–702.
- Beja P. & Alcazar R. (2003) Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. *Biological Conservation*, **114**, 317–326.
- Braby M. (2002) Life history strategies and habitat templates of tropical butterflies in north-eastern Australia. *Evolutionary Ecology*, **16**, 399–413.
- Brönmark C. & Edenhamn P. (1994) Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? *Conservation Biology*, **8**, 841–845.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New-York.
- Cruz M.J., Rebelo R. & Crespo E.G. (2006) Effects of an introduced crayfish, *Procambarus clarkii*, on the distribution of south-western Iberian amphibians in their breeding habitats. *Ecography*, **29**, 329–338.
- Curtis A.E. & Paton P.W.C. (2010) Assessing detection probabilities of larval amphibians and macroinvertebrates in isolated ponds. *Wetlands*, **30**, 901–914.
- Defos Du Rau P., Barbraud C. & Mondain-Monval J.Y. (2005) Incorporating uncertainty into analyses of red-crested pochard habitat selection. *Biological Conservation*, **125**, 355–367.
- Diaz-Paniagua C. (1990) Temporary ponds as breeding sites of amphibians at a locality in southwestern Spain. *Herpetological Journal*, **1**, 447–453.
- Diaz-Paniagua C. (1998) Reproductive dynamics of a population of small marbled newts (*Triturus marmoratus pygmaeus*) in South-Western Spain. *Herpetological Journal*, **8**, 93–98.
- Donnelly M.A. & Crump M.L. (1998) Potential effects of climate change on two neotropical amphibian assemblages. *Climatic Change*, **39**, 541–561.
- Erişmiş U.G., Arıkan H., Konuk M. & Guarino F.M. (2010) Age structure and growth in caucasian parsley frog *Pelodytes caucasicus* (Boulenger, 1896) from Turkey. *Russian Journal of Herpetology*, **16**, 19–26.
- Fiske I., Chandler R., Royle J.A. & Kery M. (2010) Unmarked: models for data from unmarked animals, R package version 0.8–6.
- Fortuna M.A., Gomez-Rodriguez C. & Bascompte J. (2006) Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society*, **273**, 1429–1434.
- Gherardi F., Renai B. & Corti C. (2001) Crayfish predation on tadpoles: a comparison between native (*Austropotamobius pallipes*) and an alien species (*Procambarus clarkii*). *Bulletin Français de la Pêche et de la Pisciculture*, **361**, 659–668.
- Gomez-Rodriguez C., Bustamante J. & Diaz-Paniagua C. (2010a) Evidence of hydroperiod shortening in a preserved system of temporary ponds. *Remote Sensing*, **2**, 1439–1462.
- Gomez-Rodriguez C., Bustamante J., Diaz-Paniagua C. & Guisan A. (2012) Integrating detection probabilities in species distribution models of amphibians breeding in Mediterranean temporary ponds. *Diversity and Distributions*, **18**, 260–272.
- Gomez-Rodriguez C., Diaz-Paniagua C., Bustamante J., Porthault A. & Florencio M. (2010b) Inter-annual variability in amphibian assemblages: implications for diversity assessment and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 668–677.

- Gomez-Rodriguez C., Diaz-Paniagua C., Bustamante J., Serrano L. & Porthault A. (2010c) Relative importance of dynamic and static environmental variables as predictors of amphibian diversity patterns. *Acta Oecologica*, **36**, 650–658.
- Gomez-Rodriguez C., Diaz-Paniagua C., Serrano L., Florencio M. & Porthault A. (2009) Mediterranean temporary ponds as amphibian breeding habitats: the importance of preserving pond networks. *Aquatic Ecology*, **43**, 1179–1191.
- Grillas P. & Battedou G. (1998) The effects of flooding date on the biomass, species composition and seed production in submerged macrophyte beds in temporary marshes in the Camargue (S. France). in: *Wetlands for the Future* (Eds A.J. McComb & J. Davis), pp. 207–218. Gleneagles Publishing, Adelaide.
- Guillera-Arroita G. (2011) Impact of sampling with replacement in occupancy studies with spatial replication. *Methods in Ecology and Evolution*, **2**, 401–406.
- Guyétant R., Temmermans W. & Avrillier J.N. (1999) Phénologie de la reproduction chez *Pelodytes punctatus* Daudin, 1802 (Amphibia, Anura). *Amphibia-Reptilia*, **20**, 149–160.
- Hecnar S.J. & M'closkey R.T. (1997) The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation*, **79**, 123–131.
- Heyer W.R., Donnelly M.A., Mcdiarmid R.W., Hayek L.A.C. & Foster M.S. (1994) *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington (USA).
- Heyer W.R., Mcdiarmid R.W. & Weigmann D.L. (1975) Tadpoles, predation, and pond habitats in the tropics. *Biotropica*, **7**, 100–111.
- Hossack B.R. & Corn P.S. (2007) Responses of pond-breeding amphibians to wildfire: short-term patterns in occupancy and colonization. *Ecological Applications*, **17**, 1403–1410.
- Ivanova N.L. & Zhigalski O.A. (2011) Demographic features of populations of the marsh frog (*Rana ridibunda* Pall.) introduced into water bodies of the Middle Urals. *Russian Journal of Ecology*, **42**, 400–406.
- Jakob C., Poizat G., Veith M., Seitz A. & Crivelli A.J. (2003) Breeding phenology and larval distribution of amphibians in a Mediterranean pond network with unpredictable hydrology. *Hydrobiologia*, **499**, 51–61.
- Joly P. & Morand A. (1994) Theoretical habitat templates, species traits, and species richness: amphibians in the Upper Rhone River and its floodplain. *Freshwater Biology*, **31**, 455–468.
- Kendall W.L. & White G.C. (2009) A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *Journal of Applied Ecology*, **46**, 1182–1188.
- Lehikoinen A., Kilpi M. & Öst M. (2006) Winter climate affects subsequent breeding success of common eiders. *Global Change Biology*, **12**, 1355–1365.
- Mackenzie D.L., Nichols J.D., Hines J.E., Knutson M.G. & Franklin A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.
- Mackenzie D.L., Nichols J.D., Lachman G.B., Droege S., Royle J.A. & Langtimm C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- Mazerolle M.J., Bailey L.L., Kendall W.L., Royle J.A., Converse S.J. & Nichols J.D. (2007) Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology*, **41**, 672–689.
- Morand A. & Joly P. (1995) Habitat variability and space utilization by the amphibian communities of the French Upper-Rhone floodplain. *Hydrobiologia*, **301**, 249–257.
- Newman R.A. (1992) Adaptive plasticity in amphibian metamorphosis: what type of phenotypic variation in adaptive, and what are the costs of such plasticity? *BioScience*, **42**, 671–678.
- Ord J. & Getis A. (1995) Local spatial autocorrelation statistics: distributional issues and an application. *Geographical analysis*, **27**, 286–306.
- Pechmann J.H.K., Scott D.E., Gibbons J.W. & Semlitsch R.D. (1989) Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology and Management*, **1**, 3–11.
- Pechmann J.H.K., Scott D.E., Semlitsch R.D., Caldwell J.P., Vitt L.J. & Gibbons J.W. (1991) Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science*, **253**, 892–895.
- Pellet J., Helfer V. & Yannic G. (2007) Estimating population size in the European tree frog (*Hyla arborea*) using individual recognition and chorus counts. *Amphibia-Reptilia*, **28**, 287–294.
- Peltonen A. & Hanski I. (1991) Patterns of Island occupancy explained by colonization and extinction rates in shrews. *Ecology*, **72**, 1698–1708.
- Petranka J., Kats L. & Sih A. (1987) Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. *Animal Behaviour*, **35**, 420–425.
- Pollock K.H. (1982) A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, **46**, 752–756.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Richter-Boix A., Llorente G.A. & Montori A. (2006) Breeding phenology of an amphibian community in a Mediterranean area. *Amphibia-Reptilia*, **27**, 549–559.
- Richter-Boix A., Llorente G.A. & Montori A. (2007) Structure and dynamics of an amphibian metacommunity in two regions. *Journal of Animal Ecology*, **76**, 607–618.
- Rowe C.L. & Dunson W.A. (1993) Relationships among abiotic parameters and breeding effort by three amphibians

- in temporary wetlands of central Pennsylvania. *Wetlands*, **13**, 237–246.
- Salvador A. & Carrascal L.M. (1990) Reproductive phenology and temporal patterns of mate access in Mediterranean anurans. *Journal of Herpetology*, **24**, 438–441.
- Serkan G., Nurhayat O., Nazan U., Kurtuluş O. & Bilal K. (2011) Body size and age structure of *Pelophylax ridibundus* populations from two different altitudes in Turkey. *Amphibia-Reptilia*, **32**, 287–292.
- Simeone A., Araya B., Bernal M., Diebold E.N., Grzybowski K., Michaels M. *et al.* (2002) Oceanographic and climatic factors influencing breeding and colony attendance patterns of Humboldt penguins *Spheniscus humboldti* in central Chile. *Marine Ecology*, **227**, 43–50.
- Smith G.R., Rettig J.E., Mittelbach J.L., Valiulis J.L. & Schaack S.R. (1999) The effects of fish on assemblages of amphibians in ponds: a field experiment. *Freshwater Biology*, **41**, 829–837.
- Snodgrass J.W., Komoroski M.J., Bryan A.L. & Burger J. (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology*, **14**, 414–419.
- Southwood T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.
- Spieler M. & Linsenmair K.E. (1998) Migration patterns and diurnal use of shelter in a ranid frog of a West African savannah: a telemetric study. *Amphibia-Reptilia*, **19**, 43–64.
- Switzer P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.
- Werner E.E., Yurewicz K.L., Skelly D.K. & Relyea R.A. (2007) Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos*, **116**, 1713–1725.
- Wilbur H.M. (1984) Complex life cycles and community organization in amphibians. in: *A New Ecology: Novel Approaches to Interactive Systems* (Eds P.W. Price, C.N. Slobodchikoff & W.S. Gaud), pp. 196–224. Wiley, New-York.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Colonization (a) and extinction (b) probabilities estimated separately for the three studied species.

Figure S2. Colonization (a) and extinction (b) probabilities estimated separately for the three studied species.

Table S1. Selection step (r), model structure, AIC_c , weight of AIC_c (w), number of parameters (k), naïve occupancy rate ($\Psi(\text{naive})$), estimated occupancy rate (Ψ), detection probability (P) and risk of imperfect detection for the single-season modeling of *Pelodytes punctatus*, *Hyla meridionalis* and *Pelophylax* spp. occupancy rates.

Table S2. Selection step (r), model structure, AIC_c , ΔAIC_c , AIC weight (w), number of parameters (k), for the multi-season occupancy modelling of *Pelodytes punctatus*, *Hyla meridionalis* and *Pelophylax* spp. among 20 ponds from the Camargue Mediterranean wetland.

Table S3. Probability of detecting the effect of $(\text{var}(H))^2$ and DE^2 on colonization and extinction rates of the three target species given the number of ponds included in the bootstrap procedure.

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