Special Section: The Value and Utility of Presence–Absence Data to Wildlife Monitoring and Research

RELATIVE IMPORTANCE OF POPULATION PROCESSES AND HABITAT CHARACTERISTICS IN DETERMINING SITE OCCUPANCY OF TWO ANURANS

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Abstract: The ecological niche is the conceptual foundation for the analysis of species distributions. Habitat variables and resources are therefore thought to determine the distribution of a species. However, metapopulation and source-sink models posit that population processes determine the local distribution of a species; metapopulation theory suggests that many suitable patches could be unoccupied and source-sink theory suggests that unsuitable patches could be occupied. We examined whether the distribution of 2 European anurans (tree frog [*Hyla arborea*] and natterjack toad [*Bufo calamita*]) was determined by habitat variables, local population size (as indexed by the number of calling males), or metapopulation characteristics are. We found that the distribution of both species was best predicted by the number of calling males in the previous years. This supports the idea that population processes are more important determinants of distribution than habitat characteristics. We suggest that future distribution models explicitly incorporate population dynamic processes. Our results suggest that there is a threshold number of calling males above which a population is almost certain to persist in the short-term. If more robust population data are not available, such a threshold should be useful for managing threatened anuran species because the number of calling males is easily determined.

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Understanding factors that govern species distribution is a central goal of ecology and is of fundamental importance to conservation biologists and wildlife managers (Hairston 1949, Andrewartha and Birch 1954, Krebs 1972, Scott et al. 2002). Only if we understand which factors determine persistence of species and which factors lead to decline can we successfully halt and reverse species declines. Therefore, modeling the distribution of species has been a long-standing interest of ecologists and has recently seen a revival, especially in conservation biology (Vos and Stumpel 1996, Boyce and MacDonald 1999, Fleishman et al. 2002*a*). Most attempts to model species distributions are based on the assumption that the distribution of a species can be explained by abiotic or biotic predictor variables that are thought to reflect the fundamental or realized niche of the species (Hutchinson 1957, James et al. 1984, Pulliam 2000, Austin 2002). Data-based models of species distributions generally assume that all patches where a species occurs are suitable for the species, whereas all unoccupied patches are unsuitable. While this reasoning is sound, we know that dissimilar communities can develop at similar sites (Gleason 1927, Jenkins and Buikema 1998, Chase 2003), suggesting that ecological requirements of species (i.e., their ecological niche) may not be the only determinant of distribution.

Austin (2002) noted that species distribution modeling is generally not well connected to ecological theory and Boyce and MacDonald (1999) argued that habitat ecology is depauperate of theory. We believe that the assumptions underlying species distribution models partly neglect 2 important bodies of ecological theory, namely source-sink dynamics and metapopulation theory (Van Horne 1983; Pulliam 1988, 2000; Hanski 1999). The concept of source-sink dynamics posits that many patches where a species occurs are in fact not suitable for the species (i.e., sinks). In contrast, metapopulation theory predicts that many suitable patches will not be occupied. In both cases, population dynamic processes determine whether a patch is occupied. It therefore

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seems worthwhile to include population dynamic processes into species distribution modeling. This is a formidable task. Here, we take the first step towards this goal. Because our interest is primarily conservation biology, we use a proxy for population dynamic processes that may be particularly relevant for conservation and management because it can relatively easily be determined in large-scale monitoring programs.

We examine whether population size in year *i*, measured as the size of the chorus of calling anurans, is a better predictor of site occupancy in year *i*+1 than abiotic habitat variables known to positively and negatively affect the distribution of 2 anurans (Pellet et al. 2004*a,b*; Pellet and Schmidt 2005; F. Zanini, Swiss Federal Institute of Technology at Lausanne, unpublished data). Anurans may be particularly well suited for such an analysis because of the largely stochastic nature of the growth rate of small populations (Beebee et al. 1996, Carlson and Edenhamn 2000, Green 2003). Thus, whether a population persists locally may be largely determined by stochastic effects on population growth and Allee effects, whereas habitat variables may be of lesser importance. Because many amphibians, including the species we study, are organized into metapopulations (Sinsch 1992*a*, Rowe et al. 2000, Carlson and Edenhamn 2000, Ter Braak and Etienne 2003), rescue effects from nearby populations may be important as well (Sinsch 1992*a*). To allow for rescue and metapopulation effects, we also examined whether the number of calling males in nearby populations affected the site occupancy in the focal site.

STUDY AREA

We surveyed the distribution of the European tree frog and the natterjack toad in the Swiss state Vaud in western Switzerland between the villages of Allaman and Bière (46°30′N; 6°25′E). The study area covered 396 km^2, of which only 0.5% constituted amphibian breeding ponds. We identified ponds based on various national databases and field knowledge (Pellet et al. 2004*a,b*). The landscape is typical of the Swiss Plateau and is a mixture of agricultural areas, forests and small villages (200–2,500 inhabitants). Villages are connected by a dense traffic network, including highways, primary roads, secondary roads, and railroads. Pellet et al. (2004*b*) provide a map of the study area.

METHODS

The treefrog and the natterjack toad are 2 European anurans that breed in temporary ponds. On the pond permanence gradient, the natterjack toad prefers very short-lived puddles, whereas the treefrogs prefers ponds with longer hydroperiod (Van Buskirk 2003). During the breeding period, males call conspicuously at the pond edges to attract females. After the breeding season, treefrogs live in hedgerows, at forest edges and similar vegetation types. Natterjack toads, in contrast, prefer open areas with little vegetation. Detailed accounts of the natural history of the 2 species are given by Beebee (1983), Stumpel and Tester (1993), Sinsch (1998), and Glandt (2004).

Data Collection

Within a larger study on the metapopulation ecology of the European treefrog (Pellet et al. 2004*a,b*), we used call surveys at 27 sites during the breeding season to assess the presence and number of calling males of the 2 species in 2001 and 2002 (Buckley and Beebee 2004, Pellet and Schmidt 2005). In 2001, we searched for anurans for 21 nights. We visited each site 1–12 times ($\bar{x}$ = 3.4). In 2002, we spent 32 nights in the field and visited each site 1–17 times ($\bar{x}$ = 3.7). We frequently visited ponds where we collected additional data for other purposes related to the larger study. We began count surveys at sundown, and we surveyed each site for 15 minutes. We walked pond shores systematically, and we counted the number of calling males. The ponds used by the 2 species were often early-successional and therefore with only little vegetation, and males of both species did not cluster together but maintained a minimum distance (Arak 1983, Tester 1990). This behavioral pattern made it easy to make accurate counts of calling males. We entered the maximum number of callers heard at a site in 2001 into the statistical analysis of site occupancy in 2002.

We extracted habitat variables from the vector 25 database, which was the vector format of the 1:25′000 topographical maps of Switzerland issued by the Swiss Federal Office of Topography (Swisstopo 2003). Data precision is approximately 3–8 meters in flat areas such as our study area (Swisstopo 2003). We extracted from the dataset the primary surfaces known to affect our 2 species distributions (i.e., first-class roads, bare soils, hedges). We measured pond area (AREA) as polygons from digitalized aerial photos.

Weather data were provided by MeteoSwiss from the Changins weather station, which is at the same altitude as the study area and located about 16 km away from the center of the study

Table 1. Model selection analysis and parameter estimates of site occupancy ($\hat{\psi}$) for *Hyla arborea* in 2002 in western Vaud, Switzerland. Site occupancy data were collected in 2001 and 2002 whereas caller counts were made only in 2001. AIC_c of the best model is 104.02, $n = 27$.

Model	−2log-likelihood	K	ΔAIC_c	Akaike weight	$\hat{\psi}$	SE($\hat{\psi}$)
ψ(COUNT2001)*p*(DAY)	94.2	4	0.00	0.352	0.693	0.085
ψ(COUNT2001, NEAR2001)*p*(DAY)	92.8	5	1.67	0.153	0.693	0.083
ψ(COUNT2001, FAR2001)*p*(DAY)	93.6	5	2.43	0.105	0.693	0.084
ψ(COUNT2001,NATURAL)*p*(DAY)[a]	94.1	5	2.89	0.083	0.691	0.084
ψ(COUNT2001, CONNECT)*p*(DAY)	94.2	5	3.04	0.077	0.693	0.085
ψ(.)*p*(DAY)	101.1	3	4.15	0.044	0.715	0.097
ψ(NEAR2001)*p*(DAY)	98.6	4	4.44	0.038	0.714	0.093
ψ(FAR2001)*p*(DAY)	99.6	4	5.38	0.024	0.708	0.094
ψ(NATURAL)*p*(DAY)	99.9	4	5.71	0.020	0.705	0.094
ψ(.)*p*(RAIN, DAY)	100.0	4	5.78	0.020	0.714	0.096
ψ(.)*p*(DAY,DAYSQUARE)	100.7	4	6.49	0.014	0.710	0.096
ψ(CONNECT)*p*(DAY)	100.8	4	6.56	0.013	0.714	0.096
ψ(AREA)*p*(DAY)	100.9	4	6.73	0.012	0.717	0.097
ψ(HEDGE1000)*p*(DAY)	101.0	4	6.84	0.012	0.713	0.097
ψ(TEMPORARY)*p*(DAY)	101.0	4	6.84	0.012	0.714	0.097
ψ(DIST2ROAD)*p*(DAY)	101.1	4	6.84	0.012	0.717	0.097
ψ(.)*p*(DAYSQUARE)	104.3	3	7.28	0.009	0.728	0.098
ψ(.)*p*(TEMP)	114.2	3	17.19	0.000	0.730	0.100
ψ(.)*p*(.)	123.4	2	23.83	0.000	0.740	0.101
ψ(.)*p*(RAIN)	123.1	3	26.10	0.000	0.740	0.102
Model averaged estimates					0.698	0.086

[a] A posteriori model.

area. We calculated temperature as the mean temperature (in °C) from 3 measurements taken during the day of the survey (morning, noon, and evening). We computed rainfall as the sum of rainfall (in mm) during the day of the survey.

During the days preceding nights of fieldwork, average rainfall was 10.3 mm (median 0.05 mm, range 0–90.8 mm). Temperature during fieldwork was on average 13.1°C (median 12.8°C, range 4.8–26.8°C). Temperature and the amount of rainfall were weakly positively correlated ($R^2 = 0.093$).

Data Analysis

We used the site occupancy models developed by MacKenzie et al. (2002) to estimate the proportion of sites occupied by tree frogs and natterjack toads and to evaluate the relative importance of population size, metapopulation effects, and habitat variables. We ran analyses in program PRESENCE (available for download at http://www.mbr-pwrc.usgs.gov/software.html). For model selection, we used the small sample Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) where sample size was the number of sites visited (i.e., $n = 27$).

We used a 2-step approach to analyze data. First, we determined which factors best explained detection probabilities. We asked whether rainfall during the day, mean daily temperature, or seasonality/breeding phenology explained detection probabilities while keeping site occupancy constant, (i.e. $\psi[.]p[variable]$). We modeled seasonality/breeding phenology using day-of-season (i.e., first day of field work = day 1). To allow for a peak in breeding season, we included models with a linear (DAY) and quadratic day-of-season (DAYSQUARE) effect. We then used the best model for detection probabilities in the second step in which we combined this model with the candidate models that represented biological hypotheses (Burnham and Anderson 2002).

Candidate Models.—Because our data set was relatively small, we kept candidate models simple (i.e., at most 2 explanatory variables for site occupancy; Tables 1, 2). Four models included habitat variables. The habitat variables were the type of habitat (NATURAL) that was a categorical variable with 2 levels: either gravel pit or a natural/seminatural habitat type. Many amphibian species live in gravel pits because human activities closely mimic the landscape dynamics of braided rivers (Meisterhans and Heusser 1970, Köppel 1995). This candidate model examines whether gravel pits with many early-successional temporary ponds are preferred over other habitat types that show less disturbance. The second habitat variable described the size of the pond (AREA). Larger patches of habitat were more

Table 2. Model selection analysis and parameter estimates of site occupancy ($\hat{\psi}$) for *Bufo calamita* in 2002 in western Vaud, Switzerland. Site occupancy data were collected in 2001 and 2002, whereas caller counts were made only in 2001. AIC_c of the best model is 84.58, n = 27.

Model	–2log-likelihood	K	ΔAIC_c	Akaikė weight	$\hat{\psi}$	SE($\hat{\psi}$)
ψ(COUNT2001)p(TEMP)	74.8	4	0.00	0.439	0.451	0.091
ψ(COUNT2001, CONNECT)p(TEMP)	73.7	5	2.01	0.161	0.455	0.092
ψ(TEMPORARY)p(TEMP)	77.1	4	2.31	0.139	0.493	0.120
ψ(COUNT2001, NEAR2001)p(TEMP)	74.8	5	3.04	0.096	0.451	[c]
ψ(DIST2ROAD)p(TEMP)	79.9	4	5.14	0.034	0.478	0.114
ψ(.)p(.)	85.6	2	5.52	0.028	0.501	0.133
ψ(.)p(RAIN)	83.8	3	6.22	0.020	0.501	0.129
ψ(.)p(TEMP)	83.8	3	6.24	0.019	0.491	0.128
ψ(.)p(DAY,DAYSQUARE)	81.6	4	6.79	0.015	0.457	0.119
ψ(.)p(DAYSQUARE)	85.4	3	7.89	0.009	0.492	0.130
ψ(.)p(RAIN, TEMP)	82.7	4	7.89	0.009	0.495	0.127
ψ(.)p(DAY)	85.6	3	8.02	0.008	0.504	0.134
ψ(NATURAL)p(TEMP)	83.5	4	8.75	0.006	0.503	0.135
ψ(AREA)p(TEMP)	83.7	4	8.97	0.005	0.493	0.131
ψ(FAR2001)p(TEMP)	83.8	4	9.00	0.005	0.493	0.130
ψ(CONNECT)p(TEMP)	83.8	4	9.02	0.005	0.491	0.129
ψ(NEAR2001)p(TEMP)	83.8	4	9.02	0.005	0.491	[c]
ψ(MINERAL500)p(TEMP)	[a]					
ψ(COUNT2001, FAR2001)p(TEMP)	[a]					
ψ(COUNT2001,TEMPORARY)p(TEMP)[b]	[a]					
Model averaged estimates					0.463	0.093

[a] Model did not converge.
[b] A posteriori model.
[c] Variance-covariance matrix not computed successfully.

likely to be inhabited by a species, and a larger habitat patch may be home to a larger population (Kindvall and Ahlen 1992, Lienert and Fischer 2003, Krauss et al. 2004). The third habitat variable was related to pond hydroperiod (TEMPORARY). Tree frogs and natterjack toads prefer temporary ponds for reproduction (Van Buskirk 2003). The fourth habitat variable was the distance to the nearest first-class road (DIST2ROAD). Roads and traffic mortality are well known to negatively affect the distribution and abundance of amphibians (Van Gelder 1973, Hels and Buchwald 2001, Pellet et al. 2004*b*). The fourth habitat model included habitat variables that described the quality of the terrestrial habitat (Pope et al. 2000). For tree frogs, this was the length of hedges (in km; HEDGE) in a circle with a radius of 1 km around the breeding pond (Fog 1993, Vos and Stumpel 1996). For natterjack toads, this was the area (in m^2) of bare soils (e.g., gravel pits, military training grounds; MINERAL) in a circle with a radius of 0.5 km around the breeding site (Sinsch 1998). For both HEDGE and MINERAL, we expected positive effects on site occupancy. The other candidate models included population size or allowed for metapopulation effects on site occupancy.

In the first of this group of models, we added the maximum number of callers at a site in the previous year (COUNT2001) as a variable for site occupancy in the current year. This model states that site occupancy was determined by previous population size, at least in the short term (Carlson and Edenhamn 2000, Barbraud et al. 2003, Buckley and Beebee 2004). Because tree frogs and natterjack toads are known to disperse during and between breeding seasons (Sinsch 1992*b*, Denton and Beebee 1993, Tester and Flory 1995, Miaud et al. 2000, Vos et al. 2000), we mapped all the calling males and then calculated the number of calling males in a circle with radius 500 m (NEAR2001) and 2 km (FAR2001), respectively. Again, we made counts in 2001 and included them into the analysis of site occupancy in 2002. We assumed the distances of 500 m and 2 km reflected dispersal within and between breeding seasons and were ad hoc measures of metapopulation structure, connectivity, and rescue effects. We also used a measure of connectivity (i.e., colonization rate) taken from metapopulation theory. We measured the connectivity measure for patch i (CONNECT) as $CONNECT_i =$

$$\sum_{i \neq j} e^{-d_{ij}} A_j$$

(Hanski et al. 1994). The distance between patch i and the neighboring patch j is d_{ij}. A_j should reflect the carrying capacity of patch j (Hanski et al. 1994); we used the mean maximal number of calling males heard in a given patch between years 2001 and 2004 as a surrogate. CONNECT thus represent a measurement of colonization pressure on pond i resulting from emigration from all other patches j. We also combined this measure of connectivity with COUNT2001. We hypothesized that a site was most likely to be occupied if it held a large population and was well connected to other populations (Ovaskainen and Hanski 2004). To account for a possible interaction between habitat and population size, we built a model that combined the best habitat variable and the best variables from the population/metapopulation models. Thus, the variables in this model were not known a priori. Finally, model $\psi(.)$ states that none of the variables described above represents the information in the data well.

We used model-averaging techniques to estimate the proportion of sites occupied (and the standard error thereof; Burnham and Anderson 2002). For model averaging, we used the estimate of the proportion of sites occupied provided by program PRESENCE for each model.

RESULTS

Tree Frog

In 2001, we detected tree frogs at 25 sites, and maximum chorus size ranged from 1 to 209 with a median maximum chorus size of 5. In 2002, we found tree frogs at 18 sites (naive site occupancy = 0.667). At 2 of those sites, we did not find tree frogs in 2001 (colonizations), while we did not find tree frogs at 9 sites where we did find them in 2001 (extinctions).

Detection probability was best modeled as a function of the linear effects of DAY. DAYSQUARE, TEMPERATURE, and RAIN explained detection probabilities substantially less well, and we found little evidence that detection probabilities were constant (Table 1). Thus, we used p(DAY) for further analysis. Based on model $\psi(.)p$(DAY), day-of-season had a positive effect on detection probability (slope on the logit scale: 0.0803 [SE 0.0218]).

Models that included COUNT2001 were substantially better than models that included habitat or metapopulation variables (Table 1). There was a positive relationship between COUNT2001 and site occupancy in 2002 (Fig. 1). Models that included metapopulation or habitat variables in addition to COUNT2001 appeared to be close competitors to the best models because ΔAIC_c was between 2 and 3 (second-best to fifth model in Table 1). We suggest that these variables do in fact have little explanatory power and are likely to be spurious (Anderson and Burnham 2002:916). This can be seen by inspecting the −2log-likelihoods (hereafter −2LL) of these models. The −2LL were all very similar to the −2LL of the best model. Hence, these variables did not improve the −2LL, and the models simply have small ΔAIC_c values because only 1

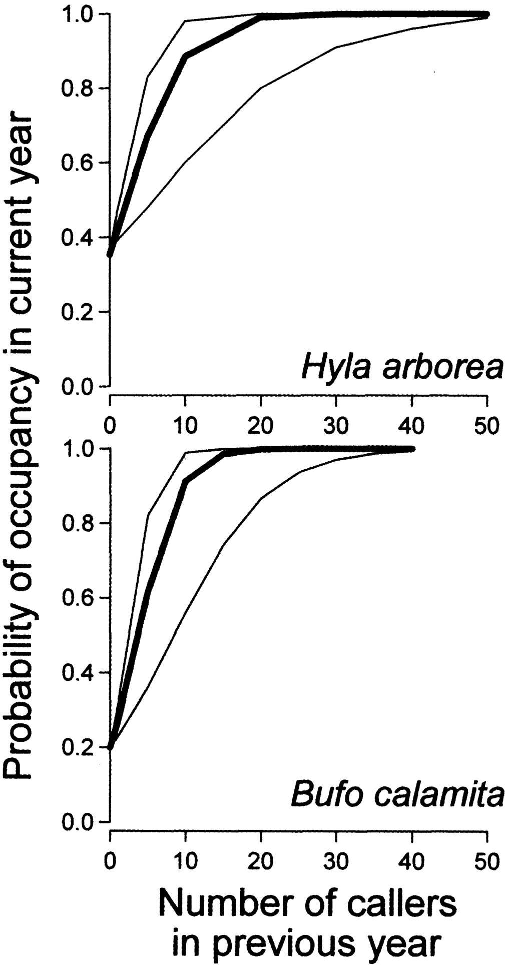

Fig. 1. The relationship between chorus size in 2001 and the probability of occupancy ($\hat{\psi}$) in 2002 for *Hyla arborea* and *Bufo calamita* in western Vaud, Switzerland, based on the best model ψ(COUNT2001)p(DAY) and ψ(COUNT2001)p(TEMP), respectively. Mean and SE are shown. Site occupancy data were collected in 2001 and 2002, whereas caller counts were made only in 2001. The maximum caller count for *Bufo calamita* was n = 40 in 2001.

parameter was added. This interpretation of the model selection analysis is supported by the fact that the slopes of the suspected spurious variables had slopes that were quite small (~0.02); estimates of SE were substantially larger than the slope estimate. Only NEAR2001 and NATURAL had larger slopes on the logit scale [ψ(COUNT2001, NEAR2001)p(TEMP): –0.3929 (SE 0.5611); ψ(COUNT2001, NATURAL) p(TEMP): –0.3936 (SE 1.1315)].

Models that included only a metapopulation or habitat variable were less well supported by the data than model y(.). This suggests that adding these variables did not substantially improve the modeling of the information in the data. All models considered estimated site occupancy within a fairly small range (Table 1). The model-averaged proportion of sites where tree frogs occurred was 0.705 (SE 0.090).

Natterjack Toad

In 2001, we detected natterjacks at 12 sites, and maximum chorus size ranged from 2 to 40 with a median maximum chorus size of 7. In 2002, we found natterjacks at 10 sites (naive site occupancy = 0.370). At 2 of those sites, we did not find natterjacks in 2001 (colonizations) while we no longer found natterjacks at 4 sites where we had found them in 2001 (extinctions).

There was uncertainty over which model was the best description of detection probability because ΔAIC_c values were small in comparison with the best model $\psi(.)p(.)$ (Table 2). Thus, we ran all candidate models in combination with all models for detection probability. We only present the results for the analysis with p(TEMP). These models had the lowest AIC_c values for all candidate models. The ranking of the best models did not depend on the choice of the model for detection probability (Pellet and Schmidt 2005). Based on model $\psi(.)p$(TEMP), temperature had a negative effect on detection probability (slope on the logit scale = –0.1138 [SE 0.0892]).

Several models did not converge. Models that included COUNT2001 were substantially better than models that included only habitat or metapopulation variables (Table 2). When in combination with COUNT2001, connectivity also explained information in the data well. CONNECT negatively influenced site occupancy. The logistic regression equations is (parameter estimates [SE] on the logit scale) logit(ψ) = –0.7714 (0.9284) – 0.2074 (0.2308) * CONNECT + 0.3837 (0.2074) * COUNT2001. TEMPORARY was also a good model ($\Delta AIC_c = 2.307$), and as we expected, natterjacks were more likely to occur in temporary than permanent ponds (effect of TEMPORARY on the logit scale: 2.9004 [SE 1.4873]). Unfortunately, model ψ(COUNT2001, TEMPORARY)p(TEMP) did not converge. The PRESENCE output suggests that this might have been the best model by far, as the –2LL was ≈ 66, which would yield an $AIC_c \approx 79$.

The range of $\hat{\psi}$ was larger in natterjacks than in tree frogs (from 0.450 to 0.511; Table 2). Models that included COUNT2001 estimated $\hat{\psi} \approx 0.45$, while models without COUNT2001 estimated $\hat{\psi} \approx$ 0.5. The latter class of models, however, had very small Akaike weights.

DISCUSSION

We used site occupancy models and information–theoretic model selection to address the question of whether the distribution of species is best described by habitat quality, population size in the previous year, or metapopulation structure. At the spatial and temporal scale of our study, models that included population size in the previous year were by far the best. Habitat and metapopulation variables generally did poorly or only gathered some support from the data when in combination with past population size. This supports the idea that population dynamic processes predict distribution far better than static habitat variables. We believe that this is because the dynamics of amphibian populations are largely stochastic (Beebee et al. 1996, Carlson and Edenhamn 2000, Green 2003).

Using the number of calling males as a variable in the models affected both model selection and parameter estimation. First, models with chorus size as a variable were the best. Second, models with chorus size as a variable generally gave smaller estimates of site occupancy and had smaller standard errors; the former may be indicative of positive bias in estimates derived from models where chorus size was not a variable. Royle (2004) modeled variation in abundance explicitly but found only a minor difference in parameter estimates of site occupancy when variation in abundance was taken into account and when it was not.

Royle and Nichols (2003) found that estimates of site occupancy are negatively biased if heterogeneity in detection probabilities induced by variation in population size is not taken into account. With anurans, variation in chorus size may be a source of heterogeneity in detection probabilities, if false absences are more likely in ponds with low anuran numbers than in ponds with high numbers. However, variation in detection probabilities was probably not a problem in our study. First, few visits are necessary to be 95% certain that a species is absent from a site (3 visits for tree frogs and 6 visits for natterjack toads; Pellet and Schmidt 2005). Thus, we probably discovered most sites where the species was present; therefore, naïve estimates of site occupancy and model-derived estimates of site occupancy were similar. Second, to test for heterogeneity in detection probability, we ran the mixture models (Pledger 2000) implemented in program PRESENCE. Unfortunately, all but 1 model did not converge. Model $\psi(.)p$(2-group mixture) for tree frogs converged. This model had $\Delta AIC_c = 48.4$, suggesting that it was not necessary to model heterogeneity in detection probability explicitly.

Both tree frogs and natterjack toads showed the same ranking of models (Tables 1, 2). Models with a variable describing population size were best, models with metapopulation variables were second best, and models with habitat variables were generally worst. Chorus size was probably the best explanatory variable for site occupancy because population growth rates in many pond-breeding amphibians are largely stochastic (Green 2003), and tree frogs and natterjack toads are no exception (Beebee et al. 1996, Carlson and Edenhamn 2000). Both species are well known for calling at ponds where reproduction fails in most years (Sinsch 1992*a*, Beebee et al. 1996, Barandun 2001). The unpredictability of successful reproduction (i.e., survival of tadpoles to metamorphosis) generates stochasticity in local population growth rates with many populations going extinct or happening to persist. In combination with common dispersal events within and between seasons, such stochasticity apparently makes the pattern of distribution independent of local habitat variables. It seems unlikely that we failed to include the most important habitat variables (e.g., habitat variables affecting tadpole survival) because we knew the best explanatory variables from an exploratory search of correlates of breeding pond use (Pellet et al. 2004*a*). Hence, the spatial pattern of presence and absence of tree frogs and natterjack toads is probably best described as a metapopulation; the concepts of the core satellite metapopulation or patchy populations are most useful (Harrison 1991, Golay et al. 1995, Rowe et al. 2000).

Even though metapopulation processes are considered as important by most authors working on natterjack toads and tree frogs (Sinsch 1992*a*, Tester and Flory 1995, Rowe et al. 2000, Carlson and Edenhamn 2000, Ter Braak and Etienne 2003), we found only little support for models containing metapopulation variables (Tables 1, 2). We expected higher connectivity would increase site occupancy. This was not the case; increased connectivity decreased the probability of site occupancy. We believe that the conspecific attraction hypothesis best explains this pattern (Ray et al. 1991, Vos 1999). If the number of males at a pond is small, the calling activity will be minor, a persistent chorus will not form (Golay et al. 1995), and females prefer ponds with large choruses (Sinsch 1992*b*). Under such conditions, theory suggests that males ought to show a tendency to leave this pond and breed elsewhere (Schmidt 2004). This appeared to be the case, but only if there were other ponds nearby. Nearby ponds with many males were likely to be most attractive because a large chorus may signal habitat quality (Stamps 1987, Cam et al. 2004). Such an anti-rescue effect that increases the likelihood that small populations go extinct should be considered when managing metapopulations (Harding and McNamara 2002). Nevertheless, there is also some evidence for positive metapopulation dynamics; patches that were empty (i.e., no callers heard in 2001) had a >20% chance of being occupied in the following year (Fig. 1).

The breeding habitat of both species could be loosely defined as early successional, temporary ponds (Van Buskirk 2003). Such a statement implies that there must be some habitat variables that explain distribution. Under which conditions and at what spatial or temporal scales would habitat variables best predict site occupancy? This is definitely an open area for research. One solution may be to restrict the analysis to large populations. Large populations show considerably less stochasticity than small populations do (Green 2003), such that deterministic processes become relatively more important. If the distribution of a species is more stable and extinctions and colonizations are rare events, then distribution may be best predicted by habitat variables. For example, Sztatecsny et al. (2004) found that egg abundance was best explained by habitat variables in *Triturus* newts and that habitat variables were more useful for explaining larval abundance than egg abundance (≈ population size).

Statistical models of the distribution of species generally assume that habitat variables are most important and that all sites where the species was present are suitable, whereas all sites where the species was absent are considered to be unsuitable. Thus, the underlying concept is the fundamental niche, or sometimes the realized niche (Hutchinson 1957, Austin 2002). Future distribution models should be based on more recent models of the ecological niche (Leibold 1995, Pulliam 2000, Tilman 2004). This might be achieved by modeling abundance rather than distribution (Boyce and McDonald 1999, Royle 2004, but see Van Horne 1983) because presence and absence are only a special case of abundance (abundance = 0 and abundance >0, respectively). Alternatively, one might model changes in distribution rather than presence/absence. This approach would be conceptually similar to time series analysis where changes in abundance rather than abundance per se are modeled (e.g., Dennis and Taper 1994).

MANAGEMENT IMPLICATIONS

Our results have implications for surveying and monitoring amphibians. First, the detection of tree frogs and natterjack toads was imperfect. Thus, surveys and monitoring program should employ methods for data analysis that take nondetection into account (Pollock et al. 2002, MacKenzie 2005). Second, the effect of temperature on detection probability was positive in tree frogs (Pellet and Schmidt 2005) and negative in natterjack toads. Thus, standardizing weather conditions for conducting a multi-species survey may be impossible. Third, there was a strong relationship between the maximum number of calling males and site occupancy in the following year (Fig. 1). Chorus size certainly underestimates the number of males present at the breeding pond and the relationship between chorus size and population size is unknown (Golay et al. 1995, Stevens et al. 2003, Schmidt 2004, Grafe and Meuche 2005). Nevertheless, chorus size may serve a useful role as a predictor of short-term population persistence. Fourth, populations of both species were almost certainly present on average in the following year if the number of callers was greater than 20 (Fig. 1). Conservationists and managers may use such a caller count as a target when managing populations of these species (Kéry et al. 2000). However, the SE are large, and a low-risk management strategy should aim for choruses that are substantially larger. Moreover, chorus size predicted persistence only in the short-term, and it remains to be tested whether chorus size predicts persistence over multiple years; the results of single-year and multiple-year analyses may be different (Fleishman et al. 2002*b*).

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