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Estimating Effects of Species Interactions on Populations of Endangered Species

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abstract: Global change causes community composition to change considerably through time, with ever-new combinations of interacting species. To study the consequences of newly established species interactions, one available source of data could be observational surveys from biodiversity monitoring. However, approaches using observational data would need to account for niche differences between species and for imperfect detection of individuals. To estimate population sizes of interacting species, we extended *N*-mixture models that were developed to estimate true population sizes in single species. Simulations revealed that our model is able to disentangle direct effects of dominant on subordinate species from indirect effects of dominant species on detection probability of subordinate species. For illustration, we applied our model to data from a Swiss amphibian monitoring program and showed that sizes of expanding water frog populations were negatively related to population sizes of endangered yellow-bellied toads and common midwife toads and partly of natterjack toads. Unlike other studies that analyzed presence and absence of species, our model suggests that the spread of water frogs in Central Europe is one of the reasons for the decline of endangered toad species. Thus, studying population impacts of dominant species on population sizes of endangered species using data from biodiversity monitoring programs should help to inform conservation policy and to decide whether competing species should be subject to population management.

Keywords: biodiversity monitoring, detection probability, habitat niche, introduced species, invasive species, *Ranidae*.

Introduction

Global change—such as climate warming, land use change, or human transport of plants and animals—leads to contracting or expanding distributional ranges of species (Sala et al. 2000; Chen et al. 2011). The direction and rates of range shifts are usually species specific, leading to a reshuffling of communities with new combinations of interacting species (Hobbs et al. 2006). Interactions such as predation, competition, parasitism, and pollination play an important role in the maintenance of biodiversity and the stability of ecosystems (Bascompte et al. 2006; Tylianakis et al. 2008). Timely monitoring the change in species composition and inferring effects of species interactions should thus be of high priority for conservation policy and population management (Dornelas et al. 2014; Sentis et al. 2014).

One readily available source of data for studying the consequences of newly interacting species is observational surveys from biodiversity monitoring or citizen science programs (Delaney et al. 2008; Dickinson et al. 2010; Couvet et al. 2011). Such approaches using observational data should account for niche differences between potentially interacting species by including variables describing the niche differences (Linder et al. 2003). Additionally, studies using observational data need to account for imperfect detection of the interacting species (Pellet and Schmidt 2005; Schmidt 2005; Tanadini and Schmidt 2011); for example, if a dominant species would influence the behavior of a subordinate species, this may affect detection probability of subordinate species, which needs to be separated from effects on population size (Waddle et al. 2010).

Recently, it was proposed to study species occurrence and co-occurrence patterns based on site-occupancy models using presence-absence data (MacKenzie et al. 2004; Waddle et al. 2010; Miller et al. 2012). However, data on presence or absence of a species provide only limited information on the actual size of a population (Dorazio and Connor 2014). Clearly, estimates of true population sizes would permit a more accurate assessment of the effects of species interactions, because a dominant species may reduce population sizes of other species without necessarily leading to their local extinction (Linder et al. 2003). Here, we aimed to develop a method to estimate true population sizes of interacting species by extending a class of models that allow the estimation of population sizes from repeated counts of individuals in the field while accounting for imperfect detection. Because local population size N is assumed to be a random variable distributed according to some mixing distribution (e.g., Pois-

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son and Binomial), this class of models is often called *N*-mixture models (Royle 2004) or binomial-mixture models (Kéry 2008). Originally, these models were developed to estimate population sizes in single species.

The extension of *N*-mixture models for interacting species that we propose is conceptually related to the work of Waddle et al. (2010), who expanded the class of occupancy models for estimating patterns of co-occurrence (presence vs. absence) of interacting species. Unlike Waddle et al. (2010), however, we aimed to estimate true population sizes. In our *N*-mixture model, we assume one species to be dominant and the other to be subordinate, and the population size and detection probability of the subordinate species is assumed to depend on the population size of the dominant species but not vice versa. Such a pattern is typical for ecological interactions between dominant species and endangered subordinate species (Waddle et al. 2010). Our model fits into the recent class of parametric models to estimate population effects of interacting species (Dorazio and Connor 2014). An advantage of using parametric modeling is that the intensity of interspecific interactions is specified as model parameters and can thus be quantified. Further, potential ecological determinants—such as habitat or other site-specific covariates—can be incorporated and their effects be estimated independently of the effects of imperfect detection.

To illustrate our approach, we analyzed population sizes of endangered amphibians in the context of recent range expansions of the so-called water frog species complex in Europe (Pagano et al. 2003). One of those species is the Eurasian marsh frog (*Pelophylax ridibundus*) that, together with other sister species, has greatly expanded its range in Central Europe (Vorburger and Reyer 2003). However, while the rapid replacement of native water frog populations (e.g., pool frogs *Pelophylax lessonae*) is now well documented, the consequences of the spread of Eurasian marsh frogs, their sister species, and hybrids on other native amphibian populations are currently unclear (Schmeller et al. 2007; Cayuela et al. 2013). We applied our model using data from an amphibian monitoring program in Switzerland, to test whether the population of water frogs (Eurasian marsh frogs, pool frogs, and their hybrids) negatively impacts populations of endangered yellow-bellied toads (*Bombina variegata*), common midwife toads (*Alytes obstetricans*), and natterjack toads (*Epidalea calamita*).

Unlike other studies that have been based on presence-absence data (Cayuela et al. 2013), our model suggests that expanding water frogs strongly negatively impact on populations of at least two of the three endangered toad species. The results indicate that estimating true population sizes instead of occurrences allows for a more accurate assessment of effects of species interactions. We thus suggest that our extension of *N*-mixture models is a useful tool for estimating effects of species interactions on populations of endangered species.

Methods

N-Mixture Model for Interacting Species

Our aim was to extend the traditional class of *N*-mixture models (Royle 2004) to estimate population sizes of two potentially interacting species. We begin by describing a model of location-specific population sizes that are not directly observable because not all individuals that are present are detected in the field. Let N_i be the latent (i.e., not observable) population size of a species at site $i = 1, \dots, R$. Each site is visited $j = 1, \dots, J$ times per year, and we assume population closure between the J visits, meaning that no birth, death, immigration, or emigration between the J visits occurred (Dail and Madsen 2011). The counts $y_{i,j}$ are then considered binomial random variables with population size N_i and detection probability $p_{i,j}$. Similar to Waddle et al. (2010), we use superscript A to denote parameters for the subordinate species and superscript B to denote parameters for the dominant species. Accordingly, the observation process that yields the counts of the subordinate and the dominant species from the latent local population sizes can be described as

$$y^{\mathrm{A}}_{i,j} \sim \mathrm{binomial}(N^{\mathrm{A}}_i, p^{\mathrm{A}}_{i,j}),$$
$$y^{\mathrm{B}}_{i,j} \sim \mathrm{binomial}(N^{\mathrm{B}}_i, p^{\mathrm{B}}_{i,j}).$$

Furthermore, we assume that the spatial variation of local population sizes N_i of the subordinate and dominant species among sites $i = 1, \dots, R$ can be described using a Poisson distribution with expected population size λ_i:

$$N^{\mathrm{A}}_i \sim \mathrm{Poisson}(\lambda^{\mathrm{A}}_i),$$
$$N^{\mathrm{B}}_i \sim \mathrm{Poisson}(\lambda^{\mathrm{B}}_i).$$

This parameterization allows us to specify site-specific covariates, including effects from co-occurring species. We assume that the expected population size of the subordinate species can be described by a number of covariates and by the latent local population size of the dominant species. Expected population sizes are expressed as

$$\log(\lambda^{\mathrm{A}}_i) = \alpha^{\mathrm{A}}_0 + \sum_{k=1}^{K} X_{i,k}\alpha^{\mathrm{A}}_k + \eta\sqrt{N^{\mathrm{B}}_i} + \varepsilon^{\mathrm{A}}_i,$$

where the expected population size of the subordinate species λ^{A}_i is described by the log-linear predictor consisting of the intercept α^{A}_0, the linear slopes α^{A}_k for the $k = 1, \dots, K$ covariates at site i with covariate value $X_{i,k}$, and the linear effect η of the square root of the latent local population size of the dominant species N^{B}_i. Note that we used the log transformation of the expected population size λ^{A}_i, which is the traditional link function in Poisson generalized linear (mixed) models (Gelman and Hill 2007). However, we used a square root transformation for the local population size, because it can have a value of 0 (i.e., the dominant species does not occur at site *i*), and a log transformation would thus not be possible. To capture the variation of the expected population size among sites that is not explained by the covariates or by the effect of the dominant species, we added the random effect $\varepsilon_i^{\mathrm{A}} \sim \mathrm{normal}(0, \sigma^{\mathrm{A}})$, where σ^{A} is the standard deviation of the random effect. Similarly, we also assume that the detection probability of the subordinate species can be described by different covariates as well as by the latent local population size of the dominant species:

$$\mathrm{logit}(p_{i,j}^{\mathrm{A}}) = \beta_0^{\mathrm{A}} + \sum_{k=1}^{K} X_{i,k}\beta_k^{\mathrm{A}} + \xi\sqrt{N_i^{\mathrm{B}}} + \mu_{i,j}^{\mathrm{A}},$$

where the detection probability of the subordinate species $p_{i,j}^{\mathrm{A}}$ is described by the logit-linear predictor consisting of the intercept β_0^{A}, the linear slopes β_k^{A} for the $k = 1, \ldots, K$ covariates at site *i* with covariate value $X_{i,k}$, and the linear effect ξ of the square root of the latent local population size of the dominant species N_i^{B}. Again, we also included a random effect $\mu_{i,j}^{\mathrm{A}} \sim \mathrm{normal}(0, \tau^{\mathrm{A}})$ with standard deviation τ^{A} to capture the variation in detection probability among sites or visits that could not be explained by the covariates or by the influence of the dominant species.

For the dominant species, however, we assume neither the local population size nor the detection probability of the dominant species to be affected by the local population size of the subordinate species:

$$\log(\lambda_i^{\mathrm{B}}) = \alpha_0^{\mathrm{B}} = \sum_{k=1}^{K} X_{i,k}\alpha_k^{\mathrm{B}} + \varepsilon_i^{\mathrm{B}},$$

$$\mathrm{logit}(p_{i,j}^{\mathrm{B}}) = \beta_0^{\mathrm{B}} + \sum_{k=1}^{K} X_{i,k}\beta_k^{\mathrm{B}} + \mu_{i,j}^{\mathrm{B}}.$$

We expect covariates to predict the local population size and detection probability of the dominant species. Note that we used the same covariates $X_{i,k}$ in the last four formulas, which does not necessarily need to be the case. To decide which covariates to include in our models, we could make the decision a priori, on the basis of what we know about the biology of the subordinate and the dominant species (which we did in our case study; see below). Alternatively, one could apply one of the many methods for model selection, particularly if the sample size is small compared with the number of covariates. For more details on model selection in a Bayesian framework, see, for example, Hooten and Hobbs (2015).

Simulation Study

To examine the performance of our model, we first applied it to simulated data that had the same structure as the data from our case study (see below). We assumed three different covariates with effects on population size and detection probability of dominant and subordinate species that randomly varied in each simulated data set. We run 100 simulations for each of four simulation scenarios: in the first scenario, we assumed the dominant species to negatively impact on the population size of the subordinate species but not on the detection probability of the subordinate species. In the second scenario, we assumed the dominant species to negatively impact on the detection probability of the subordinate species but not on its population size. In the third scenario, we assumed the dominant species to negatively affect both the population size and the detection probability of the subordinate species. The strength of these negative effects randomly varied for each data set. The fourth simulation scenario was similar to the third scenario, but additionally we used a method suggested by Martin et al. (2011) to simulate data where detection probabilities of individuals of both the dominant and the subordinate species are not independent from other individuals, thus deliberately violating one of the most important assumptions of *N*-mixture models (Martin et al. 2011).

To estimate model parameters from the simulated data, we used a Bayesian approach based on Markov chain Monte Carlo (MCMC) methods (Link et al. 2002). MCMC analyses were conducted using JAGS 3.3.0 (Plummer 2003) and were executed in R using the R add-on library rjags. We used vague priors for all parameters, and posteriors were based on two parallel chains with 200,000 iterations each, discarding the first 50,000 values and thinning the remainder by using every 100th value. The simulation study is described in more detail in the supporting information, available online, where we provide and comment on our R and JAGS codes that can be adapted to fit other study questions and other simulated or real data sets.

Case Study: Amphibian Monitoring Program

To illustrate how our method can be applied to data from existing observational studies, we analyzed the data from an amphibian monitoring program of the canton of Aargau in northern Switzerland (Schmidt 2005; Tanadini and Schmidt 2011). For a description of the monitoring protocol, see appendix A (apps. A and B available online). As far as possible, individuals of the water frog complex were identified as either Eurasian marsh frogs (*Pelophylax ridibundus*) or pool frogs (*Pelophylax lessonae*) including hybrids (*Pelophylax esculentus*), on the basis of morphological characteristics or their calls (Laufer et al. 2007). However, because of the strong phenotypic similarity of Eurasian marsh frogs, pool frogs, and their hybrids, unambiguous identification in the field is often impossible (Dubey et al. 2014). We therefore pooled the data on Eurasian marsh frogs, pool frogs, and their hybrids before analyses and used the name "water frog" for all of them. The data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.7gt4m (Roth et al. 2016).

To analyze the monitoring data, we used the Bayesian approach and the same settings as in the simulation study (see above and supporting information). Our aim was to infer whether local population sizes of yellow-bellied toads, common midwife toads, or natterjack toads (subordinate species) at a given site were negatively related to the number of water frogs (dominant species) at the same site. Note that we could have used a model that simultaneously includes all three subordinate species within a single analysis by including separate parameters for each of them. However, in a single model, each parameter would need to have an index for each species; to allow a simpler bookkeeping of parameters, we decided to run three separate models, each inferring the effect of water frogs on one of the subordinate toad species. We analyzed the data from the year of the most recent survey per site, selected from all surveys conducted between 1999 and 2013. Within a year, each site was visited twice at night, and a third visit was made during the day (see app. A). The data from the last (diurnal) visits were excluded from the analysis, because adults of several amphibian species are almost completely inactive during the day, and because population closure (i.e., no birth, death, immigration, or emigration between the visits), which is an important assumption of the applied models (Knape and Korner-Nievergelt 2015), could not be safely assumed that late in the season (third visits were made between June 15 and July 31). Further, we decided to analyze only sites that are currently suitable for amphibians by removing all sites where none of the four amphibian species had been detected. The analyzed data set contained $R = 481$ sites, and each site was visited during $J = 2$ nocturnal visits.

To model site-specific population sizes, we used as site-specific covariates (1) elevation (linear and quadratic term; mean ± SD = 405 ± 77 m asl), (2) total size of the surface of all water bodies at a site (linear and quadratic term; mean ± SD = 1,172 ± 4,177 m^2), (3) observation of fish occurrence (14% of sites), (4) whether the water level showed strong fluctuations between the two visits (13% of sites), and (5) occurrence of covering vegetation in and/or around the water bodies. Vegetation cover may be particularly important because it indicates the successional stage of water bodies. In 71% of sites, we found covering vegetation either around the water bodies or for the reed or other water plants within the water bodies. Note that we could use water surface as an offset, that is, modeling number of frogs per water surface, assuming a fixed linear increase of number of frogs with increasing water surface. Since amphibians seem to prefer water bodies of intermediate size (Semlitsch et al. 2015), and thus the number of individuals would not linearly increase with water surface, we decided to relax the assumption of a fixed slope and instead estimated a linear and a quadratic term for the effect of water surface. As covariates for detection probability, we included (1) the date when the visit was conducted (linear and quadratic term) to account for the phenology in calling activity, (2) the total size of the surface of all water bodies at a site (linear and quadratic term), and (3) the occurrence of vegetation in or around the water bodies of the site to account for the possibility that dense vegetation could be used by toads to hide from water frogs or from field workers.

The selection of covariates was mainly guided by the biology of the studied toad species (Martinez-Solano et al. 2003; Van Buskirk 2005; Warren and Buttner 2008; Cayuela et al. 2011, 2013). Note that we used the same covariates as predictors for local population size and detection probability of both the dominant species and the subordinate species. With increasing complexity of a model, the bias (i.e., the systematic difference between a parameter estimate and its true value) usually decreases, while the uncertainty of the parameter estimate increases (Korner-Nievergelt et al. 2015). Since our main aim was to infer whether and how strongly the dominant species was affecting the population size of the endangered toad species, we aimed for minimizing bias (i.e., confirmatory modeling sensu Shmueli 2010). Additionally, our sample size was relatively large compared with the number of parameters in the model. We thus decided not to apply model selection and not to reduce the complexity of our full models.

We used MCMC methods to obtain parameter estimates. We used vague priors for all parameters (for exact specification of the priors, see fig. S1 in supporting information), and posteriors were based on two parallel chains with 140,000 iterations each, discarding the first 20,000 values and thinning the remainder by using every 100th value. We assessed convergence using history plots and the Gelman-Rubin diagnostic (Brooks and Gelman 1998). We used the means of the simulated values of the posterior distributions as point estimates of the parameters and 2.5% and 97.5% quantiles as estimates of the 95% Bayesian credible intervals. Similar to Amrhein et al. (2012), we speak of a clear effect (which, in a frequentist terminology, is similar to a significant effect) if 0 was not included in the 95% Bayesian credible interval of an estimate.

We used predictive model checking with Bayesian P values to assess the goodness of fit of our statistical model (Gelman et al. 2013). The Bayesian P value is the probability that a test statistic calculated from simulated data is larger than the test statistic calculated from the observed data. Specifically, we compared the real counts of the dominant and the subordinate species with replicated data under the model using the χ^2 discrepancy as our test statistic (Kéry and Schaub 2011). Furthermore, we aimed to check for spatial autocorrelations.

Unlike when applying linear (mixed) models, however, conventional residuals are not directly available in site occupancy models when each site is visited several times. To obtain an estimate that is comparable to residuals, we calculated er_i for each site i as the mean standardized difference between observed and expected values averaged over the two visits:

$$er_i = \frac{1}{J}\sum_{j=1}^{J}\frac{y_{i,j} - N_i p_{i,j}}{N_i p_{i,j}}.$$

We used Moran's I values to explicitly test for significant spatial autocorrelation in er_i values (Dormann et al. 2007), using the R function moran.test from the package spdep (Bivand and Piras 2015). Note, however, that significance of Moran's I could be calculated using a different permutation test that is more conservative (Lichstein et al. 2002).

Results

Simulation Results

According to the simulation study (see app. B), our two-species N-mixture model succeeded well in uncovering the true effects of the covariates on population size and detection probability of the dominant and the subordinate species. In the first three scenarios, where we simulated data under our species interaction model, the model accurately uncovered effects of the dominant species on the subordinate species. Estimation bias for the effect of the dominant species on the population size of the subordinate species—expressed as the difference between estimated and true effect for each of the 100 simulated data sets—was 0.03, 0.07, and 0.07 for scenarios 1, 2, and 3, respectively. Credible interval coverage, which is the number of times the true value for the effect is contained in the 95% credible interval, was close to the nominal level of 95% (scenario 1: 0.93; scenario 2: 0.89; scenario 3: 0.91), suggesting that model assumptions were met and that our model provided estimates of species interactions with reasonable precision. Even in the fourth scenario, where we simulated data for which we violated the assumption that individuals are detected independently of each other, the model accurately uncovered effects of the dominant species on population size of the subordinate species. Estimation bias for the effect of the dominant species on the population size of the subordinate species was 0.07, and credible interval coverage was 0.91. More details on the simulation results are given in appendix B.

Observed Occurrences and Co-Occurrences

In our case study, yellow-bellied toads were observed in 35% of the 481 studied sites, common midwife toads in 22%, and natterjack toads in 12%. Although water frogs were observed in 66% of the studied sites, they were less likely to be observed in sites were the toad species occurred: water frogs were observed in 46% of the sites where yellow-bellied toads were observed (co-occurrence of water frogs and yellow-bellied toads in 16% of all studied sites), in only 21% of the sites where common midwife toads were observed (co-occurrence: 5% of all sites), and in 56% of the sites where natterjack toads were observed (co-occurrence: 7% of all sites). In 6% of the studied sites, at least one Eurasian marsh frog was identified at the species level, but only 3.4% of water frogs were identified as Eurasian marsh frogs.

Covariate Effects on Population Size and Detection Probability

Even though the studied sites covered an elevational range of <500 m (274–730 m), we detected clear differences in the elevational distributions of the four studied species (table 1; fig. 1): yellow-bellied toads and water frogs had the highest population sizes at lower elevations and common midwife toads, and natterjack toads at higher elevations. Further, habitat relationships clearly differed between the three toad species (table 1): the common midwife toad, where the males provide parental care by carrying a string of fertilized eggs on their back, did not show clear associations for particular sites. In contrast, high natterjack toad populations were clearly associated with early successional water bodies (sites with water bodies without covering vegetation in and around the water body, and sites with water bodies with strong fluctuations in water levels). Yellow-bellied toads were somewhat intermediate and were associated with sites with variable water levels and with sites without fishes. Water frogs did not show particular habitat relationships, with the exception that they were associated with sites without strong fluctuations of water level between two visits.

For two toad species and the water frogs, we found no evidence that the variation in detection probability among sites or visits was related to the investigated covariates. For the common midwife toad, however, detection probability peaked early and late during the study period, was highest at intermediate sizes of water bodies, and was reduced when there was vegetation in or around the water bodies (table 1).

Effect of Water Frogs on Native Toad Species

We found that local population sizes of yellow-bellied toads and common midwife toads were clearly negatively related to population sizes of water frogs (table 1). For the natterjack toad, the negative effect due to local water frog populations was not clear (i.e., 0 was included in the credible interval), while the estimated effect size was still negative, as for the other toad species (table 1). In contrast, however, de-

Table 1: Effects of covariates on site-specific population sizes of the subordinate species

Covariate	Yellow-bellied toad	Common midwife toad	Natterjack toad	Water frogs
Population size:				
Elevation (m):				
Linear	−.95 (−1.65 to −.38)[a]	1.10 (.65 to 1.56)[a]	1.09 (.16 to 1.99)[a]	−.97 (−1.45 to −.53)[a]
Quadratic	.13 (−.24 to .47)	−.12 (−.48 to .22)	−.23 (−.88 to .33)	.07 (−.17 to .32)
Size of water body (m^2):				
Linear	.75 (.18 to 1.25)[a]	.77 (.15 to 1.24)[a]	1.05 (.37 to 1.78)[a]	.52 (.37 to .65)[a]
Quadratic	.19 (.06 to .31)[a]	.08 (−.14 to .27)	.06 (−.18 to .30)	−.02 (−.07 to .03)
Fish occurrence[b]	−3.15 (−4.93 to −1.81)[a]	−.04 (−1.24 to 1.13)	−2.77 (−4.92 to −.52)[a]	.17 (−.42 to .74)
Vegetation cover[c]	.15 (−.85 to 1.79)	.81 (−.50 to 2.33)	−2.18 (−4.14 to −.72)[a]	.06 (−.48 to .55)
Variability of water level[d]	1.67 (.45 to 2.73)[a]	−.22 (−1.40 to .84)	2.18 (.39 to 3.85)[a]	−.68 (−1.32 to −.03)[a]
No. water frogs	−.34 (−.51 to −.07)[a]	−.88 (−1.21 to −.57)[a]	−.14 (−.40 to .12)	...
Detection probability:				
Date (Julian day):				
Linear	.13 (−.19 to .44)	.50 (.17 to .97)[a]	.57 (−.45 to 1.96)	.06 (−.18 to .32)
Quadratic	−.04 (−.12 to .02)	.08 (.02 to .17)[a]	.16 (−.06 to .46)	−.02 (−.08 to .03)
Size of water body (m^2):				
Linear	−.58 (−1.16 to .07)	−.97 (−1.54 to −.26)[a]	.18 (−1.07 to 1.42)	.09 (−.08 to .26)
Quadratic	−.09 (−.25 to .04)	−.34 (−.58 to −.06)[a]	−.05 (−.49 to .40)	.00 (−.07 to .07)
Vegetation cover[c]	−1.31 (−2.67 to .11)	−2.30 (−4.12 to −.43)[a]	.43 (−1.73 to 2.73)	.17 (−.51 to .90)
No. water frogs	.16 (−.15 to .33)	.24 (−.19 to .61)	−.02 (−.49 to .43)	...

Note: Given are means and 2.5% and 97.5% quantiles (in parentheses) of the posterior distribution. Elevation was standardized by subtracting 500 m and dividing by 100 m; size of the surface of water bodies was standardized by taking the log of the size and subtracting the log of 500 m^2.

[a] Clear effects (i.e., 0 not included in 95% credible interval).

[b] 0 = no; 1 = yes.

[c] 0 = no/few; 1 = covering around or within water body.

[d] 0 = no/little; 1 = strong.

tection probabilities of the toad species seemed not to depend on the number of water frogs present at the sites (table 1). On the basis of our models, it was possible to estimate population sizes of toads for the hypothetical case that all local population sizes of water frogs were 0. Thus, given that all water frogs were removed from the surveyed sites, the estimated total population sizes in the Swiss canton of Aargau of yellow-bellied toads, common midwife toads, and natterjack toads could potentially increase by factors of 5.5, 15.1, and 2.6, respectively (fig. 2). Note, however, that because of generally low detection probabilities (table 1), the estimates for the total population sizes had relatively low precision (i.e., large 95% credible intervals in fig. 2).

Model Adequacy

For the three models inferring the effect of water frogs on subordinate yellow-bellied toads, common midwife toads, or natterjack toads, the Bayesian P values based on χ^2 discrepancy as test statistic were between .36 and .60. A value of .5 would be perfect because this would indicate that it is equally likely that the χ^2 discrepancy of the simulated data statistic is smaller or larger than the χ^2 discrepancy of the observed data. Our results suggest that our models accurately describe the data, because Bayesian P values were in the range that is taken to indicate a good model fit (Gelman et al. 2013). Furthermore, when using Moran's I statistic testing for spatial autocorrelation in the er_i values, we detected weak but significant spatial autocorrelation for only the common midwife toad (Moran's I statistic $= 0.006$, $P = .01$), while for the two other toad species and the water frogs we could not detect significant spatial autocorrelation (yellow-bellied toad: Moran's I statistic $= 0.003$, $P = .10$; natterjack toad: Moran's I statistic $= -0.005$, $P = .80$; water frogs: Moran's I statistic $= -0.002$, $P = .46$).

Discussion

N*-Mixture Model for Interacting Species*

In this study, we extended the N-mixture model proposed by Royle (2004) to estimate effects on true population sizes of interacting species. Simulations revealed that our model is able to disentangle direct effects of dominant on subordinate species from indirect effects of dominant species on detection probability of subordinate species. Such a dominant-subordinate pattern of species interaction may be produced

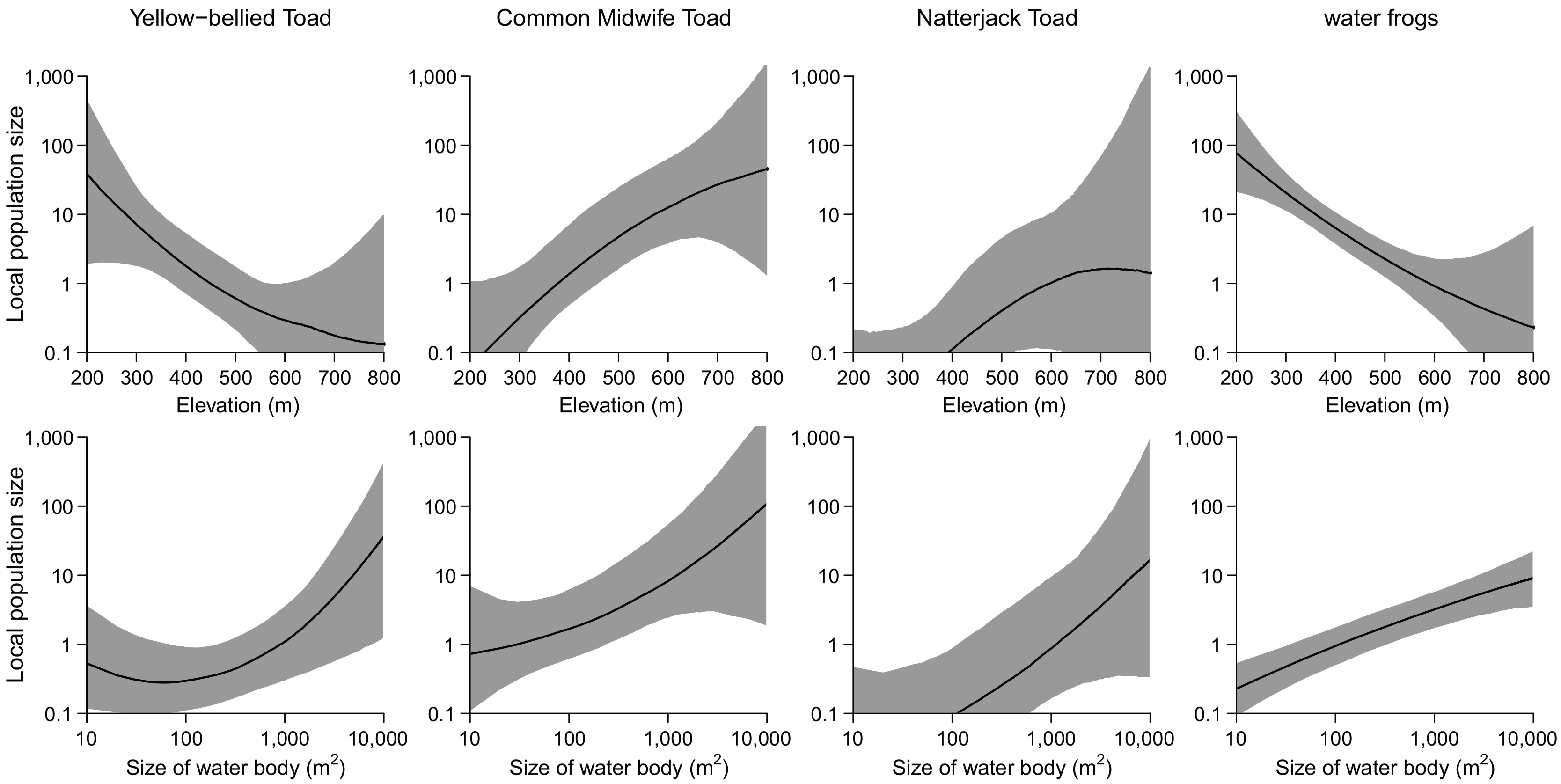

Figure 1: Predicted local population sizes (number of individuals present at a site) of yellow-bellied toads, common midwife toads, natterjack toads, and water frogs (Eurasian marsh frogs, pool frogs, and their hybrids) varied with elevation (top row) and size of water bodies (bottom row) in the Swiss canton of Aargau. Predictions of population sizes were made for an average water body with a size of 500 m^2 (top row), at an elevation of 500 m asl (bottom row), that did not contain fishes, did not have vegetation in and around it, and had no varying water level (all panels). Given are medians (lines) and 95% credible intervals (gray shading) of model predictions.

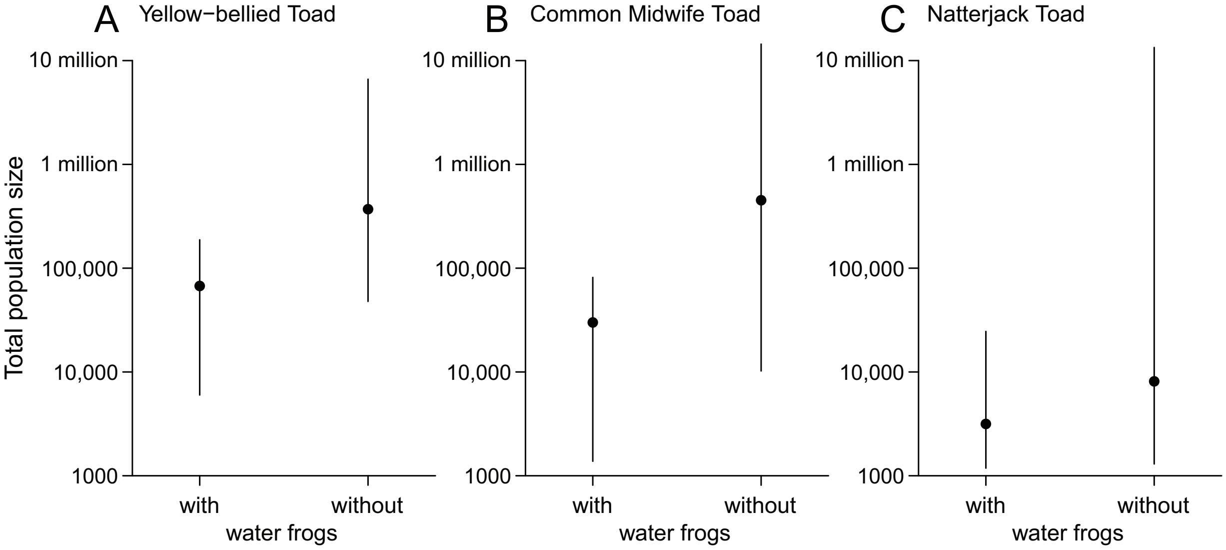

Figure 2: Total population sizes of toad species in the Swiss canton of Aargau. Total population sizes of yellow-bellied toad (*A*), common midwife toad (*B*), and natterjack toad (*C*) over all 481 surveyed sites were estimated under the current population size of water frogs (with) and under the assumption that water frogs were absent from all sites (without). Given are medians and 95% credible intervals.

by different types of ecological interactions, such as predator-prey, generalist-specialist, invasive-endangered species, or parasite-host interactions (Waddle et al. 2010).

N-mixture models are increasingly valued as a tool to account for imperfect detection for analysis of data from observational surveys. To our knowledge, however, there is only one study that extended *N*-mixture models to estimate abundances of interacting species (Dorazio and Connor 2014), in which a statistical model of counts from community-level surveys was developed to estimate the correlation in abundances between species with similar traits, accounting for imperfect detection. Their main aim was to determine "whether the effects of environment or interactions between species were more influential in determining the abundances of individual species," which is an important question of community ecology (McGill et al. 2006). In our study, we aimed to test whether a dominant species negatively impacts on populations of subordinate species and to estimate how important this impact is. This is a major issue in conservation biology, because to decide whether a species should be subject to some form of population management, decision makers need to know whether the species indeed negatively impacts on populations of endangered species (Linder et al. 2003).

There are several assumptions of our approach that need to be taken into account. For example, an important assumption of *N*-mixture models is that detection probability of individuals is independent of other individuals, which may often be violated in the field (Martin et al. 2011). This could also be the case in amphibian monitoring, because males engaged in acoustical competition with other males may increase their calling rate compared with lonely males (Bosch and Marquez 2001) and because females do not call and therefore their detection probability is lower compared with males. Such behavioral effects may cause additional variation in detection probability that is difficult to describe with visit- or site-specific covariates in the detection model. Martin et al. (2011) successfully applied a beta-binomial mixture model to account for the additional variation in detection probability due to correlated singing of individuals. Instead of using a beta distribution to model the additional variation in detection probability, we added an individual random effect to the detection model in order to account for the unexplained variance in detection probability between visits and between sites, which is conceptually similar to a beta distribution (Royle and Dorazio 2008). Simulation scenario 4 shows that our model is able to accurately estimate effects of the dominant species on the subordinate species population size also if the assumption is violated that individuals were detected independently of each other.

Another concern is that niche differences and direct interactions among species are difficult to tease apart (Wisz et al. 2013): a species might be missing at a site because of unfavorable habitat or because of competitive exclusion by other species. This is particularly problematic if (unknown) factors that influence population sizes of both the dominant and the subordinate species are not included in the models. In our case study on amphibians, it might be possible to improve the model by including further covariates to describe variation in population size among sites. For example, one could potentially include covariates describing the terrestrial habitat in the surroundings of the sites, such as the presence of busy roads or whether the site is surrounded by forested area (Van Buskirk 2005; Hartel et al. 2010; Ficetola 2015). In our study, we added random effects for the population sizes of the dominant and the subordinate species to the linear models, which likely reduced bias that would have been induced by unaccounted heterogeneity in local population sizes (Royle and Dorazio 2008).

Case Study: Effect of Water Frogs on Native Toad Species

For 8.4% of the amphibian species of the world, "invasive species or other problematic species and genes" have been listed as a threat, according to the International Union for Conservation of Nature Red List of Threatened Species (www.iucnredlist.org; accessed June 9, 2015). Predation from or competition with invasive species is thus an important factor for the worldwide decline of amphibian populations. In Central Europe, it is well established that the repeated introductions and spread of Eurasian marsh frogs had important implications on populations of the native pool frog, which now seems to be extinct in many parts of its range in which Eurasian marsh frogs have been introduced (Vorburger and Reyer 2003; Dubey et al. 2014). Note that we here use a broad definition of invasive species, encompassing species introduced by humans, as well as native species and their hybrids that rapidly become dominant (Valery et al. 2013). We therefore consider the Eurasian marsh frog as an invasive species, although it is not clear whether it should be considered native or introduced, because of the complex genetic system of water frog species and their hybrids that is possibly the result of repeated introductions or hybridization with closely related native species (Vorburger and Reyer 2003; Luquet et al. 2011; Dubey et al. 2014).

To our knowledge, the only study that assessed the impact of invasive Eurasian marsh frogs on other amphibian species found no evidence that the presence of native yellow-belied toads was negatively affected by the presence of Eurasian marsh frogs (Cayuela et al. 2013). This study was based on presence-absence data and not on counts of individuals. The authors speculated that the apparent absence of negative impacts could be due to the early stage of Eurasian marsh frog invasion at their study site. In contrast, in our study area, where the invasion of Eurasian marsh frogs is at a more advanced stage (Dubey et al. 2014), we found clear indications that the population sizes of endangered yellow-bellied toads and common midwife toads were negatively related to the population size of water frogs, while the effect was less clear in natterjack toads. Our results thus suggest that the spread of Eurasian marsh frogs and of its hybrids with the pool frog in Central Europe have resulted in a replacement of endangered toad species.

Dominant species such as water frogs may have strong effects on subordinate species through predation or competition if they occur at the same sites. Still, however, water frogs may only marginally affect the total population size of an endangered toad species if they do not share the same habitat niche and, thus, if they rarely occur at the same sites. We aimed to describe general niche differences between invasive and endangered species by including variables describing differences in water bodies (i.e., elevation, size of the surface of water bodies, occurrence of fish, strong fluctuations of water level, occurrence of covering vegetation). The estimated effect of invasive species population on endangered species population (η in our model) is then the effect if the two species occurred at the same sites. However, the flexible Bayesian modeling framework that we applied additionally allowed us to estimate the effect of water frog populations on the total population size of the endangered species at the entire study site, by comparing the total population size of an endangered species under the current abundance of water frogs with the predicted total population size under the assumption that water frogs were removed from all surveyed sites. The effect of water frogs on the total population size of an endangered species would be particularly large if the effect of water frogs occurring at the same sites as the endangered species is large (i.e., $\eta \ll 0$) and if water frogs often occur at the same sites as the endangered species. Even if the precision of the effect on the total population is relatively small, as in our study case, this effect of an invasive species on the total population size of an endangered species seems an important measure to inform decision makers about current effects of an invasive species on populations of endangered species.

Although we used relatively simple measures to describe the characteristics of the water bodies at the sites, we found clear differences in habitat relationships among the three toad species (i.e., differences in realized habitat niche): while the common midwife toad seemed not very choosy, the natterjack toad was associated with sites with early successional water bodies without covering vegetation around or within the water body and with large variation in water level. The selectivity of yellow-bellied toads was intermediate between the two other toad species in that they were associated mainly with sites with water bodies with large variation in water level (table 1). It seems important to include such covariates to describe niche differences, because if they are not accounted for, studies may report apparent negative or even positive interactions between species that may arise simply because the species prefer either different or the same habitats. As a proof of concept, we reanalyzed the data while removing all covariates from the models (results not shown), which led to estimates of true local population sizes of water frogs that were positively related to the local population size of yellow-bellied toads but negatively related to the population size of common midwife toads and natterjack toad. This indicates that our covariates were effective in describing niche differences between water frogs and toad species and suggests niche overlap between water frogs and yellow-bellied toads and niche differences between water frogs and natterjack toads and common midwife toads.

Conclusion

We suggest that our model of species abundance data is a useful extension of existing approaches by attempting to account explicitly for imperfect detection of individuals in species interactions. As shown in the case study on water frogs and toad species, the model is useful if applied to observational surveys from biodiversity monitoring programs to assess the potential impact of invasive species. According to our results, the invasion of Eurasian marsh frogs and of its hybrids with the pool frog appears to be a threat to subordinate toad species in Central Europe. To decide which dominant species should be subject to some form of population management, decision makers need to know which of the species indeed negatively impact populations of endangered species (Linder et al. 2003) and, preferably, how important the impact is. Our approach allows us to timely quantify such negative impacts of species interactions on populations of endangered species.

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