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The superpopulation approach for estimating the population size of 'prolonged' breeding amphibians: Examples from Europe

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Abstract. Individual members of a population of 'prolonged' breeding amphibian species are asynchronously present at their breeding sites. Therefore, population size estimates can be misleading when based on commonly used closed or open-population capture-mark-recapture approaches. The superpopulation approach, a modified Jolly-Seber model, has been successfully applied in taxa other than amphibians with distinct migratory behaviour and where individuals are asynchronously present at the sampling site. In this paper, we suggest that the superpopulation approach is a useful population size estimator for 'prolonged' breeding amphibian species. Two case studies on European anurans show that superpopulation estimates are much higher than simple population counts. A simulation study showed that superpopulation estimates are unbiased but that accuracy can be low when either survival or detection probabilities (or both) are low. We recommend the superpopulation approach because it matches the natural history and phenology of amphibian species with prolonged breeding seasons.

Keywords: abundance, *Bufo* (*Pseudepidalea*) *viridis*, capture-mark-recapture, *Hyla arborea*, Jolly-Seber model, POPAN, simulation.

Introduction

About one third of all known amphibian species is threatened with extinction (Stuart et al., 2008), and negative population trends have been found in almost all European species (Temple and Cox, 2009). Therefore, considerable conservation effort is needed to prevent large-scale losses of amphibian biodiversity (Stuart et al., 2004, 2008; Gascon et al., 2007). In this context, it is crucial most to know the state of amphibian populations. Because many populations decline but do not go extinct (Houlahan et al., 2000), reliable estimates of abundance – as opposed to presence/absence data – are important. To determine the size of an amphibian population, two approaches are commonly used: (i) trying to count all individuals of the population (e.g. using drift fences and pitfall traps) or (ii) estimating the population size. The first way seems attractive, but is almost impossible in many cases (Schmidt, 2004; Mazerolle et al., 2007). In any case, this method is expensive and time-consuming, and does not guarantee high and constant detection probabilities (Donnelly and Guyer, 1994; Schmidt, Schaub and Anholt, 2002). All methods of counting amphibians (adults, egg masses, or calling males) assume that detectability is perfect or at least constant, an assumption which is likely to be violated in many natural amphibian populations and which cannot be adequately tested. Therefore, the magnitude and direction of bias to remains unknown (Schmidt, 2004). It is suggested to apply methods that explicitly account for imperfect detectability. Capture-mark-recapture (CMR) methods adjust population size estimates for imperfect detection (Schmidt, 2004; Mazerolle et al., 2007). Additionally, the assumptions of these methods can be tested (Lebreton et al., 1992; Schmidt, Schaub and Anholt, 2002).

Many different estimators for abundance are available for CMR data (e.g., Williams, Nichols and Conroy, 2002). However, the question re-

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mains open which estimators are the best for amphibians, especially those with 'prolonged' breeding seasons. The best observation possibilities for amphibians are during the breeding season of pond-breeding species. Regarding the length of this breeding season, most European amphibian species can be classified either as 'explosive' or 'prolonged' breeders (Arak, 1983; Wells, 2007). In European species, the breeding season of prolonged breeders lasts for several weeks to months. Consequently, the members of the populations are asynchronously present at the breeding site and there is no period within a year with all individuals being present at the breeding site.

When estimating the size of a population of an amphibian with a prolonged breeding season, the interest is in knowing the total (or cumulative) number of individuals that use the breeding site. Closed population size estimators can estimate this number (Kendall, 1999) but assume that populations are demographically closed, i.e. that there is no immigration, birth, emigration and death during the study period. This assumption is violated in most populations, but in particular in those that have prolonged breeding. Hence, estimators for closed populations are useful only in some specific cases (Kendall, 1999). Instead, estimators for demographically open populations should be used.

The most widely used open population size estimator is the Jolly-Seber model which primarily aims to estimate abundances (Pollock et al., 1990). A drawback of this model is its unsuitability for estimating the total or cumulative number of individuals at a breeding site, as it estimates the number of individuals that are present at one particular point in time (Pollock et al., 1990; Bailey, Simons and Pollock, 2004a). Therefore, neither the closed population estimators nor the original Jolly-Seber model are suitable tools to estimate population sizes of prolonged breeding amphibians, since neither method adequately matches the natural history of amphibians with prolonged breeding seasons. Therefore, researchers have used other methods. For example, several studies used the 'robust design' (Pollock, 1982) to estimate population sizes of amphibian populations (e.g., Bailey, Simons and Pollock, 2004a; Bailey, Simons and Pollock, 2004b), including prolonged breeders (e.g., Pellet, Helfer and Yannic, 2007). The 'robust design' combines closed and open population analysis methods.

Schwarz et al. (1993) and Schwarz and Arnason (1996) developed a modification of the Jolly-Seber model that, in our opinion, may be useful for amphibians with prolonged breeding seasons. Because this model was first implemented in the software POPAN (http://www.cs.umanitoba.ca/~popan/), we call it hereafter the 'POPAN model'. Within a season, the POPAN model first estimates the number of individuals present during the first capture occasion and then estimates the number of individuals that enter the population between the first and the second capture occasion (and then the number of new entrants between all subsequent capture occasions). Thus, the POPAN model aims to estimate the number of amphibians present at any capture occasion and additionally the total or cumulative number of amphibians that use the breeding site during a season. The total or cumulative number of amphibians is estimated by adding the number of individuals present during the first capture occasion ($\hat{N}_1$) and the sum of the new entrants at subsequent capture occasions ($\hat{B}_i$):

$$\hat{N}^* = \hat{N}_1 + \sum_{i=1}^{k-1} \hat{B}_i^*.$$

This sum ($\hat{N}^*$) is called the 'superpopulation' (Schwarz and Arnason, 1996; Williams, Frederick and Nichols, 2011). The POPAN model makes the usual assumptions of Jolly-Seber models, namely that there is no heterogeneity among individuals in either survival or detection probabilities (Williams, Frederick and Nichols, 2011). Some parameters may be confounded with others (see Schwarz and Arnason, 2007).

The POPAN model has been applied successfully to different taxa with distinct migratory activity, including marine mammals (Manske, Stobo and Schwarz, 2002; Parra, Corkeron and Marsh, 2006), butterflies (Habel, Junker and Schmitt, 2010; Junker and Schmitt, 2010; Junker et al., 2010; Konvicka et al., 2010) and birds (Williams, Frederick and Nichols, 2011). Although the POPAN approach was used by some herpetologists (e.g., Wilgers et al., 2006; Hocking and Semlitsch, 2007; Vasconcellos and Colli, 2009), its ability to estimate the total number of amphibians that use a breeding site during a season is apparently not yet widely appreciated. For example, the POPAN approach was only briefly mentioned in a recent review of population analysis methods (Mazerolle et al., 2007). We believe that this estimator matches the biology and phenology of prolonged-breeding amphibians very well. To illustrate the usability of the POPAN model for use with amphibian CMR data, we used it to estimate population sizes in two species of prolonged-breeding amphibian populations in Europe. CMR data collected during one breeding season of a Green toad (*Bufo* (*Pseudepidalea*) *viridis* Laurenti, 1768) population from western Germany and data of two European tree frog (*Hyla arborea* (Linnaeus, 1758)) populations from Switzerland (Pellet, Helfer and Yannic, 2007) collected during three years serve as case studies. Furthermore, to gain insight into the properties of the POPAN superpopulation estimator when sample sizes are small as in most amphibian field studies, we conducted a small simulation study (see also Arnason and Schwarz, 2002).

Materials and methods

Field studies and data analysis

Bufo (*Pseudepidalea*) *viridis* toads were captured and marked (see below) for approximately half an hour per pond and session with a dip net by a single person (NW) in a former mining area near Camphausen, Saarland, western Germany (49°17′N, 07°01′E, about 300 m a.s.l.). Ten sessions were conducted in 2009 from the beginning to the end of the breeding season (March-June).

Two populations of *Hyla arborea* were studied, one in Camp Romain, Vaud, Switzerland (46°31′N, 06°21′E, about 600 m a.s.l.) and another one in Les Mossières, Vaud, Switzerland (46°32′N, 06°21′E, about 650 m a.s.l.). Studies were performed during the respective breeding activities in 2002, 2003 and 2004. Each year, three to four capture sessions spread across the breeding season were conducted by three persons (JP, V. Helfer, G. Yannic). For further details see Pellet, Helfer and Yannic (2007).

Green toads were individually recognised (‘marked’) by their dorsal and snout patterns (see Henle et al., 1997; Meyer and Grosse, 1997). The documentation and individual recognition was managed via a digital photograph database. Likewise, the dark lateral line in the European tree frog allowed for photographic identification of individuals (Tester, 1990).

Due to the lack of female recaptures, only data on male recapture rates was analysed for both species. The three data sets, i.e. Camphausen, Camp Romain, Les Mossières, were analysed with the software MARK (White and Burnham, 1999). All three data sets were analysed using the POPAN model. For the tree frogs, where three years of CMR data were available, we estimated abundance for each of the three years. Herein, we accounted for different time periods between field surveys. We subsequently tested for each data set whether models with constant or time-varying parameters provided a better fit to the data. We used the sinus or logit function for survival (ϕ) and detection probabilities (p). For the probability of entry (b_i), we always used the *Mlogit* link function and for N the log-link function (as recommended by Schwarz and Arnason, 2007). Best fitting models were chosen by their small sample Akaike Information Criterion values (AICc; Burnham and Anderson, 2002) and used for parameter estimation.

Simulation study

To assess the performance of the POPAN model, we simulated capture histories and used these capture histories to estimate the size of the superpopulation. We simulated capture histories in R (R Development Core Team, 2009) using an adapted version of the R function ‘simul.ch.js’ (Kéry and Schaub, 2011). Capture histories were imported into program MARK (White and Burnham, 1999) for population estimation. We simulated a study with ten capture occasions and a superpopulation size of $N = 100$. One hundred individuals is a small sample size if the goal is to assess the performance of an estimator, but we were interested in an assessment with realistically small sample sizes. Individuals entered the breeding population with probability b_i and were detected with probability p. After entry, individuals survived with probability ϕ and were detected with probability p (i.e., those probabilities were constant across time). We simulated eight scenarios in which we varied entry, survival and detection probabilities. We simulated populations in which the probability of entry (i) was the same for all occasions ($b_i = 0.1$) or (ii) where most individuals entered the populations in the middle of the study (i.e., $b_i = 0.05, 0.05, 0.05, 0.1, 0.25, 0.25, 0.1, 0.05, 0.05, 0.05$). We simulated capture histories with high and low survival probabilities ($\phi = 0.8$ and $\phi = 0.4$) and high and low detection probabilities ($p = 0.8$ and $p = 0.4$). Each scenario was simulated five times. Within program MARK, we used the POPAN option to fit two models to every simulated data set: a model where all parameters were constant and a model where capture probability was constant and survival and entry probabilities time-varying. Modelling followed Schwarz and Arnason (2007).

Results

Field studies

The best fitting models all had a time-varying probability of entry (table 1). We used these models for parameter estimation. The annual population size estimates exceeded the total number of individuals captured or were sometimes similar to them (table 2). All mean counts per capture session were lower than the per-session estimates. Likewise, all maximum numbers of captures at one occasion were much lower than the annual population size estimates (table 2, figs 1-2).

The POPAN abundance estimates for the capture events within the seasons show distinct pat-

Table 1. Best fitting POPAN models chosen by their AICc-values; K is the number of parameter. Link functions are given in parentheses for survival (ϕ) and detection probabilities (p). A log link and a Mlogit link were used for superpopulation size (N) and entry probabilities ($pent = b_i$), respectively.

Species, population, year	Model	AICc	K
Bufo (*Pseudepidalea*) *viridis*, Camphausen, 2009	$\phi(\cdot)p(\text{t})pent(\text{t})N$ (logit link for ϕ and p)	936.36	15
Hyla arborea, Camp Romain, 2002	$\phi(\cdot)p(\text{t})pent(\text{t})N$ (logit link for ϕ and p)	79.85	5
Hyla arborea, Camp Romain, 2003	$\phi(t)p(\text{t})pent(\text{t})N$ (logit link for ϕ and p)	59.71	6
Hyla arborea, Camp Romain, 2004	$\phi(\cdot)p(\text{t})pent(\text{t})N$ (logit link for ϕ and p)	98.36	6
Hyla arborea, Les Mossières, 2002	$\phi(\cdot)p(\text{t})pent(\text{t})N$ (logit link for ϕ and p)	46.77	3
Hyla arborea, Les Mossières, 2003	$\phi(\cdot)p(\cdot)pent(\text{t})N$ (sinus link for ϕ and p)	87.00	4
Hyla arborea, Les Mossières, 2004	$\phi(\text{t})p(\text{t})pent(t)N$ (logit link for ϕ and p)	172.86	7

Table 2. Total number of male individuals captured, total number of captures including recaptures, maximum number of captures at one occasion, mean number of individuals captured per session, and estimated annual population sizes. Estimates are means ± SE (95% confidence intervals in parentheses) and based on the best model shown in table 1.

Species, population, year	Total number of individuals one captured	Maximum number of captures at occasion	Mean number of individuals captured per session	Estimated annual population size (POPAN model)
Bufo viridis, Camphausen, 2009	188	84	38.1	305.14 ± 21.0 (264.0; 346.3)
Hyla arborea, Camp Romain, 2002	35	27	16	41.5 ± 3.9 (33.9; 49.2)
Hyla arborea, Camp Romain, 2003	34	21	12.3	31.9 ± 3.0 (26.0; 37.7)
Hyla arborea, Camp Romain, 2004	75	17	22	162.4 ± 35.2 (93.3; 231.5)
Hyla arborea, Les Mossières, 2002	29	22	13.3	28.7 ± 1.2 (26.3; 31.1)
Hyla arborea, Les Mossières, 2003	30	23	17.3	32.0 ± 1.0 (30.2; 33.8)
Hyla arborea, Les Mossières, 2004	45	34	22	46.2 ± 1.9 (42.5; 49.9)

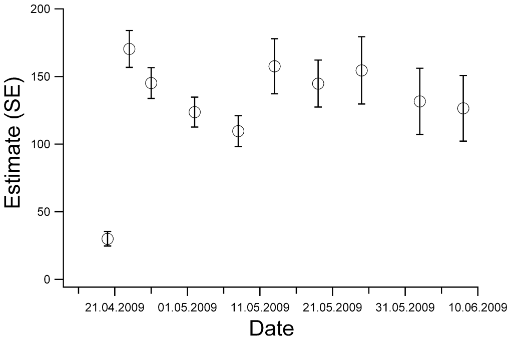

Figure 1. Estimated male population size at every capture occasion of Green toads using the POPAN model (table 1) at Camphausen (estimates are means ± SE and represent population sizes at the sampling occasions).

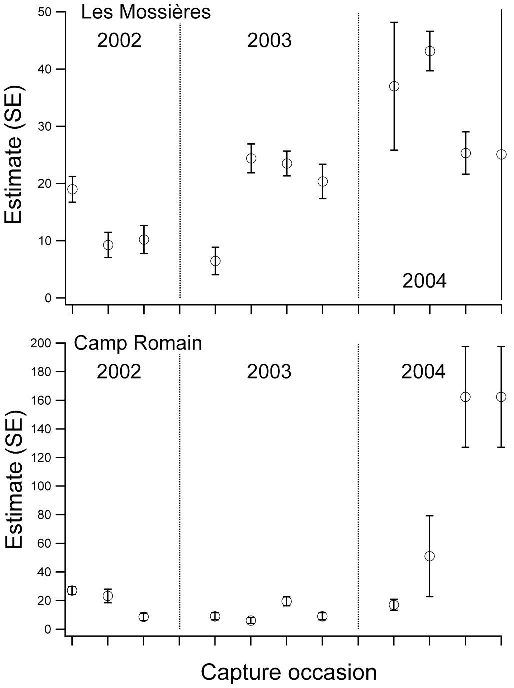

Figure 2. Estimated male population size at every capture occasion of European tree frogs using the POPAN model (table 1) at Camp Romain and at Les Mossières (estimates are means ± SE and represent population sizes at the sampling occasions).

terns (figs 1-2). The number of Green toads at the breeding site was relatively stable. However, the number of toads present at any capture event was only about 50% of the superpopulation size (table 2). Within-season survival probabilities were high but detection probabilities were often quite low and variable (table 3).

For both European tree frog populations, the POPAN within-season estimates showed relatively stable numbers of males present at the breeding site (fig. 2). Tree frog survival probabilities and detection probabilities were usually high (except for 2004). Detection probabilities were close to one, suggesting that most, and in some cases all, males present at the site were captured. As a consequence, the difference between the total number of males caught and the superpopulation estimate was small.

Simulation study

The results of the simulation study are shown in fig. 3. The figure shows the results of the superpopulation estimates based on two models. On average, there appears to be no bias but individual estimates can deviate from the true value. Estimates are best (high accuracy, i.e. minimal difference between the estimates and true superpopulation size) when both survival and capture probabilities were high ($\phi = 0.8$). When either survival or capture probabilities were low, then estimates were more variable across replicate simulations of the same scenario (i.e., reduced accuracy). Even though point estimates deviated from the true value, confidence intervals included true population size. When both survival and capture probabilities were low, then estimates were often far away from the true value. Under this scenario, confidence intervals were very wide but they nevertheless usually included the true value. Whether entry probabilities were constant or time varying had very little impact on the estimates.

Discussion

Conceptually, the POPAN model of Schwarz and Arnason (1996) is an appropriate model for the estimation of population size in prolonged breeding amphibian species. The superpopulation model provides estimates of abundance at

Table 3. Survival probabilities (ϕ) ± SE and detection probabilities (p) ± SE for the Green toad population, western Germany, and the two European tree frog populations, Switzerland. Estimates are based on the best model shown in table 1.

Species, population	Capture occasion	Survival probabilities (ϕ)± SE	Detection probabilities (p) ± SE
Bufo viridis, Camphausen	20-IV-2009	–	1.00 ± 0.04
	23-IV-2009	0.96 ± 0.01	0.18 ± 0.03
	26-IV-2009	0.96 ± 0.01	0.59 ± 0.05
	02-V-2009	0.96 ± 0.01	0.29 ± 0.05
	08-V-2009	0.96 ± 0.01	0.26 ± 0.05
	13-V-2009	0.96 ± 0.01	0.42 ± 0.06
	19-V-2009	0.96 ± 0.01	0.47 ± 0.07
	25-V-2009	0.96 ± 0.01	0.22 ± 0.05
	02-VI-2009	0.96 ± 0.01	0.05 ± 0.02
	08-VI-2009	0.96 ± 0.01	0.03 ± 0.02
Hyla arborea, Camp Romain	8-V-2002	–	1.00 ± 0.00
	14-V-2002	0.89 ± 0.02	0.53 ± 0.16
	24-V-2002	0.89 ± 0.02	1.00 ± 0.00
	23-IV-2003	–	1.00 ± 0.00
	25-IV-2003	0.82 ± 0.10	1.00 ± 0.00
	28-IV-2003	1.00 ± 0.00	0.92 ± 0.12
	8-V-2003	0.86 ± 0.04	1.00 ± 0.00
	21-IV-2004	–	1.00 ± 0.00
	27-IV-2004	1.00 ± 0.0	0.12 ± 0.08
	28-IV-2004	1.00 ± 0.0	0.08 ± 0.03
	10-V-2004	1.00 ± 0.0	0.33 ± 0.08
Hyla arborea, Les Mossières	7-V-2002	–	1.00 ± 0.00
	12-V-2002	0.83 ± 0.04	1.00 ± 0.00
	15-V-2002	0.83 ± 0.04	1.00 ± 0.00
	25-IV-2003	–	0.92 ± 0.05
	1-V-2003	0.98 ± 0.01	0.92 ± 0.05
	12-V-2003	0.98 ± 0.01	0.92 ± 0.05
	18-V-2003	0.98 ± 0.01	0.92 ± 0.05
	23-IV-2004	–	1.00 ± 0.30
	29-IV-2004	1.00 ± 0.00	0.42 ± 0.08
	3-V-2004	0.88 ± 0.03	0.59 ± 0.10
	11-V-2004	1.00 ± 1.43	0.88 ± 10.01

every sampling occasion (figs 1-2) and, most importantly, an estimate of cumulative, i.e. superpopulation, abundance (see table 2 and the equation in the introduction). Therefore, the superpopulation model is better than closed population estimators because it does not make the unrealistic assumption of demographic closure. It is better than the traditional Jolly-Seber model because it provides an estimate of cumulative abundance.

We believe that the calculation of a superpopulation in the POPAN model best matches the reproductive phenology and activity of prolonged breeding amphibians. The simulation results showed that the POPAN model recovered true population sizes well. The results of the simulation study help to identify conditions under which the superpopulation model performs best (i.e., narrow confidence intervals and high accuracy; also see Arnason and Schwarz, 2002 and Williams, Frederick and Nichols, 2011). As expected, the superpopulation model performs best when both survival and capture probabilities are high. If either probability or both are lower, superpopulation estimates are worse (fig. 3). Individual estimates can deviate from the true value and confidence intervals are wide. The confidence interval, however, usually includes the true value. Like all CMR models, the superpopulation model requires a sufficient amount of data in order to estimate demographic parameters with a satisfactory level of

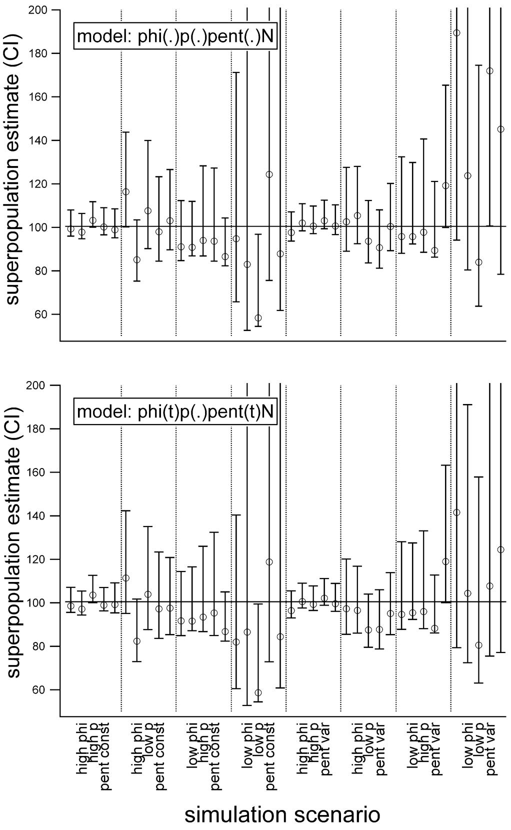

Figure 3. Results of the simulation study. Symbols show superpopulation estimates and 95% confidence intervals (some exceed the range of the y-axis) for five replicates of eight simulation scenarios. The scenarios were: (a) high survival (phi $= \phi = 0.8$), high capture probability ($p = 0.8$) and constant entry probabilities (pent $= b = 0.1$), (b) high survival (phi $= \phi = 0.8$), high capture probability ($p = 0.4$) and constant entry probabilities (pent $= b = 0.1$), (c), high survival (phi $= \phi = 0.4$), high capture probability ($p = 0.8$) and constant entry probabilities (pent $= b = 0.1$), (d), high survival (phi $= \phi = 0.4$), high capture probability ($p = 0.4$) and constant entry probabilities (pent $= b = 0.1$), (e) high survival (phi $= \phi = 0.8$), high capture probability ($p = 0.8$) and variable entry probabilities (pent; see text), (b) high survival (phi $= \phi = 0.8$), high capture probability ($p = 0.4$) and variable entry probabilities (pent; see text), (c) high survival (phi $= \phi = 0.4$), high capture probability ($p = 0.8$) and variable entry probabilities (pent; see text), (d) high survival (phi $= \phi = 0.4$), high capture probability ($p = 0.4$) and variable entry probabilities (pent; see text). The upper panel shows estimates based on a model where all parameters were constant. The lower panel shows estimates based on a model where capture probability was constant and survival and entry probabilities were allowed to vary with time. The horizontal line at $y = 100$ indicates the true superpopulation size.

confidence (Pollock et al., 1990). Thus, we suggest that researchers should try to maximize effort in the field such that capture probabilities are high.

The superpopulation approach that we described is useful if abundance has to be estimated at a single site. When abundances have to be estimated at multiple sites at the same time, the point count models by Royle (2004) and Dail and Madsen (2011) may be an even better choice, as they also account for imperfect detection (Nichols, Thomas and Conn, 2008; see Dodd and Dorazio (2004) for a case study on salamanders). Thus, those models can also deal with temporary emigration and with asynchronous presence of individuals at the sampling site (see Nichols, Thomas and Conn (2008) for a detailed discussion).

Field studies

Due to the lack of data on female individuals, only the number of males could be estimated. As this is a common problem, monitoring programmes and ecological studies often focus on males (e.g., Pellet et al., 2006). For conservation measures, herpetologists therefore have to assume that the state and dynamics of males also reflects the state and dynamics of females. However, this procedure might bear problems when proportions of males and females are changing over time, e.g., caused by ‘demasculinisation’ of amphibians by some pesticides (e.g., Hayes et al., 2006). Beside this, there is a clear need to better understand the temporal patterns of reproductive activities of individual males (Friedl and Klump, 2005; Grafe and Meuche, 2005; Broquet, Jaquiéry and Perrin, 2009). For example, the survival estimates presented in table 3 suggest that many male tree frogs spend several weeks at the breeding site (Schmidt, 2010). In contrast, several studies on sexual selection in tree frogs reported short stays at the breeding site (Friedl and Klump, 2005; Grafe and Meuche, 2005; Broquet et al., 2009).

Green toad population

High survival probabilities (table 3) suggest that most toads stay at the breeding site for most of the season (Schmidt, 2010). Detection probabilities were low and variable (table 3) even though one would expect that calling males should be easy to detect. Comparing the estimates of survival (high) and capture probabilities (low) to the results of the simulation (fig. 3), this suggests that the estimates are of intermediate quality in terms of confidence interval width and accuracy. To obtain better estimates, capture effort in the field should be increased such that detection probabilities are higher.

According to the rules defined by the German federal agency for nature conservation for population assessment under the European Habitats Directive, the Camphausen population would be declared to be in a 'good' state. This is because the maximum count at a capture occasion was $n = 88$. However, with a superpopulation estimate of ~300 male Green toads in 2009, we consider the population to be in a better state than 'good'. This highlights the fact that different methods of quantifying population size can result in different assessments of the state of a population. Indeed, the Camphausen population is the largest population of this species known in the German state of Saarland and therefore should be a special target of conservation effort. In the past, similarly larger populations were known, but they all declined, mainly due to ecological changes of the mining areas (e.g., reforestation) due to the end of coal mining (Gerstner, 2003).

Tree frog populations

Estimates of survival and capture probabilities were high (table 3) which suggests that the estimates of superpopulation size for 2002 and 2003 should be of high quality (i.e., when compared to the results of the simulation study; fig. 3). Estimates for 2004 probably are not reliable. At Camp Romain, this may be partly caused by the fact that many 'new' frogs appeared at the site at the third capture occasion while most 'old' frogs were no longer captured. The reason(s) for this turnover of individuals are unknown.

Both tree frog populations studied are source populations in a remnant metapopulation system of western Switzerland (Pellet, Maze and Perrin, 2006). They were part of a long term monitoring program aimed at the detection of early changes in breeding population sizes. The European tree frog has a relatively short life span; therefore, it is of high importance to get the best information possible on its population sizes. Thereby, conservation efforts may focus on breeding sites with decreasing population trends.

Conclusion

We believe that population estimates are more valuable than counts that are not adjusted to imperfect detection (Schmidt, 2004; Schmidt and Pellet, 2009). In our field studies, the mean counts per capture session as well as the maximum numbers of individuals captured at a single occasion were lower than the per-session estimates of abundance and much lower than the superpopulation estimate of abundance (table 2, figs 1-2). These findings support the idea that simple count data underestimate true population sizes, as also has been pointed out by other authors (e.g., Bailey, Simons and Pollock, 2004b; Dodd and Dorazio, 2004; Mazerolle et al., 2007). As described for the Green toad population, the use of counts or estimates may lead to different population status assessments.

We would like to emphasise that when using CMR methods for estimating population size of amphibians, one should carefully choose the most suitable estimator. The statistical model should account for the natural history and phenology of the species. We recommend the POPAN model to estimate population sizes of amphibians with prolonged breeding seasons because it matches the natural history and phenology of prolonged-breeding amphibians well.

Superpopulation estimates are a very useful description of the state (i.e. size) of a biological population and therefore they should be useful for the assessment of conservation status of populations of species that are listed in the EU Habitats Directive appendices. Additionally, the superpopulation estimates are in our opinion the best description of population size if the goal is to learn whether a population is stationary or declining.

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