

Estimating population size in the European tree frog (*Hyla arborea*) using individual recognition and chorus counts

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Abstract. Chorus counts are widely used to assess population abundance in breeding anurans. It is however unclear how such counts translate into true population sizes. We monitored chorus activity in two populations of the European tree frog (*Hyla arborea*) over three years, while simultaneously conducting a capture-mark-recapture (CMR) study on breeding males. Three to four capture sessions were made each year, spread across the acme of the breeding season. Individual recognition was ensured by photographs of the *linea marginalis*. We used Pollock's robust design to test several biological hypotheses and estimate demographic parameters. Male survival was estimated as mean \pm SE = 0.297 ± 0.154 . Population trends deduced from chorus counts (maximum or mean) and modelled male population sizes were not concordant. We showed that there is no simple relationship between maximum or mean chorus size and modelled male population sizes estimated from CMR study and that population trends inferred from chorus counts are likely to be biased to an unknown extent. Even though CMR methods need significant time and personnel investments in order to produce reliable results, we advocate their use in the study of pond breeding amphibians' demography, as it provides unbiased and more precise estimates.

Introduction

Understanding population dynamics and estimating demographic parameters are central issues in amphibian conservation biology (Marsh and Trenham, 2001). Without such basic information, we are unlikely to understand and reverse amphibian declines (Schmidt, Schaub and Anholt, 2002; Stuart et al., 2004). For many anurans, including the European tree frog (*Hyla arborea*), call surveys are widely used to assess both presence and abundance of species (Stumpel and Tester, 1993; Heyer et al., 1994; Edenhamn, 1996; Alford and Richards, 1999; Carlson and Edenhamn, 2000; Pellet, Maze and Perrin, in press). Although species presence can be reliably monitored by call surveys (Pellet and Schmidt, 2005), count data (even when standardized) does not allow estimating population size, because such estimates are ambiguous and biased (Hyde and Simon, 2001; Schmidt, 2004).

Capture-mark-recapture data can provide fundamental insights into the ecology of species while allowing the estimation of demographic parameters such as survival and population size.

We coupled three years of chorus counts data with a capture-mark-recapture (CMR) study on two populations of the threatened European tree frog to estimate the annual size of the breeding aggregation. We then evaluated whether chorus counts (annual maximum or mean chorus size) are reliable predictive indices for breeding population size.

Materials and methods

Chorus counts

We monitored calling activity in two populations of the European tree frog in western Switzerland from 2002 to 2004 (Pellet, 2005). The first population (Camp Romain, 46°31'20N, 6°21'05E, elevation a.s.l. 670 m) occupies a military training ground where tank activity creates multiple temporary ponds within ~3 ha. The second population (Les Mossières, 46°32'03N, 6°21'56E, elevation a.s.l. 715 m) occupies an abandoned gravel pit in which a dozen shallow temporary ponds are clustered within ~2 ha.

Each population was visited annually between five and eight times (mean \pm SD = 5.8 ± 1.5) during the acme of the breeding season to count the number of males participating in chorus. Chorus counts were made between 9:00 P.M. and midnight in optimal meteorological conditions ($>15^{\circ}\text{C}$ at sunset, Pellet and Schmidt, 2005) to ensure maximal detection probability. To count the number of males participating

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Table 1. Sampling dates and capture summary of the 172 European tree frogs captured over three years in two breeding aggregations in western Switzerland. *R* is the number of individuals captured and released on each capture session and every subsequent cell number represents the number of individuals that were recaptured in each given session.

		Recapture session									
Camp Romain	<i>R</i>	14.05.2002	24.05.2002	23.04.2003	25.04.2003	28.04.2003	08.05.2003	21.04.2004	27.04.2004	28.04.2004	
		Mark session	08.05.2002	27	7	2	0	0	5	0	0
14.05.2002	12		4	2	0	2	0	0	0	0	0
24.05.2002	9			0	0	0	0	0	0	0	0
23.04.2003	9				6	0	0	0	0	0	0
25.04.2003	6					5	1	0	0	0	0
28.04.2003	21						3	0	0	1	
08.05.2003	13							0	1	0	
21.04.2004	17								2	2	
27.04.2004	6										1

		Recapture session									
Mossières	<i>R</i>	12.05.2002	15.05.2002	25.04.2003	01.05.2003	12.05.2003	18.05.2003	23.04.2004	29.04.2004	03.05.2004	11.05.2004
		Mark session	07.05.2002	22	6	2	1	2	0	0	0
12.05.2002	8		4	1	0	0	0	0	0	0	0
15.05.2002	11			1	2	0	0	0	0	0	0
25.04.2003	6				5	0	0	0	0	0	0
01.05.2003	21					15	2	1	0	0	0
12.05.2003	23						17	2	0	0	1
18.05.2003	19							8	0	0	1
23.04.2004	34								14	4	8
29.04.2004	17									7	6
03.05.2004	15										8

in chorus, one observer walked slowly around the perimeter of the study site for 15 minutes. We thus obtained one estimate of chorus size for each visit (Heyer et al., 1994; Carlson and Edenhamn, 2000), from which we derived both an annual maximum and an annual mean chorus size for each site. Because mean annual chorus size had a smaller variance than maximum chorus size, it was likely to correlate more strongly with total male population.

Capture-mark-recapture

To estimate the size of the breeding male population, we sampled the breeding aggregations according to Pollock's robust design (Pollock, 1982; Kendall, Nichols and Hines, 1997; Bailey, Simmons and Pollock, 2004). Each year (primary session), we made three or four capture sessions (secondary sessions), spread across the acme of the breeding season (table 1). Three people walked the perimeter of the



Figure 1. The same individual photographed in 2002 (top) and 2003 (bottom). The *linea marginalis* (especially the shape of the rear "bump") allows identification of individual frogs.

site and captured by hand all frogs seen or heard (calling or non-calling males, on land or in water, as well as females). Because the two sites under study were early successional and the vegetation was not dense, the frogs were accessible and capture was relatively easy. Capture sessions were completed when no males were heard calling (usually within one hour of the first capture). We photographed each captured individual on both sides, providing us with a clear view of the *linea marginalis*, a black and white line running alongside of the body from eyes to hind legs (fig. 1). This line can be used to identify individuals (Tester, 1990) without the need for more invasive techniques such as toe-clipping or implants. By comparing pictures, we were able to create a capture history for each individual. Females accounted for only 19% ($n = 32$) of all captures. Because females are expected to have much shorter breeding pond tenure than males (Friedl and Klump, 2005), we restricted our analysis to males only. Inferences about population sizes and survival rates consequently are limited to males.

Statistical analysis

Pollock's (1982) robust design offers numerous advantages in the study of animal populations. It allows estimating capture probabilities (p), recapture probabilities (c) and popula-

Table 2. Candidate model selection. Survival [$\Phi(t)$] and population size [$N(t)$] are always year-specific. Temporary emigration is either constant [$\gamma(\cdot)$] or absent [$\gamma(\cdot) = 0$]. Capture and recapture probabilities are always equal and either year-specific [$p(t\cdot) = c(t\cdot)$] or constant [$p(\cdot\cdot) = c(\cdot\cdot)$]. K is the number of parameter and w is the Akaike weight of the models.

Site	Model number	Model	AICc	K	Δ AICc	w
Mossières	4	$\Phi(t)\gamma(\cdot) = 0$ $p(t\cdot) = c(t\cdot)N(t)$	62.990	8	0.000	0.572
	3	$\Phi(t)\gamma(\cdot)$ $p(t\cdot) = c(t\cdot)N(t)$	65.183	9	2.192	0.191
	2	$\Phi(t)\gamma(\cdot) = 0$ $p(\cdot\cdot) = c(\cdot\cdot)N(t)$	65.346	6	2.356	0.176
	1	$\Phi(t)\gamma(\cdot)$ $p(\cdot\cdot) = c(\cdot\cdot)N(t)$	67.493	7	4.503	0.060
Camp Romain	2	$\Phi(t)\gamma(\cdot) = 0$ $p(\cdot\cdot) = c(\cdot\cdot)N(t)$	-50.033	6	0.000	0.506
	4	$\Phi(t)\gamma(\cdot) = 0$ $p(t\cdot) = c(t\cdot)N(t)$	-48.614	8	1.419	0.249
	1	$\Phi(t)\gamma(\cdot)$ $p(\cdot\cdot) = c(\cdot\cdot)N(t)$	-47.804	7	2.229	0.166
	3	$\Phi(t)\gamma(\cdot)$ $p(t\cdot) = c(\cdot\cdot)N(t)$	-46.312	9	3.721	0.079

tion size (N) within primary sessions (i.e. years) while considering the population open to mortality and recruitment between primary sessions. It thus also permits us to estimate annual survival (Φ) as well as temporary emigration (γ , the probability of an individual skipping any given breeding season). This type of modeling is therefore especially well adapted to pond breeding amphibians in which some species are known to skip breeding opportunities (Schmidt, Schaub and Anholt, 2002).

Because our dataset did not allow constructing heavily parameterized models, we restricted ourselves to four major models, each representing one alternate biological hypothesis (table 2). In all four models, we assumed that both survival and population size varied between years [denoted $\Phi(t)$ and $N(t)$ respectively]. Our first model (model 1) assumed that capture probabilities were constant during the three years and that tree frogs did not show any capture response [i.e. that recapture probabilities (c) were equal to capture probabilities (p), denoted $p(\cdot\cdot) = c(\cdot\cdot)$]. Model 1 also assumed that tree frogs had a constant random probability of skipping a breeding season [$\gamma(\cdot)$], thus being inaccessible for capture, although still being alive. Following the CMR notation, we can rewrite model 1 using parentheses to describe if the parameter is constant ($\cdot\cdot$), or varying between primary sessions ($t\cdot$). Our baseline model thus reads: $\Phi(t)\gamma(\cdot)p(\cdot\cdot) = c(\cdot\cdot)N(t)$. We then hypothesized (model 2) that male tree frogs did not skip breeding seasons and that temporary emigration was thus absent [$\gamma(\cdot) = 0$]. Our third model assumed that capture and recapture probabilities, while still being equal (no trap response), varied between years [$p(t\cdot) = c(t\cdot)$], and that there is a constant random temporary emigration. Our fourth and last model was the combination of models 2 and 3, assuming no temporary emigration and time-specific capture and recapture probabilities (table 2).

We fitted our four models to the data presented in table 1 and estimated parameters using program MARK v. 4.3 (White and Burnham, 1999; Cooch and White, 2001). Because our sample was too small, we failed to obtain a goodness-of-fit statistic for our global model (model 3) using program RDSURVIV (Kendall and Hines, 1999). We ranked our models in an increasing AICc order (a modified information criterion for small samples), as recommended

when the ratio n/K (n being the sample size and K being the number of parameters included in the models) is smaller than 40 (Burnham and Anderson, 2002). We derived Akaike weights w , a relative measure of model support by the data (Burnham and Anderson, 2002; Johnson and Omland, 2004; Mazerolle, 2006). We then used model averaging procedures to estimate parameters and unconditional standard errors (Burnham and Anderson, 2002) for each population separately. Population size estimated from CMR refer to these model averaged estimates. Annual (or primary session) capture probabilities (the probability of an individual being caught at least once during the breeding season) were computed as $p^* = 1 - (1 - p)^k$, p being the single (secondary) session capture probability and k being the total number of capture sessions within each year.

Results

Our chorus counts indicated that maximum chorus size reached between 15 and 27 callers in both populations between 2002 and 2004 (table 3 and fig. 2). Mean chorus size was much lower, between 6.8 and 12.5 callers. Mean chorus count coefficients of variation (standard error divided by mean) ranged between 20% and 40%.

During our CMR study, we captured a total of 172 males, 89 in Camp Romain and 83 in Les Mossières (capture histories are summarized in table 1). Model selection (table 2) indicated that models assuming no temporary emigration best explained our data, suggesting that males did not skip the 2003-breeding season. Even if there was only a small difference in model AICc (table 2; see Burnham and Anderson, 2002), estimated values for temporary emigration in

Table 3. Maximum and mean chorus sizes, total males captured and modelled male population sizes, single session and annual capture probabilities, and survival rates in two populations of the European tree frog in western Switzerland.

	Year	Camp Romain			Les Mossières		
		Mean	SE	95% CI	Mean	SE	95% CI
Maximum chorus size	2002	27	–	–	25	–	–
	2003	18	–	–	15	–	–
	2004	20	–	–	20	–	–
Mean chorus size	2002	11.4	3.2	[5.1; 17.7]	6.9	2.8	[1.4; 12.4]
	2003	6.8	2.6	[1.7; 11.9]	7.2	2.7	[1.9; 12.5]
	2004	12.5	2.5	[7.6; 17.4]	7.3	2.8	[1.8; 12.8]
Total males captured	2002	35	–	–	29	–	–
	2003	34	–	–	30	–	–
	2004	75	–	–	45	–	–
Modelled male population size	2002	57.9	9.0	[40.3; 75.5]	38.5	5.7	[27.3; 49.7]
	2003	49.6	6.9	[36.1; 63.1]	30.8	1.3	[28.3; 33.3]
	2004	62.1	15.0	[32.7; 91.5]	46.8	2.2	[42.5; 51.1]
Single session capture probabilities (<i>p</i>)	2002	0.266	0.055	[0.158; 0.374]	0.375	0.090	[0.199; 0.551]
	2003	0.247	0.040	[0.169; 0.325]	0.548	0.057	[0.436; 0.660]
	2004	0.215	0.062	[0.093; 0.337]	0.487	0.041	[0.407; 0.567]
Annual capture probabilities (<i>p</i> [*])	2002	0.605	0.156	[0.299; 0.911]	0.756	0.246	[0.274; 1.238]
	2003	0.679	0.151	[0.383; 0.975]	0.958	0.209	[0.548; 1.368]
	2004	0.516	0.175	[0.173; 0.859]	0.931	0.154	[0.629; 1.233]
Survival rate	2002-2003	0.370	0.112	[0.150; 0.590]	0.247	0.082	[0.086; 0.408]
	2003-2004	0.106	0.082	[0.000; 0.267]	0.463	0.098	[0.271; 0.655]

models 1 and 3 were negligible, indicating that in any case, temporary emigration is very weak if not absent in both populations. Similarly, model selection did not favour constant over time-specific capture probabilities, suggesting that capture probabilities might have slightly varied between years (table 2).

Single session capture probabilities (*p*) were on average \pm SE = 0.356 ± 0.137 (table 3). Annual capture probabilities (*p*^{*}) were thus on average \pm SE = 0.741 ± 0.177 (table 3), indicating that in most cases, we had captured about three quarters of the breeding males each year.

Annual male survival rates across sites were on average \pm SE = 0.297 ± 0.154 (table 3).

Modelled male population size ranged between 31 and 62. Associated coefficients of variation ranged between 4% and 15% in Les Mossières and between 14% and 24% in Camp Romain. The estimated population size (*N*) derived from our models showed a slightly different picture than the one apparent from chorus counts. First, both maximum and mean chorus sizes underestimated total male population (table 3 and fig. 2). Second, the population trends

deduced from both chorus counts and modelled male population size were not concordant. Maximum chorus counts showed a decline in 2003 and a partial recovery in 2004 in both populations. Mean chorus counts showed a decline in 2003 followed by a complete recovery in Camp Romain and a relatively stable population in Les Mossières. Modelled male population size, on the other hand, displayed a decline in 2003 followed by a complete recovery in 2004 for both populations.

Discussion

Had we assumed that maximum chorus size reflected population size, we would have concluded that both populations had slightly declined between 2002 and 2003 before partly recovering in 2004. Detecting a clear trend in mean chorus size was difficult because of overlapping confidence intervals (fig. 2, table 3).

The comparison of these two chorus size indices to the total number of males captured or to the modelled male population size (ta-

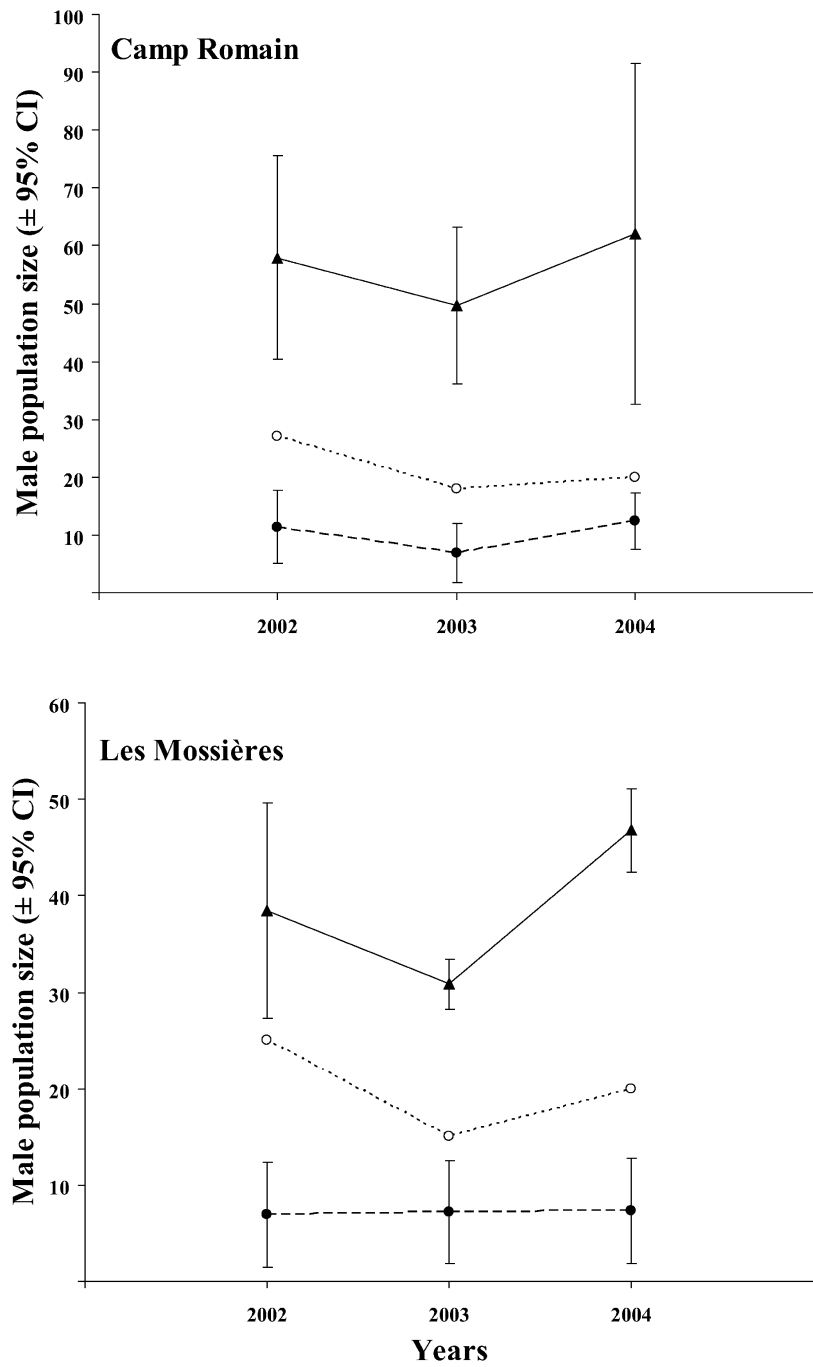


Figure 2. Estimations of male population size by maximum chorus size (white dots), mean chorus size (black dots; with 95% confidence intervals) and modelled male population size (triangles; with 95% confidence intervals) in two breeding aggregations of the European tree frog in western Switzerland.

ble 3) demonstrates that chorus counts underestimated actual population size. These results are in agreement with those published by Grafe

and Meuche (2005) showing an underestimation of population size by a factor of ~1.76 when using the maximum number of calling

males. Our data show that this fraction (modelled male population size divided by maximum chorus size; table 3) varies within the species, both between years and localities (ranging from 1.54 to 3.11). No simple linear relationship between maximum chorus counts and modelled male population sizes can thus be confirmed, as was suggested by Grafe and Meuche (2005). This is not surprising given the fact that Grafe and Meuche (2005) based their statement on a regression based on data from five different *Hyla* species having specific life histories and one of which being an obvious outlier (see fig. 2 in Grafe and Meuche, 2005). Their relationship therefore lacks robustness. Obtaining more data to refine this relationship, as proposed by Grafe and Meuche (2005), would be probably worth within a species, but we doubt that by including diverse species with specific life-histories, we could refine a within-species relationship.

As for mean chorus sizes, detecting a clear trend in modelled population size in Camp Romain was complicated by the largely overlapping 95% confidence intervals. But for Les Mossières, a clear increase can be observed between 2003 and 2004 which would not have been detected using mean chorus size. Even if detecting a clear population trend is difficult when confidence intervals are important, population size estimates derived from CMR are closer to the real population size (i.e. unbiased) than chorus counts. Furthermore, when sampling has been adequate (like in Les Mossières), population trends can be detected precisely and reliably.

Our relatively high annual capture probability (74%) is most likely due to the prolonged chorus tenure in the European tree frog, which facilitates capture throughout the breeding season (Friedl and Klump, 2005; Grafe and Meuche, 2005). In our case minimum chorus tenure, measured as the number of nights between the first and the last night an individual male was captured at the breeding site, were on average \pm SD = 11.67 ± 5.17 nights. These values are in the range of those reported by Grafe and

Meuche (2005) where chorus tenure was on average 17.0 ± 10.1 nights.

Our mean annual survival rates across sites are close to the return rates obtained by Tester (1990) (mean \pm SD = 0.303 ± 0.097) in three isolated populations of the European tree frog and the return rate value obtained by Friedl and Klump (2005) of 0.368 (14 returning males out of 38). These results are also consistent with the species life expectancy of six years (Friedl and Klump, 1997). The estimates of survival rates thus confirm previous published data and reinforce their validity when modeling demography and metapopulation persistence for this species (Pellet, Maze and Perrin, in press).

One caveat about the modeling process must nevertheless be raised. Because we failed to obtain goodness-of-fit (GOF) statistics for our global model (model 3), we can only speculate about the absolute validity of our model ranks. Overdispersion (due to non-independence in capture histories or heterogeneity between individuals) potentially induces a model lack of fit, which can be accounted for by using modified ranking variables such as QAICc (Burnham and Anderson, 2002; Schmidt, 2002). These corrections usually benefit the simpler models, the ones containing fewer parameters (i.e. models 1 and 2), thus potentially changing the ranking of our models and their relative weights. An empirical test was performed on both sets of models by changing \hat{c} from 1 to 1.5. Model ranks and weights were only slightly modified and the best model remained the same for both populations, thus suggesting that overdispersion was, in our case, of secondary importance.

Even though our results empirically demonstrate that chorus counts can hardly provide a reliable image of population size (see also Schmidt, 2004), such counts can potentially offer some insights into the species demography under some conditions. These conditions include small breeding choruses, constant proportion of satellite males, constant mean time spent at the pond, and constant overall probability of breeding through years (Pellet et al., 2006).

We conclude that, contrarily to previously published data (Grafe and Meuche, 2005), relationships between chorus size and population size do not generalize across time and populations of the European tree frog. Current methods for estimating breeding population sizes in the European tree frog using maximum chorus counts are thus inaccurate. There is an urgent need either to find a more reliable (and easily accessed) index of breeding population size or to promote the use of CMR in studies of amphibian populations. Our study, which included three to four capture sessions per year, allowed taking advantage of recent development in the science of CMR, thus permitting the estimation of demographic parameters in a relatively precise and unbiased manner. New methods based on repeated counts (Kéry, Royle and Schmid, 2005) should also be taken into consideration in the future, as they require no handling of animals and also correct for detectability biases.

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