

Sex ratio of breeding Common toads (*Bufo bufo*) – influence of survival and skipped breeding

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Abstract. Anuran sex ratio at breeding sites is typically male biased. Such sex ratios may be due to poor female survival, to females not breeding as frequently as males and/or to males becoming sexually mature earlier than females. In the present study, the first two factors are analyzed in a common toad (*Bufo bufo*) population in southern Sweden. Toads were captured, marked and recaptured at the breeding site during 5 years. Within season capture patterns were analyzed using the Jolly-Seber model and among-year captures using the Closed robust design model. Population estimates of males and females yielded an among year variation in breeding population sex ratio, ranging from 16% to 34% females. On average, 41% (proportion adult alive but not breeding) of the females skipped breeding seasons, whereas the corresponding estimate for males was less than 5%. Yearly survival averaged 42% for adult female and 63% for adult male toads. First year adult males and females had a lower survival rate than older toads. Our results demonstrate that both a female biased mortality rate and a higher proportion of skipped breeding in females contribute to the observed male biased sex ratio. However, a deterministic model suggests other factors may also be involved to obtain this degree of male biased sex ratio, the most likely being that females mature at a later age than male toads.

Keywords: breeding strategy, capture-recapture, semelparous, life history, MARK, temporary emigration.

Introduction

The adult sex ratio is a key parameter in the population and evolutionary biology of a species, dictating patterns of mate competition and mate choice, as well as affecting demographic parameters such as population growth rates (Emlen and Oring, 1977). Fisher (1930) envisioned a 1 : 1 sex ratio at birth (actually modified by any offspring sex bias in parent effort) as being evolutionary stable. However, in most anurans the effective breeding site sex ratio is more or less biased in favor of male numbers. This is partly a result of males arriving earlier to the breeding site and departing later than females (Davies and Halliday, 1979; Reading and Clarke, 1983; Kuhn, 1994). However, also when the total number of animals visit-

ing a breeding site is considered, a male-biased sex ratio is almost the norm (Howard, 1980; Berven, 1981; Guttman, Bramble and Sexton, 1991 (*Rana sylvatica*); Elmberg, 1990 (*Rana temporaria*); Grosse, Nöllert and Bauch, 1992; Friedl and Klump, 1997 (*Hyla arborea*); Gittins, Parker and Slater, 1980; Gittins, 1983; Reading and Clarke, 1983; Loman and Madsen, 1986; Hemelaar, 1988; Kiss and Laar, 1992; Arntzen, 1999 (*Bufo bufo*)), but see van Gelder and Wijands' (1987) study on *Rana arvalis*. Furthermore, in most of these studies a substantial among year variation in the sex ratio has been observed.

Numerous other processes could contribute to these sex ratios, e.g., in salamanders females more often than males skip breeding seasons (Bailey, Kendall and Church, 2004; Bailey, Simons and Pollock, 2004). Based on the irregular captures of female Common toads (*Bufo bufo*) at fenced breeding ponds, Kuhn (1994) suggested that also female toads in a German population may skip breeding seasons. The study by Kuhn did not include data on this behavior in male toads but Frétey et al. (2004) found that males in a French population did skip breed-

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ing seasons. Hemelaar (1988) mentions that females (but not males) in a high-altitude Swiss *B. bufo* population characterized by a short active season only bred every second year. Muths et al. (2006) found support for skipped breeding in male *Bufo boreas*.

Furthermore, in some anurans adult females have been suggested to have lower annual survival rates than males (Friedl and Klump, 1997 (*Hyla arborea*); Elmberg, 1990 (*R. temporaria*)), further contributing to a male-biased sex ratio.

Another process that may result in a male-biased adult sex ratio is that female anurans often mature later than males (Berven, 1990 (*R. sylvatica*); Gibbons and McCarthy, 1984; Reading, 1991 (*B. bufo*); Miaud, Guyétant and Elmberg, 1999 (*R. temporaria*)).

In the present study we analyze adult population size, adult sex ratio, adult male and female survival in a common toad (*Bufo bufo*) population, as well as the possibility that either or both sexes skip breeding opportunities.

Material and methods

Study site and field procedures

The study site, Måryd (55°40'N, 13°30'E, altitude 70 m asl) is situated in southern Sweden, 10 km east of Lund. It consists of four ponds with a maximum distance of 350 m from the easternmost to the westernmost. For a map of the study site see fig. 1 in Reading, Loman and Madsen (1991). The closest additional breeding pond is situated 1.7 km southwest of the four study ponds. A study in 1990 found no toad (in a sample of 123 toads) at this pond previously marked at the present study site (with 1298 toads marked in 1987-1989) (Reading, Loman and Madsen, 1991). We thus consider the Måryd population geographically closed in our analyses. The study was conducted during five consecutive breeding seasons, in April and early May from 1987 to 1991. During this period the ponds were visited on a total of 51 nights and 32 days. Day and night captures on the same date were always pooled. We also pooled data from some days with few captures. The number of "occasions" used in the analyses was thus 31 (appendix 1). The resulting capture histories were "reduced capture histories" in the sense of Hargrove and Borland (1994). As both males and females were observed moving between the ponds, both within and between years (Reading, Loman and Madsen, 1991), the capture data from all four ponds were pooled and hence treated as one "breeding site". At each visit all ponds were

searched. The ponds and their surroundings were searched from the shore; all toads seen in water were captured with a dip net or, on land, by hand. When a pond had been searched all toads captured were processed; measured and marked individually by toe clipping and promptly released in the pond before we proceeded to the next pond. We tried, and usually succeeded, not to separate pairs in amplexus. During the first three years of the study (1987-1989), all toads seen were captured, whereas in the last two years of the study (1991-1992), for logistical reasons, only males in amplexus and all (found) females were captured.

Population demographic analyses

Our data were analyzed to provide estimates of population size, survival and frequency of possibly skipped breeding seasons. We used the population estimation computer program MARK (White and Burnham, 1999; Cooch and White, 2007) where skipped breeding seasons is a special case of the concept "temporary emigration" (Schwarz and Stobo, 1997). We define population size as either "breeding population" or "total adult population". The "breeding population" consists of toads attending (for any number of days) the breeding area in a particular year. This estimate also includes toads that may have entered after one capture occasion and exited before the next, and thus were never available for capture (termed "Gross Population estimates" in the output from MARK's POPAN routine; Schwarz and Arnanon, 2007). The multi year analysis also estimates the "total adult population" which includes toads skipping a breeding season; living toads that have bred previously but are not present at the breeding site in a particular year. These toads may have skipped breeding altogether or bred at another site. In the present study we assume that the former situation only applies. This assumption is supported strongly by the previous compilation of data from this site (Reading, Loman and Madsen, 1991).

Data were thus analyzed using two main models provided by the program MARK. (A) The main results on survival and skipped breeding emerge from the Closed robust design model that use data from several years in one analysis. (B) In addition the POPAN model was applied to each year's data separately, for two reasons: (B1) It is known that toads may arrive at and leave the breeding site gradually. Especially males are however usually present throughout the main breeding period and most females have arrived before the height of the spawning (Reading and Clarke, 1983; Loman and Madsen, 1986). One purpose of this analysis is to study this assumed pattern of arrival to and departure from the breeding site. The assumption is used to pool data to fulfill the closure assumption of the Robust design model. (B2) In addition, comparing the estimated population sizes from two, partly independent, models provides a test of the robustness of the results.

For each of the models different simplifications were analyzed and compared. Simplifications were used (throughout or as alternatives) whenever considered biologically justified. Thus, as a global simplification, capture and recapture rates were set equal in all models. Capture rates were however always allowed to vary among dates (because this

variation was often quite substantial). Other simplifications (parameter reductions) are described under the respective model.

Models were compared using the Akaike information criterion (Anderson and Burnham, 1999). The version AIC_c (Hurvich and Tsai, 1989) that is recommended for small samples ($n/K < 40$) (Burnham and Anderson, 2002) was used. If a model did not estimate realistic values, e.g., it produced an extremely low SE for some parameters, it was discarded.

Single year estimates – POPAN. The POPAN formulation of the Jolly-Seber model (Schwarz and Arnason, 1996; Schwarz and Arnason, 2007) provides estimates of the breeding population in single years based on multiple capture-mark-recapture occasions. This model allows for successive immigration (or recruitment or birth, $pent =$ “probability to enter” in the MARK notation) and emigration (or mortality, $(1 - \phi)$ in the MARK notation) during the breeding period. In the present study actual recruitment (into the breeder/adult category) and mortality were assumed null within the capture periods. The estimated parameters ($pent$ and $1 - \phi$) thus represent only true immigration and emigration into and away from the breeding area. The model also allows for different capture probabilities during different capture occasions. This is considered essential as among-day captures differed considerably (appendix 1), most likely due to daily variation in weather conditions affecting activity and hence capture probability. Capture probability is also affected by the pooling of days with few captures (and sometimes low capture probability). The fit of the POPAN models was analyzed using program RELEASE run from MARK (table 1).

Parameters and parameter reductions – POPAN. Alternative sub-models to the Jolly-Seber model were compared. They represent different simplifications made by fixation of model parameters. These sub-models are labeled **Pa-Pc** in table 3. The full model (**Pa**) assumes and estimates temporal variation in immigration ($pent(t)$) and emigration ($\phi(t)$).

Table 1. Goodness of fit tests for the POPAN model. Tests 2 and 3 in program RELEASE as run from program MARK. Empty entries means there was not sufficient data to do the test.

	Test 2			Test 3		
	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Females						
1987	2.67	2	0.26			
1988	0.27	3	0.98	2.72	5	0.74
1989						
1990	1.96	5	0.85	7.67	7	0.36
1991	13.8	11	0.25	8.86	13	0.78
Males						
1987	78.7	5	<0.001	13.2	6	0.039
1988	3.23	4	0.52	8.24	7	0.31
1989	63.1	1	<0.001			

Although toads most likely entered the site gradually during the capture season and also left gradually before the end (as modeled by **Pa**) it is not clear how important this gradual process is when estimating parameters such as population size. Especially males are usually present throughout the main breeding period (Reading and Clarke, 1983; Loman and Madsen, 1986). An extreme simplification (**Pb**), assumes that all toads arrive at the beginning of the field season (all $pent(t) = 0$ ($t > 1$)) and that they all stay until the end of it (all $\phi(t) = 1$). A compromise approach that makes biological sense (**Pc**) was also tested: For 1987, 1988 and 1990 (with 6 capture occasions each) the first 2 emigration parameters were fixed to 1 (assuming no emigration until after the third capture occasion). The last two immigration parameters were set to 0 (assuming no further immigration after the fourth capture occasion). Correspondingly, 1 + 1 and 3 + 3 parameters were fixed for 1989 and 1991 (with 4 and 9 capture occasions respectively). Altogether, three sub-models (**Pa-Pc**) to the POPAN models were thus analyzed for each year. The breeding population was computed as a weighted average (Burnham and Anderson, 2002) of estimates from the three models, **Pa**, **Pb** and **Pc**.

Multiple year estimations – Robust design model. The Closed robust design model (Kendall, Pollock and Brownie, 1995; Kendall, Nichols and Hines, 1997) provides estimates of the breeding population number, survival and the probability that an animal temporarily emigrates from the population. The latter refers to animals that have been available for capture in one year but are missing (i.e., not available for capture, although still alive), in a subsequent year. In our study this represents skipped breeding. To analyze this model we used data from several primary capture occasions, each consisting of several secondary capture occasions. The primary capture occasions correspond to breeding season and the secondary capture occasions to the (pooled) daily samples.

As previously assumed for the POPAN model, capture rates were always allowed to vary among capture occasions (and years) but set to the same value for both recaptures and new captures on each single capture occasion.

The Robust design model (in contrast to the POPAN model) basically assumes demographically closed breeding populations within years, that is, all animals enter the breeding population before the first occasion and all exit after the last. This is a potential problem in our case. However, it is sufficient to assume that no animals enter the breeding population after the first capture occasion *or* that no animals have left the population before the last capture session (Kendall, 2007). To take a conservative approach we tried to achieve both of these conditions. Therefore we further reduced the number of capture “occasions” by pooling some of the initial and final capture occasions, respectively, that were considered separate in the POPAN analysis (appendix 1).

Based on ϕ and $pent$ values estimated by the POPAN analysis (figs 1 and 2) we now pooled the first two and also the last two occasions (except in 1989 when only the first two were pooled) for males and the first two and also the last three occasions for females (except in 1989 when only the last two were pooled).

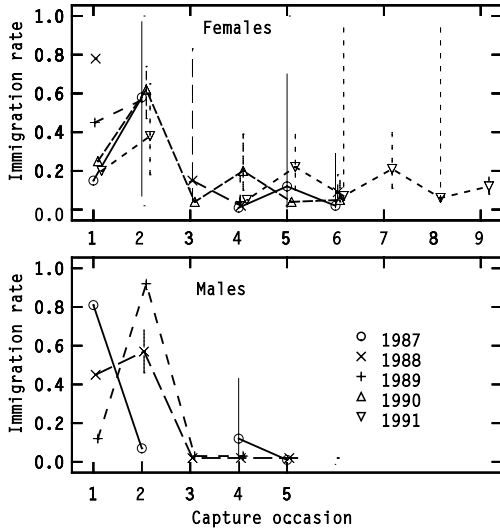


Figure 1. Immigration rates by year and capture occasion. The rate is the fraction of the total population estimated to immigrate during the interval before the respective occasion. Rates (*pent*) for occasion 2-6 (or 2-4 in 1989 and 2-9 in 1991) are estimated directly by the POPAN routine. Error bars indicate the 95% CI. Estimates for which very large CI (0-100%) were estimated were considered invalid and are not shown. The fraction arriving before the first occasion is a derived parameter and computed as 1 minus the sum of the remaining immigration rates. Each capture occasion pools captures from one or several days, this is accounted for in the appendix.

The fit of the robust models was analyzed using program RDSURVIV. This was done for the submodel with most free parameters in each data set: Females 1987-1991 (submodel **Ra1i** below) $G_{355} = 259, P = 0.99$; Females 1987-1998 (**Rb**) $G_{28} = 39.7, P = 0.07$; Males 1987-1989 (**Ra2i**) $G_{49} = 163, P < 0.001$; Paired males 1987-1991 (**Ra2ii**) $G_{725} = 256, P = 1.00$.

Parameters – temporary migration – Robust design model. In this model, allowance is made for animals that in some seasons are not available for capture. In the standard language of the model these are called “temporary emigrants”. In our case this usually means they were not present at the breeding site. When we discuss toad behaviour, rather than the model, we will use the term “skipped breeding” for this phenomenon. A different case is represented by our category of paired males. These were only available for capture if ever in amplexus with a female at the breeding site, in the respective year. All others are technically “temporary emigrants”, even if present at the breeding site. More intuitively they are simply not available for capture.

There are two different parameters that describe temporary migration. γ' is the probability to temporarily emigrate for a toad that was also not present in the previous year. γ'' is the probability to temporarily emigrate for a toad that was present in the previous year. The general case, called

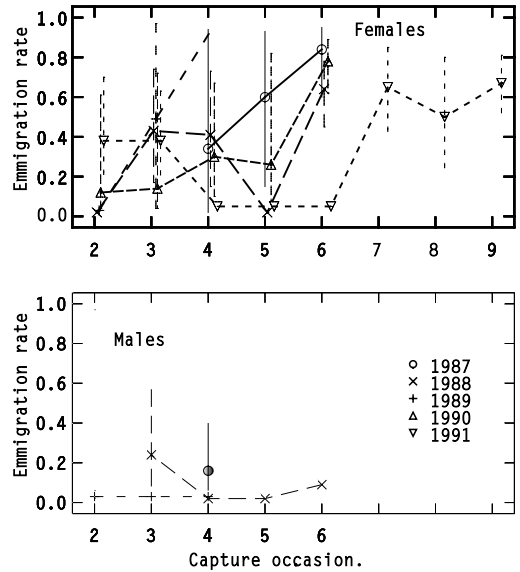


Figure 2. Emigration rates by year and capture occasion. The rate $(1 - \phi)$ indicated for an occasion is the fraction of those present at the previous occasion estimated to leave in the interval before the occasion. Error bars as in fig. 1.

Markovian migration, allows for different temporary migration rates for breeders and non breeders. Unfortunately, this model did not perform well with our data and produced unrealistically small SE's. It was not considered in our subsequent analyses. If, on the other hand, the probability of breeding in a given year is independent of whether an animal bred in the previous year or not, this is called random emigration (**Ra**). This case is modelled by the constraint $\gamma' = \gamma''$. The single parameter that is fitted is simply called γ . If we assume that animals did not ever skip breeding, we have a null model where both γ were set to 0 (**Rb**). At this step 2 submodels to the Robust design model were thus defined.

The skip parameter γ can be assumed to vary among years or to be constant. However, modeling among year variation in these parameters is only possible when using the long-term data sets from 1987 to 1991. Firstly for conceptual reasons: there was no estimable skip parameter associated with the first year (1987) and for the second year only γ'' (but not γ') was estimable (because there were no marked toads outside the breeding site in the first year). However, in the random model γ' will do as an estimate of γ for this year (1988). Futher, for numerical reasons, not all skip parameters can be estimated separately. Thus one has to fix $\gamma''_{k-1} = \gamma''_k$ and $\gamma'_{k-1} = \gamma'_k$ (Kendall, Nichols and Hines, 1997) (meaning same value for 1988 and 1989). This leaves for the 1987-1989 data only one γ parameter. Therefore, only for the 1987-1991 data we analyzed the “full random” (**Ra1**) models (with a maximum possible number of separate parameters), and the “constant random” (**Ra2**) model (with one common γ , ($\gamma' = \gamma''$) assumed for all years). For data from 1987-1989 only the last model,

“constant random” (**Ra2**) was analyzed. Thus, at this step we have three sub models for the 1987-1991 data and two sub models for the 1987-1989 data (both sets also including the null model, **Rb**).

Parameters – survival – Robust design model. Both random models were analyzed assuming either separate yearly survival rates (**Ra1i**, **Ra2i**) or a common survival rate (**Ra1ii**, **Ra2ii**) for all years. The latter was used in order to estimate a value for between sex comparison of generalized skip and survival values. At this step we thus have five sub models for the 1987-1991 data and three sub models for the 1987-1989 data.

The Robust design model allows the separate specification of survival for toads during the first year after marking and that of their survival during later years. Assuming a closed population (no transients), the former toads should on average be younger so any difference in these rates will reflect age dependent survival. This analysis was done only for the best data set for each sex; females 1987-1991 and males 1987-1989. Also it was only made as a variation of the “best” (lowest AIC_c) sub model (constant random for females and null for males) (table 8).

Parameters – population size – Robust design model. The Robust design model with random emigration provided estimates of breeding population size (N) and the probability of temporary emigration (γ). The total adult population size was estimated as $N/(1 - \gamma)$ (Kendall, Nichols and Hines, 1997; Bailey, Simons and Pollock, 2004; Dutton et al., 2005).

Results

Total number of toads captured and recaptured

In the first three years of the study (1987-1989), 1038 different males were captured a total of 2103 times and 260 different females were captured 419 times (table 2). Based on number of captured individuals, i.e., ignoring potential sex-specific capture probabilities, sex ratio varied among years between 14% and 20% females. In 1990 and 1991, when only males in amplexus were captured, 380 different males were captured on 638 times. During these two years 309 different females were captured 652 times (633 of those in amplexus). The main reason for the difference in number of males and females captured during these years was that some females were repeatedly captured with different males in amplexus. This was likely due to male competition that involves forceful removal of competitors from females (Davies and

Table 2. Captures and between year recaptures. In the “Males” section entries for 1990 and 1991 are in parentheses to indicate that males were only available for recapture if paired. In the “Paired males” section, all recapture rates refer only to males recaptured in amplexus.

	Captured	Recaptured of those			
		1988	1989	1990	1991
Females					
1987	119	18	1	1	2
1988	87		18	3	1
1989	91			11	4
1990	172				30
1991	152				
Males					
1987	484	202	35	(13)	(5)
1988	379		160	(9)	(4)
1989	574			(51)	(14)
Paired males					
1987	89	8	2	11	1
1988	73		6	3	1
1989	75			6	1
1990	182				14
1991	195				

Halliday, 1977; Loman and Madsen, 1986). Approximately 40% of the males and 20% of the females were recaptured in a year after their first capture (table 2).

Single year numbers – POPAN model

The three alternative POPAN models performed differently (and inconsistently) in terms of AIC_c for different years and sexes (table 3). Overall, there was only moderate justification for the more complex model (that allowed for continued and variable immigration and emigration during the breeding period). The seemingly realistic simplification, assuming no emigration during the beginning of the breeding period and no immigration during the end did not out-compete the other models.

Based on weighted average of the models, breeding population of females fluctuated between 132 and 329 and that of males between 526 and 1459 (table 4). Thus, sex ratio of the breeding population (in 1987-1989) varied between 13% and 31% females.

Table 3. Model selection results from three sub models of the POPAN model. ϕ (phi) is the emigration parameter, p is the capture probability parameter and $pent$ is the immigration parameter. **Pa** (“... (t)”) models allow for temporal (capture occasion) variation in the emigration and immigration parameters. In **Pb** models (“... (1.0)” and “... (0.0)”) the respective parameter is forced to 1.00 and 0.00 respectively. That is, no toads leave the site before the last capture occasion and no new toads enter after the first. **Pc** (... (t_{red})) models are a compromise; no emigration during the first few occasions and no immigration during the last few (for specifications, see “Methods”). For each sex and year, the best model is in bold face. **(Pa)**, **(Pb)** and **(Pc)** refer to sections in the Methods.

		Model	Parameters	ΔAIC_c	Weight
Females					
1987	Pa	$\phi(t)p(t)pent(t)$	14	11.10	0.00
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	12	8.21	0.02
	Pb	$\phi(1.0)p(t)pent(0.0)$	7	0.00	0.98
1988	Pa	$\phi(t)p(t)pent(t)$	12	0.00	0.76
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	9	2.41	0.23
	Pb	$\phi(1.0)p(t)pent(0.0)$	7	8.55	0.01
1989	Pa	$\phi(t)p(t)pent(t)$	7	3.69	0.13
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	8	6.66	0.03
	Pb	$\phi(1.0)p(t)pent(0.0)$	5	0.00	0.84
1990	Pa	$\phi(t)p(t)pent(t)$	13	1.91	0.25
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	11	0.00	0.64
	Pb	$\phi(1.0)p(t)pent(0.0)$	7	3.38	0.12
1991	Pa	$\phi(t)p(t)pent(t)$	20	0.00	1.00
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	15	46.89	0.00
	Pb	$\phi(1.0)p(t)pent(0.0)$	10	75.75	0.00
Males					
1987	Pa	$\phi(t)p(t)pent(t)$	12	6.25	0.04
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	11	4.20	0.10
	Pb	$\phi(1.0)p(t)pent(0.0)$	7	0.00	0.86
1988	Pa	$\phi(t)p(t)pent(t)$	10	0.00	0.52
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	9	1.16	0.29
	Pb	$\phi(1.0)p(t)pent(0.0)$	7	2.11	0.18
1989	Pa	$\phi(t)p(t)pent(t)$	5	0.00	0.47
	Pc	$\phi(t_{red})p(t)pent(t_{red})$	7	4.08	0.06
	Pb	$\phi(1.0)p(t)pent(0.0)$	5	0.00	0.47

Table 4. Breeding population (GrN) estimates from the three submodels of the POPAN model. Number after \pm is S.E.

	$\phi(t)p(t)pent(t)$		$\phi(t_{red})p(t)pent(t_{red})$		$\phi(1.00)p(t)pent(0.0)$		Averaged GrN estimate
	GrN	AIC weight	GrN	AIC weight	GrN	AIC weight	
Females							
1987	327 \pm 65	0.00	356 \pm 81	0.02	301 \pm 49	0.98	303 \pm 50
1988	131 \pm 16	0.76	138 \pm 17	0.23	124 \pm 120	0.01	133 \pm 16
1989	225 \pm 45	0.13	233 \pm 48	0.03	227 \pm 44	0.84	227 \pm 44
1990	236 \pm 14	0.25	234 \pm 14	0.64	216 \pm 10	0.12	235 \pm 114
1991	329 \pm 32	1.00	356 \pm 41	0.00	266 \pm 15	0.00	329 \pm 32
Males							
1987	712 \pm 32	0.04	713 \pm 32	0.10	684 \pm 26	0.86	688 \pm 27
1988	538 \pm 30	0.52	531 \pm 24	0.29	515 \pm 21	0.18	526 \pm 26
1989	1459 \pm 121	0.47	1459 \pm 121	0.06	1459 \pm 121	0.47	1459 \pm 121

The models were used to estimate immigration and emigration rates between the different capture occasions. For both males and females it appeared that most individuals had arrived by the second capture occasion (fig. 1). Most males stayed until the last occasion (fig. 2). In contrast, females left the ponds throughout the breeding season.

Multi-year analysis – Robust design model

For female toads, using data from all five years of study, the four random sub models with temporary emigration performed equally well with respect to AIC_c (comparing AIC_c weights) (table 5). Both constant random models (**Ra2i**, **Ra2ii**) estimated the temporary emigration at 41% (table 6). The Full random models (**Ra1i** and **Ra1ii**) estimated an annual variation in temporary emigration that ranged from 3% to 64%, with widely overlapping confidence intervals. Forcing no temporary emigration onto the data (Null model, **Rb**) resulted in a very poor AIC_c performance, compared to the other models. This supports the presence of female temporary emigration. Both the Full (**Ra1i**) and Constant random (**Ra2i**) models estimated female

yearly survival to range between about 30% and 60%, again with a substantial overlap of confidence intervals. The two constant survival models (**Ra1ii** and **Ra2ii**) both estimated average yearly survival to 42%.

For male toads the Null model (**Rb**) (assuming no temporary emigration) performed by far the best (table 5). Also the other models estimated very low rates (<5%) of temporary emigration (table 6) but with high upper 95% conf. int. Average survival (**Ra2ii**) (63%) and survival for each of both common years (1988 and 1989) (**Ra2i**) was higher than that of females (table 6). This was even more marked if males and females were compared with a null model using a restricted female data set covering the first three years of the study.

To compare females and males during all 5 years, a data set of paired males during 1987-1991 was also used. “Temporary emigration” (or unavailable for capture) in this case includes all non-breeding male toads (those never in amplexus), even if the male is at the breeding area. Thus there is no surprise the Null model (were this rate was forced to 0) performed badly (AIC weight = 0.00, table 4); obviously many males that are present at the breeding site do not breed

Table 5. Model selection results for the Closed robust model. “Males” includes all males, unpaired as well as those found in amplexus. “Paired males” is only based on males found in amplexus. γ (gamma) is random temporary emigration. For “Females” and “Males” this represents animals that were not available for capture in a year because they never visited the breeding area. For “Paired males” it represent those absent animals plus those that were at the breeding site but never were in amplexus. ϕ (phi) is survival from one year to next. (**Ra1**) etc. are labels explained in the Methods.

			Parameters	ΔAIC_c	Weight
Females 1987-1991					
Ra1i	Full random	$\gamma(t)\phi(t)$	30	0.18	0.24
Ra1ii	Full random Const. surv.	$\gamma(t)\phi(\cdot)$	27	0.14	0.24
Ra2i	Constant random	$\gamma(\cdot)\phi(t)$	28	0.08	0.25
Ra2ii	Const. random Const. surv.	$\gamma(\cdot)\phi(\cdot)$	25	0.00	0.26
Rb	Null	$\gamma(0)\phi(t)$	27	8.17	0.00
Females 1987-1989					
Rb	Null	$\gamma(0)\phi(t)$	14	0.00	1.00
Males 1987-1989					
Ra2i	Const. random	$\gamma(\cdot)\phi(t)$	17	1.58	0.30
Ra2ii	Const. random Const. surv.	$\gamma(\cdot)\phi(\cdot)$	16	5.60	0.04
Rb	Null	$\gamma(0)\phi(t)$	16	0.00	0.66
Paired males 1987-1991					
Ra2ii	Const. random. Const. surv.	$\gamma(\cdot)\phi(\cdot)$	28	0.00	1.00
Rb	Null	$\gamma(0)\phi(t)$	30	28.40	0.00

Table 6. Parameter estimates from the Robust design model. “Males” includes all males, unpaired as well as those found in amplexus. “Paired males” only includes males found in amplexus. “T. em.” is temporary emigration, (γ). For “Females” and “Males” this represents animals that were not available for capture in a year because they never visited the breeding area; skipped breeding. For “Paired males” it represent those absent plus those that were at the breeding site but never were in amplexus. “Br. pop.” is the estimated number of animals at the breeding area (restricted to those ever in amplexus for “Paired males”). **Ra1** etc. refers to sections in the Methods. Estimates are followed by 95% confidence interval, in italics, on the following line.

	Females 1987-1991					Females 1987-1989	Males 1987-1989			Paired males 1987-1991	
	$\gamma(t)\phi(t)$ Ra1i	$\gamma(t)\phi(\cdot)$ Ra1ii	$\gamma(\cdot)\phi(t)$ Ra2i	$\gamma(\cdot)\phi(\cdot)$ Ra2ii	$\gamma(0)\phi(t)$ Rb	$\gamma(0)\phi(t)$ Rb	$\gamma(\cdot)\phi(t)$ Ra2i	$\gamma(\cdot)\phi(\cdot)$ Ra2ii	$\gamma(0)\phi(t)$ Rb	$\gamma(\cdot)\phi(\cdot)$ Ra2ii	$\gamma(0)\phi(t)$ Rb
AIC _c weight	0.24	0.24	0.25	0.26	0.00	0.00	0.30	0.04	0.66	1.00	0.00
T. em. (γ) – 1988	0.15 <i>0.00-0.89</i>	0.40 <i>0.15-0.71</i>									
T. em. (γ) – 1989	0.21 <i>0.00-0.92</i>	0.03 <i>0.00-1.00</i>									
T. em. (γ) – 1990/1991	0.64 <i>0.38-0.84</i>	0.48 <i>0.28-0.68</i>									
T. em. (γ) overall			0.41 <i>0.22-0.64</i>	0.41 <i>0.23-0.62</i>	0 <i>(forced)</i>	0 <i>(forced)</i>	0.04 <i>0.00-0.47</i>	0.01 <i>0.00-0.46</i>	0 <i>(forced)</i>	0.82 <i>071-0.90</i>	0 <i>(forced)</i>
Survival (ϕ) – 1988	0.28 <i>0.16-0.45</i>		0.35 <i>0.21-0.52</i>		0.26 <i>0.17-0.38</i>	0.22 <i>0.25-0.76</i>	0.59 <i>0.52-0.65</i>		0.58 <i>0.52-0.60</i>		0.62 <i>0.31-0.86</i>
Survival (ϕ) – 1989	0.60 <i>0.25-0.87</i>		0.65 <i>0.33-0.88</i>		0.55 <i>0.32-0.55</i>	0.51 <i>0.25-0.76</i>	0.77 <i>0.59-0.89</i>		0.75 <i>0.60-0.84</i>		0.65 <i>0.25-0.91</i>
Survival (ϕ) – 1990	0.41 <i>0.19-0.68</i>		0.28 <i>0.17-0.42</i>		0.22 <i>0.14-0.33</i>						0.22 <i>0.13-0.35</i>
Survival (ϕ) – 1991	0.74 <i>0.18-0.97</i>		0.48 <i>0.28-0.69</i>		0.3 <i>0.22-0.44</i>						0.16 <i>0.10-0.25</i>
Survival (ϕ) overall		0.42 <i>0.32-0.53</i>		0.42 <i>0.32-0.52</i>				0.63 <i>0.56-0.68</i>		0.78 <i>0.51-0.92</i>	

Table 6. (Continued).

	Females 1987-1991					Females 1987-1989	Males 1987-1989			Paired males 1987-1991	
	$\gamma(t)\phi(t)$ Ra1i	$\gamma(t)\phi(-)$ Ra1ii	$\gamma(\cdot)\phi(t)$ Ra2i	$\gamma(\cdot)\phi(-)$ Ra2ii	$\gamma(0)\phi(t)$ Rb	$\gamma(0)\phi(t)$ Rb	$\gamma(\cdot)\phi(t)$ Ra2i	$\gamma(\cdot)\phi(-)$ Ra2ii	$\gamma(0)\phi(t)$ Rb	$\gamma(\cdot)\phi(\cdot)$ Ra2ii	$\gamma(0)\phi(t)$ Rb
Br. pop. – 1987	356 <i>243-575</i>	356 <i>243-575</i>	356 <i>242-575</i>	356 <i>242-575</i>	356 <i>243-375</i>	356 <i>242-575</i>	687 <i>638-754</i>	688 <i>638-754</i>	688 <i>638-754</i>	263 <i>176-437</i>	264 <i>177-437</i>
Br. pop. – 1988	138 <i>114-184</i>	138 <i>114-184</i>	134 <i>112-174</i>	138 <i>115-180</i>	142 <i>117-187</i>	135 <i>113-175</i>	511 <i>473-563</i>	528 <i>487-584</i>	518 <i>483-566</i>	151 <i>112-229</i>	296 <i>186-513</i>
Br. pop. – 1989	233 <i>165-362</i>	233 <i>165-362</i>	219 <i>162-324</i>	194 <i>151-270</i>	248 <i>179-370</i>	233 <i>165-362</i>	1003 <i>885-1167</i>	924 <i>840-1037</i>	1004 <i>885-1167</i>	163 <i>116-265</i>	421 <i>237-814</i>
Br. pop. – 1990	225 <i>205-257</i>	228 <i>207-263</i>	227 <i>206-261</i>	230 <i>208-265</i>	236 <i>213-273</i>					258 <i>232-299</i>	266 <i>237-311</i>
Br. pop. – 1991	284 <i>253-330</i>	278 <i>249-321</i>	284 <i>253-330</i>	281 <i>251-324</i>	284 <i>253-330</i>					392 <i>338-471</i>	381 <i>330-456</i>

and thus many of these males are not available for capture. For these paired males the Constant random, constant survival model predicts a “temporary emigration rate” of 82%, meaning that only 18% of the males succeeded to amplex a female (on a yearly bases), even fewer actually bred because of males displacements. This is reasonable, with a sex ratio of on average 77% males. The estimated average survival was 78%, much higher than the estimated female value of 42% (and with marginally overlapping confidence intervals).

Because the Null model (no temporary emigration) was selected as the top model in the candidate set for males, the estimated breeding population sizes (688, 518 and 1004, table 6) also represent the total adult male population.

Accepting the skip rate estimated by the Constant random model (4%), only changed these estimates marginally (table 6).

Total female population in 1987-1989 was estimated by correcting breeding population size (356, 138, 194, sub model **Ra2ii**, table 6) for temporary emigration (0.41). However also considering the total adult population, the sex ratio was male biased (table 7).

Age specific survival

Age specific survival was supported for both sexes (table 8). For males there was no overlap in 95% CI between young and old toads. For females, however, there was some overlap (table 8).

Table 7. Breeding population, total population and sex ratios. The population estimates are based on parameter estimates from the Robust design “Constant random constant survival” model (**Ra2ii**) for females and on the Robust “Constant random” model (**Ra2i**) for males. These are the “best” models for the respective sex that gives an estimate of temporary emigration. The total population is estimated as [Breeding population/(1 – temporary emigration rate)]. The latter rate is 41% for females and 4% for males.

	Breeding population			Total population		
	Females	Males	Sex ratio (% females)	Females	Males	Sex ratio (% females)
1987	356	687	0.34	614	716	0.46
1988	138	511	0.21	238	532	0.31
1989	194	1003	0.16	334	1045	0.24
1990	230			397		
1991	281			484		

Table 8. Survival estimates from Robust design Random model (**Ra2**) (females) and Null model (**Rb**) (males) with a common survival parameter for both “age classes”. Model comparison (Deviance (Δ) and weight) is within sex for models with and without age structure.

	Param.	ΔAIC_c	Weight	S all	S young	S older
Females						
$\gamma(\cdot)\phi(\cdot + \text{age})$	26	0	0.56		0.32	0.49
					0.21-0.44	0.36-0.62
$\gamma(\cdot)\phi(\cdot)$	25	0.52	0.44	0.42		
				0.32-0.52		
Males						
$\gamma(0)\phi(\cdot + \text{age})$	16	0	0.99		0.57	0.82
					0.52-0.63	0.64-0.92
$\gamma(0)\phi(\cdot)$	15	9.54	0.01	0.63		
				0.56-0.68		

Discussion

Population estimates

Estimated population sizes from the Robust design model (table 6), representing all breeding animals, were similar to those estimated by the POPAN models for single years (table 4) except for males in 1989. This year more than 50% of male catches were made on one single night (appendix 1) which is not optimal for the analysis. Also, for this year Goodness of Fit (GOF) tests (table 1) suggested problems. The GOF TEST2 that reacts to unequal catchability depending on previous capture actually reported problems for males in both 1987 and 1989. Another possible cause for this is that all toads captured in or around one pond were released together before we proceed to next pond. This may have concentrated them and made them easier to capture next time. This was less of a problem with females that anyhow mostly were captured at the actual spawning site, one or two in each pond.

Not surprisingly, the estimated number of paired males was similar to that of females. Only in one year (1991) were the estimates of paired males significantly (table 6) higher than those for the females. This suggests that, with the possible exception of 1991 (which was the breeding season of longest duration, appendix 1), male displacements (Davies and Halliday, 1977; Loman and Madsen, 1986) were not very common.

The strongly divergent results for number of paired males from models **Ra2ii** v. **Rb** in 1988 and 1989 suggest errors in either estimate. Indeed, the Null model for paired males (**Rb**) is clearly invalid because this model makes the unrealistic assumption of zero "pseudo skip rate", meaning that all males ever found in amplexus are also found in amplexus in all years (and other males hence never are found in amplexus). This is clearly not a realistic assumption as individual male mating status is likely to show temporal variation, i.e., "temporary emigration" from the paired category.

Breeding sex ratio and its immediate causes

Males far outnumbered females at the breeding site in all five years of the study (tables 2, 4, 6). This was thus true not only for observed numbers but also for numbers estimated by the CMR models. Furthermore, a male biased sex ratio was observed even when accounting for toads, mainly females, that skipped breeding opportunities (table 7). The results from our analyses highlight two factors that contribute to this pattern in toad populations. (1) A large proportion of the females skipped breeding opportunities while this seemed to be very rare for males, and (2) yearly survival was higher for male than for female toads.

Agreeing with our results, some previous studies suggest the occurrence of skipped breeding in female Common toads (Hemelaar, 1988; Kuhn, 1994; Schmidt, Schaub and Anholt, 2002). One study (Frétey et al., 2004) also finds evidence of a high proportion of males skipping breeding seasons. This is in marked contrast to our results. We suggest that one of the reasons for this may be differences in climatic or other environmental conditions. For example, in colder climates the summer might be too short for female toads to gather sufficient energy to complete an annual reproductive cycle (Hemelaar, 1988).

The sex-specific difference in Common toad annual survival rates reported here agree with results from other demographic studies of this toad (Gittins, 1983; Frétey et al., 2004). Furthermore, these studies all find survival rates in the range seen in present study. All studies, including ours, also suggest considerable among-year variation in annual survival rates. The cause of such temporal variation in survival is largely unknown but may be related to among year variation in weather (Anholt et al., 2003).

We found a tendency for lower survival in young adult toads, males and probably also females. This analysis assumes a closed population with no transient toads. Like us, Frétey et al. (2004) approximated first year adults with first captures and found a lower survival for

this male age cohort. Their data did however not allow for a similar analysis of female age-dependent mortality. In another species (*R. temporaria*), analyses of ages of breeding frogs using scelerochronology suggest relatively high mortality for first year adults (both males and females) (Gibbons and McCarthey, 1984).

Combining the estimated values for skip rate and survival, does the resulting sex ratio fit the observed data at this breeding site? Assuming same survival for males and females before sexual maturity, a model can be set up to test this. If 100 females enter sexual maturity yearly, with a survival rate of 41% and a skip rate of 42%, this results in a breeding population size of 132 females (all ages combined). The corresponding figures for 100 males (4% skip rate and 63% survival) give an estimate of 253 males. These calculations suggest that the breeding population should consist of 34% females. However, such a high proportion of females was only observed during one year of the study, suggesting that additional factors may have to be considered to explain the highly male-biased sex ratios recorded. Such a factor is a sex difference in age of maturity, unaccounted for in our study but resulting in fewer females than males recruiting each year. Indeed, Hemelaar (1988) and Reading (1991) have found that female Common toads may become sexually mature at least one year later than males. We therefore suggest that the highly male-biased sex ratios observed in our study population was caused by (1) higher male survival rates compared to females, (2) higher incidence of females, compared to males, to skip breeding opportunities and (3) female toads maturing at a later age than males.

The discussion above assumes a primary sex ratio of 1:1 and same survival for juvenile males and females. These are little studied aspect of anuran biology but Sakisaka et al. (2000) found that the average sex ratio of eggs for *Rana rugosa* was indeed 1:1 while Alho, Matsuba and Merilä (2010) found a slightly female biased primary sex ratio in *R. temporaria*.

Sex specific reproductive effort as a cause for sex effects on skip rates and survival

The weight of the ovaries of breeding female common toads may constitute up to 20% of the female's total body mass (Jørgensen, Larsen and Lofts, 1979), demonstrating that female Common toads invest a substantial amount of energy into reproduction. Similar high energy investments by females in other taxa such as adders (*Vipera berus*) (Viitanen, 1967; Madsen and Shine, 1992) and fish (Rideout, Rose and Burton, 2005) result in both increased female mortality and biennial female reproductive cycles. Although we did not measure female mass, it was evident when female toads had oviposited; they were emaciated and in quite poor condition. We suggest that between sex differences in reproductive effort is a likely explanation for the observed between sex differences in survival and possibly also for the differences between sexes in the probability of skipped breeding occasions.

An evolutionary approach

Low female survival and high female skip rates can be seen both as effects of and as an adaptation to a high reproductive effort by the females, relative to males. With a skip ratio of 41% and an adult survival of 42%, the expected number of breeding opportunities per female toad is only $1.32 (1 + (\sum 0.42^y * 0.59, y = 1, 2, 3, \dots))$. Thus, approaching a semelparous state, there is a strong incentive for a long period of growth before sexual maturity (Roff, 1992) because this will result in a large size and thus a large clutch (Kuhn, 1994; van Gelder, 1995) at the first, and possibly the only, breeding opportunity. This may be the reason females were larger than males in this (table 9) as well as in other toad populations.

Migration pattern

Previous studies and analyses (including one on this population) suggest that males tend to arrive earlier and stay longer while females

Table 9. Male and female average size (mm, snout – urostyle). Data from 1990 and 1991 is not included because the sample of males was in these years biased by including those in amplexus only.

	Males			Females		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
1987	60.9	4.19	491	74.5	4.35	122
1988	61.3	3.62	386	75.7	4.04	88
1989	61.4	4.07	583	76	4.79	95

arrive later and leave the breeding site shortly after spawning, causing a more gradual decrease in their number at the breeding site (Gittins, Parker and Slater, 1980; Reading and Clarke, 1983; Kuhn, 1984; Loman and Madsen, 1986; Kiss and Laar, 1992). In contrast, our results suggest that there is little difference among the sexes in the timing of arrival at the breeding site (fig. 1, appendix 1). However, findings from the previous studies tend to agree with our result of a sex difference in the timing of departure from the breeding site (fig. 2).

Practical lessons for conservation

Skipped breeding and sex ratio constitute two important population demographic parameters in amphibian conservation. Breeding site censuses are often useful for monitoring purposes. However, if one is interested in knowing the true number of animals in a superpopulation such censuses may be misleading unless the frequency of breeding skip rates is known.

Furthermore, in order to assess a population's long term viability the effective population size should be measured (Brede and Beebee, 2006). One important parameter influencing the effective population size is the population's sex ratio (Frankham, 1995). The effect of sex ratio on the genetic effective population size is influenced mainly by the breeding number of the rarer sex (Falconer, 1981), in anurans thus usually females. From this respect, spawn counts that are popular means of censusing anurans (Loman and Andersson, 2007) should give a relevant measure. However, in species with spawn that is difficult to count, counts of males (that spend

more time at the breeding site, in some species' call loudly and thus are easier to catch) give more reliable figures (but restricted to this sex) than estimates of the female or total population. This is typically the case with toads (Brede and Beebee, 2006) and, although useful for analyses of trends, it does not inform on effective population size, unless the actual sex ratio is known or can be assessed from studies of similar populations.

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Appendix 1. Total catches by year and date. The number of raw captures is indicated in the columns "Day" and "Night". Only females and paired males were captured in 1990 and 1991. Days with few captures were pooled in the analyses. Individuals captured at both day and night or during several pooled days counted only as one here. Pooled rows are indicated by double vertical bars. The "Pooled" columns give the number of individuals entered in the POPAN analyses. For the Robust design model the number of capture occasions was further reduced by a second pooling. Single vertical bars indicate which rows were combined to form the reduced samples (occasions). The reduced pooled samples size is entered in the columns labelled "Red.". The value used in the analysis is the number of different individuals captured at least once during the period. Again, this may be less than the total in the individual cells of the previous row if some toads were captured more than once within the respective period. The first pooling was made to deal with very small samples on some days. The second pooling (giving the reduced samples) was made to fulfil the assumption of closure within capture year. Both the pooled and reduced capture occasions resulted in reduced capture histories in the sense of Hargrave and Borland (1994).

Date (day/month)	Females						Males				Paired males			
	Day		Night		Both		Day	Night	Both		Day	Night	Both	
	Total	Paired	Total	Paired	Pooled	Red.			Pooled	Red.			Pooled	Red.
1987														
22/4			10	3				52				3		
23/4			34	25		40		184		202		25		25
25/4			24	20		23		127		126		19		18
26/4			7	0		7		17		17		0		0
27/4	17	17	14	11		27		17	86	92	92	16	12	26
28/4	9	9	17	12		25		9	172	172		9	12	21
29/4	8	8	8	2				8	69			7	3	
30/4	4	3						4				3		
1/5	1	1	3	2				1	48			1	3	
2/5	2	2						2				2		
4/5	0	0	1	0		22		0	2		127	269	0	0
1988														
20/4			50	45		49			238	227			45	45
22/4			6	5		6		52	60	58		267	6	6
23/4			18	8		17		17	51	43		43	9	9
24/4			7	7		7			9	9		9	7	7
25/4			27	9		26			111	110			9	9
26/4			15	5					6				6	
27/4			8	2					2				2	
28/4			1	0					0				0	
3/5	2	2	4	3				2	106			2	3	
5/5			1	0		26		44	29		127	203	0	0

Appendix 1. (Continued).

Date (day/month)	Females						Males				Paired males			
	Day		Night		Both		Day	Night	Both		Day	Night	Both	
	Total	Paired	Total	Paired	Pooled	Red.			Pooled	Red.			Pooled	Red.
1989														
13/4			31	28	30	30		159	153			29	26	
14/4			43	36	39	39		348	339	487		36	35	61
15/4	16	15	15	9	26		12	93	100	100	12	8	18	18
16/4	3	2	10	4			2	76			2	4		
20/4			2	0	13	37		1	76	76		0	5	5
1990														
2/4			48	42	48						0	39	39	
3/4	29	29	57	57	80	110					29	57	82	110
4/4	7	7	45	45	50	50					6	44	49	49
5/4	17	17	37	36	49						17	36	47	47
6/4	8	8	30	29	36						8	28	33	
7/4	4	4	10	10							4	10		
8/4	5	5	13	11							5	12		
10/4	3	3	4	4							3	4		
11/4			5	4	33	91					0	4	31	55
1991														
2/4			6	5								5		
3/4			9	8								8		
4/4			38	37	47							37	47	
5/4	2	2	27	27	28	68					2	27	28	68
6/4	1	1	31	31	31	31					1	28	29	29
7/4			27	27	27	27						25	24	24
8/4	5	5	36	36	40	40					6	35	40	40
9/4	12	12	30	28	37	37					11	28	39	39
10/4	5	5	16	16	21						4	16	19	19
11/4	7	7	28	26	32						7	27	33	
12/4	4	4	12	12							4	12		
13/4	5	5	12	13							5	17		
14/4	6	6	7	7							5	7		
15/4	2	2	2	2							2	2		
16/4			1	0	43	76						0	47	69