

# Unbiased survival estimates and evidence for skipped breeding opportunities in females

Erin Muths<sup>1\*</sup>, Rick D. Scherer<sup>1,2</sup> and Brad A. Lambert<sup>3</sup>

<sup>1</sup>US Geological Survey Fort Collins Science Center, Fort Collins, CO 80526-8118, USA; <sup>2</sup>Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523-1474, USA and <sup>3</sup>Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO 80523, USA

## Summary

1. Estimates of demographic parameters for females, in many organisms, are sparse. This is particularly worrisome as more and more species are faced with high extinction probabilities and conservation increasingly depends on actions dictated by complex predictive models that require accurate estimates of demographic parameters for each sex and species.

2. This study assesses demographic parameters, specifically temporary emigration and survival, for females, a class that has been difficult to investigate historically because of lack of data. Amphibians provide a particularly good example because there is global concern about amphibian decline; yet most demographic parameter estimates are based on data from males, which we show can lead to erroneous conclusions.

3. We use 10 years of capture–recapture data from boreal toads (*Bufo boreas*) and the multi-state open robust design model to provide evidence for the occurrence of skipped breeding opportunities (i.e. temporary emigration) in females. This is the first time that the open robust design model has been applied to an analysis of an amphibian population that we are aware of.

4. We determined that the transition from breeder to non-breeder is obligate and the probability of a non-breeder remaining a non-breeder is 64%; thus, temporary emigration is first-order Markovian in nature, where breeding probability is dependent on the previous year's activity, i.e. if a female did not breed in year one, there is a 36% chance that she will breed in year two. With temporary emigration accounted for, we estimated between-year female survival at 87%.

5. Establishing the occurrence of temporary emigration not only reduces bias in estimates of survival probabilities but also provides information about expected breeding attempts by females, a critical element in understanding the ecology of an organism and the impacts of outside stressors and conservation actions.

**Key-words:** boreal toad, capture–recapture, Colorado, multi-state open robust design, survival, temporary emigration

## Introduction

Understanding the demographic processes that drive population dynamics is a central focus of ecology (Krebs 2001) and identifying threats to species' well-being is predicated on such knowledge (Richter & Seigel 2002; Tomillo *et al.* 2008). An understanding of these processes is limited to males for many species. In particular, information on the demographics of pond-breeding bufonids (true toads) is sparse and only a handful of studies (Kuhn 1994; Schmidt & Anholt 1999; Reading 2007; Vasconcellos & Colla 2009) have addressed demographic

parameters of female anurans (frogs or toads). In spite of great concern over declining amphibian populations and data that indicate over 32% of the world's amphibians are at risk (Stuart *et al.* 2004), comprehensive demographic data are unavailable for most amphibian species (Biek *et al.* 2002).

Increasingly, scientists are using predictive models of greater complexity in the management and conservation of species (e.g. population viability models, Stevens & Baguette 2008; extinction risk assessments, Purvis *et al.* 2000). As these models become more complex, species- and sex-specific parameter estimates are important if demographic population models are to be relevant to conservation science. With amphibians having a current extinction rate of 221 times their background rate (McCallum 2007), conservation efforts become more urgent,

\*Correspondence author. E-mail: erin\_muths@usgs.gov  
Correspondence site: <http://www.respond2articles.com/MEE/>

escalating the need for such targeted data. Given that bufonids are one of the most threatened families of amphibians (Collins & Crump 2009), this paucity of basic knowledge about female bufonids is alarming and limits our ability to make sound conservation decisions.

Amphibians are often sampled at breeding ponds, and individuals that are not present at a breeding site in a particular breeding season are considered temporary emigrants in capture–recapture models (Nichols *et al.* 1987). Temporary emigration refers to temporary absence from the study area rather than permanent dispersal. In some cases, temporary emigration is equivalent to skipping a breeding opportunity. Boreal toads, for example, are philopatric to breeding ponds (Olson 1992; Carey *et al.* 2005). Therefore, we assume temporary emigrants are skipping a breeding opportunity and not breeding in a different pond. Nichols *et al.* (1987) describe two kinds of temporary emigration, random and Markovian: in a Markovian process, temporary emigration depends on whether an individual bred in the previous breeding season and in a random system, temporary emigration is independent of an individual's behaviour previously. For females we might suppose that temporary emigration, if it occurs, is linked to reproductive state in the previous breeding season and thus follows a Markovian pattern (*sensu* Church *et al.* 2007). Temporary emigration is of interest biologically because it provides information about behaviour and reproduction. It is also interesting computationally because the presence of Markovian temporary emigration can bias estimates of survival from the Cormack–Jolly–Seber (CJS) models (Kendall, Nichols, & Hines 1997; Frétey *et al.* 2004; Schaub *et al.* 2004), subsequently affecting results from elasticity analyses or other applications that depend on reliable estimates of demographic parameters.

A number of authors allude to the presence (or absence) of temporary emigration in bufonids (Olson 1992; Kuhn 1994; Williamson & Bull 1996; Corn, Jennings, & Muths 1997; Schmidt & Anholt 1999; Frétey *et al.* 2004; Henle 2005; Bull & Carey 2009), but published reports typically focus on males or data sets where both sexes are lumped together (and are generally highly male biased). Most do not attempt to quantify temporary emigration specifically for females and the studies that present data on this phenomenon in male bufonids present divergent results, from evidence against (Vasconcellos & Colli 2009) to evidence for (Schmidt, Schaub, & Anholt 2002; Frétey *et al.* 2004; Muths *et al.* 2006; Bull & Carey 2009).

In contrast to the phenomenon of temporary emigration, a few studies have estimated annual survival probabilities in female bufonids. Researchers estimating survival probability have primarily used the CJS model (Schmidt & Anholt 1999; Schmidt *et al.* 2002; Reading 2007), although Vasconcellos & Colli (2009) apply multi-state modelling to a 3-year data set.

Estimation of demographic parameters under models that are currently available rely on recaptures of individuals (Williams, Nichols, & Conroy 2002), yet a common trait of capture–recapture data from populations of bufonids is a high proportion of captures and recaptures of males compared with that of females, making precise estimates for parameters specific to females difficult. For example, Frétey *et al.* (2004)

captured more than 1500 males, but only 728 females in a 16-year study of *Bufo bufo* in France. Of the 728 females, only 31 (4%) were captured more than one time during the study. By contrast, over 400 (55%) of the males were captured multiple times. In a 6-year study of *Bufo boreas* in northern Colorado, Corn *et al.* (1997) captured 401 males and 87 females. While 96 (24%) of the males were captured more than once, only six (7%) of the females were recaptured. Another long-term study of *B. bufo* in Britain reported the capture of 3178 females, but only 453 (14%) were recaptured more than once (Reading 2007). Kuhn (1994) documented the capture of 2385 female common toads with only 329 (14%) recaptured. In a more recent, but shorter (3-year), study of two tropical bufonids, *B. schneideri* and *B. rubescens*, Vasconcellos & Colli (2009) captured 141 males (*B. schneideri*: 66, *B. rubescens*: 75) and 22 females (*B. schneideri*: 9, *B. rubescens*: 13). These authors noted that 40% of the individuals for both species were only captured once but did not provide statistics specific to each sex.

These studies are consistent in their relatively low numbers of recaptures for females. We hypothesize that female bufonids are captured less frequently for the following reasons: (1) they are not present at the breeding site because females skip breeding opportunities (i.e. temporary emigration is occurring); and (2) when they do breed, they remain at the breeding site for a shorter period of time because females congregate and disassemble in a more random fashion than males (i.e. in a typical explosive breeding situation the congregation of males is relatively synchronous). These hypotheses follow the generally accepted paradigm for female bufonid behaviour: arriving after males, breeding, then retreating to summer habitat (Davies & Halliday 1978; Stebbins & Cohen 1995; Frétey *et al.* 2004), but these hypotheses lack quantitative support.

Male survival rates are often used in models because data on females is lacking (e.g. Biek *et al.* 2002; Vonesh & De la Cruz 2002). For example, ecological sensitivity analyses indicate that adult survival has a strong influence on population growth rates of several species of western anurans (Biek *et al.* 2002). They targeted female survival rate as a focal parameter because females produce the offspring, but in practice they substituted male survival estimates (Biek *et al.* 2002). Substituting male-specific data (i.e. survival rates) may lead to erroneous conclusions. To address this lack of information for female bufonids, we applied the multi-state open robust design (MSORD) (Schwarz & Stobo 1997; Kendall & Bjorkland 2001; Kendall & Nichols 2002) to a 11-year capture–recapture data set from a single population of boreal toads (*B. boreas*) in central Colorado, USA. Our goals were to assess temporary immigration as manifested in the transition between breeding and non-breeding states in a female bufonid and to provide an unbiased estimate of survival.

## Materials and methods

We collected data using the robust design framework (Pollock 1982; Kendall & Nichols 1995). Within each breeding season from 1999 to 2009, we conducted multiple sampling sessions at the breeding pond of a population of boreal toads (*B. boreas*) at Denny Creek

(Colorado) (3360 m elevation). Animals were captured by hand, at night (for site description and detailed methods, see Scherer, Muths, & Lambert 2008). This species has suffered population declines in the Rocky Mountains since the mid-1990s (Carey 1993; Muths *et al.* 2003) and has been considered for listing under the federal Endangered Species Act. Recently, the US Fish and Wildlife Service (USFWS) has been served with a 'Notice of Intent to Sue' by a non-governmental conservation organization (T. Ireland, USFWS, pers. comm.) indicating that the federal status of the boreal toad is unresolved.

We refer to the period of time over which sampling was conducted each year as the primary period and to the sampling sessions conducted within each primary period as capture occasions. During each capture occasion, the site, including adjacent wetlands and terrestrial areas, was searched and toads were captured in individual plastic bags. New captures received a passive integrated transponder (PIT) tag with a unique number. Recaptured animals were measured, their PIT tag number recorded and then released.

We used two models to analyse the data. For the majority of the analysis, we used the relatively new, multi-state, open robust design model (MSORD; Kendall & Bjorkland 2001) in program MARK (White & Burnham 1999). This model incorporates information on within-year dynamics in addition to our target parameters of survival and temporary emigration. For reasons discussed below, we also used the multi-state model for live recaptures (multi-state mark-recapture, MSMR; Brownie *et al.* 1993) to assess potential bias in the parameter estimates from the MSORD model. We assumed that females in the population were in one of two states each year: breeder (present at the breeding site and available for capture) or non-breeder (absent from the breeding site). As non-breeders were not present at the breeding site and, therefore, were not available for capture, the 'non-breeder' state was unobservable (*sensu* Schaub *et al.* 2004; Vasconcellos & Colli 2009).

#### MULTI-STATE OPEN ROBUST DESIGN

There are two elements in the MSORD model: (1) parameters for modelling movement dynamics and capture probability across capture occasions within each primary period (i.e. within years) and (2) parameters for modelling the changes in demographic values (survival probability and temporary emigration) between primary periods (i.e. between years).

##### Element 1

In general, movement and sampling processes within primary periods are modelled with two types of parameters:  $\text{pent}_i^s$ , the probability that an individual in state  $s$  (i.e. breeder or non-breeder) enters the study area just before capture occasion  $j$  within primary period  $i$  and  $\phi_i^s$ , the probability that an individual in state  $s$  remains in the study area between capture occasions  $j$  and  $j + 1$  within primary period  $i$  given that it had previously entered the study area. The probability of capture,  $p_i^s$ , is the probability that an individual in state  $s$  is detected on occasion  $j$  of primary period  $i$  given that it is in the study area. The model allows individuals to enter and exit the population once during a primary period (i.e. individuals cannot enter the study area again after exiting within the same year) (Kendall & Bjorkland 2001).

##### Element 2

Changes in demographic parameters between primary periods are modelled by  $S_i^s$ , the probability that an individual in state  $s$  survives

from primary period  $i$  to  $i + 1$ :  $\psi_i^{\text{B} \rightarrow \text{NB}}$ , the probability that an individual transitions from a breeder to a non-breeder state between  $i$  and  $i + 1$  (i.e. becomes a temporary emigrant) and  $\psi_i^{\text{NB} \rightarrow \text{NB}}$ , the probability that an individual remains a non-breeder between  $i$  and  $i + 1$ .

In the application of this model to our data, we assumed that non-breeding females would not be at the breeding pond at all and, therefore, set the probability of entry into the study area for non-breeders ( $\text{pent}_i^{\text{NB}}$ ) to 0. As our data were relatively sparse, we evaluated models with few parameters. Previous studies have noted that female bufonids congregate and disassemble in a more random fashion than males, and generally arrive at breeding sites later in the breeding season than males (Davies & Halliday 1978; Frétey *et al.* 2004; Stebbins and Cohen 1995; EM & RDS, pers. obs.). Therefore, we hypothesized that  $\text{pent}_i^{\text{B}}$  would be higher in later capture occasions. We chose to examine this pattern in the probability of entry via linear,  $\text{pent}(\text{linear})$ , and quadratic,  $\text{pent}(\text{quad})$ , models as well as evaluating models that allowed the linear and quadratic relationships to vary between years (i.e. time):  $\text{pent}(t \times \text{linear})$  and  $\text{pent}(t \times \text{quad})$ . We also allowed  $\text{pent}$  to vary among all capture occasions and all primary periods [ $\text{pent}(\text{fulltime})$ ]. Finally, we hypothesized that the  $\text{pent}_i^{\text{B}}$  would be the same across capture occasions  $j$  but would vary among primary periods  $i$ :  $\text{pent}(\text{primary})$ .

Once individuals have entered the population,  $\phi_i^s$  describes the probability that they remain at the breeding site for subsequent capture occasions. As we assumed that non-breeders were not present at the breeding site, we set all  $\phi_i^{\text{NB}}$  to 0. For breeders, we hypothesized that the probability of remaining at the breeding site would be a function of the length of time that an individual had already been at the breeding site (i.e. the number of capture occasions since the individual arrived at the breeding site) and denoted this model as  $\phi(\text{stay})$ . We expected estimates of  $\phi_i^{\text{B}}$  to be low (i.e. females do not stay at the breeding site very long) and to be smaller the longer an individual was present at the breeding site based on our supposition (above) that females move into and away from the breeding site quickly relative to males. We also evaluated models in which  $\phi_i^{\text{B}}$  varied among all capture occasions and all primary periods,  $\phi(\text{fulltime})$ , and model structures where  $\phi_i^{\text{B}}$  was constant across capture occasions  $j$  and primary periods  $i$ :  $\phi(t)$ .

We set the capture probability of non-breeders,  $p_i^{\text{NB}}$ , to 0. We evaluated three models of capture probability for breeders,  $p_j^{\text{B}}$ , 'fulltime' and 'x' models (as described above for the  $\text{pent}_i^{\text{B}}$  and  $\phi_i^{\text{B}}$ ) and a model where  $p_j^{\text{B}}$  was allowed to vary among primary periods but not among capture occasions within primary periods [denoted as  $p(\text{primary})$ ].

After evaluating structures for primary period parameters (element 1), we turned to the between-year parameters (element 2); the probabilities of annual survival and temporary emigration. As non-breeders are not observable, the model requires that we assume that survival probability in breeders is equal to survival probability in non-breeders ( $S_i^{\text{B}} = S_i^{\text{NB}}$ ) (Kendall & Bjorkland 2001).

We assessed two models for  $S_i^{\text{B}}$ : one representing an average annual probability of survival [ $S(\cdot)$ ] and one allowing variation in the probability of survival among years [ $S(t)$ ] such that survival probability was estimated for each year.

Transition probabilities ( $\psi$ ) describes the probability of a breeding individual becoming a non-breeding individual ( $\psi^{\text{B} \rightarrow \text{NB}}$ ) and a non-breeding individual remaining a non-breeder ( $\psi^{\text{NB} \rightarrow \text{NB}}$ ). Boreal toad females, among other bufonids, are thought not to breed every year, but to skip one or more years between breeding (Olson 1992; Corn *et al.* 1997; Carey *et al.* 2005; Bnli & Carey 2009; but see Vasconcellos & Colli 2009). The physiological requirements of female toads (e.g. acquiring adequate energy to yolk eggs) support the phenomenon of skipping breeding opportunities (i.e. temporary emigration). These

physiological efforts require adequate resources during the growing season, and can be compromised by a particularly early winter or late, cold spring (Jørgensen 1992; Reading 2007).

Hypothesizing that females may be physiologically unable to breed every year, we expected that the probability of transitioning from breeder to non-breeder ( $\psi^{B,NB}$ ) would be greater than transitioning from non-breeder to non-breeder state ( $\psi^{NB,NB}$ ). That is, it is more likely to become a non-breeder once an individual has been a breeder. This scenario, where breeding status depends on the breeding status of the previous year exemplifies first-order Markovian (i.e. non-random) temporary emigration (Kendall, Nichols & Hines 1997). Furthermore, given the constraints associated with living in a harsh environment, 'resting' (i.e. skipping an opportunity) after a year of breeding may be obligatory. In view of these hypotheses, we evaluated several models. First we assessed  $\psi(\text{state})$ , which reflects differences in transition probabilities between states (i.e. Markovian temporary emigration ( $\psi^{NB,NB} \neq \psi^{B,NB}$ )). Second, we tested a model that fixed the transition from breeder to non-breeder to 1,  $\psi(B \rightarrow NB = 1)$ , which tests the supposition that if an individual is a breeder in year 1, then that individual is obliged to be a non-breeder in year 2. Third, we allowed differences in transition probabilities and variation across years ( $t = \text{time}$ ):  $\psi(\text{state} \times \text{time})$  and finally, we evaluated the model  $\psi(\cdot)$ , that transition probabilities breeding to non-breeding and non-breeding to breeding are not different (i.e. random temporary emigration) (Table 1).

#### MODELLING PROCEDURE AND GOODNESS OF FIT

Although we were primarily interested in estimating survival and transition probabilities for females, appropriate assessment of movement dynamics and capture probability within each primary period (element 1 in the MSORD model) was essential to avoid bias and imprecision in the parameters of interest. We began our analysis by using the most highly parameterized model of the between-year parameters, that is, we structured survival probability as time-specific [ $S(t)$ ] and transition probability as state and time dependent ( $\psi(\text{state} \times \text{time})$ ), then kept this structure constant while we evaluated models of  $\text{pent}_i^b$ ,  $\phi_i^b$  and  $p_i^b$ . The evaluation of the within-year parameters yielded four models with  $\Delta\text{AIC}_c < 20$  (Burnham & Anderson 2002). These structures on  $\text{pent}_i^b$ ,  $\phi_i^b$  and  $p_i^b$  were retained when evaluating between-year parameters using all possible combinations of models for  $S$  and  $\psi$ . We assessed goodness of fit of the MSORD using program `ODDSURVIV` (Kendall & Bjørkland 2001).

#### MULTI-STATE MARK-RECAPTURE

Goodness-of-fit testing suggested that a general MSORD model fit the data poorly. It is important to note, however, that this test (the Pearson chi-squared goodness-of-fit test) can too frequently reject the null hypothesis of adequate fit when the data are sparse (Kendall & Bjørkland 2001; Williams *et al.* 2002). On the other hand, a possible cause of the poor fit of the MSORD model to the data is multiple

entrances and exits of individuals into the site within primary periods (i.e. between capture occasions). If the model fits the data poorly, parameter estimates from the model may be biased. Therefore, we chose to analyse the data using a second model to look for evidence of bias in parameter estimates.

We used the MSMR model (Browne *et al.* 1993) which requires pooling data across capture occasions within a primary period (i.e. each individual is considered captured or not for each primary period). By pooling across capture occasions within each primary period, we eliminated the potential problem of multiple entries and exits and the estimation of the movement parameters within primary periods ( $\text{pent}_i^b$  and  $\phi_i^b$ ). The remaining parameters from the MSORD model are included in the MSMR model ( $S_j^b$ ,  $S_j^{NB}$ ,  $\psi_j^{B,NB}$ ,  $\psi_j^{NB,NB}$ ,  $p_j^b$  and  $p_j^{NB}$ ), although  $p_j^b$  and  $p_j^{NB}$  have a slightly different interpretation:  $p_j^b$  is the probability of detecting a breeder at least once during primary period  $j$  and  $p_j^{NB}$  is 0.

The set of models we evaluated using the MSMR model were structurally similar to the models we evaluated using the MSORD model and we continued to assume equivalent survival probabilities for breeders and non-breeders,  $S_j^{NB} = S_j^b$ . With this constraint in place, we evaluated models in which survival probability varied for each year [ $S(t)$ ], and was constant across years [ $S(\cdot)$ ]. We evaluated four structures on transition probability: (i) transition probability from breeder to non-breeder varies over time and is different from the transition probability from non-breeder to non-breeder ( $\psi[\text{state} \times t]$ ), (ii) transition probability from breeder to non-breeder does not vary over time but is different from the transition probability from non-breeder to non-breeder ( $\psi[\text{state}]$ ), (iii) transition probability from breeder to non-breeder is one and is different from the transition probability from non-breeder to non-breeder ( $\psi[\text{state}, B \rightarrow NB = 1]$ ) and (iv) transition probability to non-breeder does not vary across time or depend on an individual's state in the previous breeding season ( $\psi[\cdot]$ ). Finally, we evaluated two structures on  $p_j^b$ . We allowed variation across years [ $p(t)$ ], or assumed it was constant across years [ $p(\cdot)$ ]. We evaluated every possible combination of the model structures for these parameters and derived model-averaged estimates of  $S_j^b$ ,  $\psi_j^{B,NB}$  and  $\psi_j^{NB,NB}$ . To evaluate potential bias in parameter estimates from the MSORD model, we compared those estimates with the model-averaged estimates from the MSMR model. We used the median catch procedure in program `MARK` to estimate the level of over-dispersion,  $\hat{c}$ , in the data for the most parameterized MSMR model.

A common problem in analyses of capture-recapture data is failure of the estimation procedure to produce estimates of some parameters in a model. In particular, the failure to generate an estimate can occur when the estimate is near the bounds of the range of possible values (i.e. an estimate of survival probability near 0 or 1). Instances in which some parameters are not estimated are important to consider because non-estimation of a parameter can cause bias in estimates of other parameters. In this analysis, the estimation procedure failed to produce estimates for some parameters in many models. In every case, the parameters that were not estimated were nuisance parameters (i.e. they were not the parameters of primary interest, survival and

Table 1. Results of model selection for the assessment of within-year parameters (element 1,  $\text{pent}$ ,  $\phi$  and  $p$ )

Model	QAIC <sub>c</sub>	Delta QAIC <sub>c</sub>	w(t)	k	QDeviance
{ $S(t)$ , $\psi(\text{state} \times t)$ , $\text{pent}(\text{primary})$ , $\phi(\text{stay})$ , $p(\cdot)$ }	607.6	0	0.86	44	496.4
{ $S(t)$ , $\psi(\text{state} \times t)$ , $\text{pent}(\text{primary})$ , $\phi(\cdot)$ , $p(\cdot)$ }	611.2	3.6	0.14	41	509.4
{ $S(t)$ , $\psi(\text{state} \times t)$ , $\text{pent}(t \times \text{linear})$ , $\phi(\cdot)$ , $p(\cdot)$ }	622.4	14.8	< 0.01	51	488.1
{ $S(t)$ , $\psi(\text{state} \times t)$ , $\text{pent}(t \times \text{linear})$ , $\phi(\text{stay})$ , $p(\cdot)$ }	628.5	20.9	< 0.01	54	483.6

transition probabilities.) To deal with this problem, we examined the raw data to determine if the value of a parameter that was not estimated was near 0 or 1. If that was the case, we fixed the parameter to the relevant value and ran the model again. For example, in the top model from the MSMR analysis, capture probabilities in years 2000 and 2001 were not estimated. Examination of the raw data indicated that  $p$  for 2000 was close to 0 (i.e. no toads were re-captures in 2000) and  $p$  for 2001 was close to 1 (i.e. many individuals were re-captures). Therefore, we set these capture probabilities to 0 and 1, respectively, and ran the model again. Resulting estimates of the target parameters were nearly identical to our original models.

## Results

### DATA SUMMARY

We captured 124 female toads over 11 years (11.3 per year). The results of the goodness-of-fit test for the MSORD model indicated poor fit to the data ( $\chi^2 = 87.59$ ,  $P = 0.0002$ ) and moderate over-dispersion in the data ( $\hat{c} = 1.95$ ).

### MSORD MODEL SELECTION AND PARAMETER ESTIMATES – WITHIN-YEAR (ELEMENT 1)

Using the general structure for survival and transition probabilities,  $S(t)$  and  $\psi(\text{state} \times t)$ , we explored different structures for the within-primary period parameters (Table 1). In the set of candidate models, the data provided strong support ( $w_i = 0.86$ ) for a single structure: pent(primary),  $\phi(\text{stay})$ ,  $p(\cdot)$  (Table 1). Contrary to our hypotheses, estimates of  $\text{pent}_{ij}^B$  from the top model suggest that the highest proportion of females were present at the breeding site during the first capture occasion each year, and that smaller proportions arrived later. For example, the estimate of  $\text{pent}_{ij}^B$  for the first occasion in 2001 is 0.88 and estimates of  $\text{pent}_{ij}^B$  for the remaining capture occasions in that year are  $< 0.05$ . The top model indicated that once at the breeding site, the probability that a female remained at the breeding site in subsequent capture occasions ( $\phi$ ), varied by the length of time the female had already been at the site. Due to the sparseness of the data, only one estimate of  $\phi$  was returned from the top model; therefore, we present the average value for  $\phi$  from the second ranked model:  $\hat{\phi} = 0.56$  (95% CI 0.32–0.78) and provide information from the raw data to illustrate the behaviour measured by this parameter. No females were captured in *consecutive years* and only 61 (49%) were captured more than once during the entire study. Of the 61 that were recaptured, only 39 were captured more than once *within*

a primary period. Seventy-seven per cent (30 of 39) of the individuals that were encountered in more than one capture occasion per primary period were captured in *consecutive occasions*. If we use the estimate of 0.56 for  $\phi$ , the probability of remaining in the study area for two consecutive capture occasions would be  $0.56 \times 0.56 = 0.31$  and then decrease by 56% for each capture occasion thereafter.

Finally, the structure of  $p_{ij}$  in the top model suggested low capture probability for females and low variability in capture probability across primary periods and capture occasions within breeding seasons ( $p_{ij} = 0.22$ , 95% CI 0.15–0.30).

### MSORD MODEL SELECTION AND PARAMETER ESTIMATES – BETWEEN-YEAR (ELEMENT 2)

The data provided support for the first two models (combined  $w_i = 0.95$ ), although the top model received considerably higher support. The top two models differed only in the structure of  $\psi_i^{B \rightarrow NB}$ : the top model fixed  $\psi_i^{B \rightarrow NB}$  to 1 (i.e. breeders always transit to non-breeders the following year) and the second model allowed  $\psi_i^{B \rightarrow NB}$  to be estimated from the data. Estimates from the two models were nearly identical; therefore, we report the estimates from the top model only (Table 2 and Table 3).

The structure of the top ranked model indicated that survival probability in boreal toad females varied little between years ( $S = 0.87$ , 95% CI 0.73–0.95) and that the transition from breeder to non-breeder was obligatory (i.e.  $\psi_i^{B \rightarrow NB} = 1$ ). The probability that an individual remained a non-breeder after skipping breeding the previous year,  $\psi_i^{NB \rightarrow NB}$  was 0.64 (95% CI 0.38–0.84) (Table 3). Therefore, temporary emigration in female boreal toads is Markovian: the probability that

**Table 3.** Estimates of key demographic parameters: survival probability for breeders and non-breeders,  $S_i^B$ ; the probability of transition from breeder to non-breeder,  $\psi_i^{B \rightarrow NB}$ ; and the probability of transition from non-breeder to non-breeder,  $\psi_i^{NB \rightarrow NB}$  from the MSORD (top model) and MSMR (model-averaged) models

Parameter	MSORD	MSMR
$S_i^B$	0.87 (0.73–0.95)	0.90 (0.74–0.97)
$\psi_i^{B \rightarrow NB}$	1.00 (fixed)	1.00 (0.98–1.00)
$\psi_i^{NB \rightarrow NB}$	0.64 (0.38–0.84)	0.65 (0.44–0.82)

Numbers in parentheses represent 95% confidence intervals. In the top model from the MSORD,  $\psi_i^{B \rightarrow NB}$  was fixed to 1 and was not estimated.

**Table 2.** Results of model selection for the assessment of between-year parameters (element 2: survival and  $\psi$ )

Model	QAIC <sub>c</sub>	Delta QAIC <sub>c</sub>	$w(t)$	$k$	QDeviance
{ $S(\cdot)$ , $\psi(B \rightarrow NB = 1)$ , pent(primary), $\phi(\text{stay})$ , $p(\cdot)$ }	551.0	0.0	0.73	18	511.5
{ $S(\cdot)$ , $\psi(\text{state})$ , pent(primary), $\phi(\text{stay})$ , $p(\cdot)$ }	553.4	2.4	0.22	19	511.5
{ $S(\cdot)$ , $\psi(B \rightarrow NB = 1)$ , pent(primary), $\phi(\cdot)$ , $p(\cdot)$ }	557.4	6.4	0.03	15	525.0
{ $S(\cdot)$ , $\psi(\text{state})$ , pent(primary), $\phi(\cdot)$ , $p(\cdot)$ }	559.7	8.8	0.01	16	525.0

Models with Delta QAIC<sub>c</sub>  $> 10$  not shown

a female skips breeding in a particular year depends on her breeding status the previous year. These results supported our observations from the raw data (no females were encountered in consecutive years) and our hypothesis that females skip breeding opportunities frequently. It is important to note that some parameters were not estimated despite the relatively low number of parameters in the top two models. We discuss the issue of non-estimation earlier in the modelling procedure section.

#### MULTI-STATE MARK-RECAPTURE MODEL

Under the MSMR model, estimates of the over-dispersion parameter,  $\hat{c}$ , were small ( $\hat{c} = 0.96$ , 95% CI 0.63–1.30). This suggests that pooling across capture sessions within primary periods addressed some of the lack of fit of the MSORD model. Model-averaged estimates of  $S_i^B$ ,  $\psi_i^{B,NB}$  and  $\psi_i^{NB,NB}$  from the MSMR model were nearly identical to those from the top model from the analysis using MSORD (Table 3).

#### Discussion

There are reasons why precise estimates of demographic parameters for female bufonids are rare. Differences in breeding behaviour and the assumptions of traditional capture-recapture models (e.g. the CJS model) conspire to bias demographic studies and information resulting from them, towards males. Despite the difficulties, it is unreasonable to expect ecologically accurate conclusions and predictions about females – and hence populations – based on models that use data only from males. Given the current world-wide amphibian crisis, demographic data that accurately reflect an entire population and not one sex only, are even more vital.

We used contemporary capture-recapture models to estimate survival and transition probability between breeding and non-breeding bufonid females in the temperate zone, capitalizing on a recently developed model (MSORD) that relaxes some of the problematic assumptions of earlier models. The goodness-of-fit test suggested poor fit of the MSORD model to the data, and not all parameters were estimated, even in the top models. Notably  $\phi_{ij}^*$  (probability of entry) and  $\phi_{ii}^*$  (probability of staying once the animal has arrived at the site) were not estimated in the MSORD model. Because of these difficulties, typical with sparse data, we also assessed the data using the MSMR model. The fact that model results were quite similar suggests that the un-estimated parameters were not of direct consequence to our focal parameters of  $\psi$  and  $S$  and therefore did not affect the estimates.

#### ESTIMATING SURVIVAL AND THE PHENOMENON OF TEMPORARY EMIGRATION ARE ENTWINED

Estimates of survival from the CJS model are biased in the presence of non-random (Markovian) temporary emigration such that use of the CJS model implies that no temporary emigration occurs. A cursory examination of female bufonid physiology and ecology, especially of those species living at

higher elevations, strongly suggests that it is biologically unrealistic to assume that some sort of temporary emigration does not occur. As 'capital breeders' (*sensu* Bonnet, Bradshaw, & Shine 1998), female bufonids acquire and store energy for egg production prior to the breeding season rather than during the breeding season [e.g. in temperate zone anurans, fat (energy) is not accumulated until after the completion of breeding, Jørgensen 1992]. Animals living at the edge of their climatic range are probably faced with harsh environmental conditions that potentially restrict available resources and the opportunity to access them. This scenario allows for a prolonged period of energy acquisition (e.g. more than a year) and thus skipped breeding opportunities.

Boreal toads in the Rocky Mountains are a good example of such a temperate zone bufonid. These toads typically live at elevations over 2286 m (Muths & Nanjappa 2005) at sites with short growing seasons and harsh winters. Females have greater energetic requirements than males (Carey *et al.* 2005), limited time to acquire resources and a relatively long life span (10 or more years) (Olson 1992; Carey *et al.* 2005). These characteristics suggest that females are physiologically and environmentally constrained such that skipping breeding opportunities may be obligatory.

#### TEMPORARY EMIGRATION

Temporary emigration is an important and understudied component of bufonid behaviour. We present evidence that female boreal toads skip breeding opportunities, that the transition from breeder to non-breeder is obligatory and the probability of transitioning from non-breeder to non-breeder is 64%. Incorporating our estimated survival probability (0.87) and taking into account obligate non-breeding the first year after a breeding event, we expect that 27% of females will breed the year following a skipped opportunity (survival in year 1  $\times$  survival in year 2  $\times$  the probability of transitioning from NB to B =  $0.87 \times 0.87 \times 0.36 = 0.27$ ). Following that logic, 73% will skip two or more breeding opportunities ( $1 - 0.27 = 0.73$ ). These findings quantify the idea that some iteroparous animals, including bufonids, skip breeding opportunities (Bull & Shine 1979).

We contend that skipping breeding opportunities facilitates the accumulation of energy necessary for breeding, perhaps a critical concern in areas where high elevations and low temperatures potentially curtail foraging, growth and vitellogenesis (Bull & Shine 1979; Duellman & Trueb 1986; Feder & Burggren 1992). Furthermore, the probability of temporary emigration in female boreal toads is higher than in male boreal toads, where temporary emigration for most years is low (0.03–0.23, Muths *et al.* 2006). Our results support early reports of breeding intervals of greater than 1 year in bufonids (Bragg 1940; Blair 1943) and more recent studies that allude to temporary emigration (see Introduction).

Understanding temporary emigration in female bufonids and recognizing potential differences between populations or species at high and low elevations in the frequency of skipped breeding can be instructive and sets the stage for evolutionary

questions about lifetime fecundity, selection and the influence of environmental constraints

#### SURVIVAL

We assumed equal survival probabilities for breeders and non-breeders because survival is inestimable for the unobserved state (non-breeder). This assumption can be supported or refuted based on standard life-history theory. It can be argued that non-breeders do not bear the cost of reproduction (travel, egg yolking and competition) and therefore might have higher survival (although in this case, some energy would be expended in the protracted effort of yolking eggs). On the other hand, it can also be argued that only very fit toads breed so that even with the increased risk, survival in breeders is about equal to the less fit non-breeders. This is relevant to how we interpret our estimates of survival and longevity. Estimates of survival probability of females from this analysis are high (87%), consistent across years and higher than the survival probability reported for common toad females in Europe (38%, Schmidt *et al.* 2002) and toads in a neotropical savanna (~37%, based on estimates of monthly survival probability of 92%, Vasconcellos & Colla 2009). The estimates for female boreal toads are also higher than values reported for male boreal toads (Corn *et al.* 1997, Scherer *et al.* 2005, 2008; 0.74–0.83). However, if the survival rate is constant among breeders and non-breeders, few animals will survive up to the age of 10 years and further exploration of survival differences between breeders and non-breeders would be instructive. Use of survival estimates from our analysis for female boreal toads (rather than the male estimate used) would not change the conclusions of the previous sensitivity analyses of Biek *et al.* (2002) and Yonesh & De la Cruz (2002) because the male estimate they used in their models was also relatively high (78%). If anything, their conclusions that a reduction in adult survival rate would have stronger effects on population growth rates than reductions in other vital rates are magnified when female survival is higher. However, if female survival was substantially lower than the survival estimates for males used in the analyses, their conclusions may have been different.

This particular example, where survival rates between male and female toads were similar, would be unlikely to influence a conservation decision negatively, but as long as results derived from single sex parameter estimates are applied to entire populations, without knowledge about sex-based parameter differences, the potential for such a misinformed decision is present.

#### IMPLICATIONS

Sample size issues make it difficult to pinpoint the exact pattern of the arrival and departure of females to the breeding site during a primary period, but our evaluation of parameters within primary periods provides some insights into these patterns. Our work and earlier studies (Davies & Halliday 1978; Stebbins & Cohen 1995; Frétey *et al.* 2004) suggest that females arrive and depart in a fashion different from

males. Contrary to our *a priori* hypotheses, the top model suggested that most females were present at the breeding site at the first capture occasion, and smaller proportions entered the breeding site prior to later capture occasions in each primary period. Our results also indicated that about half of the females that were present at the breeding site on one capture occasion left prior to the next capture occasion. Muths *et al.* (2006) found little evidence that males entered the breeding site individually or that males left the breeding site during a primary period. Rather, those data suggested that males remained at the breeding site from the first to the last capture occasion in most years. Additionally, we may be dealing with an unobserved state nested within an observed state, that is, females may enter the breeding site, breed, then stay at the breeding site but move to adjacent terrestrial sites (underground or otherwise camouflaged), removed from the risks of breeding yet unavailable for capture. This unobserved state, occurring at the breeding site where we are assuming observability, could be affecting the arrival and departure data and possibly contributing to the observed lack of fit and the low (0.22) capture probability. The current analysis suggests that earlier, and perhaps more frequent, capture occasions within the breeding season may help to clarify arrival and departure patterns of female bufonids and thus benefit subsequent analyses.

#### Conclusions

Understanding the behavioural components of breeding activity (e.g. temporary emigration), and the impacts on survival is necessary to thoroughly comprehend the demography of a species. The continued decline in amphibian populations, set against the backdrop of ecological disturbance – climate change, disease or introduced predators – further emphasizes this need. This study highlights the importance of acquiring sex-specific estimates for critical demographic parameters, especially when behaviour suggests that such estimates might be different, and provides an applied example of the use of the open robust design model to elucidate population dynamics. Our example highlights the information gained by establishing the occurrence and pattern of temporary emigration in a population. Specifically, we are able to provide an unbiased estimate of the probability of survival and quantitative evidence that female boreal toads skip breeding opportunities in a non-random (Markovian) fashion – information that provides important insights into expected patterns in breeding efforts.

#### Acknowledgements

This study was partially funded by the USGS Amphibian Research and Monitoring Initiative, The Colorado Natural Heritage Program and the Colorado Division of Wildlife. We thank L. Bailey and W. Kendall for conversations about the modelling and L. Bailey, R. Reed and B. Schmidt for suggestions that improved the manuscript. All procedures used in handling animals were approved by the USGS Animal Care and Use Committee. Any use of trade product or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

## References

- Bick, R., Funk, W.C., Maxell, B.A. & Mills, L.S. (2002) What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology*, **16**, 728–734.
- Blair, W.T. (1962) Population structure in toads. *American Naturalist*, **77**, 563–568.
- Bonnael, X., Bradshaw, B. & Shine, R. (1998) Capital versus income breeding: an ectothermic perspective. *Oikos*, **83**, 333–342.
- Bragg, A.N. (1940) Observations on the ecology and natural history of Anura. I. Habits, habitat and breeding of *Bufo constrictus* Say. *American Naturalist*, **74**, 424–438.
- Browne, C., Hines, J.E., Nichols, J.D., Pollock, K. & Hestbeck, J.B. (1993) Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics*, **49**, 1173–1187.
- Bull, T. & Carey, C. (2009) Breeding frequency of western toads (*Bufo boreas*) in northeastern Oregon. *Herpetological Conservation and Biology*, **3**, 282–288.
- Bull, T.J. & Shine, R. (1979) Iteroparous animals that skip opportunities for reproduction. *The American Naturalist*, **114**, 296–303.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: A Practical Information Theoretic Approach*, 2nd edn. Springer-Verlag, New York, New York, USA.
- Carey, C. (1993) Hypotheses concerning the causes of the disappearance of boreal toads from the mountains of Colorado. *Conservation Biology*, **7**, 355–367.
- Carey, C., Corn, P.S., Jones, M.S., Livo, L.J., Muths, E. & Loftler, C.W. (2005) Environmental and life history factors that limit recovery in the southern Rocky Mountain populations of boreal toads (*Bufo boreas*). *Amphibian Decline: The Conservation Status of United States Species* (ed. M. Lannoo), pp. 222–236. University of California Press, Berkeley, California, USA.
- Church, D.R., Bailey, L.L., Wilbur, H.M., Kendall, W.L. & Hines, J.E. (2007) Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology*, **88**, 891–903.
- Collins, J.C. & Crump, M.L. (2009) *Extinction in Our Times*, 273 pp. Oxford University Press, Oxford.
- Corn, P.S., Jennings, M.L. & Muths, E. (1997) Survey and assessment of amphibian populations in Rocky Mountain National Park. *Northwestern Naturalist*, **78**, 54–55.
- Davies, N.B. & Halliday, T.R. (1978) Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.
- Duellman, W.F. & Trueb, L. (1986) *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Feder, M.E. & Burggren, W.W. (1992) *Environmental Physiology of the Amphibians*. The University of Chicago Press, Chicago, Illinois, USA.
- Fréchet, J., Curé, F., Legault, P. & Moisan, J. (2004) Adult survival and temporary emigration in the Common Toad. *Canadian Journal of Zoology*, **82**, 859–872.
- Harde, K. (2005) Analysis of recapture data from breeding populations of amphibians on temporary emigration: model assumptions, bias, and common toads. *Amphibia-Reptilia*, **26**, 7–16.
- Jørgensen, C.B. (1992) Growth and reproduction. *Environmental Physiology of the Amphibians* (eds M.E. Feder & W.W. Burggren), pp. 439–466. University of Chicago Press, Chicago, Illinois, USA.
- Kendall, W.L. & Bjorkland, R. (2001) Using open robust design models to estimate temporary emigration from capture–recapture data. *Biometrics*, **57**, 1113–1122.
- Kendall, W.L. & Nichols, J.D. (1995) On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics*, **22**, 751–762.
- Kendall, W.L. & Nichols, J.D. (2002) Estimating state-transit or probabilities for unobservable states using capture–recapture/resighting data. *Ecology*, **83**, 3276–3284.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997) Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology*, **78**, 563–578.
- Krebs, C.J. (2001) *Ecology: The Experimental Analysis of Distribution and Abundance*, 5th edn. Benjamin-Cummings Publishing Company, San Francisco, California, USA.
- Kuhn, J. (1994) Lebensgeschichte und Demographie von Erdkrötenweibchen *Bufo bufo* (L.) *Zoologische Feldherpetologie*, **1**, 3–87.
- McCullum, M.L. (2007) Amphibian decline or extinction? Current declines dwarf background extinction rate. *Journal of Herpetology*, **41**, 483–491.
- Muths, E. & Nanjappa, P. (2005) Family Bufonidae: *Bufo boreas* Baird and Girard, 1852 western toad. *Amphibian Decline: The Conservation Status of United States Species* (ed. M. Lannoo), pp. 392–396. University of California Press, Berkeley, California, USA.
- Muths, E., Corn, P.S., Pessier, A.P. & Green, D.E. (2003) Evidence for disease-related amphibian decline in Colorado. *Biological Conservation*, **110**, 357–365.
- Muths, E., Scherer, R.D., Corn, P.S. & Lambert, B.A. (2006) Estimation of the probability of male toads to return to the breeding site. *Ecology*, **87**, 1048–1056.
- Nichols, J.D., Hepp, G.R., Pollock, K.H. & Hines, J.E. (1987) The Hasting dilemma: a methodological note. *Ecology*, **68**, 213–217.
- Olson, D.H. (1992) Ecological susceptibility of amphibians to population declines. Proceedings of the symposium on biodiversity of Northwestern California, October 28–30, Santa Rosa, California, USA.
- Pollock, K.H. (1982) A capture–recapture design robust to unequal probability of capture. *The Journal of Wildlife Management*, **46**, 752–757.
- Purvis, A., Gittleman, J.L., Cowlshaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society B*, **267**, 1947–1952.
- Reading, C.J. (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, **151**, 125–131.
- Richter, S.C. & Seigel, R.A. (2002) Annual variation in the population ecology of the endangered gopher frog *Rana sierrae* Con. and Selting. *Copeia*, **2002**, 962–972.
- Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. (2004) Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology*, **85**, 2107–2113.
- Scherer, R.D., Muths, E., Noon, B.R. & Corn, P.S. (2005) An evaluation of weather and disease as causes of decline in two populations of boreal toads. *Ecological Applications*, **15**, 2150–2160.
- Scherer, R.D., Muths, E. & Lambert, B.A. (2008) Effects of weather on survival in populations of boreal toads in Colorado. *Journal of Herpetology*, **42**, 508–517.
- Schmidt, B.R. & Anholt, B.R. (1999) Analysis of survival probabilities of female common toads, *Bufo bufo*. *Amphibia-Reptilia*, **20**, 97–108.
- Schmidt, B.R., Schaub, M. & Anholt, B.R. (2002) Why you should use capture–recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, over-dispersion, and common toads. *Amphibia-Reptilia*, **23**, 375–388.
- Schwarz, C.J. & Stobo, W.T. (1997) Estimating temporary migration using the robust design. *Biometrics*, **53**, 178–194.
- Stebbins, R.C. & Cohen, N.W. (1995) *A Natural History of Amphibians*. Princeton University Press, Princeton, New Jersey, USA.
- Stevens, V.M. & Bagnette, M. (2008) Importance of habitat quality and landscape connectivity for the persistence of endangered waterjack toads. *Conservation Biology*, **22**, 1194–1204.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.
- Tominello, P.S., Saba, V.S., Pedraza, R., Paladino, F.V. & Spotila, J.R. (2008) Effects of illegal harvest of eggs on the population decline of leatherback turtles in Las Baulas Marine National Park, Costa Rica. *Conservation Biology*, **22**, 1216–1224.
- Vasconcellos, M.M. & Colli, G.R. (2009) Factors affecting the population dynamics of two toads (Anura: Bufonidae) in a seasonal neotropical savanna. *Copeia*, **2009**, 266–276.
- Vonesh, J.R. & De la Cruz, O. (2002) Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia*, **133**, 325–333.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(Suppl.), 126–130.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, California, USA.
- Williamson, I. & Bull, C.M. (1996) Population ecology of the Australian frog *Crynobatrachus signifer*: adults and juveniles. *Wildlife Research*, **23**, 249–266.

Received 4 January 2010; accepted 24 February 2010

Handling Editor: Robert P. Freckleton