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ESTIMATION OF TEMPORARY EMIGRATION IN MALE TOADS

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Abstract. Male boreal toads (*Bufo boreas*) are thought to return to the breeding site every year but, if absent in a particular year, will be more likely to return the following year. Using Pollock's robust design we estimated temporary emigration (the probability a male toad is absent from a breeding site in a given year) at three locations in Colorado, USA: two in Rocky Mountain National Park and one in Chaffee County. We present data that suggest that not all male toads return to the breeding site every year. Our analyses indicate that temporary emigration varies by site and time (for example, from 1992 to 1998, the probability of temporary emigration ranged from 10% to 29% and from 3% to 95% at Lost Lake and Kettle Tarn, respectively). Although the results provide weak evidence that males are more likely to return after a year's hiatus, a general pattern of state-dependent temporary emigration was not supported. We also hypothesized relationships between temporary emigration and a number of weather variables. While some competitive models included weather covariates, imprecise and variable estimates of the effects of these covariates precluded fully defining their impact on temporary emigration.

Key words: amphibian; boreal toad; Bufo boreas; *capture–recapture; Colorado, USA; robust design; temporary emigration.*

Introduction

As amphibian populations decline or are deemed to be threatened, precise and unbiased estimates of heretofore un-estimated or poorly estimated demographic parameters have become increasingly important to conservation and management (Biek et al. 2002, Schmidt et al. 2002). For example, estimates of demographic parameters are critical components of two important tools: population viability analyses (White 2000) and ecological sensitivity analyses (Biek et al. 2002). Previously, capture–recapture data have been used with ad hoc estimators (Husting 1965, Clarke 1977), the Lincoln Petersen estimator (Nelson and Graves 2004), and the Jolly-Seber model (Nichols et al. 1987, Smith 1987, Corn et al. 1997) to examine demographic parameters in amphibian populations. Estimates of some parameters from these methods are not robust to violations of assumptions (Carothers 1973, Nichols and Pollock 1983, Kendall 1999) such that the study of demographics in amphibian populations is fraught with challenge. High variation in capture probabilities over time (Schmidt and Anholt 1999) and across individuals, uncertainty in the completeness of closure (Williams et al. 2002), and difficulties in marking and tracking post metamorphic and juvenile animals exacerbate problems inherent to these methods.

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A number of models developed recently are available for analysis of capture–recapture data (e.g., Kendall et al. 1997), but few of these models have been applied to studies of amphibian populations in the published literature (but see Wood et al. 1998, Schmidt and Anholt 1999, Schmidt et al. 2002, Bailey et al. 2004*a*, *b*). These models expand the range of demographic parameters that can be estimated from capture–recapture data and improve the robustness of many of the estimators.

For example, Kendall et al. (1997) allow the estimation of temporary emigration (γ_i) and provide the tools to distinguish between two forms; random or state-dependent (i.e., Markovian). Under a Markovian form, a toad that is absent from the breeding site at $i-1$ (state 1), will have a different probability of temporary emigration at time i than a toad that was present at the breeding site at $i-1$ (state 2) (sensu Bailey et al. 2004*a*). For capture–recapture studies of amphibians at breeding ponds, $\gamma_i' =$ probability that a male toad is absent from the breeding site at time i if absent at time $i-1$; and $\gamma_i'' =$ probability that a male toad is absent at time i if present at time $i-1$. Under a random form, the probability of temporary emigration at time i will be the same regardless of whether an individual was present or absent from the breeding site at $i-1$ ($\gamma_i' = \gamma_i''$). Capture–recapture studies of amphibians are often conducted during the breeding season, so individuals not present at the breeding site in a given year are unavailable for capture (Bailey et al. 2004*a*). Biologically, we believe

that it is likely that toads not present at the breeding pond are skipping breeding for the year although this has not been tested empirically. This is relevant to amphibian studies because the paradigm generally accepted of breeding behavior for adult male boreal toads (*Bufo boreas*) is annual visits to a breeding site and, therefore, by definition, no temporary emigration. This paradigm is based on observations from studies that indicate toads are generally philopatric and return to their natal pond to breed (Olson 1992 [*B. boreas*]; Reading et al. 1991 [*B. bufo*]; Sinsch 1992, Sinsch and Dagmar 1995 [*B. calamita*]), and the belief that physiologically, male toads do not have to spend much time and energy preparing to breed (e.g., Carey et al. 2005). For example, nutritional condition affects gonadal development less in males than in females (Feder and Burggren 1992), and starving toads have been shown to continue to produce sperm (Van Oordt 1960), suggesting that male toads are capable of breeding immediately after hibernation and lean years may not preclude breeding activity. Furthermore, boreal toads are relatively long-lived (>10 years; Olson 1992), such that skipping a breeding opportunity would not necessarily be maladaptive.

To our knowledge, temporary emigration has received little quantitative attention in amphibian demographic studies (but see recent work by Bailey et al. 2004*a*, *b*). Husting (1965) noted that some *Ambystoma maculatum* were not captured in one year, and then recaptured in subsequent years. He suggested that these animals had skipped breeding for a year and used an ad hoc estimator to determine the proportion of the population breeding. Gill (1985) explained observed absences of *Notpopthalmus viridescens* as sampling error and mortality. Nichols et al. (1987) pointed out the similarity between Gill's (1985) model and capture–recapture models, used capture–recapture methodology to reanalyze both Gill's and Husting's work, and concluded there was evidence for temporary emigration in both studies.

Studies of *B. boreas* and other amphibians using capture–recapture methodologies have reported a high degree of temporal variation in capture probability (Olson 1992, Corn et al. 1997, Schmidt and Anholt 1999, Retallick et al. 2004, Carey et al. 2005). Recent studies have acknowledged the possibility of temporary emigration, but they have not quantified it rigorously (Williamson and Bull 1996, Corn et al. 1997, Schmidt and Anholt 1999). We suggest that some of the variation in capture probabilities is due to temporary emigration.

Since sampling of individuals in capture–recapture studies of pond-breeding amphibians often takes place at the breeding site, some individuals will not be available for capture in the presence of temporary emigration. Consequently, if temporary emigration occurs and is random in pattern, more commonly used models such as Jolly-Seber and Cormack-Jolly-Seber underestimate capture probability in the population (Kendall et al. 1997, Kendall 1999). In the presence of temporary emigration, capture probability of the sampled portion of the population (i.e., breeders) is underestimated because it is the product of detection probability (P) and the probability that an individual is available for capture (1 − the probability of temporary emigration; Kendall et al. 1997, Kendall 1999). In most capture–recapture models, the probability of an animal being available for capture is assumed to be 1 because these models assume the probability of temporary emigration is 0. When capture probability is underestimated, estimates of the number of animals at the breeding site are positively biased and have larger confidence intervals (Kendall et al. 1997, Bailey et al. 2004*a*). Using the robust design and the temporary emigration model, the probability of an animal being available for capture is estimated, rather than assumed to be 1. Temporary emigration is thus a potentially influential parameter.

Although habitat loss is acknowledged as the cause of many amphibian declines (Pechmann and Wilbur 1994, Corn 2000), other declines have been attributed to "enigmatic" causes (Stuart et al. 2004), such that the value of deriving precise and unbiased estimates of demographic parameters increases. For example, recruitment rate and population size are affected by reproductive success, which is linked directly to the probability that a toad returns to the breeding site. The accurate assessment of demographic parameters is critical in advancing our understanding of amphibian population dynamics and declines, enigmatic or otherwise. The aim of this paper is to evaluate multiple models of temporary emigration including models that incorporate weather covariates, using methods described in Kendall et al. (1997) to elucidate the form, and to estimate the magnitude of temporary emigration using data collected on *B. boreas* in Colorado between 1991 and 2003.

Materials and Methods

Field methods

We studied *B. boreas* at Kettle Tarn and Lost Lake, two sites along the North Fork drainage of the Big Thompson River in the northeastern corner of Rocky Mountain National Park (RMNP), Larimer County, and at Denny Creek, a site in the Collegiate Peaks, Chaffee County, Colorado, USA. Details of the study area, breeding sites, and data collection methods are described elsewhere (for RMNP see Corn et al. [1997], Muths et al. [2003], and Scherer et al. [2005]; for Chaffee County see Lambert [2003]). *B. boreas* breed just after breeding sites are free of ice, and data from previous studies suggest boreal toads are highly philopatric and return to the same breeding site year after year (Olson 1992). We used data collected in 1991–1998 and 1998–2003 for sites in RMNP and Chaffee County, respectively.

Data were collected under Pollock's robust design; we distinguish between capture–recapture sampling at two temporal scales: primary and secondary (Kendall et al.

1997). Data were collected during the breeding season (primary period). Primary periods began approximately one week after the first observation of a toad at a breeding site and lasted approximately four weeks. We assumed each population to be closed to gains and losses within each primary period (see *Analysis methods* below for a test of this assumption). Lost Lake and Kettle Tarn were each visited in eight primary periods (1991–1998); Denny Creek was visited in six primary periods (1998–2003). There were two to six capture–recapture surveys (= secondary periods) at each site during each primary period. During each capture–recapture survey, breeding ponds and their surrounding terrestrial habitats were searched, and toads were captured by hand. We measured snout–vent length, determined sex and mass, and marked each toad by subcutaneous injection of a uniquely numbered passive integrated transponder (PIT) tag (dorsal side; Corn et al. 1997). Toads were released immediately after processing. Secondary periods were separated by 3–7 days. Using these data, we applied the temporary emigration model (Kendall et al. 1997) to test for the presence and estimate the probability of temporary emigration, to distinguish between random and Markovian patterns of emigration, and to evaluate hypothesized relationships between temporary emigration and selected weather covariates.

Hypotheses and predictions

We predicted that: (1) γ_i' and γ_i'' would both be low, because adult males are physiologically able to breed each year and are expected to be present at the breeding site each year to maximize their reproductive efforts; (2) temporary emigration would be Markovian (state dependent) in a pattern where γ_i' is lower than γ_i''; and (3) environmental covariates would influence temporary emigration through potential physiological or physical activity of the toads. For example, in boreal toad populations living at the upper limit of their elevational range (Muths and Nanjappa 2005), air temperature and active period determine how much energy can be consumed and stored as fat or reproductive resources per season.

Weather data

We used data from nearby weather stations (<30 km away), to represent weather conditions at our three sites and to examine possible effects of four weather and weather-related covariates on the probability of temporary emigration. We used active period (AP, the number of days when the temperature in the previous growing season was >3.89°C for each year) as a covariate and predicted a negative relationship with temporary emigration. For example, a longer active period in the previous year might allow male toads to go into hibernation in better condition, and therefore decrease the probability that toads would emigrate temporarily. In addition, we used air temperature (T_a, mean daily temperature from 1 June to 31 August of the previous growing season) as a covariate and predicted a negative relationship. Higher temperatures during the active period of the previous year may allow male toads to go into hibernation in better condition (Carey et al. 2005) and, therefore, decrease the probability that toads would emigrate temporarily. Finally, we used a value representing the amount of snowpack (snow water equivalents [SWE], a measure of the water content in the snowpack) just prior to the breeding season and melt out (days after 1 May of the current breeding season when SWE reached 0) as covariates. We predicted a positive relationship between each of these covariates and temporary emigration. Greater snowpacks and later melt out dates may make it more probable that a male toad would emigrate temporarily, possibly because of difficulty in physically getting to the breeding site.

Analysis methods

Testing for closure and goodness of fit.—We tested the assumption of closure within primary periods using Program CloseTest (Stanley and Burnham 1999). CloseTest was the most appropriate test to apply because our model selection results indicated temporal variation in capture probability between primary periods, and model M_t is the null model in CloseTest (Stanley and Burnham 1999). In addition, temporal variation in capture probability (P) causes an alternative test for closure (Otis et al. 1978) to reject above the nominal level.

We tested the fit of the data for each site to a global model using RDSURVIV (Hines 1996, sensu Bailey et al. 2004*a*). None of the predefined models in RDSURVIV were equivalent to our global model, so we modified one of the predefined models ($p(t, bt)$, $S(t)$, $\gamma(\cdot)$) by expanding the number of parameters. Our global model was $p\,(t, t+b)$, $s(t)$, $\gamma'(t)$, $\gamma''(t)$. To avoid confounding gamma parameters, the last two γ_i'' values and last two γ_i' values were set equal to one another. We calculated $\hat{c}$ (variance inflation factor; Anderson et al. 1994) by dividing the Pearson χ^2 value by the degrees of freedom and used that $\hat{c}$ value to adjust for overdispersion in our data.

Modeling approach.—The temporary emigration model (Kendall et al. 1997) is composed of three parameters: capture probability, apparent survival rate, and probability of temporary emigration. We defined a unique set of candidate models and used the step-down approach (Lebreton et al. 1992) to evaluate each of these parameters. In brief, we determined the top model of capture probability by comparing the three models in the candidate set while keeping the dimensionality of the apparent survival rates and temporary emigration probabilities high and constant (Lebreton et al. 1992). After determining the top model of capture probability, we used that model to compare each of the candidate models of apparent survival rate (again, we kept the dimensionality of the temporary emigration probabilities high and constant). These results were then used in

our evaluation of the candidate set of models of temporary emigration. We define each parameter and briefly describe the candidate set of models for each parameter in the following subsections.

Modeling capture probability.—Capture probability is a measure of the probability that a toad is captured at each secondary sampling period in each primary period, given that the animal is alive and present in the area that is sampled (Kendall et al. 1997). Failure to adequately model variation in capture probability may bias the estimates of target parameters (Lebreton et al. 1992). We evaluated three models of capture probability (M_t, M_b, and M_{t+b} [sensu Otis et al. 1978]).

Modeling apparent survival rate.—Models of apparent survival rate, Φ (the probability that an animal survives and is present at the site) for the Kettle Tarn and Lost Lake populations were available from previous analyses of these data (Scherer et al. 2005). The data from Denny Creek had not been analyzed previously, so we evaluated four models of apparent survival rate: $\Phi(t)$ (apparent survival rate varies across years), Φ(first-year effect) (apparent survival during the first year after marking is different than apparent survival in years after the first year; see Scherer et al. [2005] for further discussion of the first-year effect), $\Phi(t+\text{first-year effect})$, and $\Phi(\cdot)$ (apparent survival is constant over time). (All notation is sensu Lebreton et al. [1992].)

Modeling temporary emigration.—We evaluated the following models of the temporal variation in temporary emigration: (1) γ_i', $\gamma_i''(t)$ (the probability of temporary emigration varies across time); (2) γ_i', $\gamma_i''(\cdot)$ (the probability of temporary emigration does not vary across time); (3) $\gamma_i' = \gamma_i'' = 0$ (no temporary emigration); (4) γ_i', γ_i'' (the probability of temporary emigration is correlated with one of four weather covariates); (5) γ_i', γ_i'' (the probability of temporary emigration is a function of an additive model including every possible pair of weather covariates; since the SWE and melt out were related measures of snowpack, we did not combine them into an additive model); and (6) γ_i', γ_i'' (the probability of temporary emigration is a function of an additive model including every combination of three weather covariates [as in point 5, the SWE and melt out covariates were not combined]). Both random and Markovian forms were assessed for each of these models (Appendix A).

Model selection and parameter estimation.—The values for $\Delta QAIC_c$ and Akaike weights, w_i, were used to determine which model(s) best described the information in the data (Burnham and Anderson 1998). Fisher's method of maximum likelihood was used for estimation of parameters and their standard errors (Lebreton et al. 1992).

Results

Closure tests

The assumption that the populations are geographically and demographically closed within primary sampling periods was supported by the results of the closure tests for all three sites. Closure was supported in 79% (15 of 19) of years with data adequate to assess closure ($P \geq 0.05$, df varied from 1 to 10; Appendix B). The Stanley and Burnham (1999) test does not have the power to detect closure violations with less than three capture sessions. Therefore, we were unable to assess closure at Lost Lake in 1996, and at Denny Creek in 1998 and 2000.

Goodness of fit tests (RDSURVIVE)

Evidence of overdispersion was present in the data at all sites (Kettle Tarn, $\hat{c} = 2.61$ [$\chi^2 = 75.7$, df = 29]; Lost Lake, $\hat{c} = 1.18$, [$\chi^2 = 73.7$, df = 62]; Denny Creek, $\hat{c} = 1.93$ [$\chi^2 = 73.4$, df = 38]). In addition to overdispersion, the ratio of sample size to the number of parameters in the global model was small. Therefore, we used $QAIC_c$ as our model selection criterion, and we report adjusted standard errors for all parameter estimates using $\hat{c}$ for each site (sensu Bailey et al. 2004*a*).

Model selection

Capture probability.—The top model of capture probability for data from Kettle Tarn and Denny Creek was M_t. The two remaining models had little support in the data from either site (Akaike weights ≤ 0.03). The top model for data from Lost Lake was M_{t+b}. The two remaining models had no support (Akaike weights ≤ 0.001).

Apparent survival probability.—Models of Φ for Kettle Tarn and Lost Lake came from a previous analysis of those data (Scherer et al. 2005), thus, there are no model selection results to report for those sites. The top model for Denny Creek held apparent survival constant, $\Phi(\cdot)$. The model including a first-year effect, Φ(first-year effect), was also supported (Akaike weight = 0.11). The remaining two models received no support (Akaike weights ≤ 0.0001; Table 1).

Temporary emigration.—There was a significant amount of uncertainty in model selection for all three data sets (Table 1). Overall, there was considerable support for the occurrence of temporary emigration. Although the model of no temporary emigration was the top model for Lost Lake and Denny Creek, the sums of Akaike weights for models that did include temporary emigration were 0.80 (Lost Lake) and 0.68 (Denny Creek). The Akaike weights of models with no temporary emigration were only marginally higher than models with some form of temporary emigration. At Kettle Tarn, the sum of Akaike weights for models that included temporary emigration was >0.99, and all of the top models provided evidence for temporary emigration (the model of no temporary emigration had an Akaike weight <0.01).

Generally, the model selection results provided greater support for models of random temporary emigration ($\hat{\gamma}' = \hat{\gamma}''$), although models of Markovian temporary emigration were among the top models at Lost Lake and Denny Creek. Models that included environmental

TABLE 1. List of the top models of capture–recapture data collected from boreal toads (*Bufo boreas*) at three sites in Colorado, USA (see Appendix A for a complete list of models).

Model	No. parameters	$\Delta QAIC_c$	Akaike weights	QDev†
Kettle Tarn (Rocky Mountain National Park)				
$\gamma(T_a$ + AP + melt out) (random)	50	0	0.69	172.4
$\gamma(T_a$ + melt out) (random)	49	2.6	0.19	167.4
Lost Lake (Rocky Mountain National Park)				
$\gamma = 0$ (no temporary emigration)	49	0	0.20	375.2
$\gamma(\cdot)$ (Markovian)	51	0.5	0.15	371.3
$\gamma(\cdot)$ (random)	50	1.0	0.12	374.0
γ(SWE) (random)	51	1.2	0.11	372.0
γ(AP) (random)	51	1.3	0.10	372.0
γ(melt out) (random)	51	2.4	0.06	373.2
γ(Ta) (random)	51	3.0	0.05	373.7
γ(AP) (Markovian)	51	3.2	0.04	369.4
Denny Creek (Chaffee County)				
$\gamma = 0$ (no temporary emigration)‡	28	0	0.19	303.7
$\gamma(\cdot)$ (random)‡	29	0.6	0.14	302.2
$\gamma = 0$ (no temporary emigration)	29	1.1	0.11	302.6
γ(SWE) (random)‡	30	2.1	0.07	301.4
γ(melt out) (random)‡	30	2.2	0.06	301.5
$\gamma(\cdot)$ (Markovian)‡	30	2.5	0.05	301.8
γ(Ta) (random)‡	30	2.6	0.05	301.9
γ(AP) (random)‡	30	2.7	0.05	302.0

Notes: The model of capture probabilities was M_t for data from Kettle Tarn and Denny Creek and M_{t+b} for Lost Lake (t represents time, and b represents behavior). The same structure on apparent survival rates, including a first-year effect, was used for every model unless noted otherwise. Covariate descriptions are: T_a, air temperature (mean daily temperature from 1 June to 31 August of the previous growing season); AP, active period (the number of days when the temperature in the previous growing season was >3.89°C for each year); and SWE, snow water equivalents (a measure of the water content in the snowpack).

† Qdeviance = −2 log-likelihood/$\hat{c}$.

‡ The model of apparent survival for these models is $\Phi(\bullet)$.

covariates were present in at least one of the top models in the data from all three sites. Weather covariates were included in the top two models of the data from Kettle Tarn and also had considerable support in the data from Denny Creek and Lost Lake (Table 1).

Parameter estimation

Because of the uncertainty in the model selection results, we used model averaging to generate estimates of γ' and γ'' (Burnham and Anderson 1998). Model-averaged parameter estimates also provide strong support for the occurrence of random temporary emigration ($\hat{\gamma}' = \hat{\gamma}''$; Table 2). Estimates of γ' and γ'' were nearly equal in all years, particularly when one considers the low precision of these estimates (Table 2).

Confidence intervals (95%) around the estimates of the regression coefficients for the environmental covariates in the competitive models included 0 for all cases, although estimates were admittedly imprecise. The regression coefficients for SWE (from the top models that included this covariate) at both Denny Creek and Lost Lake (−0.19, 95% CI = −0.66–0.22; and −1.01, 95% CI = −2.9–0.90, respectively) indicate that as snowpack increases, the probability of temporary emigration decreases. This is the reverse of our predictions, suggesting that the amount of snowpack is not a deterrent in moving from hibernacula to the breeding site. The regression coefficients for active period (also from the top model that included this covariate) at Lost Lake (−2.33, 95% CI = −5.48–0.82) indicates that, as the length of the active period increases, the probability of temporary emigration decreases. This relationship matches our predictions, suggesting that as more energy is acquired during the summer, the individual is more likely to be ready and able to breed and, therefore, less likely to temporarily emigrate (be present at the breeding site). Although the support for the environmental covariates was equivocal, the covariates that we examined are biologically plausible and deserve additional investigation.

DISCUSSION

Demographic and geographic closure within primary periods is an important assumption of the temporary emigration model (Kendall et al. 1997, Williams et al. 2002). Existing closure tests are not robust to individual and behavioral heterogeneity and, consequently, reject for the null hypothesis of closure above the nominal level in the presence of such heterogeneity (Otis et al. 1978, Stanley and Burnham 1999). However, tests on our data provide evidence that the closure assumption holds at all sites although our power to detect non-closure is low in some years.

The model selection results and estimates of γ_i' and γ_i'' suggest that temporary emigration is occurring over primary periods, and suggest strongly that it is random in nature. That is, the probability of the animal being at the breeding pond is not dependent on its presence at the

TABLE 2. Model-averaged estimates of temporary emigration (γ_i' = probability that a male toad is absent from the breeding site at time i if absent at time $i-1$; γ_i'' = probability that a male toad is absent at time i if present at time $i-1$).

Site and year	γ'	CI	γ''	CI
Kettle Tarn	0.50		0.55	
1992			0.9	0.59–0.98
1993	0.04	0.001–0.68	0.03	0.001–0.61
1994	0.11	0.004–0.79	0.09	0.003–0.78
1995	0.23	0.05–0.63	0.21	0.05–0.58
1996	0.81	0.49–0.95	0.80	0.49–0.95
1997	0.95	0.43–0.99	0.95	0.43–0.99
1998	0.87	0.52–0.98	0.87	0.50–0.98
Lost Lake	0.17		0.21	
1992			0.21	0.03–0.69
1993	0.23	0.021–0.81	0.29	0.05–0.74
1994	0.17	0.007–0.85	0.21	0.02–0.77
1995	0.18	0.02–0.73	0.23	0.05–0.63
1996	0.18	0.013–0.78	0.23	0.4–0.69
1997	0.14	0.007–0.79	0.18	0.02–0.68
1998	0.10	0.002–0.86	0.14	0.009–0.73
Denny Creek	0.13		0.07	
1998			0.06	0.003–0.56
1999	0.12	0.003–0.89	0.06	0.003–0.57
2000	0.1	0.003–0.81	0.07	0.004–0.53
2001	0.17	0.007–0.85	0.10	0.008–0.62
2002	0.13	0.004–0.84	0.08	0.006–0.59

Note: Means of model-averaged values are in the same row as each site name and include all models in the candidate set (both random and Markovian); therefore, the value for γ' and γ'' are not identical.

breeding site the preceding season. For example, environmental conditions (e.g., length of active period in previous season) may trigger the "decision" to breed, resulting in a random pattern of temporary emigration. Estimates of temporary emigration for Kettle Tarn showed more temporal variation, but were more precise than at the other sites. The data from Kettle Tarn are unique in that they include data from years (1996, 1997, and 1998) with low numbers of captured toads. Muths et al. (2003) and Scherer et al. (2005) presented evidence that a die-off occurred at Kettle Tarn between 1996 and 1997. The rate of temporary emigration at Kettle Tarn shows a marked increase in 1996 prior to the die-off. One possible mechanism for this dramatic increase in temporary emigrants is that toads were skipping a breeding opportunity because they were too ill (e.g., Muths et al. 2003) to return to the breeding site. This phenomenon, if real, bears further investigation.

There was some evidence for Markovian (state-dependent) emigration at all three sites, more so at Lost Lake and Denny Creek. Under Markovian temporary emigration, γ_i', the probability of a toad being absent from the breeding site at time i if absent at time $i-1$; and γ_i'', the probability of a toad being absent at time i if present at time $i-1$, are not equal. We predicted that if a toad was absent from the breeding site at time $i-1$, it would be more likely to be present at time i ($\gamma_i' < \gamma_i''$). The poor precision of point estimates of γ_i' and γ_i'' preclude a rigorous evaluation of this prediction; however, estimates of γ_i' and γ_i'' from the Lost Lake data are consistent with this line of reasoning (Table 2). Estimates of γ_i' and γ_i'' from Denny Creek are not consistent with our prediction, while the point estimates from the Kettle Tarn data are nearly identical suggesting a completely random pattern of temporary emigration (Table 2). Results reported in Sinsch (1988) support the hypothesis that not all adults breed (or return to the breeding site) every year (26% did not return, but were still alive; U. Sinsch, *personal commmunication*). That study further suggests that endogenous factors play a significant role in determining the amount of locomotory activity in the common toad (*Bufo bufo*) and hence drive emigration distances and presence at the breeding site (Sinsch 1988). The idea that such an internal mechanism (e.g., condition) affects behavior is consistent with a pattern of Markovian, or state-dependent, temporary emigration. Schmidt et al. (2002) also present data that support the presence of Markovian temporary emigration in *B. bufo*. In addition, it is possible that we do not have enough power to detect Markovian temporary emigration in our data set. The extent of Markovian temporary emigration in a particular population may be related to differences in site characteristics, weather, incidence of disease in the population, or other unidentified variables. Evidence for Markovian temporary emigration was strongest at Lost Lake. It is the highest elevation site of our three study sites, situated at the upper end of a drainage connected to appropriate habitat surrounding the lake and continuing down the drainage for at least 2 km. Breeding has been documented at only one site nearby (<1 km) in the last 10 years (E. Muths, *personal observation*). In addition, it is possible that an unknown environmental factor is masking a truly Markovian pattern. For example, body condition may drive the Markovian pattern, but an exceptionally warm spring might override this factor such that toads return to a breeding site regardless of body condition. Further investigation is warranted to determine what variables might trigger Markovian temporary emigration and to what extent it may occur.

Models that included weather covariates received support. One or a combination of two or more of the covariates was present in competing models for all sites. Due to model selection uncertainty, it is unclear which of the evaluated covariates are the most important in modeling temporary emigration. In our analyses, there is some evidence that the length of the active period in the previous year and the depth of snowpack just prior to the breeding season have some effect on temporary emigration. The negative direction of the relationship of active period to temporary emigration is consistent with our hypothesis that temporary emigration will be lower in breeding seasons that follow a longer active period as male toads will be able to gather more resources and, consequently, be more likely to return to the breeding sites.

The relationship suggested between snowpack and temporary emigration is the opposite of our prediction although previous work suggests that snowpack, rather than temperature is more relevant to the onset of breeding in montane habitats (Corn and Muths 2002, Corn 2003). Difficulties in interpretation of the influence of environmental covariates may be due to the lack of on-site, fine-grain data for these variables or selection of inappropriate covariates. Additional covariates that warrant examination include the physical size of the breeding site, population size, and sex ratio. While a case can be made for how each of these covariates can influence the return of toads to a breeding site in the spring (e.g., temperature affects the rate and onset of spermatogenesis [Van Oordt 1960], and see Scherer et al. 2005), results from the model selection involving covariates are inconclusive.

The general paradigm for *B. boreas* suggests a high propensity for males to return to the breeding site each year (Olson 1992, Corn et al. 1997) and that if a male toad is absent in a particular year, it is even more likely that it will be present at the breeding site the following year. Contrary to this paradigm, we provide evidence that temporary emigration is occurring in these populations and that it varies among years. The $\hat{\gamma}'$ value was >0 for all sites, and generally >0.10, supporting the idea that temporary emigrants may stay away from the breeding site more than one year at a time. Although our model results favor random temporary emigration, we suggest that further study is warranted given the biological arguments for Markovian temporary emigration and the inclusion of weather covariates in some of the competitive models.

We were not able to determine the form of temporary emigration with certainty, but we are confident that we are observing temporary emigration rather than instances of toads simply breeding at alternative sites. Our data and our field experience, particularly at Kettle Tarn and Lost Lake, led us to this assertion. The nearest potential breeding site to either Kettle Tarn or Lost Lake is at least 1 km away. Although movements between sites have been documented, they are few (of >1900 captures, 17 males and 3 females were captured at a site different from where they captured previously). In addition, evidence of breeding has been observed rarely (4 instances in 15 years) at sites in the drainage other than Kettle Tarn and Lost Lake. Temporary emigration at Denny Creek is more equivocal, while the nearest potential breeding site to Denny Creek is also $\sim$1 km away, evidence of breeding has been noted more frequently. In spite of this, model results from Denny Creek are quite similar to the results from other sites suggesting a similar situation.

If temporary emigration is occurring, a more realistic estimate of the size of the population present at the breeding site is achieved by using the temporary emigration model (Kendall et al. 1997). Corn et al. (1997) assessed population sizes for Lost Lake and Kettle Tarn using the same data used in this analysis and program JOLLY, which estimates the size of the entire population (breeders + nonbreeders = "super population" sensu Kendall et al. 1997) using the Jolly-Seber model. This model assumes that all animals are available to be captured at the breeding site during secondary sessions. Our population size estimates from the temporary emigration model are lower because this model does not assume that all animals are available for capture. In general, models that do not take temporary emigration into account will overestimate the population size (but not necessarily the super population size) and underestimate capture probability.

These data raise a number of questions that include, but are not limited to the following. (1) Is $>10\%$ temporary emigration an isolated phenomenon in Colorado, where populations of *B. boreas* have been declining for >10 years? Perhaps a combination of drought conditions and other stressors such as disease (Muths et al. 2003) have influenced animals to emigrate temporarily from breeding sites. (2) Is there a cost to reproduction in the male toad that has not been assessed adequately that might explain "decisions" to forego breeding for one or more years? Basic amphibian biology suggests that males are prepared to breed as they emerge or shortly after they emerge from hibernation, even when the cycle of spermatogenesis is discontinuous (Van Oordt 1960, Jorgensen 1992). Different species of amphibians have developed multiple patterns of synchronizing testicular cycles (e.g., spermatogenesis) with breeding seasons (Rastogi and Iela 1980) and boreal toads are likely to exhibit discontinuous spermatogenesis because of their elevational range (2286–3048 m; Hammerson 1999). Temperature, an environmental parameter that is quite variable during the breeding season at higher elevations, is the major factor in determining spermatogenesis in amphibians (Van Oordt 1960), along with light (Rastogi and Iela 1980). Additionally, predation at breeding sites has been documented (Corn 1993, Olson 1989) but not quantified. The aforementioned costs to reproduction are environment based and may be affected by climate change. (3) Are there environmental changes (e.g., pollution) affecting physiological processes such as spermatogenesis? While experiments have focused on frogs in water contaminated presumably from run-off, wind and precipitation can also deposit chemicals (e.g., Davidson et al. 2002). Although the connection is speculative, the possibility is noteworthy. Atrazine, an herbicide belonging to the triazine family, is mobile and has been found in pristine areas in the Alps (Royte 2003) and in the nearby (<315 air km) North Platte River, Carbon County, Wyoming (Hayes et al. 2003). Atrazine converts androgens to estrogens, and while the inhibition of spermatogenesis is not a direct effect of exposure to Atrazine, it is a likely secondary effect of androgen depletion (Hayes et al. 2003).

Our study suggests that at least 10% of male boreal toads emigrate temporarily from these breeding sites. The results of these analyses suggest that temporary emigration varies among years and is primarily random in structure. Weather covariates appear to factor into the mechanics of temporary emigration but require further investigation. Temporary emigration is an under-evaluated demographic parameter and has the potential to play an important role in the determination of management strategies for endangered or threatened populations. For example, when temporary emigration is associated with the probability of breeding, the ramifications of poorly estimated parameters can be serious. Ignoring this parameter can have significant impact on the estimation of other demographic parameters such as population size. Estimation of temporary emigration can serve as a tool to investigate more complex demographic fluctuations in anuran populations and physiological aspects of the probability of the return of male toads to breeding sites.

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APPENDIX A

The complete list of the models of temporary emigration (*Ecological Archives* E087-060-A1).

APPENDIX B

Results of the closure tests for each site and year (*Ecological Archives* E087-060-A2).