## Canadian Journal of Zoology

 Revue canadienne de zoologie
## First Estimates of the Probability of Survival in a Smallbodied, High Elevation Frog or, how Historical Data Can Be Useful

| Journal: | Canadian Journal of Zoology |
| ---: | :--- |
| Manuscript ID | cjz-2016-0024.R1 |
| Manuscript Type: | Article |
| Date Submitted by the Author: | 14-Apr-2016 |
| Complete List of Authors: | Muths, Erin; USGS Fort Collins Science Center, <br> Scherer, Rick; Conservation Science Partners, 501 Old Town Square <br> Amburgey, Staci; Pennsylvania State University, Ecosystem Science and <br> Management; <br> Matthews, Terry; 1414 Nunn Creek Ct <br> Spencer, Albert; Fort Lewis College - emeritus, Department of Biology <br> Corn, P. Stephen; U.S. Geological Survey, Northern Rocky Mountain <br> Science Center |
| Keyword: | chorus frog, conservation, data reclamation, mark-recapture, Pseudacris <br> maculata |
|  |  |

SCHOLARONE ${ }^{m}$
Manuscripts

## Canadian Journal of Zoology Revue canadienne de zoologie

## First Estimates of the Probability of Survival in a Smallbodied, High Elevation Frog or, how Historical Data Can Be Useful

| Journal: | Canadian Journal of Zoology |  |  |
| ---: | :--- | :---: | :---: |
| Manuscript ID | cjz-2016-0024.R1 |  |  |
| Manuscript Type: | Article |  |  |
| Date Submitted by the Author: | 14-Apr-2016 |  |  |
| Complete List of Authors: | Muths, Erin; USGS Fort Collins Science Center, <br> Scherer, Rick; Conservation Science Partners, 501 Old Town Square <br> Amburgey, Staci; Pennsylvania State University, Ecosystem Science and <br> Management; <br> Matthews, Terry; 1414 Nunn Creek Ct <br> Spencer, Albert; Fort Lewis College - emeritus, Department of Biology <br> Corn, P. Stephen; U.S. Geological Survey, Northern Rocky Mountain <br> Science Center |  |  |
| Keyword: | chorus frog, conservation, data reclamation, mark-recapture, Pseudacris <br> maculata |  |  |
|  |  |  |  |
|  |  |  |  |

SCHOLARONE ${ }^{\text {m }}$
Manuscripts

# First Estimates of the Probability of Survival in a Small-bodied, High Elevation Frog or, how Historical Data Can Be Useful 

E. Muths ${ }^{1}$, R. D. Scherer ${ }^{2}$, S. M. Amburgey ${ }^{3}$, T. Matthews ${ }^{4}$, A. W. Spencer ${ }^{5}$, P. S. Corn ${ }^{6}$
${ }^{1}$ Corresponding author, U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave. Bldg C, Fort Collins, Colorado 80526, USA, muthse@usgs.gov, 970-226-9474
${ }^{2}$ Conservation Science Partners, 501 Old Town Square, Fort Collins, Colorado 80524 USA, scherer@rams.colostate.edu
${ }^{3}$ Department of Ecosystem Science and Management, Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, Pennsylvania 16802, USA, sma279@psu.edu
${ }^{4} 1414$ Nunn Creek Ct., Fort Collins, Colorado 80526 USA, terry.matthews42@gmail.com
${ }^{5}$ Emeritus, Fort Lewis College, Department of Biology, Durango, Colorado 81301, USA
${ }^{6}$ U.S. Geological Survey, Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, Missoula, Montana 59801, USA, corn.stephen@gmail.com

Short title: Survival estimates for boreal chorus frogs

# First Estimates of the Probability of Survival in a Small-bodied, High Elevation Frog or, how Historical Data Can Be Useful 

E Muths, R. D. Scherer, S. M. Amburgey, T. Matthews, A. W. Spencer, P. S. Corn


#### Abstract

In an era of shrinking budgets yet increasing demands for conservation, the value of existing (i.e., historical) data is elevated. Lengthy time-series on common, or previously common, species are particularly valuable and may be available only through the use of historical information. We provide first estimates of the probability of survival and longevity $(0.67-0.79 ; 5-7 \mathrm{yr})$ for a subalpine population of a small-bodied, ostensibly common amphibian, the boreal chorus frog (Pseudacris maculata (Agassiz 1850; Platz 1989)), using historical data and contemporary, hypothesis-driven information-theoretic analyses. We also test a priori hypotheses about the effects of color morph (as suggested by early reports) and of drought (as suggested by recent climate predictions) on survival. Using robust mark-recapture models, we find some support for early hypotheses regarding the effect of color on survival, but we find no effect of drought. The congruence between early findings and our analyses highlights the usefulness of historical information in providing raw data for contemporary analyses and context for conservation and management decisions.


Key words: chorus frog, conservation, data reclamation, mark-recapture, Pseudacris maculata

## Introduction

Conservation science is confronted by multiple challenges; one of the most difficult to address is the lack of data with which to reliably estimate historic abundance, demographic rates, and species richness. There is substantial literature comparing historical and recent abundance and distribution of species, but there are few published demographic studies that allow such a comparison by spanning multiple decades (notable exceptions include Kellner and Green 1995; Daszak et al. 2005; Schmidt et al. 2005; Pellet et al. 2006). Fewer than $15 \%$ of long-term studies focused on population declines use data more than 100 years old (Bonebrake et al. 2010).

Without these estimates, change in contemporary animal populations and communities cannot be quantified rigorously, and the urgency with which conservation measures should be enacted is difficult to characterize (Bonebrake et al. 2010). The paucity of historic data has a variety of explanations. In part, demographic studies were not in vogue until models capable of estimating vital rates were developed (e.g., Williams et al. 2002); but also, species are often of little interest until declines in their numbers are evident. Species may be inherently difficult to study because they occupy inaccessible habitats or are distributed sparsely (e.g., caecilians, Gower and Wilkinson 2003). Populations may be few and small, such that the concerns of harming remaining animals, or computational concerns (e.g., lack of recaptures), hamper or preclude data collection and analysis (Williams et al. 2002). In some cases, the paucity of data is perceived rather than actual. Historical data are often discounted because the collection and analysis methods are considered to be outdated, thus (theoretically) compromising the utility of the data. This dearth, or marginalization of existing historical data, can cause "shifting baseline syndrome" (Pauly 1995), where reference conditions are continually re-set, tracking the start of
careers or monitoring programs, and thus compromise comparisons between "baseline" and contemporary data.

Baseline information (e.g., estimates of survival probability) is important in selecting appropriate management actions and should be an established metric based on the earliest available data rather than a shifting target. In the absence of contemporary data, relevant historical data may provide information and context to guide formulation of hypotheses and design of contemporary studies. Baseline data are particularly important in adaptive management strategies where observed changes (from a previous state to the current state, e.g., population size or survival estimates) guide future actions, and without baseline data for context, contemporary data (either extant or yet to be collected) are of limited utility.

The value of data collected historically has been noted. Tingley and Beissinger (2009) suggest that historical species occurrence data can contribute to ecological inference. Lindborg and Ehrlen (2002) show that long-term historical data can complement short-term data to better capture changes in plant demography, and Rosenberg et al. (2005) apply historical data in determining biomass of cod as a benchmark for rebuilding fisheries. We suggest that additional information can be drawn from historical data. Increasingly, funding constraints and directed research dictate that few modern datasets are long-term or are focused on organisms that lack conservation or commercial "value" such that retrospective analyses of historical data may be the only alternative when developing the information needed to guide management actions.

Such an example of historic data exists for boreal chorus frogs (Pseudacris maculata [Agassiz1850; Platz 1989]) in northern Colorado where individuals were captured for nine years prior to 1975. These data were published as part of other studies, but modern analytical methods allow a rigorous estimation of survival over almost a decade. Boreal chorus frogs are currently
broadly distributed in ephemeral ponds in wet-meadow habitats typical at high elevations in the Rocky Mountains (Hammerson 1999; Dodd 2013). Boreal chorus frogs are a good example of the use of historical data because they are broadly distributed and likely have utility as model organisms for understanding the response of pond-breeding amphibians to climate change (Amburgey et al. 2012; 2014). This data set, in particular, is long-term (3 to 4 generations of frog) and thus allows for an examination of interannual variation in vital rates and population size that is not possible with more typically-available single-year estimates from historic studies. Most species, similar to boreal chorus frogs, receive little attention until declines are noticed, which illustrates the great value of baseline data and highlights the potential value of historical data to conservation.

Boreal chorus frogs are small-bodied frogs (mean SVL $=32.44 \mathrm{~mm} ; n=619$ at elevations $>2600 \mathrm{~m}$, P.S.C. and E.M., unpublished data), with a gradient in body size from low to high elevation (Pettus and Angleton 1967; Funk et al. 2015). Boreal chorus frogs typically breed in May in the Rocky Mountains, but the timing of emergence from hibernation is tied to snowpack (Corn and Muths 2002). Tadpoles metamorphose and emerge from the pond in mid- to late- summer, disperse to terrestrial habitat, and find hibernacula in the fall. There is limited information to assess the persistence of boreal chorus frog populations at the landscape level, but this species is perceived to be widespread and of least conservation concern (IUCN Red List, http://www.iucnredlist.org/details/136004/0, accessed 24 January 2016). However, Seburn et al. (2014) indicate widespread decline of the boreal chorus frogs in eastern Ontario.

Early work on boreal chorus frogs in the Rocky Mountains focused on natural history (Pettus and Spencer 1964), reproduction (Pettus and Angleton 1967), color polymorphism (Matthews 1971; Tordoff and Pettus 1977; Hoppe 1981; Hoppe and Pettus 1984), inheritance of
color (Matthews and Pettus 1966), allele frequencies (Matthews 1971; Tordoff et al. 1976), survival differences relative to color (Matthews 1971), and predation (Tordoff 1980). These efforts aimed to obtain demographic estimates but also to investigate potential relationships between color and survival. Color variation tends to be greater in high elevation versus lower elevation populations, and variation in, and prevalence of, color (dorsal and spot) within high elevation populations can be striking (Spencer 1964; Matthews and Pettus 1966; Matthews 1968; Hoppe and Pettus 1984; E.M. and P.S.C., unpublished data). Genetic mechanisms underlying color variation in boreal chorus frogs were explored by Matthews and Pettus (1966) and Matthews (1971) proposed that differences in spot and background color were due to environmental variables with different conditions favoring color phenotypes or characteristics associated with color. Tordoff (1980) found that jays (Perisoreus canadensis, Linnaeus 1766) and robins (Turdus migratorius, Linnaeus 1766) differentially select frogs that contrast with the substrate on which they are presented in the laboratory, suggesting a link between color and survival. However, color investigations were not linked quantitatively with demographic analyses, nor were other environmental aspects of the habitat. Recent studies have focused on speciation (Moriarty-Lemmon et al. 2007, Funk et al. 2015), the effects of hydroperiod (Amburgey et al. 2012), the effects of climate change (Corn and Muths 2002), predation (Amburgey et al. 2014), and genetic connectivity (Watts et al. 2015).

Alterations to high elevation wetland habitats (i.e., changes in water availability), can be linked to changes in climate (Corn 2003, Adam et al. 2009, Matthews 2010), and quality of wetland habitat (i.e., presence and capacity to hold water [no drought]) is important in determining genetic connectivity and persistence in boreal chorus frogs populations (Watts et al. 2014). Thus, we might expect a negative relationship between drought and survival, an
expectation that highlights the need to understand these relationships for use in in mitigating deleterious effects of climate change on amphibians.

We applied modern analytical methods to an historical data set from a population of boreal chorus frogs in northern Colorado to estimate annual survival probability and illustrate the value of historical data. We also used the available data to examine the influence of color (dorsal and spot) and drought on survival. Baseline information is critical to meet expected challenges as climate changes (e.g., Magurran et al. 2010), and understanding how the demography of chorus frogs is functionally tied to high elevation wetland habitats may help predict the response of this community to expected changes in the timing and form of precipitation (sensu Lacan et al. 2008; Corn 2005; Matthews et al. 2013).

We assessed the following hypotheses: 1) Survival during the active season, after breeding and before hibernation, depends on color (spot, dorsal). We expected survival to be higher in green frogs than in frogs that were not green (i.e., interaction between habitat characteristics and predation, e.g., color matching in green wet meadow habitat alters predation risk [Tordoff 1980]). 2) Dry conditions (as represented by PHDI, Palmer hydrological drought index [NOAA 2013]) during the active season affect survival negatively. We surmised that this effect would be especially evident for green frogs as drier conditions create a color mismatch, (greater contrast between green frogs and a brown environment) which then increases predation risk.

## Materials and Methods

## Species and Site

Lily Pond is an ephemeral pond/wet meadow at 2969 m elevation near the summit of Cameron Pass in the Never Summer Mountains of the Colorado Front Range (Fig. 1). The pond is surrounded by lodgepole pine, Engleman spruce and subalpine fir (Pettus and Spencer 1966; Matthews 1971). Logging (thinning to clear-cuts) has occurred within 750 m of Lily Pond since 1953, but the vegetation and canopy cover at the immediate pond margin (at least $100 \mathrm{~m}, \mathrm{D}$. Oberlag and R. Edwards, USFS, personal communication) has changed only naturally. Melt-out of the pond occurs in late May to mid-June (Corn and Muths 2002). Peak breeding for boreal chorus frogs, determined by calling activity assessed over 16 years, is variable, occurring 20 May - 16 June (Corn and Muths 2002).

Field data collection and assembling capture-mark-recapture dataset

From 1963 to 1968 and 1970 to 1972, boreal chorus frogs (metamorphosed animals, juveniles and adults) were captured by hand or in pitfall traps and marked (Spencer 1964; Matthews 1968). Pitfall traps extended outward from Lily Pond in concentric circles up to 275 m. Spencer (1964) and Matthews (1968) used toe clipping (Martof 1953) to mark adults individually but in the first year of the study (1961) field notes state that "a simpler and different" system [from Martof 1953] was used to mark 51 male and 29 female boreal chorus frogs. After the first year, the Martof system (Martof 1953) was used exclusively and allowed 6400 marks using no more than 2 toes per foot. From field notes it is clear that the marking system, both the "simpler" system and Martof (1953) were carefully applied such that we have no concerns about misidentifying individuals. If there was any uncertainty or incongruity in duplicate numbers for animals (i.e., we were not convinced that the information represented a
recapture), those individuals were removed. Capture occasions were not defined formally but lasted from 1-27 days May-Sept. These data were originally collected to track phenotype frequency and assess survival of different phenotypes (using return rates).

Original paper records (2593 pages) and field notes were used to construct capture histories for individual animals. In contrast to the original objectives (Spencer 1964; Matthews 1968), we were interested in modeling yearly demographic estimates for the breeding population. Therefore, we truncated the data set, limiting our investigation spatially by retaining only records of animals found in traps $\leq 122 \mathrm{~m}$ from the pond. We did this to focus on animals near to the breeding site and therefore most likely part of the breeding population. We also included data collected only during the breeding season (May-July). Although some individuals were captured multiple times within a year, we pooled the data such that each individual was recorded as captured or not for each year.

The original field notes recorded color for individual frogs but the designations were complex (ranging from green to bronze to pink) and subjective (colors determined under differing light conditions). We simplified dorsal colors to "green" or "not green" by looking at the color descriptions in the original field notes. If green was listed as the prominent color, an individual was designated as green (Gr). If green was not listed at all or was not in the top two colors listed for dorsal color (e.g., Copper/Red/Green), an individual was designated as not green (NGr). Spot color was determined in a similar way (Table 1).

The historical data were sorted and assessed critically. Context for decisions in building the dataset came from discussions among authors and detailed interpretation of the field notes, protocols, and marking schemes by AWS and TM. For example, to be counted as a "recapture", the record for that frog had to match the original "capture" record in approximate dorsum color,
spot color, sex, and toe clip number. Ambiguous identities or recaptures were eliminated, resulting in a conservative data set including less than half of the $>4000$ records. Our final dataset consisted of capture histories for 1617 individuals (1266 male: 351 female) with information on sex, dorsal color, and spot color ${ }^{1}$.

## Data Analysis

We used the Cormack-Jolly-Seber (CJS) model in Program MARK to analyze the data (Lebreton et al. 1992; White and Burnham 1999). The CJS model is composed of two parameters: apparent survival probability, $\widehat{\varphi}_{l}$, where $i$ indexes year, and $p_{i}$, capture probability. Apparent survival probability is defined as the probability that a marked individual in the population during the sampling period at time $i$ survives and stays in the population until sampling period at time $i+1$ (Lebreton et al. 1992; Williams et al. 2002). 'Apparent' is used because animals that emigrate permanently cannot be distinguished from animals that die (Williams et al. 2002). Little is known about the population dynamics of boreal chorus frogs, but rates of permanent emigration in adults of other pond-breeding amphibians in similar landscapes are low (Funk et al. 2005; Muths et al. 2006; Matthews and Preisler 2010). Therefore, we consider $\varphi_{i}$ to represent true survival for boreal chorus frogs. Capture probability, $p_{i}$, is defined as the probability that a marked individual in the population is captured during sampling period $i$. Because we did not sample the population in 1969, the interval after 1968 is 2 years. We derived estimates of annual survival probability for 1968 to 1969 and 1969 to 1970 by computing the square root of the 2-year estimate.

[^0]
## Hypotheses and Modeling Approach

We developed separate sets of hypotheses to assess the causes of temporal and individual variation in survival and capture probability. We developed mathematical models to represent each hypothesis and refer to the representations of these hypotheses as sub-models (sensu Taylor et al. 2005). We fit models to the data in two steps and used $\Delta \mathrm{AIC}_{c}$ values and Akaike weights ( $w_{m}$, where $m$ indexes model) to evaluate models at each step. Both $\Delta \mathrm{AIC}_{c}$ values and Akaike weights quantify the strength of evidence for a particular model relative to in the set of models being evaluated (Burnham and Anderson 2002).

In the first step, we evaluated sub-models of capture probability during which we retained the time-dependent model for survival. We assessed the hypothesis that capture probability of males and females would differ. We supposed that it would be higher for males because they are expected to be at the breeding site longer than females (e.g., males arrive earlier [Semlitsch 2008]) and leave later [P.S.C. and E.M., personal observation]); and the majority of our data were from the breeding season. Additional sub-models included effects of year, where year was treated as a fixed effect, background color of dorsum (green or not green), and spot color on dorsum (green or not green). We included an effect of year in all sub-models and combined the effect with every possible combination (additive and interactive) of sex and spot or background color.

In the second step, we assessed sub-models of the probability of survival. Because we were interested primarily in the effect of color, we did not include sex of the individual in the model. There is little information on boreal chorus frog demography, but studies of closely related species at lower elevations generally report low survival and short life spans. For
example, species in the $P$. triseriata complex are reported to live 1-3 yr (Caldwell 1987). In a 2yr study of $P$. maculata on Isle Royale, Smith (1987) reported yearly adult survival as 0.14 . We expected survival in the chorus frogs in our study area to be higher because our recent capture-mark-recapture data (1987-2014) suggest > 5 yr lifespans for some individuals (E.M. and P.S.C., unpublished data).

We predicted that green colored frogs would have higher survival than brown colored frogs based on the premise that in typical habitat (predominantly green), green colored frogs would be better camouflaged and avoid predation at a higher rate than brown frogs. We further predicted that this effect would vary depending on drought conditions, with a decrease in green frog survival as habitats dried and became less green.

To evaluate these hypotheses, we assessed sub-models of survival probability by combining them with the highest ranked sub-model of capture probability identified in the first step. We initially fit a sub-model of survival probability with fixed effects of year and a submodel with no variation in survival probability among years. While we found evidence for high annual variation, we experienced estimation problems (results not reported). Instead, we used the Palmer Hydrological Drought Index (PHDI, classification of drought conditions each year), to represent variation across years. We assessed models that represented an effect of color on survival and interactions between PHDI and color. We fit sub-models that included individual effects of background color, spot color, and PHDI, as well as sub-models with additive and interactive effects of these covariates.

Due to the 2-yr gap between sampling in 1968 and 1970, we fit models with a set of PHDI values for each year that included 1968, and separate models in which the value for 1968 was
replaced by the value for 1969 . Finally, we estimated average lifespan, $\bar{L}$, for adult boreal chorus frogs using the equation:

$$
\bar{L}=-\frac{1}{\ln (\hat{\varphi})}
$$

where $\widehat{\varphi}$ indicates an estimate of apparent survival.

## Results

We captured 1,913 individuals, but capture numbers per year were highly variable (Table 1). Most (65\%) captured frogs were not green (dorsum, spot or both, Table1).

The highest ranked model of capture probability was the model with fixed effects of year. Four other models had $\Delta \mathrm{AIC}_{c}$ values $<3.00$ and included effects of dorsal color, spot color and sex. However, $95 \%$ confidence intervals around estimates of regression coefficients for each of these effects included 0 . Of these effects, the evidence is strongest for a positive effect of green spots on capture probability (i.e., a frog with green spots is more likely to be recaptured). The effect is included in the second-ranked model $\left(\Delta \mathrm{AIC}_{c}=1.34\right)$, and the estimate of the regression coefficient was 0.20 ( $95 \% \mathrm{CI}:-0.23-0.64$ ). Model-averaged estimates of capture probability were generally low $(0.03[0.01-0.08]$ to $0.18[0.09-0.34]$, and $>70 \%$ of the capture probability estimates were $<0.15$.

Model-selection results were uncertain for survival probability (Table 2); nine models had $\Delta$ AIC $_{\mathrm{C}}$ values $<3.00$. Two models had lower $\mathrm{AIC}_{\mathrm{C}}$ values than the model of no variation in survival probability, but estimates of regression coefficients for the effects in these models were imprecise, and 95\% confidence intervals for their regression coefficients included 0 . Modelaveraged estimates of survival probability ranged from $0.68(0.56-0.78)$ to $0.79(0.63-0.89)$.

Based on estimated survival probabilities, we calculated the lifespan of boreal chorus frogs at Lily Pond as 5-7 yr (3 yr to reach breeding size [A.S., T.M., and P.S.C. personal observation] plus 2-4 yr post-breeding [from eq. 1]).

Model-selection results indicated that survival estimates were similar for all color combinations (e.g., between individuals with green and not green spots and dorsal colors,), although spot color was present in 3 of the top 5 models and suggested that green-spotted individuals survived at a higher rate (but confidence intervals overlapped 0). There was little support for an interaction between spot or dorsal color and drought.

## Discussion

Our assessment of this nine-year historical data set provides first estimates of survival and longevity for a small bodied, high elevation amphibian. We also describe how specific hypotheses can be generated and tested based on historic data. This is important because it first illustrates how historical data, with appropriate caveats, can be used to gain conservation context for planning, and second because it provides baseline values for a widespread amphibian that is ostensibly "secure" (IUCN Red List, http://www.iucnredlist.org/details/136004/0, accessed 24 January 2016). Predictions of future amphibian declines include "hundreds of species of amphibian can be expected to go extinct over the next few decades." (Stuart et al. 2004), to"catastrophic future losses" (McCallum 2007). The persistence of boreal chorus frog populations may be particularly challenged by changes in hydroperiod of breeding pools (Amburgey 2014) driven by expected changes in precipitation pattern - more precipitation as rain than snow with significant effects on the amount of snowpack (e.g., Barnett et al. 2005).

Overall predictions of amphibian decline and the vulnerability of boreal chorus frogs to changing climate factors increase the value of these historical data.

## Survival

Annual survival was relatively high (range $0.67-0.79$ ) compared to populations at lower elevations in Colorado ( $<1 \%$ recaptures/yr, P.S.C., unpublished data), a pattern also shown for common frogs (Rana temporaria, Linneus, 1758) in Switzerland (Ryser 1996). Low capture probabilities (e.g., $<0.15$ ) cause imprecision in survival estimates (Mazerolle et al. 2007) and low capture probabilities can cause a small negative bias in survival estimates (Schmidt et al. 2014). Therefore, true survival of frogs at Lily Pond may be higher than our estimates. Achieving high capture probabilities is typically a challenge with small, cryptic animals in large populations without highly intensive field work (Hanson et al. 2015) and may be a common disadvantage to historical data sets.

Survival might be expected to be higher at higher elevations because elevation can influence life history traits (e.g., survival in common frogs, Rana temporaria [Linnaeus 1758], Ryser 1996; body size in wood frogs, Lithobates sylvatica [LeConte 1825], Bervan 1982, and in boreal chorus frogs [Pettus \& Spencer 1964; Pettus and Angleton 1967]). Additionally, boreal chorus frogs inhabiting cold climates typically hibernate for more than half of the year (PSC, EM pers. obs.). Hibernation is associated with increased survival (Turbill et al. 2013), albeit for mammals, but the same principles of reduced physiological needs during hibernation apply to amphibians. During hibernation amphibian breathing, blood flow, and heartbeat are suspended (Storey and Storey 1987) thus potentially prolonging life (e.g., Ruf et al. 2012; Keil et al. 2015).

Comparisons of our survival estimate to earlier work on the P. triseriata complex are untenable because of differences in methods. For example, survival estimates from Isle Royale (0.14, Smith 1987) do not take capture probability into account. In addition, differences in climate (high alpine versus maritime) may also contribute to the differences in our estimates compared to Smith (1987). Recent work on the Baja California treefrog (P. hypochrondriaca, Hallowell 1854), provides annual survival estimates of 0.01-0.29 (Luja et al. 2015) but these estimates were based on two years of data only and are for a low-elevation species.

Model selection results suggested that spot and dorsal color were not the most important factors explaining differential survival. However, the conspicuous contrast in color between low and high elevation chorus frogs, and among individuals in a single population, remains interesting from evolutionary, adaptive, and behavioral perspectives, and the inclusion of spotcolor in our top models argues for additional investigation. Despite a plausible mechanism for a link among color, drought and survival (i.e., a mismatch in the color of frog and environment after prolonged drought, favoring selection for brown frogs and the subsequent loss of the green color morph [sensu Matthews and Pettus 1966; Matthews 1971]), we found little evidence to support this hypothesis. Additional information about the effects of drought (i.e., a finer-scale, site-level assessment), and the role of color, in survival would benefit an understanding of these potential relationships.

## Veracity of the data

There are assumptions associated with analysis of CMR data (Kendall et al. 1997): 1) no marks are lost or misread, 2) sampling is instantaneous, and 3) there is no heterogeneity in
capture or survival probabilities, or it is modeled adequately. However, few studies meet assumptions completely. Despite the fact that the historical study at Lily Pond was not designed as a CMR study and that effort varied among years, we think that the assumptions were met, albeit with caveats: 1) Boreal chorus frogs do not regenerate toes (P.S.C. and E.M., personal observation), and we are confident that our constructed capture histories are accurate (see below). 2) To address the second assumption, we included captures over three months to maximize the number of captures but minimize the duration of sampling. Finally, inference to the unmarked portion of this population may not be appropriate because multiple toes on single limbs were clipped occasionally. Altwegg and Reyer (2003) reported that the number of toes clipped did not affect survival in juvenile Pelophylax lessonae (Camerano 1882) but more recently, Swanson et al. (2013) found that survival in juvenile boreal chorus frogs declined when the number of toes clipped increased. The details of the "simpler" toe clip protocol used in year one have been lost and this lack of information compromises our ability to retrospectively identify the numbers of toes clipped for the 80 individuals captured in 1961. Without this information it is difficult to model the effect of the number of toes clipped on survival for this historic dataset. However, preliminary analyses from a more recent data set on boreal chorus frogs indicates that the number of toes clipped relative to the color of the animal is uniform (Muths unpublished data), suggesting that while there is a potential for the survival estimate to have a negative bias, we would expect it to be the same across colors such that comparisons of survival probability between colors are valid.

## Using historical data

Our use of a large historical dataset provides first estimates of survival probability and longevity for a small-bodied, subalpine frog that is common in high elevation, ephemeral wetlands in the Rocky Mountains. These frogs are of particular interest because of their nearly ubiquitous distribution (Moriarty and Lannoo 2005; Dodd 2013) and their lack of obvious response to the presence of the amphibian chytrid fungus, (Reeder et al. 2012; E.M., unpublished data). Such demographic estimates are generally lacking and are useful to studies of life history (Biek et al. 2002) and population viability analyses (e.g., Doak et al. 1994). We argue for the value and usefulness of historic data for several reasons. There has been a cultural shift away from natural history and intensive field research, to limited presence of personnel in the field and the application of sophisticated modeling techniques to fill data gaps. Historical data can help to assess the validity of the modeled data. Establishing baseline knowledge from data collected well before contemporary perturbations can provide context from which to evaluate current trends. For example, if baseline survival probabilities in boreal chorus frogs are $0.67-0.79$ for the 1960s, substantially lower modern estimates might trigger management actions. Historical data can be flawed but still offer a useful view of historical conditions. We illustrate that the judicious use of historical data is tenable and that these datasets are an important resource for conservation efforts.

## Acknowledgments

We thank to D. Oberlag and R. Edwards, USFS for information regarding logging. The manuscript is dedicated to the memory of D. Pettus for scientific and mentoring contributions. This is contribution no. 542 of the U.S. Geological Survey's Amphibian Research and

Monitoring Initiative and was funded partially by the U. S. Geological Survey's Data Rescue Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Supporting Information

Capture histories (raw data) for boreal chorus frogs Pseudacris maculata in Colorado from 19631972 is available in online Appendix A1.

## References

Adam, J. C., Hamlet, A. F., and Lettenmaier, D. P. 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. Hydrol. Processes, 23: 962-972.

Agassiz, L. 1850. Lake Superior, its Physical Character, Vegetation, and Animals, Compared with Those of Other and Similar Regions, with a Narrative of the Tour, by J. Elliot Cabot, and Contributions by Other Scientific Gentlemen. Part. II. Natural History Gould, Kendall and Lincoln, Boston, USA.

Altwegg, R., and Reyer, H.U. 2003. Patterns of natural selection on size at metamorphosis in water frogs. Evolution, 57: 872-882.

Amburgey, S., Funk, W.C., Murphy, M.A., and Muths, E. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (Pseudacris maculata). Herpetologica, 68: 456-467.

Amburgey, S., Bailey, L.L., Murphy, M., Muths, E., and Funk, W.C. 2014. The effects of hydroperiod and predator communities on amphibian occupancy. Can. J. Zool. 92: 927937.

Ashton, K.G. 2002. Do amphibians follow Bergmann's rule? Can. J. Zool. 2002, 80(4): 708-716, 10.1139/z02-049.

Barnett, T.P., Adam, J.C., and Lettenmaier, D.P. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature, 438: 303-309.

Biek, R., Funk, W.C., Maxell, B.A., and Mills, L.S. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conserv. Biol. 16: 728-734.

Blouin, M.S. 1989. Inheritance of a naturally occurring color polymorphism in the ornate chorus frog, Pseudacris ornata. Copeia 4: 1056-1059.

Bonebrake, T.C., Christensen, J., Boggs, C.L., and Ehrlich, P.R. 2010. Population decline assessment, historical baselines, and conservation. Conserv. Lett. 3: 371-378.

Berven, K.A. 1982. The genetic basis of altitudinal variation in the wood frog Rana sylvatica. I. An experimental analysis of life history traits. Evolution, 36: 962-983.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Inference: A Practical Information - Theoretic Approach. New York, NY, USA: Springer-Verlag.

Caldwell, J.P. 1987. Demography and Life History of Two Species of Chorus Frogs (Anura: Hylidae) in South Carolina. Copeia, 1: 114-127.

Camerano, L. 1882 "1881". Recherches sur les variations de la Rana esculenta et du Bufo viridis dans le Bassin de la Méditerranée. Comptes Rendus de l'Association Française pour l'Avancement des Sciences. Paris 10: 680-690.

Corn, P.S., 2003. Amphibian breeding and climate change: importance of snow in the mountains. Conserv. Biol. 17: pp.622-625.

Corn, P.S. 2005. Climate change and amphibians. Anim. Bio. Conserv. 28: 59-67.

Corn, P.S., and Muths, E. 2002. Variable breeding phenology affects the exposure of amphibian embryos to ultraviolet radiation. Ecology, 83: 2958-2963.

Daszak, P., Scott, D.E., Kilpatrick, A.M., Faggioni, C., Gibbons, J.W., and Porter, D. 2005. Amphibian population declines at the Savannah River Site are linked to climate, not chytridiomycosis. Ecology, 86: 3232-3237.

Doak, D., Kareiva, P., and Klepetka, B. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecol. Appl. 4: 446-460.

Dodd, C.K. 2013. Frogs of the United States and Canada. Johns Hopkins University Press, Baltimore, MD, USA. Vo1. 1 pp 371-384.

Funk, W. C., Murphy, M. A., Hoke, K. L., Muths, E., Amburgey, S. M., Lemmon, E. M., and Lemmon, A. R. 2015. Elevational speciation in action? Restricted gene flow associated with adaptive divergence across an altitudinal gradient. J. Evol. Biol. 29: 241-252. DOI: 10.1111/jeb. 12760.

Funk, W.C., Blouin, M.S., Corn, P.S., Maxell, B.A., Pilliod, D.S., Amish, S., and Allendorf, F.W. 2005. Population structure of Columbia spotted frogs (Rana luteiventris) is strongly affected by the landscape. Mol. Ecol. 14: 483-496.

Gower, D.J., and Wilkinson, M. 2005. Conservation Biology of caecilian amphibians. Conserv. Biol. 19: 45-55.

Hallowell, E. 1854. Descriptions of new reptiles from California. Proc. Acad. Nat. Sci. Philadelphia 7: 91-97.

Hammerson, G.A. 1999. Amphibians and reptiles in Colorado. Second edition. University of Colorado Press and Colorado Division of Wildlife, Boulder, Colorado, USA.

Hoppe, D.M. 1981. Chorus frogs and their colors. Ecology of reptiles and amphibians in Minnesota. Proceedings of a symposium March 13-15, 1981, Headwaters Regional Environmental Education Council, Bemidji State University, Minnesota Department of Natural Resources, Bell Museum of Natural History, University of Minnesota Science Museum, Minnesota Audubon Council, U.S. Forest Service, U.S. Fish and Wildlife Service, and Minnesota Environmental Education Board, pp 7-8.

Hoppe, D.M., and Pettus, D. 1984. Developmental features influencing color polymorphism in chorus frogs. J. Herpetol. 18: 113-120.

Keil, G., Cummings, E., and de Magalhães, J.P. 2015. Being cool: how body temperature influences ageing and longevity. Biogerontology 2015: 1-15.

Kellner, A., and Green, D.M. 1995. Age structure and age at maturity in Fowler's toads, Bufo woodhousii fowleri, at their northern range limit. J. Herpetol. 29: 485-489.

Kendall, W.L., Nichols, J. D., and Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78, 563-578.

Lacan, I., Matthews, K., and Feldman, K. 2008. Interaction of an introduced predator with future effects of climate change in the recruitment dynamics of the imperiled Sierra Nevada yellow-legged frog. Herpetol. Conserv. Biol. 3: 211-223.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62: 67-118.

Le Conte, J. E. 1825. Remarks on the American species of the genera Hyla and Rana. Annals of the Lyceum of Natural History of NewYork 1: 278-282.

Lindborg, R., and Ehrlen, J. 2002. Evaluating the extinction risk of a perennial herb:
demographic data versus historical records. Conserv. Biol. 16: 683-690.
Linnaeus, C. 1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima, reformata. (in Latin). Holmiae. (Laurentii Salvii). p. 292.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 10th Edition. Volume 1. Stockholm, Sweden: L. Salvii.

Luja, V.H., Rodriguez-Estrella, R., Schaub, M., and Schmidt, B.R. 2015. Among-population variation in monthly and annual survival of the Baja California treefrog, Pseudacris hypochondriaca curta, in desert oases of Baja California Sur, Mexico. Herpetol. Conserv. Biol. 10: 112-122.

McCallum, M.L., 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. J. Herpetol. 41: 483-491.

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield P.J., and Watt, A.D. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol. Evol. 25: 574-582.

Martof, B. 1953. Home range and movements of the green frog, Rana clamitans. Ecology 34: 529-543.

Matthews, J.H. 2010. Anthropogenic climate change impacts on ponds: a thermal mass perspective. BioRisk 5: 193-209.

Matthews, T.C. 1968. Some evolutionary aspects of color polymorphism in a population of boreal chorus frogs. PhD thesis, Colorado State University, Fort Collins, Colorado.

Matthews, T.C. 1971. Genetic changes in a population of boreal chorus frogs (Pseuadacris triseriata) polymorphic for color. Am. Midl. Nat. 85: 208-221.

Matthews, T.C., and Pettus, D. 1966. Color inheritance in Pseudacris triseriata. Herpetologica 22: 269-275.

Matthews, K.R., and Preisler, H.K. 2010. Site fidelity of the declining amphibian Rana sierra (Sierra Nevada yellow-legged frog). Can. J. Fish Aquat. Sci. 67: 243-255.

Matthews, J. H., Funk, W. C., and Ghalambor, C.2013. Demographic approaches to assessing climate change impact: An application to pond-breeding frogs and shifting hydropatterns. in: Wildlife Conservation in a Changing Climate. Edited by J. F. Brodie, E. Post, and D. Doak. University of Chicago Press, Chicago. pp. 58-85.

Mazerolle, M. J., Bailey, L.L., Kendall, W.L., Royle, A.J., Converse, S.J., and Nichols, J.D. 2007. Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies. J. Herpetol. 41: 672-689.

Moriarty, E., and Lannoo, M.J. 2005. Pseudacris triseriata complex. In Amphibian decline: the conservation status of U.S. species. Edited by M.J. Lannoo. University of California Press, USA. pp. 485-488.

Moriarty-Lemmon, E., Lemmon, A.R., and Cannetella, D.C. 2007. Geological and climatic forces driving speciation in the continentally distributed trilling chorus frogs (Pseudacris). Evolution 61: 2086-2103.

Muths, E., Scherer, R.D., Corn, P.S., and Lambert, B.A. 2006. Estimation of temporary emigration in male toads. Ecology 87: 1048-1056.

NOAA 2013. National Climatic Data Center. <http://www.ncdc.noaa.gov/oa/climate/ research/prelim/drought/palmer.html> 15 May 2013. (Accessed Sept 2015).

Pauly, D. 1995. Anecdotes and shifting baseline syndrome of fisheries. Trends Ecol. Evol. 10: 430.

Pettus, D., and Spencer, A.W. 1964. Size and metabolic differences in Pseudacris triseriata (Anura) from different elevations. Southwest. Nat. 9: 20-26.

Pettus, D., and Angleton, G.M. 1967. Comparative reproductive biology of montane and piedmont chorus frogs. Evolution 21: 500-507.

Pellet, J., Schmidt, B.R., Fivaz, F., Perrin, N., and Grossenbacher, K. 2006. Density, climate and varying return points: an analysis of long-term population fluctuations in the threatened European tree frog. Oecologia 149: 65-71.

Platz, J. E. 1989. Speciation within the chorus frog Pseudacris triseriata: Morphometric and mating call analyses of the boreal and western subspecies. Copeia 1989: 704-712.

Reeder, N.M., Pessier, A.P., and Vredenburg, V.T. 2012. A reservoir species for the emerging amphibian pathogen Batrachochytrium dendrobatidis thrives in a landscape decimated by disease. PLoS ONE 7: e33567.

Rosenberg, A.A., Bolster, W.J., Alexander, K.E., Leavenworth, W.B., Cooper, A.B., and McKenzie, M.G. 2005. The history of ocean resources: modeling cod biomass using historical records. Front. Ecol. Environ. 3: 78-84.

Ruf, T., Bieber, C., and Turbill, C. 2012. Survival, aging, and life-history tactics in mammalian hibernators. In Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations. Edited by T. Ruf, C. Bieber, W. Arnold and E. Millesi. Springer Science and Business Media. pp. 123-132.

Ryser, J., 1996. Comparative life histories of a low-and a high-elevation population of the common frog Rana temporaria. Amphibia-Reptilia. 17: 183-195.

Schmidt, B.R., Feldmann, R., and Schaub, M. 2005. Demographic processes underlying population growth and decline in Salamandra salamandra. Conserv. Biol. 19: 11491156.

Schmidt, B.R., Itin, E. and Schaub, M., 2014. Seasonal and annual survival of the salamander Salamandra salamandra salamandra. J. Herpetol. 48: 20-23.

Seburn, D. C., Gunson, K., and Schueler, F. W. 2014. Apparent widespread decline of the Boreal Chorus Frog (Pseudacris maculata) in eastern Ottawa. Can. Field Nat. 128: 151-157.

Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. J. Wildl. Manage. 72: 260-267.

Smith, D.C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. Ecology, 68: 344-350.

Spencer, A. 1964. The relationship of dispersal and migration to gene flow in the boreal chorus frog. PhD thesis, Colorado State University, Fort Collins, Colorado

Storey, K.B., and Storey, J.M. 1987. Persistence of freeze tolerance in terrestrially hibernating frogs after spring emergence. Copeia, 3: 720-726.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S., Fischman, D.L. and Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science, 306: 1783-1786.

Swanson, J., Bailey, L.L., Muths, E., and W.C. Funk. 2013. Factors influencing survival and mark retention in post metamorphic boreal chorus frogs. Copeia 4: 670-675.

Taylor, M.K., Laake, J., McLoughlin, P.D., Born, E.W., Cluff, H.D., Ferguson, S.H., RosingAsvid, A., Schwinsburg, R., and Messier, F. 2005. Demography of a hunted population of polar bears. Arctic, 58: 203-214.

Tingley, M.W., and Beissinger, S.R. 2009. Detecting range shifts from historical species occurrences: new perspectives on old data. Trends Ecol. Evol. 24: 623-633.

Tordoff, W. III. 1980. Selective predation of gray jays, Perisoreus Canadensis, upon boreal chorus frogs, Pseudacris triseriata. Evolution, 34: 1004-1008.

Tordoff, W. III, and Pettus, D. 1977. Temporal Stability of Phenotypic Frequencies in Pseudacris triseriata (Amphibia, Anura, Hylidae). J. Herpetol. 11: 161-168.

Tordoff, W. III, Pettus, D., and Matthews, T. 1976. Microgeographic variation in gene frequencies in Pseudacris triseriata (Amphibia, Anura, Hylidae). J. Herpetol. 10: 35-40.

Turbill, C., Bieber, C. and Ruf, T., 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc. R. Soc. Lond. B Biol. Sci. 278: 3355-3363.

Watts, A., P. Schlichting, S. Billerman, B. Jesmer, S. Micheletti, M. Fortin, W.C. Funk, P. Hapeman, E. Muths, M.A. Murphy. 2015. How spatio-temporal habitat connectivity affects amphibian genetic structure. Front. Genet. 6: 275. DOI: 10.3389/fgene.2015.00275.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement): 120-138.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press,San Diego, CA, USA.

Table 1: Number of captures and recaptures by year for each sex. Numbers in the color columns represent the number of individuals (of the total captured for that year) with the indicated color combination ${ }^{*}$.

| Year | Males |  |  |  |  |  | Females |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Color |  |  |  |  |  | Color |  |  |  |  |  |
|  | $\begin{gathered} \text { Total \# } \\ \text { of } \\ \text { captures } \\ \hline \end{gathered}$ | $\begin{gathered} \# \\ \text { recaps } \end{gathered}$ | $\begin{gathered} \mathrm{Gr} / \\ \mathrm{Gr} \end{gathered}$ | $\begin{aligned} & \mathrm{Gr} / \\ & \mathrm{NGr} \end{aligned}$ | $\begin{gathered} \mathrm{NGr} / \\ \mathrm{Gr} \end{gathered}$ | $\begin{aligned} & \text { NGr/ } \\ & \text { NGr } \end{aligned}$ | Total \# of captures | $\begin{gathered} \# \\ \text { recaps } \end{gathered}$ | $\begin{gathered} \mathrm{Gr} / \\ \mathrm{Gr} \end{gathered}$ | $\begin{aligned} & \mathrm{Gr} / \\ & \mathrm{NGr} \end{aligned}$ | $\begin{gathered} \mathrm{NGr} / \\ \mathrm{Gr} \end{gathered}$ | $\begin{aligned} & \text { NGr/ } \\ & \text { NGr } \end{aligned}$ |
| 1963 | 363 | 0 | 2 | 56 | 93 | 212 | 30 | 0 | 1 | 9 | 6 | 14 |
| 1964 | 42 | 27 | 1 | 5 | 11 | 25 | 7 | 3 | 0 | 2 | 2 | 3 |
| 1965 | 213 | 25 | 32 | 5 | 48 | 128 | 123 | 9 | 11 | 3 | 27 | 82 |
| 1966 | 191 | 52 | 24 | 5 | 40 | 122 | 83 | 17 | 12 | 0 | 22 | 49 |
| 1967 | 74 | 25 | 10 | 1 | 14 | 49 | 31 | 13 | 4 | 1 | 9 | 17 |
| 1968 | 21 | 6 | 2 | 2 | 1 | 16 | 16 | 5 | 1 | 4 | 5 | 6 |
| 1970 | 122 | 17 | 4 | 13 | 9 | 96 | 32 | 0 | 2 | 4 | 2 | 24 |
| 1971 | 236 | 39 | 3 | 27 | 30 | 176 | 13 | 1 | 0 | 1 | 2 | 10 |
| 1972 | 265 | 70 | 5 | 38 | 32 | 190 | 69 | 5 | 3 | 13 | 8 | 45 |

[^1]Table 2: Model selection results for survival (Phi) ${ }^{*}$. Note, because there was a 2-yr gap between sampling in 1968 and 1970, we fit models with PHDI values for each year that included 1968, and a separate set of models in which the value for 1968 was replaced by the value for 1969. The null model (no effect) is Phi(.) p(t).

| Model | AICc | Delta <br> AICc | AICc <br> Weights | Number <br> Parameters | Deviance |
| :---: | :---: | :---: | :---: | :---: | :---: |
| \{Phi(PHDI 69) p(t) \} | 2317.4 | 0.0 | 0.18 | 10 | 469.7 |
| \{Phi(spot+PHDI 69) p(t) \} | 2317.7 | 0.3 | 0.15 | 11 | 468.0 |
| \{Phi(.) p(t) \} | 2317.9 | 0.5 | 0.13 | 9 | 472.3 |
| \{Phi(spot) $\mathrm{p}(\mathrm{t})$ \} | 2318.2 | 0.8 | 0.12 | 10 | 470.5 |
| \{Phi(spot*PHDI 69) $\mathrm{p}(\mathrm{t})$ \} | 2318.8 | 1.4 | 0.09 | 12 | 467.0 |
| \{Phi(PHDI 68) $\mathrm{p}(\mathrm{t})$ \} | 2319.3 | 1.9 | 0.07 | 10 | 471.6 |
| \{Phi(dorsal+PHDI 69) $\mathrm{p}(\mathrm{t})$ \} | 2319.4 | 2.0 | 0.06 | 11 | 469.9 |
| \{Phi(spot+PHDI 68) $\mathrm{p}(\mathrm{t})$ \} | 2319.6 | 2.2 | 0.06 | 11 | 469.9 |
| \{Phi(dorsal) p(t) \} | 2320.0 | 2.6 | 0.05 | 10 | 472.3 |
| \{Phi(spot*PHDI 68) $\mathrm{p}(\mathrm{t})$ \} | 2321.0 | 3.6 | 0.03 | 12 | 469.3 |
| \{Phi(dorsal*PHDI 69) $\mathrm{p}(\mathrm{t})$ \} | 2321.1 | 3.7 | 0.03 | 12 | 469.4 |
| \{Phi(dorsal+PHDI 68) $\mathrm{p}(\mathrm{t})$ \} | 2321.3 | 3.9 | 0.02 | 11 | 472.0 |
| \{Phi(dorsal*PHDI 68) $\mathrm{p}(\mathrm{t})$ \} | 2323.3 | 5.9 | 0.01 | 12 | 471.6 |

[^2]Figure 1: Study site location. Lily Pond is near the summit of Cameron Pass (3,132 m) in Larimer County, CO. The pass is between the north end of the Never Summer Mountains and the south end of the Medicine Bow Mountains.

$279 \times 361 \mathrm{~mm}(300 \times 300$ DPI)

First Estimates of the Probability of Survival in a Small-bodied, High Elevation Frog or,
how Historical Data Can Be Useful
Muths, Scherer, Amburgy, Matthews, Spencer and Corn
Supplementary Material
Capture histories for boreal chorus frogs (Pseudacris maculata), Colorado 1963-1972.

| individual |  |  |  |  |  |  |  |  | sex |  |  | rsa |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1970 | 1971 | 1972 M | F |  |  |  |  |  |
| 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 9 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 11 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 21 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 23 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 26 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 27 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 31 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 33 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 34 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 42 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 51 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 53 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| 54 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 60 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 75 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 83 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 92 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 96 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 97 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 101 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 103 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 104 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 105 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 106 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 109 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 120 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 124 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 138 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 142 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 143 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 151 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 155 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| 165 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 172 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 188 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 194 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 200 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 203 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 204 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 205 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 206 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 209 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 211 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 212 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 213 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 215 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 216 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 221 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 222 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 223 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 224 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 225 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 226 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 227 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 228 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 229 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 230 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 231 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 232 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 233 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 234 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 235 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 236 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 237 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
















1000
$100 J$
100 J
112 J
1200 U
1250 l
121
1592 J
1600 U
1609ر
1641 J
1650 J
1769
1775 J
1801 U
18025
1885J
1923J
$1923 J$
$1980 J$
2047J
2250J
2654J
$2660 J$
$2670 J$
$2873 J$
$2892 J$
2892
$295 J$
3042 J
3100 J
3125 J
31271

| 3164 J |
| :--- |
|  |

3232 J
$3234 J$
$3237 J$
3248J
3249 J
3265 J
3286J
3305 J
3307 J
3330J
33521
33541
35211
3530 J
3538 J
35391
3587J
3606 J
3611 J
3686J
4004J
4019 J
4019
2J U 1

## OU

1J J 5J 7 J J J 3J J J J 2 J 7J 5 J 2 J 1J 39J 11J 19J

5445
5445
5446

5447
5448 5449 5450 541 5452
5453 453 5456 5457 5458 5467 5470 5472 5486 5600 5632 6312 6600 7920
,
$\square$ 0
0
0 000

0
0
0 0 0
0
0
$\square$
$\square$
000
$4-4$
0
 1


3891
3902
3904 3904
3913 3935
3936
3936
3941 3951
3953
4052
4053
4054
4092
4095
4096
4131
4285
4341
4342
4343
4344
4345
4355
4457
4464
4521
4540
4693
4766
4809
4826
4838
4849
4855
4876
4877
4912
4927
4940
4946
4965
5069
5143
5198
5205
5290
5292
5294
5329
5334
5337
5338
5346
5365
5380
5413
5415
5416
5417
5424
5436
5441
5443
5455
5457
5458
5459
5460
5461
5462
5463
5464
5465




[^0]:    ${ }^{1}$ Supplementary material 1

[^1]:    ${ }^{*} \mathrm{Gr} / \mathrm{Gr}=$ green dorsum + green spots; $\mathrm{Gr} / \mathrm{NGr}=$ green dorsum + spot color NOT green; $\mathrm{NGr} / \mathrm{Gr}$ $=$ dorsum color NOT green + green spots; $\mathrm{NGr} / \mathrm{NGr}=$ dorsum color NOT green + spot color NOT green

[^2]:    *PHDI $=$ Palmer Hydrological Drought Index; spot $=$ spot color; dorsal $=$ dorsal color

