

DEMOGRAPHY AND POPULATION DYNAMICS OF AMPHIBIANS IN
DESERT MOUNTAIN CANYONS

by

Erin Rae Zylstra

Copyright © Erin R. Zylstra 2018

A Dissertation Submitted to the Faculty of
THE SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN NATURAL RESOURCES

In the Graduate College

THE UNIVERSITY OF ARIZONA

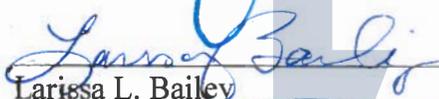
2018

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Erin R. Zylstra, titled Demography and Population Dynamics of Amphibians in Desert Mountain Canyons and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.



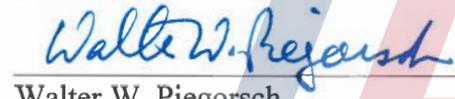
Robert J. Steidl Date: 12 April 2018



Larissa L. Bailey Date: 12 April 2018



David Christianson Date: 12 April 2018



Walter W. Piegorsch Date: 12 April 2018

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.



Dissertation Director: Robert J. Steidl Date: 12 April 2018

STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of the requirements for an advanced degree at the University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that an accurate acknowledgement of the source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his or her judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Erin R. Zylstra

ACKNOWLEDGMENTS

This work would not have been possible without the help and support of numerous people. I am extremely thankful for each and every one of them.

First, I have to thank my advisor, Bob Steidl, from whom I learned a great deal about ecology, statistics, writing, and more. Bob challenged me to pursue goals that I had assumed were out of reach, gave me the freedom to explore a wide range of questions and projects, and provided encouragement at every step along the way. I am extremely grateful for the experience and will be sad to see this chapter end.

I am also thankful for all the support and thoughtful insights provided by my committee: Larissa Bailey, Dave Christianson, and Walt Piegorsch. I'm grateful to Larissa for asking challenging questions and offering her expertise in both amphibian ecology and statistics. I also greatly appreciated her encouragement and support, especially as I began to think about post-graduate pursuits. I enjoyed discussions with Dave about applications and extensions of our work to other species and environments, and I owe Walt thanks for encouraging me to pursue an M.S. in Statistics and providing statistical advice and expertise along the way. In addition to my committee, I also want to thank Ed Bedrick, Dean Billheimer, Joe Watkins, and others in the Statistics GIDP at the University of Arizona for helping me develop the quantitative skills I needed to finish the statistics degree and apply that knowledge to my dissertation research.

It is not an overstatement to say that my accomplishments as a graduate student, and this project in particular, would not have happened without Don Swann. Over the years, I have been lucky to consider Don a mentor, collaborator, and friend. In many ways, this work is an extension of projects that Don initiated more than 20 years ago, and many of the questions I pursued stemmed from our ongoing discussions about frogs and aquatic resources in the Sky Island region.

This kind of research is always collaborative, and I have been fortunate to work with great people, several of which will be co-authors on the published papers that result from this work. In addition to Bob and Don, Blake Hossack and Erin Muths contributed to the project in several ways, most importantly sharing their knowledge and expertise with regards to amphibian declines in the western U.S. They also helped to secure funding and provided valuable feedback on reports and earlier versions of the papers.

I am very grateful to those who ventured in the field with me, as those days were often long, hot, and exhausting. In particular, I thank Patrick Brown, Bruce Weise, Ben Beal, Dave Prival, and James Borgmeyer. Many other people helped get me up to speed on all things frog-related, including Cecil Schwalbe, Mike Sredl, Kevin Bonine, Brent Sigafus, Dennis Caldwell, Kim Baker, Kris Ratzlaff, and David Hall.

One of my dissertation chapters is based largely on long-term monitoring data from Saguaro National Park. It would be impossible to thank all of the people who contributed to those efforts, but several people deserve special recognition, including Mike Ward, Natasha Kline, Cecil Schwalbe, Scott Stonum, and Kara O'Brien.

This project was made possible by grants from the U.S. Geological Survey Amphibian Research and Monitoring Initiative, T & E, Inc, and the Tucson Herpetological Society. Funding for long-term monitoring efforts was provided by Saguaro National Park, the Western National Parks Association, and Friends of Saguaro National Park. I received additional support from The Wildlife Society, the Graduate and Professional Student Council at the University of Arizona, and a number of scholarships through the School of Natural Resources and the Environment and the College of Agriculture and Life Sciences.

Finally, and most importantly, I thank my family, and my partner, Bruce. For your constant encouragement, your support, and your patience, I am forever grateful.

TABLE OF CONTENTS

LIST OF TABLES	9
LIST OF FIGURES	10
ABSTRACT	12
CHAPTER 1 : DROUGHT-MEDIATED EXTINCTION OF AN ARID-LAND AMPHIBIAN: INSIGHTS FROM A SPATIALLY EXPLICIT DYNAMIC OCCUPANCY MODEL	14
ABSTRACT	14
INTRODUCTION	15
METHODS	18
<i>Study area</i>	18
<i>Field surveys</i>	19
<i>Occupancy model</i>	20
<i>Environmental covariates</i>	23
<i>Site-level covariates</i>	23
<i>Season-level covariates</i>	24
<i>Survey-level covariates</i>	25
<i>Model implementation and inferences</i>	26
<i>Forecasting effects of climate on metapopulation persistence</i>	29
RESULTS	30
<i>Field surveys</i>	30
<i>Occupancy</i>	31
<i>Forecasts</i>	33
DISCUSSION	33
<i>Conclusions</i>	38
CHAPTER 2 : LOW SURVIVAL OF AN ARID-LAND AMPHIBIAN CONTRIBUTES TO POPULATION DECLINES	48
ABSTRACT	48
INTRODUCTION	49
METHODS	51
<i>Study area</i>	51

<i>Field surveys</i>	53
<i>Identifying individuals</i>	54
<i>Encounter histories</i>	56
<i>Environmental covariates</i>	57
<i>Model structure and inferences</i>	59
RESULTS	60
<i>Field surveys</i>	60
<i>Survival and recapture probability</i>	61
DISCUSSION	62
CHAPTER 3 : A BAYESIAN STATE-SPACE MODEL FOR SEASONAL GROWTH OF TERRESTRIAL VERTEBRATES IN DYNAMIC ENVIRONMENTS	74
ABSTRACT	74
INTRODUCTION	75
METHODS	78
<i>Growth model</i>	78
<i>Growth of canyon treefrogs</i>	81
<i>Study area</i>	81
<i>Field surveys</i>	82
<i>Model selection</i>	83
<i>Model implementation</i>	85
RESULTS	86
<i>Model assessment</i>	86
<i>Growth of canyon treefrogs</i>	86
DISCUSSION	88
APPENDIX A: EVALUATING THE RELATIONSHIP BETWEEN DROUGHT INDICES AND SURFACE WATER AVAILABILITY	99
APPENDIX B: VARIATION IN DETECTION PROBABILITY OF LOWLAND LEOPARD FROGS ON VISUAL ENCOUNTER SURVEYS AS A FUNCTION OF COVARIATES	101
APPENDIX C: ACCOUNTING FOR BIAS IN ESTIMATES OF SURVIVAL OF LOWLAND LEOPARD FROGS	102

APPENDIX D: SIMULATIONS TO ASSESS BIAS OF PARAMETER ESTIMATES IN GROWTH MODELS	107
APPENDIX E: EXAMPLE JAGS CODE FOR A SEASONAL MODEL OF GROWTH.....	110
REFERENCES	112

LIST OF TABLES

TABLE 1.1. Summaries of environmental covariates used to explain variation in initial occupancy, extinction, colonization, and detection probability of lowland leopard frogs surveyed in two watersheds (South, North) in the Rincon Mountain, Arizona, USA between 1996 and 2017..	39
TABLE 1.2. Posterior mean and standard deviation (SD) for parameters from a dynamic occupancy model for lowland leopard frogs in southern Arizona, USA.	40
TABLE 2.1. Descriptions of six stream reaches in the Rincon Mountains surveyed for lowland leopard frogs between May 2013 and November 2015.	66
TABLE 2.2. Results from surveys for lowland leopard frogs in two watersheds (South, North) in the Rincon Mountains in water years 2013 (May 2013–Sep 2014), 2014 (Oct 2013–Sep 2014), and 2015 (Oct 2014–Sep 2015).	67
TABLE 2.3. Parameter estimates on the logit scale, Wald Z-statistics, and associated <i>P</i> -values from a model describing apparent survival and recapture probabilities of post-metamorphic lowland leopard frogs in southern Arizona, USA between 2013 and 2015.....	68
TABLE 3.1. Deviance information criterion (DIC) for models of growth in canyon treefrogs that evaluated the effect of sex on asymptotic size, L_{∞} , and the effects of sex and year (1 Oct–30 Sept) on characteristic growth rate, k	93
TABLE 3.2. Mean, standard deviation (SD), and 95% credible intervals (CRI) of posterior distributions for parameters in a seasonal, von Bertalanffy model of growth for canyon treefrogs captured in the Rincon Mountains, Arizona, USA, 2014-2016.....	94

LIST OF FIGURES

FIGURE 1.1. Maps of pool complexes surveyed for lowland leopard frogs in two watersheds (North, South) in the Rincon Mountains.....	41
FIGURE 1.2. A timeline illustrating relationships among sampling periods, seasons, and periods when we measured covariates.....	42
FIGURE 1.3. Estimated proportion of sites occupied by lowland leopard frogs in two watersheds of the Rincon Mountains, Arizona, USA in spring (16 May–15 Jul) and fall (1 Oct–30 Nov) sampling periods between 1996 and 2017.....	43
FIGURE 1.4. Extinction probabilities for populations of lowland leopard frogs in (a) summer (16 Jul–30 Sep) and (b) winter (1 Dec–15 May) as a function of mean Palmer Drought Severity Index (PDSI) during the previous six months and water reliability (permanent sites had ≥ 1 pools that never went dry; low-reliability sites went dry during 75% of spring and fall sampling periods).....	44
FIGURE 1.5. Baseline colonization probabilities for populations of lowland leopard frogs in summer and winter as a function of (a) mean Palmer Drought Severity Index (PDSI) during the previous larval period (Jan–Aug) and (b) precipitation during current summer and winter seasons.	45
FIGURE 1.6. Seasonal estimates of the proportion of sites occupied by lowland leopard frogs in two watersheds of the Rincon Mountains, Arizona, USA, 1996–2014, as a function of Palmer Drought Severity Index (PDSI) averaged over the preceding 12 months.....	46
FIGURE 1.7. Proportion of sites occupied over 30 years in simulated metapopulations of lowland leopard frogs under three climate scenarios: 1) neutral conditions, 2) persistent, mild drought, and 3) extreme three-year droughts occurring once per decade..	47
FIGURE 2.1. Maps of six stream reaches surveyed for lowland leopard frogs in two watersheds (South, North) in the Rincon Mountains.....	69
FIGURE 2.2. Schematic of a spot pattern that was mapped completely (a) and three partially-mapped spot patterns (“partial spot maps”; b-d).....	70
FIGURE 2.3. Surface-water availability (mean water depth relative to maximum pool depth) in one of the reaches in the south watershed and in the middle-elevation reach in the north watershed.	71
FIGURE 2.4. Apparent monthly survival (a) and recapture probabilities (b) of post-metamorphic lowland leopard frogs as a function of surface-water availability (mean water depth relative to maximum pool depth) and water year.....	72

FIGURE 2.5. Apparent monthly survival of post-metamorphic lowland leopard frogs between October 2013 and November 2014 (i.e., water year 2014) as a function of minimum daily temperature and dew point. 73

FIGURE 3.1. Predicted growth of individuals based on a model that allowed growth to vary seasonally (solid black line) and a model that assumed constant growth (solid gray line). 95

FIGURE 3.2. Proportion of surveys, across all reaches and years, when we observed canyon treefrog eggs (top) or metamorphs (bottom) by date (gray bars). 96

FIGURE 3.3. Predicted growth of post-metamorphic female and male canyon treefrogs emerging from larval stages with an SVL of 22.5 mm in late spring (1 Jul) and late summer (1 Sep), 2013-2015. 98

ABSTRACT

Changes in the distribution and abundance of species reflect variation in underlying demographic rates, including survival, reproduction, growth, and dispersal. Understanding how natural and anthropogenic processes affect demography and dynamics of species with patchy distributions can be challenging, but it is critical for developing reliable conservation strategies for landscapes that are changing at unprecedented rates. We studied amphibians that inhabit isolated, intermittent streams in mountain canyons of the desert southwest, a region where drought conditions have prevailed over the last 30 years and where the availability of surface water is likely to decrease further in response to changes in climate. Specifically, we used detection-nondetection data from 22 years of biannual visual encounter surveys with recent capture-recapture data to better understand survival, growth, and metapopulation dynamics of lowland leopard frogs (*Lithobates yavapaiensis*) and canyon treefrogs (*Hyla arenicolor*). We used a spatially-explicit metapopulation model to describe the distributional dynamics of leopard frogs in eight canyons in southern Arizona, and found that local frog populations were more likely to go extinct during periods of drought, particularly at sites that lacked deep or spring-fed pools that held water reliably. Leopard frogs were also less likely to colonize unoccupied sites when larval or dispersal periods were drier than normal or when sediment levels in pools increased following high-elevation wildfires. In one of the two watersheds we surveyed, occupancy by leopard frogs declined markedly in the latter half of the study, and we observed no frogs in this watershed after 2015. We used frequent capture-recapture surveys (≥ 1 survey every two weeks) based on in-situ photographs to demonstrate that the apparent extirpation was

due, at least in part, to drought-mediated decreases in post-metamorphic survival. Seasonal and spatial variation in survival were governed largely by surface-water availability, and survival was particularly low at sites where water levels were lowest. Finally, seasonal variation in demographic rates was not limited to survival, as we found strong evidence of temporal variation in somatic growth of post-metamorphic canyon treefrogs. Growth rates were highest during the summer monsoon season, when both ambient temperatures and water levels in pools were typically high. Given the effects of climate and surface-water availability on demography of leopard frogs and treefrogs, distribution and abundance of these species may decline if future changes in climate reduce the quantity or quality of aquatic resources available in mountain canyons. Moreover, because leopard frog populations tend to be small and geographically isolated, they are unlikely to persist at a regional scale if increased drought frequency or severity limits the ability of individuals to disperse among populations through an increasingly arid landscape.

**CHAPTER 1: DROUGHT-MEDIATED EXTINCTION OF AN ARID-LAND
AMPHIBIAN: INSIGHTS FROM A SPATIALLY EXPLICIT DYNAMIC
OCCUPANCY MODEL**

ABSTRACT

Understanding how natural and anthropogenic processes, especially changes in climate, affect population dynamics of species with patchy distributions is critical to predicting their responses to future environmental changes. To facilitate exploring the effects of these processes on distributional dynamics, we extended a spatially explicit metapopulation model to allow extinction and colonization probabilities to vary over space and time as a function of environmental covariates. We apply this framework to 22 years of biannual survey data for lowland leopard frogs, *Lithobates yavapaiensis*, an amphibian that inhabits arid mountain canyons in southeastern Arizona, USA. Colonization and extinctions of local populations were more likely during summer than winter. Local extinctions occurred more frequently during periods of drought, particularly at sites that lacked pools with reliable surface water. Colonizations of unoccupied sites increased when larval and dispersal periods were wetter than normal, increasing the probability that potential emigrants metamorphosed and reached neighboring sites. Frogs were less likely to colonize sites that had moderate or high levels of sediment ($\geq 25\%$ of pool volume), a consequence of erosion that followed high-elevation wildfires. Between 1996 and 2008, the proportion of sites occupied in each of two watersheds we surveyed fluctuated between 0.20 and 0.61. Between 2009 and 2017, however, occupancy continued to fluctuate similarly in one watershed, but declined

precipitously in the other; we observed no frogs in this watershed after spring 2015.

Although effects of a severe drought (annual Palmer Drought Severity Index ranged from -2.4 to -5.2) between 2011 and 2014 affected metapopulation dynamics of leopard frogs in both watersheds, frogs persisted only where sediment levels were low and where most sites held water consistently. The framework we advanced has application to many species that inhabit patchy environments, can improve our understanding of factors that govern metapopulation dynamics, and can inform strategies for conservation of imperiled species.

INTRODUCTION

Ongoing and anticipated changes in climate, disturbance regimes, and land use are expected to alter the distributions of many species (Parmesan 2006, Ehrlén and Morris 2015). The effects of climate might be particularly important, as distributional limits often have a direct physiological basis defined by a species' tolerance to climatic conditions (Gaston 2003). Changes in climate also might induce changes in distributions indirectly by shifting distributions of predators and competitors and by altering the quantity and quality of habitat available to species (Gaston 2003). Numerous studies have evaluated whether recent, rapid changes in climate have contracted or expanded the limits of species' distributions (Parmesan 2006, Chen et al. 2011, and sources therein), but climate impacts may not be limited to range margins, especially if habitat for a species is discontinuous (Stewart et al. 2017). Identifying processes associated with changes in distributions of species that inhabit patchy environments can be especially challenging, particularly in dynamic systems (Hodgson et al. 2009, Miller et al. 2012). If

these environments are surveyed consistently for long periods, however, extirpation and colonization events can be linked more directly to climate, disturbances, or other temporal processes through a metapopulation framework (Yackulic et al. 2015). This information can then be used to predict species responses to future environmental changes, which provides a foundation to inform conservation strategies for imperiled species that depend on patchy resources in dynamic environments.

Approaches for modeling dynamics of metapopulations have evolved considerably since Levins (1969) introduced the first deterministic, non-spatial models. Most contemporary approaches treat site occupancy as a stochastic process, where the current occupancy state of a site depends on occupancy at the previous time step and extinction and colonization (i.e., transition) probabilities. Approaches that are spatially explicit better reflect metapopulation theory by allowing transition probabilities to vary with the spatial arrangement of sites and dispersal capabilities of the target species through an incidence function (Hanski et al. 1996, Hanski 1999, Risk et al. 2011) or by integrating other measures of connectivity (Franken and Hik 2004, Heard et al. 2013, Sutherland et al. 2014). Many recent spatial models incorporate a state-space approach to overcome the limitations of imperfect surveys (Bled et al. 2011, Yackulic et al. 2012, Heard et al. 2013, Sutherland et al. 2014, Chandler et al. 2015, Broms et al. 2016). Most frequently, these spatial models have been used to 1) estimate site-specific rates of extinction, colonization, or turnover, 2) assess metapopulation viability, and 3) evaluate whether observed distributional dynamics of species match theoretical expectations. Rarely, however, have studies explored temporal variation in extinction and colonization probabilities, despite substantial evidence that demographic rates and dispersal behaviors

vary over time in response to changes in climate, land use, or disturbance processes (e.g., O'Brien et al. 2003, Robinson et al. 2007, Knowlton and Graham 2010). Even when long-term data are available, temporal effects are seldom explored because existing models 1) assume that dynamic parameters remain constant over time or vary only with patch area or degree of connectivity (Risk et al. 2011, Chandler et al. 2015), 2) require supplementary demographic data (Harrison et al. 2011, Heard et al. 2013, Sutherland et al. 2014), or 3) make assumptions about dispersal processes that may not hold for all species (Bled et al. 2011, Yackulic et al. 2012, Eaton et al. 2014, Broms et al. 2016).

Here, we extend the spatially explicit dynamic occupancy model developed by Chandler et al. (2015) to allow extinction and colonization probabilities to vary over both space and time as a function of environmental covariates. We apply the model to 22 years of biannual survey data for lowland leopard frogs (*Lithobates yavapaiensis*), a species of conservation concern in the southwestern U.S. and northern Mexico (Sredl et al. 1997). In southeastern Arizona, lowland leopard frogs primarily inhabit stream reaches in arid mountain canyons, environments that are rare on the landscape, are highly dynamic, and are likely to change in response to anticipated shifts in climate and other anthropogenic threats (Grimm and Fisher 1992, Sredl 2005, Wallace et al. 2010, Jaeger et al. 2014). Although abundance and distribution of lowland leopard frogs fluctuate in response to hydrologic conditions (Zylstra et al. 2015), there is growing evidence of systematic declines and extirpations in populations across this region (Sredl et al. 1997, Witte et al. 2008, Savage et al. 2011). Identifying factors associated with these declines is a conservation priority and can provide insight into the dynamics of this and other sensitive species that depend on surface water in arid mountain systems.

The objectives of our paper are three-fold. First, we present a spatially explicit framework for metapopulations that facilitates exploring factors with the potential to explain both spatial and temporal variation in extinction and colonization probabilities. This framework requires only binary data and depends on few assumptions about the dispersal process. Second, we illustrate this approach using long-term survey data from lowland leopard frogs to evaluate how extinction and colonization rates varied over time. We highlight the value of biannual surveys that facilitate assessing the relative influence of multiple threats, including disease, which vary seasonally. Finally, we use simulations to forecast metapopulation dynamics of lowland leopard frogs under a range of climate scenarios and to identify characteristics of sites where frogs are likely to persist over the long term.

METHODS

Study area

We studied population dynamics of lowland leopard frogs in the Madrean Sky Island region of southeastern Arizona, where isolated mountain ranges are separated by large expanses of desert and semi-desert grasslands. We surveyed frogs in the Rincon Mountains, east of Tucson, Arizona. The Rincon Mountains range from 900 m to 2640 m elevation and encompass at least four distinct vegetation communities that range from Sonoran desertscrub to mixed-conifer forests (Brown 1982, Bowers and McLaughlin 1987). The area is bisected by a ridge formation that runs SW to NE with deeply-incised canyons forming the headwaters of two watersheds, one north and one south of the ridge (Valentine-Darby et al. 2017). The landscape outside of these canyons, particularly

below 1500 m elevation, is arid, with little to no surface water. Flow in most stream reaches is intermittent, with seasonal variation reflecting a bimodal pattern of annual precipitation (300–700 mm/yr, depending on elevation; Brown 1982, Bowers and McLaughlin 1987). In winter (Dec–Apr), pools are often connected by continuous flow produced by widespread cool-season rains whereas in late spring (May–Jun) and fall (Oct–Nov), channels between pools dry frequently (Grimm and Fisher 1992, Wallace et al. 2010). During monsoon season (Jul–Sep), localized, high-intensity storms can trigger sporadic flash floods. Because lowland leopard frogs in the Sky Island region inhabit low-order streams below approximately 1400 m elevation, we restricted surveys to canyon reaches at middle elevations (870–1370 m), where pools are associated frequently with bedrock outcroppings. Most pools are <2 m deep with surface areas 3–12 m², and limited soil-bank development (Wallace et al. 2010).

Field surveys

We surveyed leopard frogs in eight canyons, four in the north watershed and four in the south watershed (Fig. 1.1). Canyons contained 213 pools that were likely to contain water much of the year and provide habitat for frogs. Between May 1996 and June 2017, we surveyed streams when they typically were not flowing, in both spring (16 May–15 Jul) and fall (1 Oct–30 Nov), which we defined as sampling periods ($n = 43$; Fig. 1.2). Each stream reach was surveyed 0–13 times per sampling period by 1–3 observers, at least one of which had surveyed these canyons for leopard frogs previously. Observers followed standard protocols for diurnal visual encounter surveys (VES; Zylstra et al.

2015), and at each pool recorded whether water was present and whether they observed ≥ 1 post-metamorphic (i.e., juvenile or adult) lowland leopard frog.

Although surveyors recorded observations of leopard frogs at each pool, many pools were in close proximity and did not function as independent habitat patches. Therefore, we aggregated data among pools < 150 m apart (stream distance) and refer to these aggregations as pool complexes. We delineated pool complexes based on the expectation that when streams were not flowing (i.e., during spring and fall sampling periods) frogs were unlikely to move among complexes. This resulted in 55 pool complexes, 32 in the northern watershed and 23 in the southern watershed. In most instances, all pools in a complex were surveyed in a single day. Occasionally, however, surveys of large complexes (≥ 8 pools) spanned two days within a five-day period; we considered these as one survey in our analyses.

Occupancy model

We extended the spatially explicit dynamic occupancy model of Chandler et al. (2015) to allow extinction and colonization probabilities to vary over space and time as a function of environmental covariates. We used a state-space formulation, with variation in survey data decomposed into a state or ecological process (here, occupancy of frogs over time and space) and an observation process (Royle and Kéry 2007). Survey data consisted of $y_{i,k,t} = 1$ if observers detected ≥ 1 leopard frog or $y_{i,k,t} = 0$ if observers detected no frogs at pool complex i ($i = 1, \dots, 55$ sites) on survey k ($k = 1, \dots, 13$) in sampling period t ($t = 1, \dots, 43$). We assumed closure within sampling periods, and allowed occupancy to vary between spring and fall sampling periods (i.e., during summer and

winter seasons; Fig. 1.2). We considered the ecological process to be Markovian, with occupancy after the first sampling period conditional on occupancy in the previous sampling period. Our model consisted of two dynamic parameters, namely the probability of colonization if the site was unoccupied previously (γ) and probability of persistence (ϕ) if the site was occupied previously. Unlike the model of Chandler et al. (2015), which assumed occupancy in the first sampling period was known with certainty, we modeled the true occupancy state of site i in the first sampling period, $z_{i,1}$, as a Bernoulli random variable with probability of initial occupancy, $\psi_{i,1}$:

$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1})$. We modeled occupancy in subsequent sampling periods as:

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(\gamma_{i,t}(1 - z_{i,t}) + \phi_{i,t}z_{i,t}) \quad (1.1)$$

where $\gamma_{i,t}$ is the probability that an unoccupied site was colonized between time t and $t+1$ and $\phi_{i,t}$ is the probability an occupied site remained occupied between t and $t+1$.

Consistent with metapopulation theory (Hanski 1999), we allowed colonization and persistence probabilities to vary with proximity to other occupied sites. We began by modeling pairwise colonization probabilities, defined as the probability that site i was colonized by at least one individual from site j between sampling period t and $t+1$, $\delta_{i,j,t}$:

$$\delta_{i,j,t} = \delta_{B,i,t} \exp(-d_{i,j}^2/(2\theta^2))z_{j,t} \quad (1.2)$$

where $\delta_{B,i,t}$ is the “baseline” colonization probability for sites coincident to site i , $d_{i,j}$ is the distance between sites, and θ is the scale parameter in a Gaussian dispersal kernel governing how colonization probability decreases with distance (Chandler et al. 2015). Most metapopulation models use Euclidian distances to approximate the minimum distance individuals must travel to colonize a neighboring site. If movements of individuals between sites are unlikely to follow straight-line paths, however, other

distance measures may be more appropriate. Similar to many dendritic stream networks, we expected aridity, landscape structure, and topography to constrain movements of lowland leopard frogs among sites. Specifically, we assumed that high-elevation ridges and ephemeral flow of valley-bottom streams would prevent frogs from moving between watersheds, and therefore delineated two metapopulations based on watershed boundaries. For sites in the same canyon that were flow-connected (*sensu* Peterson et al. 2013), we used stream distances instead of Euclidean distances, as this likely reflected how frogs move within canyons. For sites in the same watershed that were not flow-connected, we used minimum out-of-stream distances after restricting movement paths to areas below 1370 m because frogs have only been observed infrequently above this elevation (Wallace et al. 2010). Most out-of-stream distances were considerably larger than stream distances between sites that were flow-connected (Fig. 1.1).

After defining pairwise colonization probabilities, we calculated the cumulative probability that site i was colonized between sampling period t and $t+1$ as:

$$\gamma_{i,t} = 1 - \left\{ \prod_{j=1}^{N_i} 1 - \delta_{i,j,t} \right\} \quad (1.3)$$

where N_i is the number of other sites in the same watershed as site i . We allowed for the possibility that sites could go extinct and be recolonized between consecutive sampling periods (i.e., a pseudo-rescue effect, Hanski 1999, Sutherland et al. 2014, Chandler et al. 2015): $\phi_{i,t} = 1 - \varepsilon_{i,t}(1 - \gamma_{i,t})$, where $\varepsilon_{i,t}$ is the probability site i goes extinct between sampling period t and $t+1$.

Finally, we modeled the observation process separately from ecological processes because observers may fail to detect frogs when a site is truly occupied (Royle and Kéry 2007, Zylstra et al. 2015). Because we assumed changes in occupancy would occur only

between sampling periods, multiple surveys of a site within a sampling period allowed us to estimate detection probability (p) or the probability of detecting ≥ 1 post-metamorphic frogs if the site is occupied. We assumed a Bernoulli distribution for detection-nondetection data: $y_{i,k,t} \sim \text{Bernoulli}(z_{i,t} \times p_{i,k,t})$.

We modeled extinction and baseline colonization probabilities ($\varepsilon_{i,t}$ and $\delta_{B,i,t}$), as well as initial occupancy and detection probabilities (ψ_i and $p_{i,k,t}$), as logit-linear functions of site-, season- and survey-level covariates. We used the same general structure for each linear model, where probability on the logit scale was modeled as a function of an intercept (α) and a set of fixed effects (β) describing the relationship between covariates (\mathbf{X}) and probability of extinction, colonization, initial occupancy, or detection probability (e.g., $\text{logit}(\psi_i) = \alpha_\psi + \mathbf{X}_i\beta_\psi$). We standardized all continuous covariates prior to analysis. In the following sections, we describe relevant covariates and specify the linear model for each parameter.

Environmental covariates

Site-level covariates.—For each complex (i.e., site), we determined the number of pools (n_{pools}) and mean elevation ($elev$) across pools. We estimated the area of each basin that drained into the lowest-elevation pool in each complex ($area$) using hydrology tools in ArcGIS 10.1. Reliability of surface water in canyons is governed by several factors, including pool depth and groundwater connectivity (Valentine-Darby et al. 2017). Because these measures were not available for all pool complexes, we used information on water availability collected during VES surveys to create an index of water reliability for each site across the 22-year study period. For each pool, we

determined the number of sampling periods the pool was surveyed at least once and calculated the proportion of those sampling periods during which the pool did not go dry. We then used the maximum value among pools within each complex as an index of surface-water reliability (*reliability*). This resulted in values that ranged from 0 (all pools in a complex went dry during every sampling period the complex was surveyed) to 1 (at least one pool in a complex always held water).

Season-level covariates.—We identified a number of time-varying factors that might explain changes in site occupancy during summer and winter seasons. Wildfire and subsequent erosion can fill pools with sediment, decreasing their capacity to hold water for months to decades after a fire, which can influence colonization and extinction rates (Parker 2006). We created a discrete index of sediment levels in each of eight canyons over time (*sediment*) based on repeated measurements of sediment volume from 24 pools (0–7 pools/canyon), data collected during VES surveys, and descriptions of sediment levels in one canyon from an unrelated study of wildfire in the Rincon Mountains (Parker 2006). For each summer and winter season, we assigned all complexes within a canyon the same *sediment* value. We classified sediment levels as low (*sediment* = 0) when either mean sediment volume for measured pools was <25% of pool volume, or, for those canyons where sediment volume was not quantified, <20% of the watershed had burned in the preceding 10 years (Parker 2006). We classified sediment levels as moderate (*sediment* = 1) when mean sediment volume of pools was approximately 25–50% and high (*sediment* = 2) when mean sediment volume was $\geq 50\%$.

We expected that colonization and extinction probabilities might vary over time in response to weather and its effects on surface-water availability. Specifically, we

hypothesized that drought could increase extinction probabilities by decreasing the amount of surface water available for frogs, particularly at the beginning of summer and winter seasons. We estimated the effect of drought for each canyon using downscaled, monthly measures of Palmer Drought Severity Index (PDSI) between 1996 and 2017 (Abatzoglou, McEvoy, & Redmond, 2017).¹ For each summer (Jul–Sep) and winter (Dec–May), we calculated mean PDSI during the preceding six-month period (Jan–Jun and Jun–Nov, respectively; *6mo.PDSI*; Fig. 1.2) because this measure was associated with surface-water availability at the end of spring and fall sampling periods (Appendix A).

We expected that weather might affect colonization probabilities in two ways: 1) drought could reduce the number of juveniles available to colonize other sites by reducing the number of tadpoles that reach metamorphosis, and 2) decreases in precipitation during summer or winter could increase desiccation-related mortality rates of individuals moving between sites. To explore the first possibility, we calculated mean PDSI over an eight-month period (Jan–Aug) leading up to and including when the most recent cohort of juveniles emerged (hereafter, the larval period; *JA.PDSI*; Fig. 1.2). To explore the second possibility, we obtained downscaled, monthly estimates of precipitation and 30-year normals (1981–2010) for each canyon from the PRISM Climate Group.² For each summer and winter, we calculated the percentage of precipitation normals from July–September and December–May, respectively (*precip*; Fig. 1.2).

Survey-level covariates.—Because we expected surface-water availability to affect frog activity patterns and detection probability during VES surveys (Zylstra et al. 2015),

¹ <https://wrcc.dri.edu/wwdt>; Accessed 4 Sep 2017

² <http://prism.oregonstate.edu>; Accessed 4 Sep 2017

we calculated the proportion of pools in each complex with water during each survey (*water*). We also created a binary variable to differentiate surveys that were led by observers with limited experience (<10 previous surveys; *inexp.obs*) from those led by individuals with extensive survey experience (≥ 10 previous surveys).

Model implementation and inferences

We modeled variation in the probability of occupancy among sites in spring of 1996 as a function of basin area, number of pools in each complex, and mean elevation. We included a quadratic term for elevation to allow for non-linear relationships between initial occupancy and elevation:

$$\begin{aligned} \text{logit}(\psi_{i,1}) = & \alpha_{\psi} + \beta_{\psi.area}(area_i) + \beta_{\psi.pools}(npools_i) \\ & + \beta_{\psi.elev}(elev_i) + \beta_{\psi.elev2}(elev_i^2) \end{aligned} \quad (1.4)$$

where α_{ψ} is the mean probability of initial occupancy across all sites on the logit scale.

We allowed extinction and colonization probabilities to vary between summer and winter seasons, and to vary with basin area, surface-water reliability, and sediment levels. In addition, we allowed extinction probabilities to vary as a function of drought over the preceding six-month period, and included an interaction term to allow the effect of drought to differ between summer and winter:

$$\begin{aligned} \text{logit}(\varepsilon_{i,t}) = & \alpha_{\varepsilon} + \beta_{\varepsilon.area}(area_i) + \beta_{\varepsilon.rel}(reliability_i) + \beta_{\varepsilon.sed}(sediment_{i,t}) \\ & + \beta_{\varepsilon.win}(winter_t) + \beta_{\varepsilon.dr}(6mo.PDSI_{i,t}) + \beta_{\varepsilon.windr}(winter_t \times 6mo.PDSI_{i,t}) \end{aligned} \quad (1.5)$$

where α_{ε} is the probability of extinction in summer for sites with low sediment levels on the logit scale. We modeled baseline colonization probabilities as a function of drought during the preceding larval period and precipitation during summer and winter. Similar

to the model for extinction, we included interactions between hydrologic variables and season:

$$\begin{aligned} \text{logit}(\delta_{B,i,t}) = & \alpha_{\delta} + \beta_{\delta.area}(area_i) + \beta_{\delta.rel}(reliability_i) + \beta_{\delta.sed}(sediment_{i,t}) \\ & + \beta_{\delta.win}(winter_t) + \beta_{\delta.dr}(JA.PDSI_{i,t}) + \beta_{\delta.windr}(winter_t \times JA.PDSI_{i,t}) \\ & + \beta_{\delta.precip}(precip_{i,t}) + \beta_{\delta.winprecip}(winter_t \times precip_{i,t}) \end{aligned} \quad (1.6)$$

where α_{δ} is baseline colonization probability in summer at sites with low sediment levels on the logit scale. For site-level covariates, we assumed baseline colonization probabilities varied with characteristics of the recipient site (i). Alternatively, we might have modeled $\delta_{B,i,j,t}$ instead of $\delta_{B,i,t}$ and incorporated covariates to represent differences in habitat characteristics between sites i and j , similar to other gradient-based approaches that have been used for birds (Broms et al. 2016). We opted for the simpler approach given that lowland leopard frogs have limited dispersal capabilities and low rates of post-metamorphic survival (Chapter 2). Finally, we allowed detection probability to vary between spring and fall sampling periods, vary with observer experience, and vary with availability of surface water:

$$\begin{aligned} \text{logit}(p_{i,k,t}) = & \alpha_p + \beta_{p.fall}(fall_t) + \beta_{p.obs}(inexp.obs_{i,k,t}) \\ & + \beta_{p.water}(water_{i,k,t}) + \beta_{p.water2}(water_{i,k,t}^2) \end{aligned} \quad (1.7)$$

where α_p is mean detection probability of experienced observers in spring on the logit scale.

We specified vague priors for all parameters. We specified a logistic prior for intercepts in regression models, $\alpha \sim \text{Logistic}(\mu = 0, \sigma = 1)$, which implied a Uniform(0, 1) prior for ψ , δ_B , ε , and p when all covariates were equal to zero (Northrup and Gerber 2018). We specified Normal($\mu = 0, \sigma^2 = 10$) priors for all regression coefficients

describing effects of covariates on initial occupancy, colonization, extinction, and detection probabilities on the logit scale. Finally, we specified a Uniform prior for theta, the scale parameter describing the rate of decay in colonization probability with distance: $\theta \sim \text{Uniform}(0, 15)$. We fit our model in JAGS executed from R using the package jagsUI (Kellner 2015, R Core Team 2016). We ran three Markov chains initiated at random values for 85,000 iterations. We discarded the first 5,000 iterations as adaptation and burn-in and retained 1 of every 40 iterations thereafter to summarize the posterior distribution. We assessed convergence by inspecting trace plots and checking that Gelman-Rubin \hat{R} statistics were < 1.1 (Gelman and Rubin 1992).

We assessed the extent to which each covariate explained variation in colonization, extinction, initial occupancy, or detection probability by calculating a posterior probability (PP) value, defined as the proportion of samples from the posterior distribution that were > 0 if the mean of the posterior was positive or < 0 if the mean was negative. For example, if the mean of the posterior distribution for $\beta_{\psi.area}$ was positive, but 20% of posterior samples were negative (PP = 0.80), we would conclude there was only weak evidence that probability of initial occupancy was associated positively with basin area. We generated posterior distributions for the proportion of sites occupied in each watershed during each of the 43 sampling periods (1996–2017) and used a Bayesian beta regression model (Ferrari and Cribari-Neto 2004) to assess the relationship between these posterior occupancy probabilities and drought indices averaged over the preceding 12 months (spring: Jun–May; fall: Oct–Sep). Unless noted otherwise, we used 95% credible intervals (95% CI) to characterize uncertainty of estimates based on posterior distributions.

Forecasting effects of climate on metapopulation persistence

We used simulations to forecast effects of potential changes in climate on persistence of leopard frog metapopulations in arid mountain canyons. We assessed the probability that a metapopulation would persist over a 30-year period under three climate scenarios: 1) neutral conditions, with monthly PDSI = 0 and precipitation equal to 30-year normals; 2) persistent mild drought, with PDSI = -1.5 and precipitation in summer and winter equal to 75% of normals; and 3) periodic extreme drought, with PDSI = -4.5 and precipitation equal to 50% of normals for three years followed by seven years of mild drought conditions, repeated three times. We simulated occupancy dynamics for four hypothetical metapopulations, each consisting of 48 sites distributed evenly among eight canyons, to evaluate the relative importance of water reliability and distance between sites. Specifically, we established metapopulations in areas where water reliability was either high (30% of sites with permanent water, mean reliability = 0.85) or low (15% of sites permanent, mean reliability = 0.60) and distances between sites were either short (distances between adjacent canyons ranged from 1 to 5 km, mean distance between all pairs of canyons = 8.6 km) or long (range of distances = 2–8 km, mean = 13.6 km). For each metapopulation, we fixed initial occupancy equal to 0.50, sediment levels as low, and basin area of each site equal to the observed mean. We assumed the effects of drought and precipitation on extinction and colonization probabilities were identical to those we observed between 1996 and 2017. We predicted occupancy of sites in each metapopulation over time, with associated uncertainty, by combining posterior draws from extinction and colonization parameters based on observed data with projected PDSI

and precipitation values under each climate scenario. For each metapopulation and climate scenario, we calculated the proportion of 48 sites that were occupied in each spring and fall sampling period and computed probability of metapopulation extinction as the proportion of MCMC iterations in which no sites were occupied after 30 years. We expected our estimates of extinction probabilities to be conservative, as 48 sites represents a large metapopulation relative to those we studied and others in the region.

RESULTS

Field surveys

We surveyed 55 pool complexes distributed among eight canyons, with each complex containing between 1 and 16 pools (mean = 3.9 pools). Basin area of complexes averaged 9.4 km², with those in the southern watershed averaging 3.7 km² larger than complexes in the northern watershed (Table 1.1). In 75% of complexes ($n = 41$), at least one pool held water during $\geq 50\%$ of all sampling periods (*reliability* ≥ 0.50); 25% of complexes ($n = 14$) held water permanently (*reliability* = 1.0). Water was less reliable in complexes from the northern than southern watershed, as 37.5% of northern complexes ($n = 12$) and only 8.7% of southern complexes ($n = 2$) were dry during $>50\%$ of sampling periods (*reliability* < 0.50 ; Table 1.1). Sediment reached high levels (mean sediment volume $\geq 50\%$) in two of eight canyons, both in the northern watershed (Table 1.1). In these two canyons, sediment levels peaked approximately 1.5 years after wildfires in 1999 and 2003 and remained high for 5–7 years.

On average, we surveyed each pool complex in 26.0 (SE = 0.87) of 43 sampling periods (range = 12–39 sampling periods/complex) and visited complexes an average of

1.7 (SE = 0.05) times during each of those sampling periods (range = 1–13 surveys/sampling period/complex). More than 82% of surveys were led by observers with extensive survey experience. Most complexes (84%, $n = 46$) were visited more than once within multiple sampling periods, providing information about detection probability; there was a slight positive trend in the mean number of surveys per sampling period per complex over time (slope = 0.02, 95% CI = 0.00–0.04). There was more surface water available for frogs during fall surveys (mean proportion of pools in a complex with water = 0.84) than spring (0.65), although drought conditions prevailed throughout much of the study. Both mean PDSI and precipitation were well below normal (PDSI = -1.7 ; monthly precipitation = 84% of 30-year normals), with exceptional drought conditions observed in most canyons between 2013 and 2014 (minimum monthly PDSI ranged from -4.8 to -6.2). Observers were more likely to detect frogs in fall (318 of 944 surveys, 34%) than in spring (411 of 1410 surveys, 29%). Post-metamorphic leopard frogs were detected at least once in 71% of pool complexes ($n = 39$).

Occupancy

Across all sites, probability of initial occupancy averaged 0.52 and was higher for complexes with more pools and larger basin areas (Table 1.2). From 1996–2008, the first 13 years of the study, the proportion of sites occupied in each watershed fluctuated between 0.20 and 0.61, and peaked in fall 2008 (Fig. 1.3). Shortly thereafter, occupancy declined precipitously in the northern watershed, with no observations of lowland leopard frogs after spring 2015 (Fig. 1.3). In contrast, occupancy in the southern watershed continued to fluctuate between 0.38 and 0.61 for the remainder of the study.

In general, local populations were more dynamic during summer than winter, with both extinction and colonization probabilities lower during winter, except during severe droughts (Table 1.2; Figs. 1.4 and 1.5). Local populations were more likely to go extinct (probabilities >0.2) at sites where surface water was less reliable (*reliability* ≤ 0.25) than sites where at least one pool held water permanently (probabilities <0.2 , except during extreme drought; Fig. 1.4). Extinction probabilities did not vary with sediment levels or basin area after accounting for season, water reliability, and drought (PP = 0.70 and 0.50, respectively; Table 1.2).

During winter, sites were unlikely to be colonized (probabilities <0.12), regardless of hydrologic conditions or site characteristics (Fig. 1.5). During summer, sites were more likely to be colonized when the preceding larval period (Jan–Aug) was wetter than normal and when precipitation during summer monsoons was above average (Fig. 1.5). Colonization probabilities also varied with site characteristics. Specifically, the odds that frogs colonized an adjacent site were 4.2 times higher (95% CI = 1.1–15.2) when sediment levels at the recipient site were low rather than high, regardless of sediment levels at the site of origin. Frogs were also more likely to colonize sites in close proximity to their natal site. Sites were 2.2 times (95% CI = 1.1–8.3) more likely to be colonized by frogs from a site 150 m away compared to a site 1.5 km away, assuming the recipient site had little to no sediment.

Effects of drought on occupancy differed between watersheds. Between 1996 and 2014, estimates of the proportion of sites occupied were associated positively with PDSI (i.e., lower occupancy during drought) in the northern watershed (slope on the logit scale

= 0.21, 95% CI = 0.14–0.29) but not the southern watershed (slope = 0.04, 95% CI = –0.03 to 0.11; Fig. 1.6).

Observers were likely to detect leopard frogs when they were present (mean p = 0.82), especially when the site was surveyed more than once during a sampling period (mean p >0.95 when experienced observers surveyed a complex ≥ 2 times). Detection probability was higher in fall than spring and peaked at intermediate levels of surface-water availability (proportion of pools with water = 0.70; Appendix B: Fig. B1).

Forecasts

In the absence of drought, metapopulations of lowland leopard frogs comprised of 48 sites are unlikely to go extinct within 30 years (extinction probabilities <0.03). When mild or extreme droughts occur, however, some metapopulations are vulnerable to extinction, particularly if few sites have pools that hold water reliably (extinction probabilities = 0.11–0.41; Figs. 1.7a and 1.7c). When extreme droughts occur at least once per decade, all metapopulations are vulnerable to extinction within 30 years, regardless of water reliability and distances between sites. In the absence of wildfires, the spatial arrangement of sites has less of an effect on persistence than does water reliability (Fig. 1.7), although sites are less likely to be recolonized following severe drought if distances between adjacent canyons are large (2–8 km).

DISCUSSION

Changes in climate, especially increases in drought frequency and severity, have been implicated in declines of many amphibians in the western U.S. and around the world

(Daszak et al. 2005, Scheele et al. 2012, Hossack et al. 2013a). These changes have altered demographic rates (e.g., Reading 2007, Cayuela et al. 2016), shifted phenology of life-history events (e.g., Todd et al. 2011, Benard 2015), and reduced the quantity and quality of aquatic environments on which many amphibians depend (McMenamin et al. 2008, Werner et al. 2009, Pilliod et al. 2015). By extending existing analytical frameworks to allow dynamic parameters to vary as a function of time-varying covariates, we were able to demonstrate that for lowland leopard frogs, both extinction and colonization processes were affected by drought-mediated factors, specifically reductions in surface water in arid mountain canyons.

Changes in occupancy or transition probabilities of amphibians that are active during only part of the year in temperate environments have been linked to variation in hydrologic conditions through data from annual surveys (Werner et al. 2009, Ray et al. 2016). Data from biannual surveys that spanned 22 years allowed us to explore seasonal variation in extinction and colonization processes for a species that is active year-round (Sredl 2005). Periods of severe drought, during either spring or fall, decreased the amount of surface water available to post-metamorphic frogs in early summer or winter (Appendix A), which increased extinction probabilities (Fig. 1.4). In summer, colonization rates reflected both the number of potential emigrants and hydrologic conditions that affected the ability of emigrants to reach new sites. The number of emigrants arriving at a site is often assumed to scale with the area of neighboring occupied sites (Hanski 1999), but for many aquatic-breeding amphibians, recruitment fluctuates in response to precipitation and hydroperiod, such that temporal variation is likely more important than patch area or other site-level characteristics (Pechmann et al.

1991, Daszak et al. 2005). For lowland leopard frogs, drought conditions during larval periods (Jan–Aug) increased the probability of recruitment failure, which decreased colonization rates the following summer (Fig. 1.5a). When recruitment was successful, however, individuals that metamorphosed were more likely to colonize neighboring pool complexes when monsoon rainfall was above average (Fig. 1.5b). Like cane toads (*Rhinella marina*) that reduce the frequency or spatial extent of movements during drought (Schwarzkopf and Alford 2002, Tingley and Shine 2011), lowland leopard frogs might have been less likely to emigrate from natal pools during dry summers, reducing colonization rates. Moreover, because rates of evaporative water loss are high in *Lithobates* spp. (Spotila and Berman 1976), low colonization rates during dry summers might have resulted from increased mortality of emigrants rather than, or in addition to, decreased probabilities of emigration. In winter, colonization rates of unoccupied sites were low, regardless of hydrologic conditions (Table 1.2; Fig. 1.5).

Although drought-mediated processes influenced occupancy dynamics and persistence of metapopulations, sites with pools that were spring-fed or sufficiently deep to retain water year-round reduced those effects, likely by functioning as refugia (Table 1.2, Figs. 1.7b and 1.7d; Keppel et al. 2012). Our results are consistent with other studies of amphibian metapopulations in the western U.S. where persistence depended on sites that held water year-round or at least longer than the time required for tadpoles to reach metamorphosis (Chandler et al. 2015, Ray et al. 2016). Generally, surface-water reliability is a strong predictor of extinction but explains less variation in recolonization rates of unoccupied sites (Chandler et al. 2015, Ray et al. 2016; Table 1.2). The distribution of these hydrologic refugia might explain why occupancy of lowland leopard

frogs in the southern watershed, where surface water was reliable at more than half of sites, did not decrease appreciably when drought conditions were severe (Fig. 1.6). In contrast, occupancy in the northern watershed, where water was reliable at less than a third of sites, decreased markedly as drought severity increased (Fig. 1.6). Like other amphibians in arid regions, persistence of leopard frogs in the Sky Island region likely depends on these refugia, the quantity and quality of which are likely to decrease with anticipated changes in climate and disturbance regimes (Westerling et al. 2006, Seager et al. 2007, Cook et al. 2015).

Effects of wildfire on amphibian populations have been studied in forest ecosystems (Dunham et al. 2007, Hossack et al. 2013b), but not in deserts. In low-elevation deserts that have not been invaded by nonnative grasses, wildfires are generally rare and low intensity (McLaughlin and Bowers 1982, Brooks and Matchett 2006). Wildfires in these areas are unlikely to cause direct mortality of stream-dwelling species, as fuels in and near stream channels are often insufficient to sustain fire. Stand-replacing fires in forests at higher elevations, however, can affect species that inhabit downstream reaches because post-fire erosion often transports large amounts of sediment from the upper watershed to pools below (Parker 2006, Goode et al. 2012). Though increases in sedimentation were not associated with extinctions of leopard frog populations during our study, frogs were less likely to recolonize sites with moderate to high levels of sediment (average sediment volume $\geq 25\%$; Table 1.2). Because sediment levels declined slowly (high levels persisted for an average of 6.2 years at sites affected by high-elevation fires), affected sites were likely to remain unoccupied for many years following fire. Our study is one of the first to associate amphibian declines with wildfire-caused sedimentation, yet we

expect these secondary effects of fire to occur more frequently as the number of severe, large-scale wildfires is expected to increase in the western U.S. (Westerling et al. 2006, Goode et al. 2012).

In addition to climate-related processes, amphibian declines have been attributed to a number of other factors including habitat loss, disease, invasions by nonnative species, and pollutants (Collins and Storfer 2003, Whitfield et al. 2016). Although we found that declines in lowland leopard frogs were associated with drought and the downstream consequences of wildfire, other factors may have influenced their population dynamics. *Batrachochytrium dendrobatidis* (Bd), a fungal pathogen that causes chytridiomycosis, has been implicated in declines or extinctions of several montane amphibians in the western U.S. (Bradford 1991, Kagarise Sherman and Morton 1993, Muths et al. 2003). With few exceptions, most amphibian populations in the warmer deserts of the southwestern U.S. persist with low rates of infection (Schlaepfer et al. 2007, Savage et al. 2011); disease-related mortality, when it occurs, is generally expected in cooler winter months (Forrest and Schlaepfer 2011, Savage et al. 2011). Although we did not test for presence of Bd throughout the study, our analyses suggest that factors other than disease were the primary drivers of the declines we documented, as most local extinction events occurred during summer. We note, however, that extirpation of lowland leopard frogs from a canyon near our study area in 2011 was linked to high rates of Bd infection (Savage et al. 2011).

Conclusions

As anthropogenic activities decrease the quantity and continuity of habitat for many species, applications for metapopulation theory are likely to increase (Hanski 1999). In most spatially explicit models of metapopulation dynamics, colonization and extinction probabilities are assumed to vary among sites solely as a function of patch area and connectivity, despite evidence indicating that these dynamic processes reflect variation in climate, hydrology, or other environmental factors (Royle and Kéry 2007, Ray et al. 2016). The ability to explore these processes can be limited by the lack of data from periods that capture meaningful variation in environmental conditions. For example, many empirical studies of occupancy dynamics in vertebrates have been based on ≤ 7 years of data, which limits the extent to which environmental conditions can be linked to state transitions (Franken and Hik 2004, Risk et al. 2011, Heard et al. 2013, Chandler et al. 2015, Broms et al. 2016, Ray et al. 2016). This limitation is especially important for long-lived species or for species with life stages >1 year in duration. Although it seems reasonable to assume that transition rates remain constant over short time periods, insights about mechanisms that govern distributional dynamics are more likely to emerge from long-term studies, which are likely to capture a wider range of environmental variation. These insights can contribute to conservation of imperiled species. For example, results from our study will help managers identify locations for potential reintroductions of lowland leopard frogs, prioritize areas for habitat restoration based on the reliability of surface water, and determine whether populations should be translocated following catastrophic fires or similar landscape-level disturbances.

TABLE 1.1. Summaries of environmental covariates used to explain variation in initial occupancy, extinction, colonization, and detection probability of lowland leopard frogs surveyed in two watersheds (South, North) in the Rincon Mountain, Arizona, USA between 1996 and 2017. We summarized values of covariates separately for pool complexes in each watershed. For season-level covariates, we provide the mean value across all summer and winter seasons and for survey-level covariates we provide the mean value across all surveys in each spring or fall sampling period. We used a discrete index to classify sediment levels (0 = low; 1 = moderate; 2 = high), Palmer Drought Severity Index to characterize drought (negative values indicate drought; positive values indicate wetter than normal conditions), and continuous indices that ranged from 0 to 1 to characterize water reliability and surface-water availability during each survey.

Covariate	Label	South ($n = 23$)		North ($n = 32$)	
		Mean	Range	Mean	Range
<i>Site-level</i>					
No. pools	<i>npools</i>	4.0	1, 13	3.8	1, 16
Elevation (m)	<i>elev</i>	1137	962, 1357	1056	873, 1359
Basin area (km ²)	<i>area</i>	11.6	3.9, 32.9	7.9	1.9, 18.1
Water reliability	<i>reliability</i>	0.85	0.19, 1.00	0.63	0.10, 1.00
<i>Season-level</i>					
Sediment levels	<i>sediment</i>	0.54	0, 1	0.88	0, 2
Drought (prior 6 months)	<i>6mo.PDSI</i>	-1.9	-5.4, 4.5	-1.6	-4.6, 4.7
Drought (larval period)	<i>JA.PDSI</i>	-2.0	-5.2, 4.4	-1.7	-4.6, 4.6
Precipitation (% normals)	<i>precip</i>	88	16, 203	89	17, 206
<i>Survey-level</i>					
Surface-water availability	<i>water</i>	0.84	0.00, 1.00	0.66	0.00, 1.00

TABLE 1.2. Posterior mean and standard deviation (SD) for parameters from a dynamic occupancy model for lowland leopard frogs in southern Arizona, USA. For regression coefficients (β), we report the proportion of samples from the posterior distribution > 0 if the mean is positive or < 0 if the mean is negative (PP).

Parameter	Mean	SD	PP
<i>Initial occupancy</i>			
α_ψ	0.15	1.31	
$\beta_{\psi,\text{area}}$	2.68	1.67	0.99
$\beta_{\psi,\text{pools}}$	3.09	2.18	0.97
$\beta_{\psi,\text{elev}}$	0.21	1.85	0.57
$\beta_{\psi,\text{elev2}}$	-0.33	2.28	0.58
<i>Colonization</i>			
α_δ	-2.47	0.55	
$\beta_{\delta,\text{area}}$	0.87	0.40	1.00
$\beta_{\delta,\text{rel}}$	0.11	0.19	0.71
$\beta_{\delta,\text{sed}}$	-0.72	0.33	0.98
$\beta_{\delta,\text{win}}$	-1.11	0.92	0.90
$\beta_{\delta,\text{dr}}$	0.39	0.21	0.97
$\beta_{\delta,\text{windr}}$	-1.13	0.98	0.88
$\beta_{\delta,\text{precip}}$	1.12	0.44	1.00
$\beta_{\delta,\text{winprecip}}$	-1.11	0.53	0.99
θ	1.90	0.82	
<i>Extinction</i>			
α_ϵ	-0.13	0.71	
$\beta_{\epsilon,\text{area}}$	0.16	0.68	0.50
$\beta_{\epsilon,\text{rel}}$	-1.85	0.45	1.00
$\beta_{\epsilon,\text{sed}}$	-0.24	0.44	0.70
$\beta_{\epsilon,\text{win}}$	-1.92	0.91	0.99
$\beta_{\epsilon,\text{dr}}$	-0.44	0.48	0.82
$\beta_{\epsilon,\text{windr}}$	-1.17	0.86	0.92
<i>Detection</i>			
α_p	1.30	0.15	
$\beta_{p,\text{fall}}$	1.23	0.21	1.00
$\beta_{p,\text{obs}}$	-0.68	0.23	1.00
$\beta_{p,\text{water}}$	-0.14	0.15	0.83
$\beta_{p,\text{water2}}$	-1.03	0.16	1.00

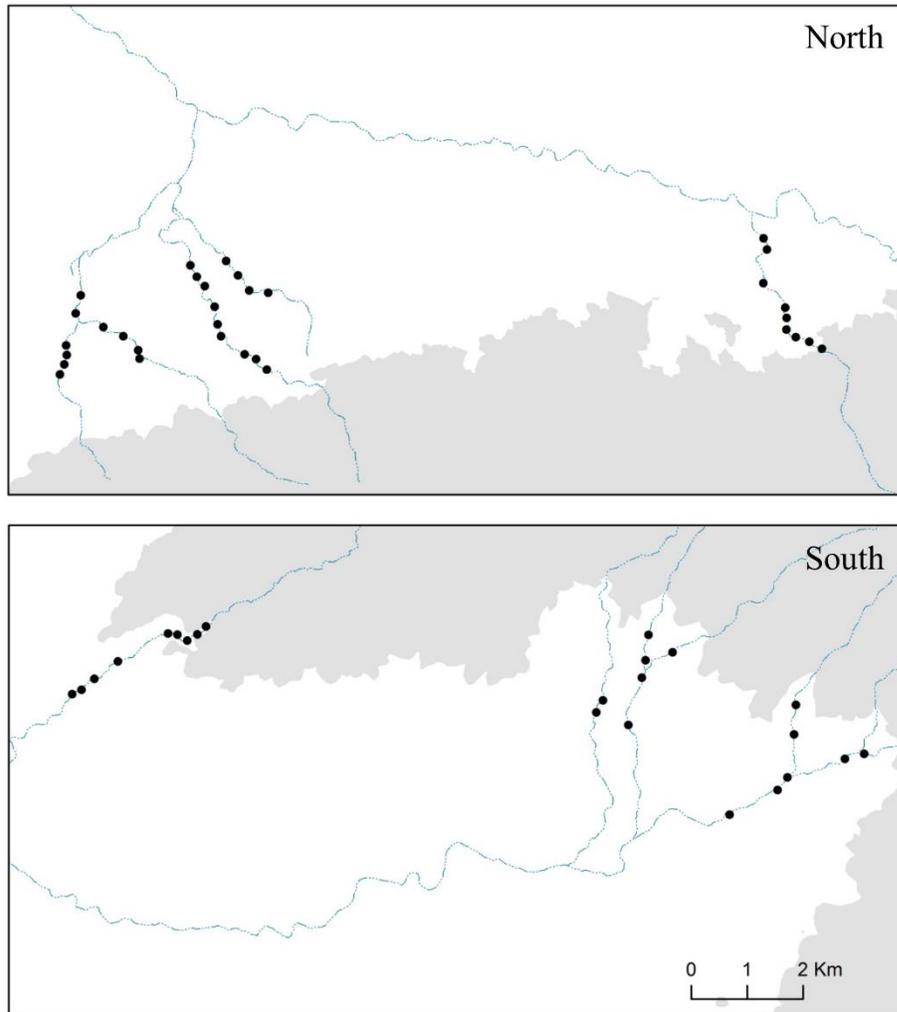


FIGURE 1.1. Maps of pool complexes surveyed for lowland leopard frogs in two watersheds (North, South) in the Rincon Mountains. Each black dot represents the approximate midpoint of a pool complex. Areas above 1370 m elevation are shaded gray.

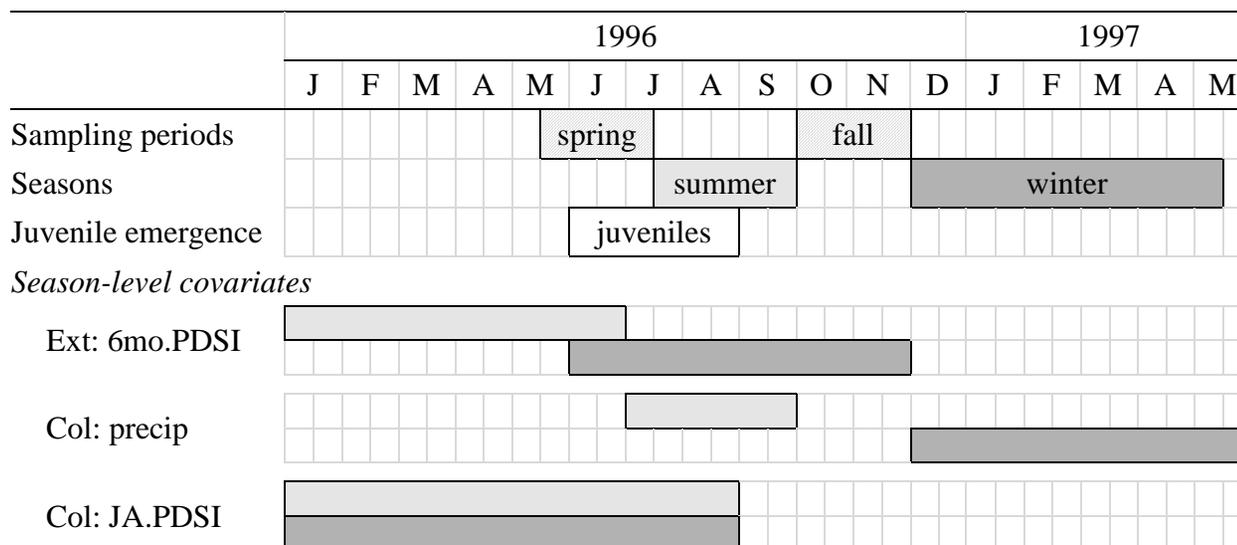


FIGURE 1.2. A timeline illustrating relationships among sampling periods, seasons, and periods when we measured covariates. For simplicity, we illustrate these relationships from January 1996 to May 1997, a period that encompasses only the first two sampling periods (of 43) and seasons of the 22-year study. Each box represents an approximate 15-day period (i.e., the first or second half of each month). We surveyed for post-metamorphic leopard frogs during spring and fall sampling periods (diagonal hatch), and assumed colonization and extinction events occurred during the intervening summer and winter seasons (light gray and dark gray, respectively). We related extinction probabilities (Ext) in summer and winter to Palmer Drought Severity Index averaged over the preceding six-month period (6mo.PDSI; shaded to correspond with associated season). We related colonization probabilities (Col) during summer and winter to current precipitation (precip) and to drought indices averaged over the eight-month period leading up to and including when the most recent cohort of newly-transformed juveniles emerged (JA.PDSI).

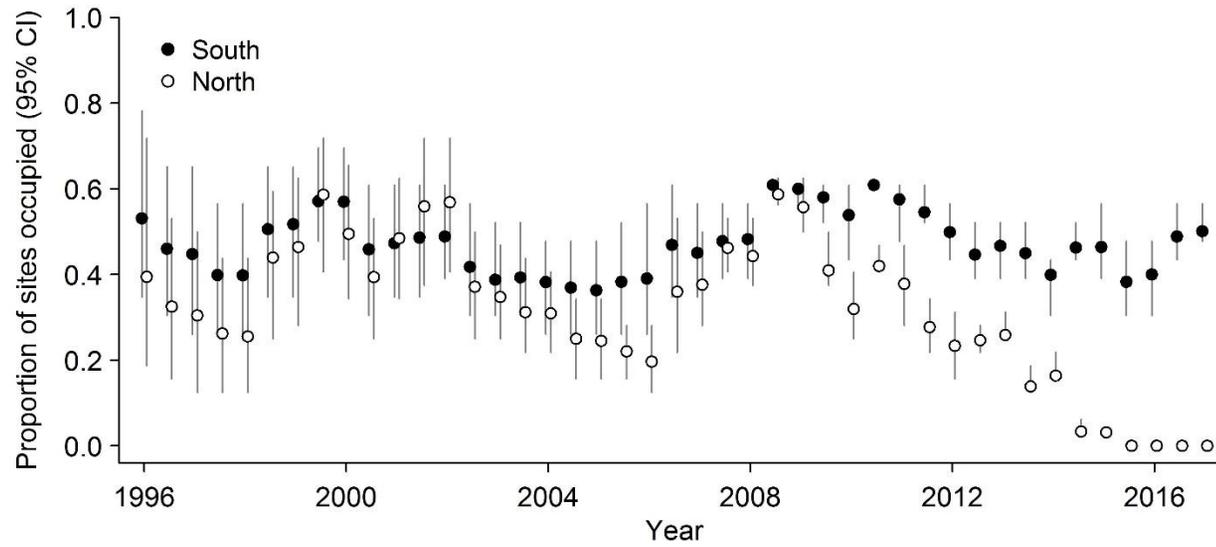


FIGURE 1.3. Estimated proportion of sites occupied by lowland leopard frogs in two watersheds of the Rincon Mountains, Arizona, USA in spring (16 May–15 Jul) and fall (1 Oct–30 Nov) sampling periods between 1996 and 2017.

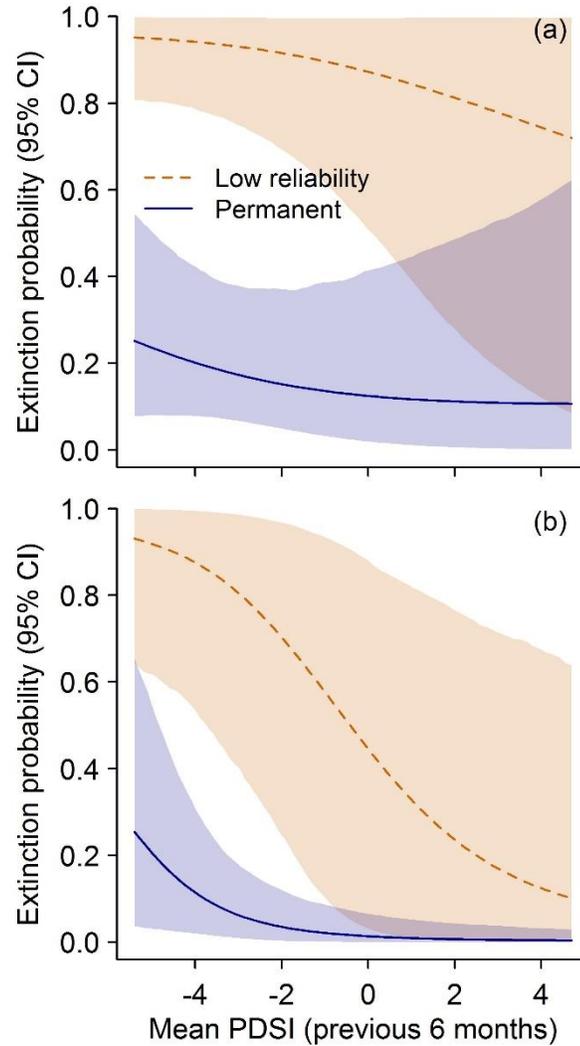


FIGURE 1.4. Extinction probabilities for populations of lowland leopard frogs in (a) summer (16 Jul–30 Sep) and (b) winter (1 Dec–15 May) as a function of mean Palmer Drought Severity Index (PDSI) during the previous six months and water reliability (permanent sites had ≥ 1 pools that never went dry; low-reliability sites went dry during 75% of spring and fall sampling periods). Negative PDSI values indicate drought; positive PDSI values indicate wetter than normal conditions. To predict extinction probabilities, we assumed sediment levels were low and basin area was equal to the mean across all pool complexes.

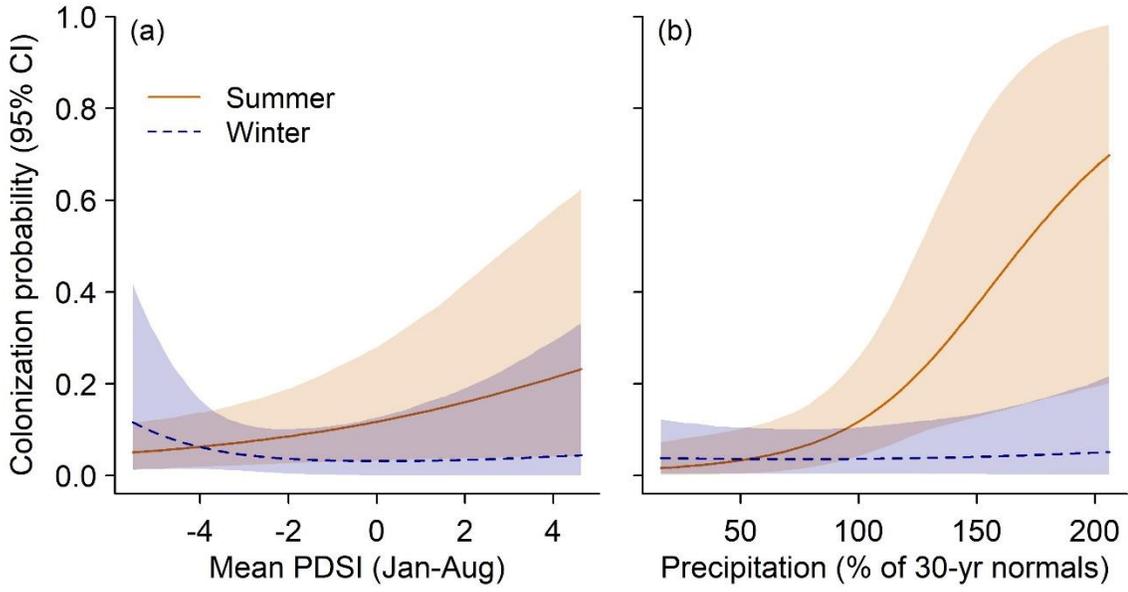


FIGURE 1.5. Baseline colonization probabilities for populations of lowland leopard frogs in summer and winter as a function of (a) mean Palmer Drought Severity Index (PDSI) during the previous larval period (Jan–Aug) and (b) precipitation during current summer and winter seasons. Negative PDSI values indicate drought; positive PDSI values indicate wetter than normal conditions. To predict colonization probabilities as a function of drought, we fixed basin area and water reliability equal to their means across all pool complexes, sediment levels as low, and precipitation to its mean across all pool complexes and seasons. We similarly fixed basin area, reliability, sediment, and PDSI values to their means when predicting colonization probabilities as a function of precipitation.

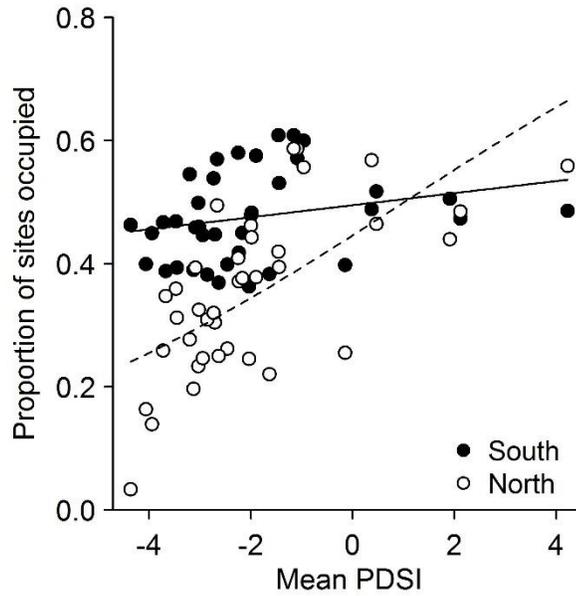


FIGURE 1.6. Seasonal estimates of the proportion of sites occupied by lowland leopard frogs in two watersheds of the Rincon Mountains, Arizona, USA, 1996–2014, as a function of Palmer Drought Severity Index (PDSI) averaged over the preceding 12 months. Proportion of sites occupied was positively associated with PDSI in the northern watershed (dashed line; slope on logit scale = 0.21, 95% CI = 0.14–0.29), but not the southern watershed (solid line; slope = 0.04, 95% CI = –0.03 to 0.11).

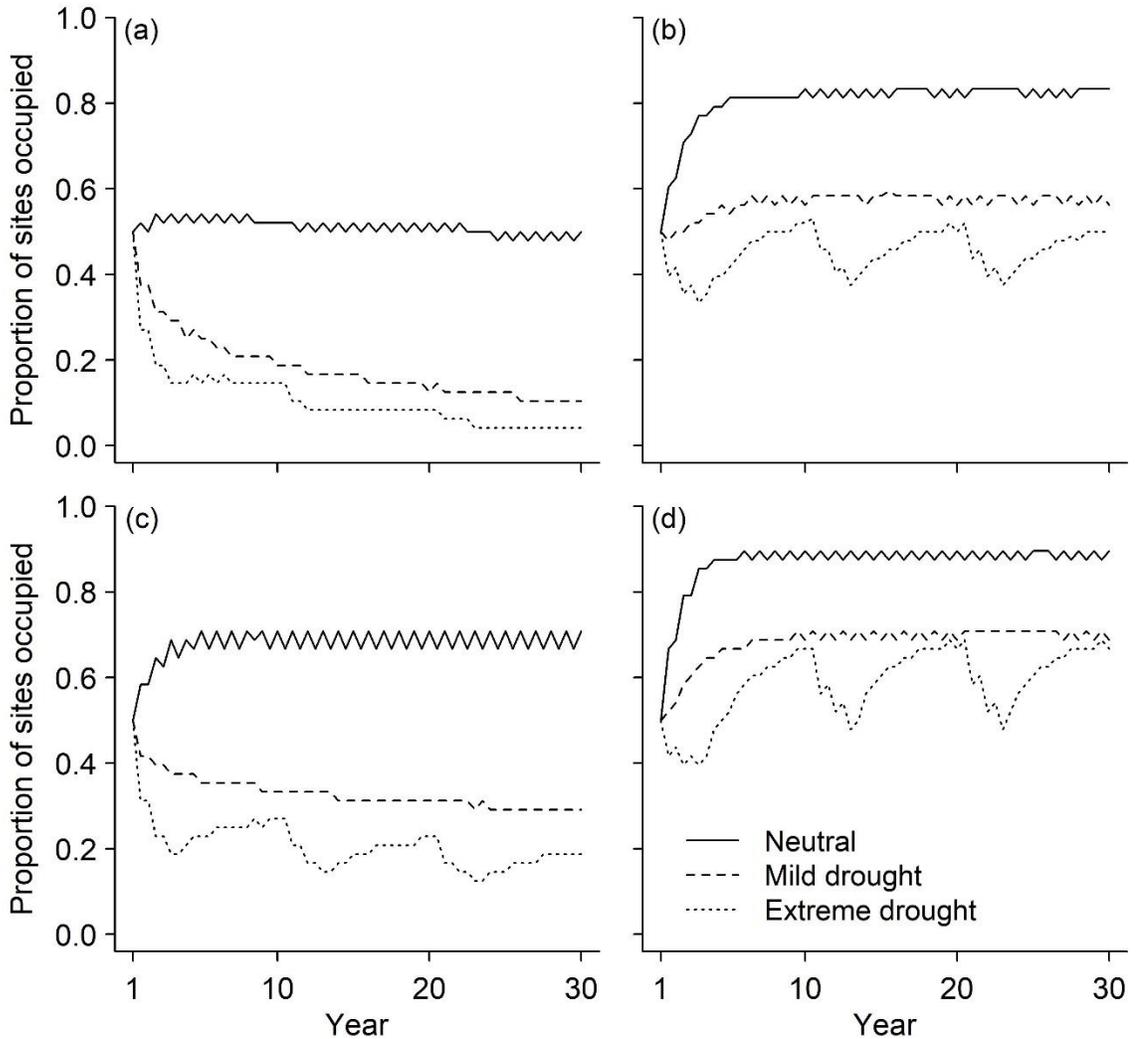


FIGURE 1.7. Proportion of sites occupied over 30 years in simulated metapopulations of lowland leopard frogs under three climate scenarios: 1) neutral conditions, 2) persistent, mild drought, and 3) extreme three-year droughts occurring once per decade. Metapopulations were characterized by a) low water reliability and long distances between sites, b) high water reliability and long distances between sites, c) low water reliability and short distances between sites, and d) high water reliability and short distances between sites. Lines represent the medians of posterior distributions. In all simulations, we assumed 50% of sites were occupied in the first year.

CHAPTER 2: LOW SURVIVAL OF AN ARID-LAND AMPHIBIAN CONTRIBUTES TO POPULATION DECLINES

ABSTRACT

Declines in populations of amphibians have been linked to a number of factors, including changes in climate. Decreases in precipitation, for example, can reduce or shift the distribution of aquatic resources that are integral to reproduction and larval development of many species. How changes in climate might affect other demographic parameters is less well known, particularly for species that are active year-round. To explore this question, we studied survival of lowland leopard frogs (*Lithobates yavapaiensis*) in arid mountain canyons in southern Arizona, where the availability of surface water varies markedly within and among years. Between 2013 and 2015, we surveyed frogs 33–74 times in each of six stream reaches distributed among two watersheds and used capture-recapture methods based on in-situ photographs to identify individuals. We used Cormack-Jolly-Seber models to explore how surface-water availability, weather, and vegetation influenced seasonal variation in survival of post-metamorphic frogs. Overall, mean annual survival in this dynamic environment was low ($\hat{\phi} = 0.11$, 95% CI = 0.07–0.14). Survival varied with ambient temperature, dew point, perimeter groundcover, and year, but especially with surface-water availability. Mean monthly survival was high ($\hat{\phi} \geq 0.88$) when water levels were at or near 100% maximum pool depths, but declined sharply ($0.12 \leq \hat{\phi} \leq 0.85$) when water levels dropped below 50%. Decreased survival of post-metamorphic frogs during severe drought almost certainly contributed to the extirpation of frogs from one watershed in 2015. Predicted

increases in frequency or severity of drought will likely decrease the probability of lowland leopard frogs persisting in this region over the long-term, as droughts are likely to increase the rate of local extirpations and limit the ability of individuals to disperse through an increasingly arid landscape.

INTRODUCTION

Effective conservation of rare species depends on understanding the factors that govern their population dynamics (Caughley and Gunn 1996). Because local abundance reflects a balance between the number of individuals gained through local recruitment plus immigration and the number of individuals lost through mortality plus emigration (Williams et al. 2002), population declines can result from changes in any or all of these demographic parameters. Understanding the relative contribution of different demographic processes to population dynamics, and the environmental factors that govern demography over time and space, can help to inform strategies to ameliorate threats effectively and stem declines.

Throughout the U.S. and worldwide, the abundance and distribution of many amphibians are declining (Stuart et al. 2004, Adams et al. 2013). Many of these declines have been attributed to increases in mortality from disease (e.g., Pilliod et al. 2010, DiRenzo et al. 2017) or increases in mortality and decreases in immigration from habitat loss or fragmentation (e.g., Carr and Fahrig 2001, Harper et al. 2008). Numerous declines have also been linked to recruitment failure during periods of drought or changes in land use that reduced the availability of surface water (e.g., Pechmann et al. 1991, Daszak et al. 2005, Anderson et al. 2015). Decreases in recruitment resulting from

reductions in surface water are unsurprising given that most amphibians rely on water for reproduction and larval development (Duellman and Trueb 1986). What is less clear, however, is the extent to which drought or surface-water availability affects post-metamorphic survival and contributes to population declines (but see Grafe et al. 2004, Church et al. 2007, Cayuela et al. 2016) .

Survival rates of post-metamorphic amphibians are estimated commonly using capture-recapture methods, where individuals are surveyed annually during a relatively short breeding season (<3 months) (e.g., Church et al. 2007, Cayuela et al. 2016). Typically, variation in survival is related to environmental factors that are summarized annually, potentially masking important processes that act over shorter time scales. Moreover, annual capture-recapture data cannot be used to explore within-year variation in survival, which may be particularly important for short-lived species or for species that inhabit environments that allow them to remain active year-round.

To identify factors that govern variation in post-metamorphic survival and population dynamics of an arid-land amphibian, we used innovative capture-recapture methods and frequent surveys to characterize survival of lowland leopard frogs (*Lithobates yavapaiensis*). Though once common in valley-bottom streams of southern Arizona, lowland leopard frogs are now listed as a species of species concern in Arizona, as groundwater depletion and reductions in streamflow have resulted in widespread declines and extirpations (Sredl 2005). Many extant populations in this region are comprised of few individuals that inhabit isolated, arid mountain canyons with intermittent streamflow (Wallace et al. 2010, Zylstra et al. 2015).

We surveyed lowland leopard frogs frequently in six stream reaches during a 30-month period to explore how survival of post-metamorphic frogs varied over time and space as a function of environmental factors. One of our primary objectives was to understand how the availability of surface water influenced survival of lowland leopard frogs given recent changes in climate and anthropogenic activities that have altered the hydrologic landscape of this arid region (Hendrickson and Minckley 1985, Grimm et al. 1997). In particular, the mountain canyons now inhabited by many lowland leopard frogs are more arid than the cienegas and permanent streams that once formed the core of their historical distribution in southern Arizona (Clarkson and Rorabaugh 1989, Sredl 2005). In addition to identifying factors that affect survival, we used estimates of survival in concert with estimates of reproductive output to explain the apparent extirpation of frogs at one site during our study. Our findings illustrate the value of seasonal capture-recapture data, particularly for short-lived species, and provide information to guide conservation strategies for species that depend on limited surface water in arid environments.

METHODS

Study area

We studied lowland leopard frogs in the Madrean Sky Island region of southern Arizona and northern Mexico, where isolated mountain ranges are surrounded by desert and semi-desert grasslands. Specifically, we surveyed frogs in the Rincon Mountains east of Tucson, Arizona. Vegetation communities range from Sonoran desertscrub and desert grassland below 1500 m elevation to mixed conifer forests between 2100 m and

2640 m elevation (Brown 1982, Bowers and McLaughlin 1987). The Rincon Mountains are bisected by a ridge formation that runs SW to NE, with deeply-incised canyons forming the headwaters of two watersheds, one north and one south of the ridge (Valentine-Darby et al. 2017). Like many mountain ranges in the region, most surface water is limited to bedrock pools in canyon bottoms. Flow in most stream reaches is intermittent, with seasonal variation reflecting a bimodal pattern of annual precipitation (300–700 mm/yr, depending on elevation; Brown 1982, Bowers and McLaughlin 1987). In winter (Dec–Apr), pools are connected frequently by continuous flow in response to widespread cool-season rains, whereas in late spring (May–Jun) and to a lesser extent in fall (Oct–Nov), pools are isolated as stream channels between pools dry (Grimm and Fisher 1992, Wallace et al. 2010). During monsoon season (Jul–Sep), localized, high-intensity storms can trigger sporadic flash floods. Because lowland leopard frogs in this region inhabit streams below approximately 1400 m elevation, we restricted surveys to reaches at low and middle elevations (870–1370 m). Typically, pools in these reaches are <2 m deep with surface areas of 3–12 m² and limited soil-bank development; pools provide habitat for post-metamorphic leopard frogs when surrounding stream channels dry (Wallace et al. 2010).

We surveyed leopard frogs in six stream reaches, three in each watershed (Table 2.1, Fig. 2.1). In the south watershed, the three survey reaches were distributed across three canyons. These reaches ranged from 598 m to 1944 m in length and each contained between 14 and 24 pools that held water in spring and fall of most years. In the north watershed, we surveyed three stream reaches in the same canyon. The lower reach (870 m to 932 m elevation) contained 14 pools, the middle reach (942 to 1015 m elevation) 23

pools, and the upper reach (1063 to 1233 m elevation) 19 pools. A minimum of 215 m stream distance separated each reach and we never documented leopard frogs moving among survey reaches.

Field surveys

We surveyed for leopard frogs between 13 May 2013 and 8 November 2015. We surveyed four reaches (three in the north watershed, one in the south watershed) in all years of the study and two reaches in 2014 and 2015 (Table 2.1). Between March and early November, we surveyed each of the six reaches approximately once every nine days (range of intervals between surveys in the same reach = 1–60 days). To assess frog activity and survival during winter, we surveyed one reach in the south watershed approximately once every 14 days (range = 5–33 days) between mid-November and February. On all but two surveys, we searched for lowland leopard frogs during daylight hours because rugged canyons are difficult to traverse in the dark and detection probabilities during diurnal surveys are sufficiently high (≥ 0.1) to estimate survival (Wallace et al. 2010, Zylstra et al. 2015). Typically, we started surveys 1–3 hours after sunrise and completed surveys in the late morning or early afternoon.

During each survey, 1–3 observers (mean = 1.2) traversed the survey reach, using binoculars to scan the perimeter of pools and emergent aquatic vegetation for leopard frogs with estimated snout-vent length (SVL) ≥ 50 mm (hereafter, post-metamorphic leopard frogs). When we detected a leopard frog, one observer approached the area quietly and used a camera equipped with a 70–300 mm telephoto lens to photograph the dorsum, left flank, and right flank of the frog. We obtained 1–7 photographs of each

frog, and refer to this sequence of photographs as a photoset. Multiple photographs often were necessary to document spots across all three body regions, as features were sometimes obscured by physical obstructions (e.g., vegetation, rocks), poor lighting (e.g., glare), or frog posture. In addition to surveying for post-metamorphic frogs, we scanned pools for leopard frog eggmasses or clusters of newly hatched tadpoles; for simplicity, we refer to observations of newly hatched tadpoles as eggmasses. Observers also measured the depth of water in each pool, and measured air temperature, relative humidity, and wind speed at the start and end of each survey.

Identifying individuals

Estimating demographic parameters for populations of rare or threatened species, like lowland leopard frogs, is often challenging (Caughley and Gunn 1996). Typically, researchers seek to minimize adverse impacts to individuals, which can be difficult when estimates of survival, growth, or lifetime reproductive output require repeated interactions with individuals. Limiting the number of individuals studied or the frequency of interactions, however, lowers precision of parameter estimates (Williams et al. 2002). To balance ethical and legal obligations with the need for precise estimates of survival and other demographic parameters, some capture-recapture studies have used non-invasive marks, such as unique patterns or scars that can be photo-documented (Langtimm et al. 2004, Morrison et al. 2011) or DNA from hair or scat (Boulanger et al. 2004, Marucco et al. 2009). As with previous studies of salamanders and ranid frogs (Bailey 2004, Ferner 2010), we identified individual leopard frogs based on their unique natural markings. Unlike previous studies of amphibians, however, we used photographs

taken in-situ, which eliminated the need to capture individuals and allowed us to survey frequently without causing undue stress to animals.

Many studies that have used photographs to identify animals have focused on natural markings from one region of the body that can be captured in a single image (e.g., left flank; Holmberg et al. 2008, Nair et al. 2012). Recently, this approach has been extended to include markings from two regions (e.g., left and right flank), where repeated photographs of each region can be tracked independently to estimate abundance or survival (Hiby et al. 2013, McClintock et al. 2013). Because we photographed frogs in-situ, however, we were able to document markings on three contiguous body regions: the dorsum, left flank, and right flank. We refer to individual spots or small clusters of spots as features and the collection of all features across all three regions as a spot pattern. Each post-metamorphic individual has one unique spot pattern that does not change appreciably with age.

For most frogs (62%, $n = 215$), we were able to map all features on all three body regions (i.e., we were able to construct a “complete spot map” for an individual), either from a single photoset or from multiple photosets where features overlapped (Fig. 2.2). For other individuals (39%, $n = 137$), we were able to map features on one or more regions but not the entire spot pattern. We refer to a map that included some, but not all, features on an individual’s spot pattern as a “partial spot map.” Because spot patterns are unique, each partial spot map could represent only one frog. It is possible, however, that one frog was represented by multiple, partial spot maps that did not overlap in extent (Fig. 2.2).

To determine whether we had rephotographed (hereafter, recaptured) an individual, we compared photosets manually rather than using computer-based pattern-matching algorithms. We chose this alternative because 1) photosets were often comprised of multiple photographs rather than a single image, 2) the orientation and posture of frogs varied greatly among photographs, and 3) bodies of leopard frogs are not laterally or dorso-ventrally compressed. We concluded that two photosets represented the same individual when we matched ≥ 2 unique features definitively. We note that it was possible to recapture individuals whose spot patterns had not been mapped completely if ≥ 2 features within the mapped region matched. We processed photosets chronologically, comparing each photoset with all complete and partial spot maps that we observed previously in the same watershed. We assumed frogs could move between survey reaches within the same watershed but could not move between watersheds (71 km stream distance, 8 km straight-line distance).

Encounter histories

Typically, data from capture-recapture surveys are assembled into encounter histories that indicate the occasions when individuals were recaptured. Because we surveyed each reach 33–74 times during the study and rarely surveyed multiple reaches on the same day, there were a large number of survey occasions (259) and short intervals (1–33 days, median = 2 days) between survey occasions. For frogs whose spot patterns we had mapped completely, it was straightforward to construct an encounter history for each individual, with a 1 or 0 indicating whether the individual was observed on that survey occasion and a “.” indicating that the reach was not surveyed on that occasion. For frogs

whose spot patterns were not mapped completely, we created separate encounter histories for each partial spot map, recognizing that one frog could be associated with more than one encounter history.

Because the number of encounter histories might have exceeded the number of frogs we observed, which could bias estimates of survival (Link et al. 2010; Appendix C), we implemented an ad-hoc strategy to account for false rejection errors (i.e., failing to recognize that two partial spot maps were associated with the same frog; Morrison et al. 2011). False rejection errors can result in multiple encounter histories for an individual, often with a single encounter. To reduce bias in estimates of survival resulting from a lack of independence among encounter histories (Yoshizaki 2007), we censored the initial observation of each spot map (Morrison et al. 2011). This strategy resulted in the exclusion of all histories with a single encounter event (105 of 137 partial spot maps [77%] and 42 of 215 individuals with a complete spot map [20%] were excluded). We discuss the trade-offs in this strategy and alternative approaches to account for potential bias in Appendix C.

Environmental covariates

We anticipated that survival of leopard frogs and the probability of photographing a frog might vary in response to weather, hydrologic conditions, and vegetation cover along pool perimeters. To characterize weather conditions during each survey, we calculated minimum temperature, mean percent relative humidity, and maximum wind speed based on measures recorded at the start and end of each survey. To characterize weather conditions between survey occasions (i.e., during each survival interval), we

used downscaled, daily estimates of temperature and dew point from the PRISM Climate Group.¹ For each watershed, we calculated the mean dew point and mean of daily minimum temperatures during each survival interval, inclusive of the start and end dates.

To characterize surface-water availability, we related survey-specific measurements of water depth to maximum pool depths. We measured the maximum depth of each pool within six months of commencing surveys in each reach; when sediment levels in pools changed as the result of erosion or flash floods (Parker 2006), we remeasured maximum depths. Each time we surveyed a pool, we related water depth to maximum pool depth, resulting in a proportion ranging from 0 (pool was dry) to 1 (pool was full of water). We used the mean of these proportions across all pools in each reach as a survey-level index of surface-water availability. To characterize availability of surface water during each survival interval, we computed the index based on measurements taken during survey and non-survey dates (68% of index values from survey dates, 32% from non-survey dates). We then used linear interpolation to impute missing daily values in each reach using the `imputeTS` package in R (R Core Team 2016, Moritz and Bartz-Beielstein 2017), and calculated the mean value for each survival interval, inclusive of the start and end dates.

During each spring (May–Jun) and fall (Oct–Nov) season, we estimated visually the percentage of each pool perimeter (<1 m from pool edge) that contained groundcover vegetation (0–0.5 m). Within each of three water years (2013: May 2013–Sep 2013; 2014: Oct 2013–Sep 2014; 2015: Oct 2014–Sep 2015), we calculated mean perimeter groundcover across all pools in each reach as this could affect the quality of habitat for

¹ <http://prism.oregonstate.edu>; Accessed 10 Jan 2018

leopard frogs (Wallace et al. 2010) as well as the ability of observers to detect leopard frogs when present.

Model structure and inferences

We used a Cormack-Jolly-Seber model to estimate apparent survival (ϕ), or the probability that post-metamorphic frogs survived and remained in the study area between consecutive survey occasions, adjusted for recapture probability (p), which we defined as the probability of photographing a spot pattern that we observed previously (Lebreton et al. 1992). We specified the duration of each survival interval in days, and therefore assumed constant rates of daily survival between consecutive survey occasions. We based inferences on a model that included all environmental covariates we thought had potential to explain variation in survival (surface-water availability, temperature, dew point, and perimeter groundcover) and recapture probability (surface-water availability, temperature, humidity, wind, and perimeter groundcover). We included quadratic terms between surface-water availability and both survival and recapture probabilities to allow for non-linear relationships. We also included year as a covariate to account for temporal variation in survival and recapture probabilities beyond that explained by weather and hydrologic conditions. Specifically, we included indicator variables for water years 2014 and 2015; we included data we collected in October and November 2015 with water year 2015 as data were too sparse to estimate parameters for water year 2016. We standardized all continuous covariates prior to analysis, and used program MARK (White and Burnham 1999) through the RMark package (Laake 2013) in R to estimate model parameters.

RESULTS

Field surveys

Across the 30-month study period, we surveyed six stream reaches for lowland leopard frogs 310 times, with 64, 116, 113, and 17 surveys in water years 2013 through 2016, respectively. We observed between 0 and 37 leopard frogs with estimated SVL ≥ 50 mm on each survey (median = 2) and photographed an average of 70% of frogs we observed on each survey. We obtained 1082 photosets of individual frogs, each of which included between 1 and 7 photographs (mean = 2.4). We catalogued 352 unique spot maps, 215 (62%) of which were complete and mapped all features of an individual, and 137 (39%) of which were partial and mapped only a subset of features. We observed 81% of complete spot maps more than once (range = 2–15 observations, $n = 173$) and 23% of partial spot maps more than once (range = 2–5 observations, $n = 32$). The number of leopard frog observations in the north watershed declined over time (Table 2.2), and we observed no post-metamorphic frogs in this watershed after June 2015.

We observed 97 eggmasses, 52 in late winter and early spring (Feb–Apr; 26 eggmasses/season) and 45 in early fall (Aug–Oct; 15 eggmasses/season; Table 2.2). We observed only 3 of 97 eggmasses (3%) in the north watershed, all of which were oviposited prior to fall 2014. No leopard frog tadpoles were observed in the north watershed after July 2014.

Surface-water availability varied over time and space in ways that likely affected survival of leopard frogs. Within-year variation in surface-water availability was substantial (Fig. 2.3); surface-water availability was lowest in June (mean = 0.43, range =

0.06–0.90 across reaches and years) and highest in March (0.98, 0.87–1.00). Surface-water availability also varied among years, particularly during the dry season; mean water levels in June were considerably higher in 2015 (0.70) than in 2013 (0.33) or 2014 (0.21). Although seasonal patterns in water availability were similar in both watersheds, the total amount of water available in any given season varied among reaches, particularly in the north watershed. Large, deep pools in the highest elevation reach held water throughout the duration of the study (median surface-water availability = 0.90, range = 0.26–1.00), whereas water levels in pools at low- and middle-elevation reaches dropped markedly in both winter (minimums = 0.48, 0.28) and summer (0.06, 0.03) of 2014 (Fig. 2.3).

Survival and recapture probability

Mean annual survival of post-metamorphic leopard frogs across all sites was 0.11 (95% CI = 0.07–0.14), which we estimated from 205 encounter histories. Across all reaches and years, there was strong evidence of seasonal (within-year) variation in survival that was associated with variation in hydrologic conditions. Monthly survival was high (mean >0.83) when surface-water availability was ≥ 0.6 and declined sharply as availability dropped below 0.6 (Fig. 2.4). In addition, survival increased as minimum ambient temperature increased and as dew point decreased (Table 2.3; Fig. 2.5). Survival did not vary appreciably with vegetation cover after accounting for weather and hydrologic conditions (Table 2.3). Recapture probabilities averaged 0.26 (95% CI = 0.24–0.28) and increased as surface-water availability decreased (Fig. 2.4). Recapture probabilities also increased as ambient temperature increased, were lower where pool

perimeters had more vegetation cover, and were lower in 2014 than 2013 or 2015 (Table 2.3; Fig. 2.4). Lastly, recapture probabilities decreased slightly as wind speed increased (Table 2.3).

DISCUSSION

For many amphibians that inhabit temperate environments, estimating annual survival between consecutive breeding seasons is sufficient to characterize population dynamics. For species that are short-lived, are active year-round, or have multiple or prolonged breeding seasons within a year, annual estimates of survival may not capture short-term variation in this important demographic parameter. Underestimating interannual, and presumably intraannual, variability in demographic parameters can overestimate population growth rates, particularly for short-lived species (Morris et al. 2008). Therefore, understanding the extent to which survival and other demographic rates vary temporally, as well as the environmental factors that govern such variation, is necessary to assess long-term population viability and to inform conservation strategies in light of impending stressors, such as climate change.

Temporal variation in post-metamorphic survival of lowland leopard frogs reflected the highly dynamic nature of these mountain canyon environments. Survival was higher during late spring and summer than in winter when ambient temperatures often fall below 5 °C (Fig. 2.5, Table 2.3). This pattern corroborated previous findings based on an independent source of data (long-term counts; Zylstra et al. 2015) as well as our incidental observations of lethargic frogs at pool edges on very cold winter mornings. Contrary to our expectations, however, apparent survival decreased as dew point

increased. This result might reflect increased rates of emigration rather than mortality, as leopard frogs may have been more likely to leave survey reaches or make long-distance movements when risk of desiccation was lower (Chapter 1), similar to other amphibians in arid environments (Schwarzkopf and Alford 2002, Tingley and Shine 2011).

After adjusting for weather, surface-water availability accounted for much of the seasonal, annual, and spatial variation in post-metamorphic survival (Table 2.3). Whether a consequence of physiological stress, reductions in food resources, or increased vulnerability to predators, survival dropped precipitously when surface-water availability was low (Fig. 2.4), which typically occurred when ≥ 1 pool in a stream reach dried. Although other studies have linked survival of post-metamorphic amphibians to total annual precipitation or binary indicators of drought (Grafe et al. 2004, Church et al. 2007, Cayuela et al. 2016), our study provides evidence that survival rates of amphibians can vary markedly within a season in response to short-term, local changes in hydrologic conditions.

Unlike populations in other parts of their range, lowland leopard frogs in southeastern Arizona seem to be declining in both distribution and abundance (Clarkson and Rorabaugh 1989, Sredl et al. 1997, Witte et al. 2008, Savage et al. 2011). Remaining populations are often small (<100 individuals; Sartorius and Rosen 2000, Wallace et al. 2010, Savage et al. 2011), increasing the risk of extirpation from demographic stochasticity (Caughley and Gunn 1996, Melbourne and Hastings 2008). Although we do not know the proximate cause of the extirpation of leopard frogs in the north watershed, severe drought almost certainly contributed to these declines. Unusually dry conditions in the lower reaches of this watershed—a consequence of prolonged, severe drought

(annual precipitation in water years 2012–2014 was 58–84% of 30-year normals²)—reduced both post-metamorphic survival and reproductive output (Table 2.2). When drought conditions subsided in late 2014 and 2015, few frogs remained (we observed only two individuals after Aug 2014) and did not reproduce; the population subsequently went extinct in 2015.

Even during a relatively wet year in 2015, annual survival of lowland leopard frogs in the populations we studied was low compared to other ranids, including closely related species that inhabit arid environments (0.27 in *Lithobates onca*, Bradford et al. 2004; 0.27 in *Lithobates chiricahuensis*, Howell et al. 2016). It is unclear whether low rates of survival in lowland leopard frog populations are a recent phenomenon or whether survival rates in these populations have always been low. Historically, populations of leopard frogs and other aquatic vertebrates that inhabited mountain canyons were likely peripheral to core populations along perennial watercourses in valley bottoms (Clarkson and Rorabaugh 1989, Sredl 2005, Hall and Steidl 2007). Based on ecological theory, we might expect these peripheral populations to have lower and more variable densities and lower rates of reproduction or survival (Brown 1984). Alternatively, survival in these peripheral populations might have been higher historically and only declined in the last several decades as the southwestern U.S. has become increasingly arid (Weiss et al. 2009, Balling and Goodrich 2010). Reductions in the surface and subsurface waters that feed streams in these mountain canyons have likely reduced the quantity and quality of aquatic resources on which leopard frogs depend (Dahm et al. 2003).

² National Weather Service: <https://www.weather.gov/twc>; Accessed 4 Sep 2017

In addition to altering the hydrology of mountain canyons, long-term drying at the regional scale is likely to reduce the probability of lowland leopard frogs persisting in southern Arizona by decreasing connectivity among these isolated, remnant populations (Walls et al. 2013). Until recently, dispersal of leopard frogs among stream reaches and canyons has allowed the species to persist in this region despite low rates of survival and occasional extinctions of local populations (Chapter 1). If drought reduces the spatial distribution of aquatic refugia or reduces the frequency with which sites are connected hydrologically, however, dispersing individuals may be unlikely to reach unoccupied sites. These environmental changes are likely to reduce the probability that metapopulations will persist over the long-term. The impact of drought on networks of ponds with varying hydroperiods and the amphibians that inhabit these environments has been explored theoretically and empirically (e.g., Fortuna et al. 2006, Chandler et al. 2015). This research indicates that metapopulations are likely to persist despite frequent or severe drought when 1) density of inhabitable sites is high, 2) a significant proportion of sites are spring-fed or sufficiently deep to retain water during drought, or 3) species are capable of dispersing long distances (Fortuna et al. 2006, Chandler et al. 2015). Metapopulations of lowland leopard frogs in the Sky Island region may be less resilient to drought than other amphibians, however, because drought has the potential to affect post-metamorphic survival, recruitment, and dispersal adversely. As sites with reliable surface water become increasingly rare and geographically isolated, sources of potential emigrants will decrease and distances among habitable sites will increase, reducing the chances that unoccupied sites are recolonized and increasing the probability that local populations go extinct.

TABLE 2.1. Descriptions of six stream reaches in the Rincon Mountains surveyed for lowland leopard frogs between May 2013 and November 2015.

Watershed	Reach length (m)	Elevation (m)		No. pools	Years surveyed	No. surveys
		Min.	Max.			
South	598	1036	1069	24	2013–2015	74 ^a
	1944	1022	1208	14	2014–2015	33
	1104	1083	1291	18	2014–2015	38
North	681	870	932	14	2013–2015	45
	1229	942	1015	23	2013–2015	57
	1011	1062	1233	19	2013–2015	63

^a Includes surveys between mid-November and the end of February.

TABLE 2.2. Results from surveys for lowland leopard frogs in two watersheds (South, North) in the Rincon Mountains in water years 2013 (May 2013–Sep 2014), 2014 (Oct 2013–Sep 2014), and 2015 (Oct 2014–Sep 2015). We report minimum surface-water availability (mean water depth relative to maximum pool depth) observed in any survey reach, seasonal reproductive output (number of pools where eggmasses were observed and total number of eggmasses), maximum number of post-metamorphic leopard frogs (snout-vent-length [SVL] ≥ 50 mm) observed during a survey in any reach, and number of photosets.

	South			North		
	2013	2014	2015	2013	2014	2015
Number of reaches surveyed	1	3	3	3	3	3
Minimum surface-water availability	0.26	0.09	0.30	0.16	0.03	0.43
Spring reproduction (no. pools) ^a		8	14		1	0
Spring reproduction (no. eggmasses) ^a		22	29		1	0
Fall reproduction (no. pools) ^b	3	7	12	2	0	0
Fall reproduction (no. eggmasses) ^b	9	13	21	2	0	0
Max. count of post-metamorphic frogs	37	36	25	10	4	1
Number of photosets	234	364	248	91	62	4

^a Eggmasses observed between February and April. Reaches were not surveyed in spring 2013.

^b Eggmasses observed between August and October. We included observations in October 2014 with water year 2014 and observations in October 2015 with water year 2015.

TABLE 2.3. Parameter estimates on the logit scale, Wald Z-statistics, and associated *P*-values from a model describing apparent survival and recapture probabilities of post-metamorphic lowland leopard frogs in southern Arizona, USA between 2013 and 2015. Year:2014 is an indicator variable for water year 2014 (Oct 2013–Sep 2014), and Year:2015 is an indicator variable for the period between October 2014 and November 2015. All other covariates were standardized relative to their means and standard deviations. See the Methods section for detailed descriptions of covariates.

Parameter	Covariate	Estimate	SE	Z	<i>P</i>
Survival	Intercept	2.61	0.39		
	Year:2014	-0.31	0.41	-0.76	0.450
	Year:2015	-0.55	0.39	-1.41	0.159
	Surface-water availability	0.27	0.25	1.12	0.265
	Surface-water availability ²	-0.32	0.14	-2.37	0.018
	Temperature	0.51	0.26	1.96	0.050
	Dew point	-0.64	0.29	-2.21	0.027
	Perimeter groundcover	-0.05	0.09	-0.59	0.555
Recapture	Intercept	-0.49	0.17		
	Year:2014	-0.59	0.18	-3.28	0.001
	Year:2015	0.04	0.19	0.22	0.826
	Surface-water availability	-0.39	0.10	-3.94	<0.001
	Surface-water availability ²	-0.04	0.06	-0.70	0.487
	Humidity	-0.04	0.07	-0.57	0.569
	Wind	-0.09	0.07	-1.34	0.180
	Temperature	0.13	0.06	2.19	0.029
Perimeter groundcover	-0.20	0.05	-3.65	<0.001	

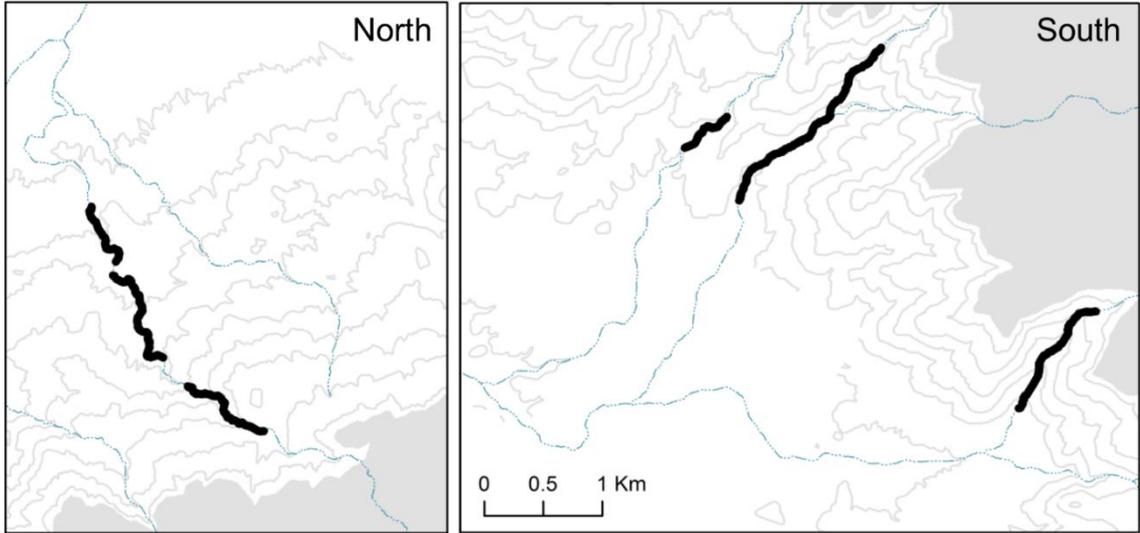


FIGURE 2.1. Maps of six stream reaches surveyed for lowland leopard frogs in two watersheds (South, North) in the Rincon Mountains. Light gray lines are 60-m elevation contours; areas above 1370 m elevation are shaded gray.

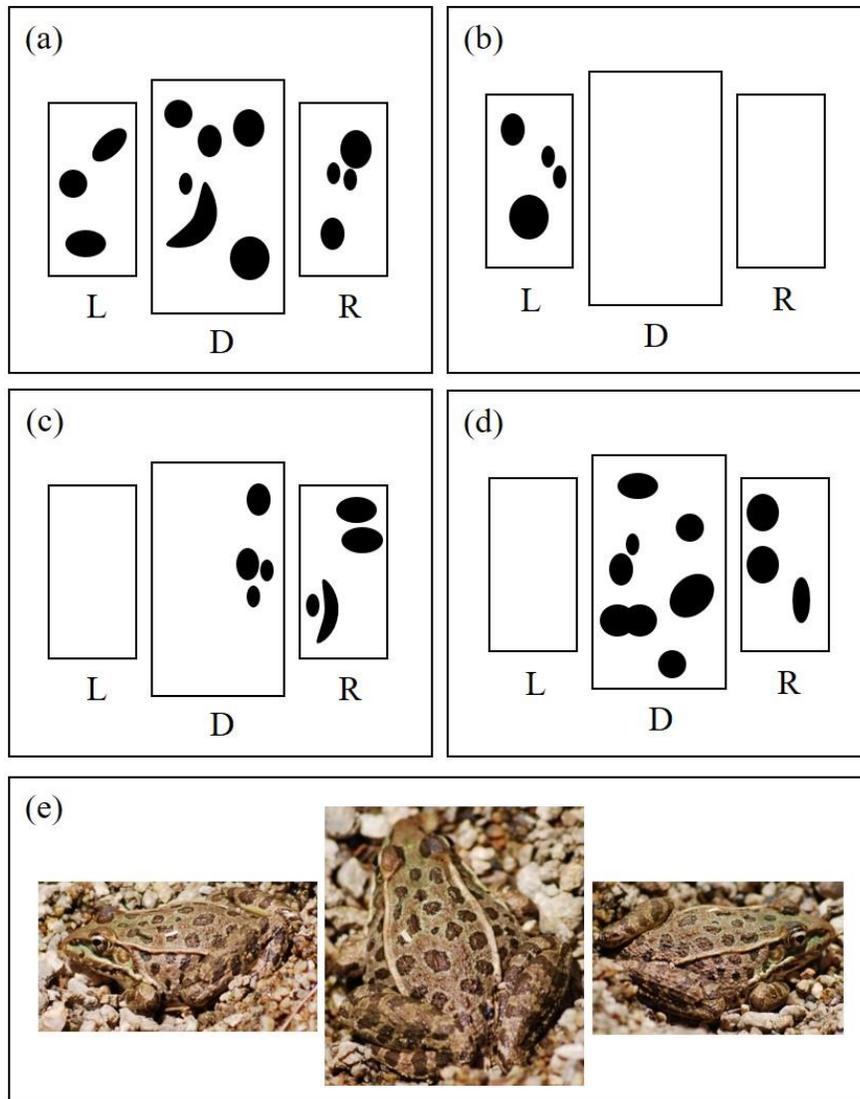


FIGURE 2.2. Schematic of a spot pattern that was mapped completely (a) and three partially-mapped spot patterns (“partial spot maps”; b-d). Boxes above the letter “L” depict features on the left flank, boxes above “D” depict features on the dorsum, and boxes above “R” depict features on the right flank. The partial spot maps in panels (c) and (d) cannot represent the same frog, as they overlap in extent and have no matching features. The partial spot map in panel (b) can represent the same frog as that represented in panel (c) or (d), however, as there is no overlap between (b) and the other partial spot maps (c, d). In panel (e) we present images of a frog whose spot pattern was mapped completely.

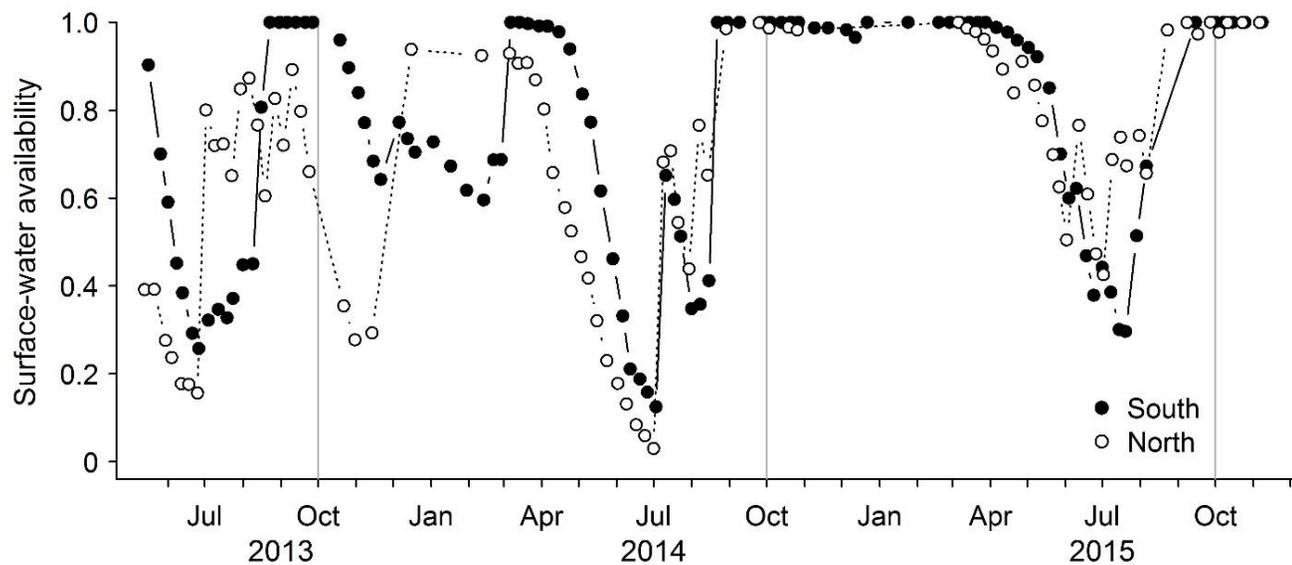


FIGURE 2.3. Surface-water availability (mean water depth relative to maximum pool depth) in one of the reaches in the south watershed and in the middle-elevation reach in the north watershed. Vertical gray lines represent the start of each water year.

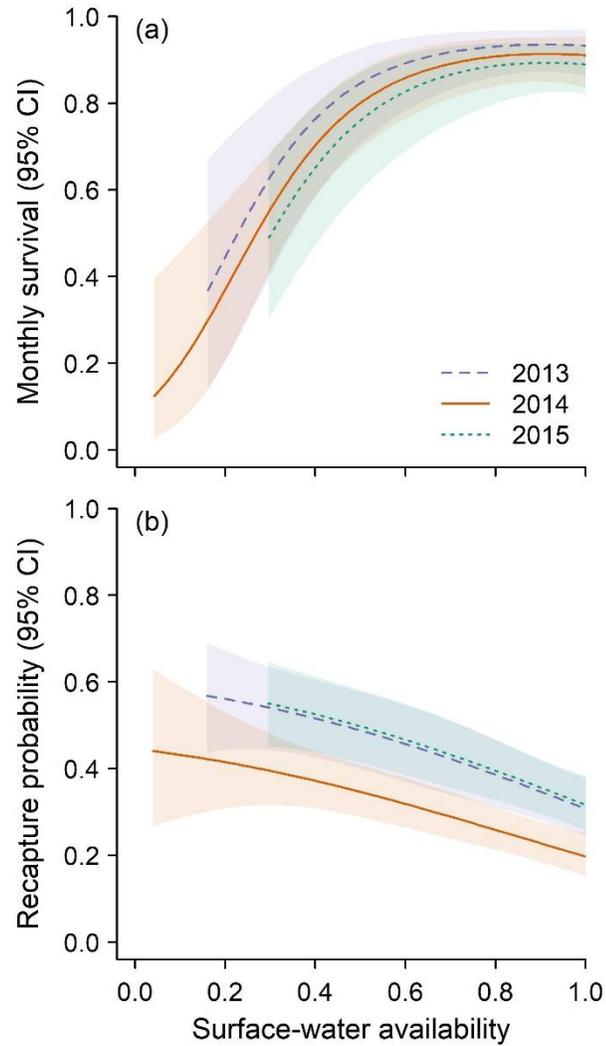


FIGURE 2.4. Apparent monthly survival (a) and recapture probabilities (b) of post-metamorphic lowland leopard frogs as a function of surface-water availability (mean water depth relative to maximum pool depth) and water year. We predicted survival and recapture probabilities across the range of surface-water availability values we observed in each water year, while fixing all other covariates at their mean values.

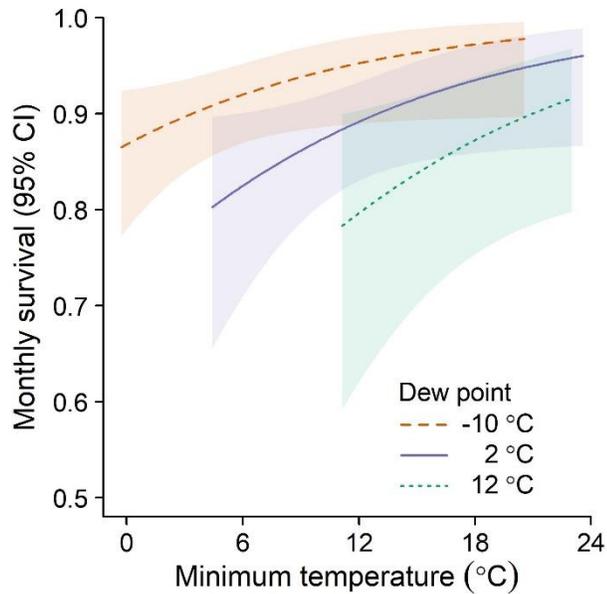


FIGURE 2.5. Apparent monthly survival of post-metamorphic lowland leopard frogs between October 2013 and November 2014 (i.e., water year 2014) as a function of minimum daily temperature and dew point. We only predicted survival for temperatures that were observed when mean dew point was within 4 °C of selected values (e.g., we predicted survival for a mean dew point of -10 °C based on temperatures observed when mean dew point ranged from -14 °C to -6 °C). We fixed surface-water and vegetation covariates at their observed means.

CHAPTER 3: A BAYESIAN STATE-SPACE MODEL FOR SEASONAL GROWTH OF TERRESTRIAL VERTEBRATES IN DYNAMIC ENVIRONMENTS

ABSTRACT

Somatic growth determines the rate at which individuals reach sexual maturity and transition among life stages, which along with survival and reproduction, are principal factors governing population rates of change. For short-lived species that inhabit dynamic environments, such as many post-metamorphic amphibians, accounting for seasonal fluctuations in somatic growth can improve inferences about population dynamics. We describe a Bayesian, state-space formulation of a von Bertalanffy growth model that integrates a sinusoidal model for seasonal growth while also accounting for individual heterogeneity and measurement error. We use this model to describe growth of canyon treefrogs, *Hyla arenicolor*, that inhabit arid mountain canyons in the southwestern United States, based on capture-recapture data from 404 individuals. Our model provided unbiased estimates of characteristic growth rate, k , and mean asymptotic size, L_∞ , when growth fluctuates seasonally. In contrast, a traditional model that assumed growth was constant overestimated k , biasing estimates of time to sexual maturity and other life stages. For canyon treefrogs, we found strong evidence that growth varied seasonally and annually, with maximum growth rates during the summer monsoon season. Females grew faster than males (mean difference in characteristic growth rate = 0.52 yr^{-1}) and reached asymptotic sizes that averaged 5.1 mm larger than males. Projected growth curves from the model were consistent with length-frequency

histograms for all treefrogs captured during each survey occasion. Collectively, our results indicate that treefrogs in this region are shorter-lived and have higher rates of population turnover than other co-occurring amphibians. Failure to account for seasonal fluctuations in growth can bias inferences, particularly when using growth-related parameters to describe population dynamics of fast-growing species that reproduce more than once per year or inhabit environments with strong seasonal signals. We present a straightforward approach for using repeated length measurements from individuals of unknown age to estimate growth while accounting for seasonality and individual heterogeneity, sources of variation common in many vertebrate populations.

INTRODUCTION

Life-history traits, including rates of survival, reproduction, and somatic growth, govern dynamics of vertebrate populations, therefore understanding how traits vary over time, across space, and among individuals is essential for predicting population rates of change (Caswell 2001). For many terrestrial species, research has focused on survival and reproduction, with less effort focused on characterizing somatic growth or age at first reproduction (Crouse et al. 1987, Caswell 2001, Sibly and Hone 2002). The rate at which individuals reach sexual maturity or transition between distinct life stages, however, has important consequences for both the fitness of individuals and for dynamics of populations (Semlitsch et al. 1988, Stearns 1992). For example, individuals with higher rates of somatic growth may be more likely to survive to sexual maturity by reducing the duration of earlier life stages when predation mortality is highest (Werner and Gilliam 1984, Werner 1986). Further, for iteroparous species, individuals that reach sexual

maturity earlier may increase lifetime reproductive output (Cole 1954, Lewontin 1965, Oli et al. 2002).

Unlike many vertebrates, growth of most amphibians is biphasic, a consequence of abrupt changes in body structure at metamorphosis (Duellman and Trueb 1986). Growth of pre-metamorphic, or larval, amphibians can vary markedly in response to a number of extrinsic factors, including density of conspecifics (Semlitsch and Caldwell 1982), presence of predators or competitors (Skelly 1992, Relyea 2004), temperature (Harkey and Semlitsch 1988), and hydrologic conditions (Rowe and Dunson 1995). Numerous studies have focused on growth of individuals in early life stages because of its effect on age and size at metamorphosis, which can affect post-metamorphic survival, reproductive output, and locomotor performance (Berven and Gill 1983, Semlitsch et al. 1988, Ficetola and De Bernardi 2006). Most growth of amphibians, however, occurs after metamorphosis (80-99% of adult size; Werner 1986). Growth during this period affects a series of life-history traits, including the transition from juvenile to adult life stages, which can have strong effects on dynamics of some amphibian populations (Biek et al. 2002).

Models of somatic growth, particularly those for post-metamorphic amphibians, have relied traditionally on tools such as skeletochronology to relate age to body size (Hemelaar 1988, Tinsley and Tocque 1995, Liao and Lu 2010). Inferences based on these methods, however, can be limited by sample size or high uncertainty of age estimates (Sullivan and Fernandez 1999, Eden et al. 2007, Sinsch 2015). Although body size is measured commonly when animals are captured, such as when capture-recapture methods are used to estimate survival, only a few studies have explored somatic growth

of post-metamorphic individuals (Blackwell et al. 2003, Hamer and Mahony 2007, Lee et al. 2012). These studies may be limited, in part, because traditional growth models do not accommodate seasonal fluctuations in growth that occurs in many temperate species (Martof 1956, Turner 1960). Further, individual heterogeneity in growth can bias estimates of growth parameters (Sainsbury 1980, Zhang et al. 2009). We outline an approach for modeling growth of post-metamorphic amphibians based on repeated measures of body size that overcomes these limitations. Specifically, we describe a Bayesian, hierarchical formulation of the von Bertalanffy growth model to account for both seasonal fluctuations in growth and individual heterogeneity in growth parameters (Zhang et al. 2009, Tang et al. 2014). We use a state-space framework (Kéry and Schaub 2012) to separate measurement error from variation in growth associated with season, year, or differences among individuals.

We begin with a general description of the growth model and use simulations to assess bias of model estimates. We then apply the model to growth of the canyon treefrog, *Hyla arenicolor*, a small-bodied, short-lived frog that inhabits arid mountain canyons in the southwestern United States (Painter 2005). Treefrogs in this region can reproduce twice per year, with cohorts emerging from larval stages at the beginning and end of the summer monsoon season (Gehlbach 1965). Growth is likely to vary seasonally in treefrogs because temperature and hydrologic conditions can differ markedly among cohorts of newly-transformed individuals and because treefrogs retreat to rock crevices for several months in winter (Hammerson 1999, Baker 2010). To make broader inferences about the life-history of canyon treefrogs in the region, we complement our estimates of growth with data from visual encounter surveys describing

the phenology of reproduction and recruitment events, providing new insights into demography and population dynamics of this understudied species.

METHODS

Growth model

For wild animals, it is rare to be able to characterize attributes or “states” of individuals or populations perfectly because field methods are imperfect; for example, researchers can overlook individuals that are present or quantify their traits incorrectly. Consequently, state-space approaches have been applied increasingly to ecological data because they decompose survey data (e.g., counts of individuals, measures of length and mass) into variation attributable to the true state (i.e., the process model) and variation attributable to the sampling or measurement process (i.e., the observation model; Kéry and Schaub 2012). The process model we developed is a growth-interval form of the von Bertalanffy model, modified to allow seasonal variation in post-metamorphic growth of amphibians (Fabens 1965, Somers 1988). We model growth as a sine function with a period of one year, such that

$$L_{i,t+d} - L_{i,t} = (L_{\infty,i} - L_{i,t})(1 - \exp[-k_{i,t}d + S(i,t) - S(i,t+d)]), \quad (3.1)$$

where

$$S(i,t) = Ck_{i,t}/2\pi * \sin[2\pi(t - t_s)], \quad (3.2)$$

$L_{i,t}$ is length of individual i at time t (in fractions of a year after 1 Jan), d is the time elapsed in years between consecutive observations, $L_{\infty,i}$ is asymptotic length of individual i , $k_{i,t}$ is the characteristic growth rate of individual i at time t , C is the magnitude of seasonal oscillations in the growth rate, and t_s is the time (in fractions of a year) at which

the growth rate is maximized (Frazer and Ehrhart 1985, Somers 1988, Robins et al. 2006). Although commonly referred to as a growth rate, units for k are yr^{-1} rather than length/yr given that k reflects the “exponential rate of approach to asymptotic size” (Schnute and Fournier 1980); consequently, k is not comparable directly among species. In this seasonal parameterization, C ranges from 0 to 1, with a value of 1 indicating that growth ceased during some portion of each year and a value of 0 indicating that growth did not fluctuate seasonally. Importantly, to apply this model, measurements must be made in more than one season per year (i.e., the duration of some intervals $[d]$ must be <1 year).

Traditionally, growth models have assumed that L_∞ and k are identical for all individuals in a population (Fabens 1965). Estimates of growth parameters can be biased, however, when models do not account for heterogeneity in growth among individuals, particularly in L_∞ (Sainsbury 1980, Eveson et al. 2007, Zhang et al. 2009). Individual heterogeneity in growth parameters can be modeled as a function of measured covariates (e.g., ectoparasite load) or with an individual-level random effect. We use a hybrid approach that allows L_∞ and k to vary among groups of individuals (e.g., males and females or individuals at different sites) and include a random effect for L_∞ to account for unmodeled heterogeneity within groups. Specifically, we consider individual asymptotic length, $L_{\infty,i}$, to be a random variable drawn from a normal distribution with mean equal to the group mean and variance representing heterogeneity in asymptotic length among individuals:

$$L_{\infty,i} \sim N(\bar{L}_{\infty,g(i)}, \sigma_{\infty,g(i)}^2),$$

where $\bar{L}_{\infty,g(i)}$ is the mean asymptotic length of individuals in the group that includes individual i and $\sigma_{\infty,g(i)}^2$ is the variance in asymptotic length among individuals within that same group.

We modeled the characteristic growth rate of individual i at time t with a linear model:

$$k_{i,t} = \boldsymbol{\beta}_g \mathbf{X}_{g(i)} + \boldsymbol{\beta}_y \mathbf{X}_{y(t)}, \quad (3.3)$$

where $\boldsymbol{\beta}_g$ and $\boldsymbol{\beta}_y$ are vectors of estimated coefficients for group- and year-level effects, respectively; $\mathbf{X}_{g(i)}$ is a vector of ones and zeros indicating group membership of individual i and $\mathbf{X}_{y(t)}$ is a vector of environmental conditions in year y or a vector of ones and zeros indicating the year of observation t . We restrict $\mathbf{X}_{y(t)}$ to conditions that vary annually ($\mathbf{X}_{y(t)}$ rather than modeling time directly as \mathbf{X}_t) because we assume seasonal oscillations of k within years. We specify a fixed year effect when annual data on environmental conditions are not available, but a random effect could also be specified. To increase model efficiency and ensure that all parameters are identifiable, we assume k to be constant among individuals in the same group and year.

For the observation model, we compare measured and predicted growth between consecutive observations of each individual. Specifically, we assume a normal distribution for observed growth of individual i between time t and $t+d$:

$$y_{i,t} \sim N(L_{i,t+d} - L_{i,t}, \sigma_{\Delta L}^2)$$

where $L_{i,t+d} - L_{i,t}$ represents the true change in length of individual i and $\sigma_{\Delta L}^2$ represents the variance associated with measurement error. Similar to other models, ours contains an implicit assumption that length at first capture was measured without error (Jiao et al. 2010, Tang et al. 2014, Dzul et al. 2017). We adopted this approach because it decreases

the time required for the model to converge and has minimal effect on parameter estimates.

We used simulations to evaluate the reliability of the model and to characterize bias in parameter estimates. We simulated 100 datasets, each containing length measurements for 600 females across eight survey occasions in each of two consecutive years. To ensure all individuals had ≥ 2 measurements in a given year, we assumed all individuals were recaptured during the survey immediately after they were marked; subsequently, we assumed an annual survival rate of 0.50 and recapture rate of 0.70. We simulated length measurements assuming seasonal, but not annual variation in growth rates. For each dataset, we estimated \bar{L}_∞ , σ_∞ , k , t_s , and $\sigma_{\Delta L}$ from a seasonal model where C was fixed equal to one (eqn 3.1) and estimated \bar{L}_∞ , σ_∞ , k , and $\sigma_{\Delta L}$ from a model where growth was assumed constant:

$$L_{i,t+d} - L_{i,t} = (L_{\infty,i} - L_{i,t})(1 - e^{-k_{i,t}d}). \quad (3.4)$$

To assess whether our seasonal model was robust to misspecification, we simulated 100 new datasets where growth rate was constant throughout the year and estimated \bar{L}_∞ , σ_∞ , k , t_s , C , and $\sigma_{\Delta L}$ from the seasonal model. Additional details about the simulations appear in Appendix D.

Growth of canyon treefrogs

Study area.—We studied canyon treefrogs in the Madrean Sky Island region of southeastern Arizona, where isolated mountain ranges are separated by vast expanses of desert and semi-desert grasslands. Specifically, we surveyed treefrogs in mid-elevation (850–1300 m) reaches of four canyons in the Rincon Mountains east of Tucson, Arizona

in Saguaro National Park. Streams in these reaches are deeply incised, characterized by shallow, bedrock-lined pools. Most pools are <2 m deep with surface areas 3–12 m², limited soil-bank development, and limited aquatic vegetation (Wallace et al. 2010). Stream flow varies seasonally, a product of a bimodal precipitation regime (Brown 1982). Perennial pools are often connected by shallow riffles and runs between December and April in response to widespread winter rains. Between July and September, localized and high-intensity monsoon storms cause sporadic flash floods. In late spring (May–Jun) and late fall (Oct–Nov), stream channels between perennial pools typically remain dry (Grimm and Fisher 1992, Wallace et al. 2010).

Field surveys.—We used capture-recapture methods to survey treefrogs along four stream reaches that ranged in length from 500 m to 2900 m. Between April 2014 and June 2016, we captured canyon treefrogs on 11 different survey occasions. During each occasion, we spent 4–10 days capturing treefrogs, with consecutive surveys on each reach separated by 1–7 months. We captured treefrogs in spring (Apr, May, and Jun) and fall (late Sep–early Oct, late Oct–early Nov) when treefrogs congregated near perennial pools. During the final survey occasion on each reach and when we observed <100 treefrogs on a reach, we attempted to capture all individuals with snout-vent length (SVL) ≥ 35 mm. When we observed ≥ 100 treefrogs on a reach, we focused our effort on segments where treefrogs were present consistently and accessible to surveyors.

We captured treefrogs by hand and released individuals after processing at the capture location. For each treefrog captured, we measured SVL and classified sex of adults (SVL ≥ 40 mm) based on throat color (Wylie 1981, Baker 2010). Infrequently, individuals that were captured as adults ≥ 2 times were classified as male and female on different

occasions (<10% of adults). For analysis, we used sex assigned at last capture because secondary sex characteristics (i.e., dark-colored throats in males) are more likely to be evident when individuals are sexually mature. We marked each individual uniquely by injecting a 1.2 mm x 2.7 mm alphanumeric tag in the left calf, where skin was transparent. We handled treefrogs with vinyl gloves and disinfected equipment between handling individuals to prevent spread of disease. Our protocol was approved by the University of Arizona's Institutional Animal Care and Use Committee (protocol 13-450).

To evaluate the time required for post-metamorphic treefrogs to reach reproductive age and 90% of asymptotic size, we used visual encounter surveys to document reproduction and recruitment events. We surveyed the same stream reaches for treefrogs once every 5–10 days between March and October, 2014–2015, excluding periods of high stream flow when reaches were inaccessible and treefrogs were difficult to detect. During each survey, we recorded the number and location of individuals observed in each stage class (eggs, tadpoles, metamorphs [Gosner stages 42–45], juveniles [estimated SVL <40mm], adults; Gosner 1960). We considered observations of eggs or newly hatched tadpoles as evidence of reproduction and presence of metamorphs or newly emerged juveniles (estimated SVL <25 mm) as evidence of recruitment.

Model selection.—To establish a model for inference for growth of canyon treefrogs, we began by constructing a rich model that included seasonal fluctuations in growth rates and allowed L_{∞} and k to vary with sex and k to vary with year (defined as 1 Oct–30 Sep to correspond with hydrologic water year, an interval used frequently in studies of stream systems):

$$L_{\infty,i=F} \sim N(\bar{L}_{\infty,F}, \sigma_{\infty,F}^2)$$

$$L_{\infty,i=M} \sim N(\bar{L}_{\infty,M}, \sigma_{\infty,M}^2)$$

$$k_{i,t} = \beta_0 + \beta_1 x_{i=M} + \beta_2 x_{i,t=y2015} + \beta_3 x_{i,t=y2016} \quad (3.5)$$

where $L_{\infty,i=F}$ and $L_{\infty,i=M}$ are asymptotic lengths (mm) of individual i for females and males, respectively; $x_{i=M}$ is an indicator equal to one if individual i is male; and $x_{i,t=y2015}$ and $x_{i,t=y2016}$ are indicators of water years 2015 (defined as Oct 2014–Sep 2015) and 2016 (Oct 2015–Jun 2016), respectively, for individual i at time t . In this parameterization, the intercept, β_0 , represents growth of females in water year 2014 (Apr–Sep 2014). For individuals that were never captured with SVL >40 mm and therefore never classified as male or female (7% of recaptured individuals), we modeled sex as a random variable and assumed a 50:50 sex ratio:

$$x_{i=M} \sim \text{Bern}(0.5), \quad i = 1, \dots, n,$$

where n is the number of individuals of unknown sex.

We then evaluated whether there was sufficient evidence of seasonal fluctuations in post-metamorphic growth of canyon treefrogs. We constructed a model with the same error structure and the same covariates for L_{∞} and k , but did not include a seasonal component (eqn 3.4). We used deviance information criterion (DIC), a composite measure that reflects model fit while incorporating a penalty for added model complexity, to compare models and proceeded with the model that had the lower DIC (Spiegelhalter et al. 2002). Finally, we assessed whether sex and year explained variation in L_{∞} and k . We constructed eight models with all combinations of covariates for L_{∞} and k and selected the model with the lowest DIC value for inference. We predicted length of average treefrogs over time based on the top model, assuming 1) SVL was 22.5 mm at

metamorphosis (Wylie 1981), 2) metamorphosis occurred on 1 July and 1 September (based on our visual encounter surveys), and 3) growth rates immediately after metamorphosis were similar to those of individuals with SVL ≥ 35 mm.

Model implementation.—We specified uniform priors for mean asymptotic lengths of females and males: $\bar{L}_{\infty,F} \sim U(40, 60)$ and $\bar{L}_{\infty,M} \sim U(40, 60)$. We specified a uniform prior for growth rate of females in 2014, $\beta_0 \sim U(0, 5)$, and normal priors for regression coefficients associated with the effects of sex and year on k ($\beta_1 \sim N(0, 1)$, $\beta_2 \sim N(0, 1)$, $\beta_3 \sim N(0, 1)$). We limited variances of the prior distributions for β_1 , β_2 , and β_3 because we expected characteristic growth rates to range between zero and five (Wylie 1981, Liao and Lu 2010). We specified uniform priors for the standard deviation of growth measurements, $\sigma_{\Delta L} \sim U(0, 10)$, and individual variation in asymptotic lengths, $\sigma_{\infty,F} \sim U(0, 10)$ and $\sigma_{\infty,M} \sim U(0, 10)$, as recommended for hierarchical models (Gelman 2006). Finally, we assigned uniform priors on the unit interval for both C and t_s .

We fit models in JAGS executed from R using the package rjags (Plummer 2003, R Core Team 2016); example JAGS code is provided in Appendix E. For each model, we ran three Markov chains initiated at random values for 250,000 iterations. We discarded the first 50,000 iterations as burn-in and retained 1 of every 20 iterations thereafter to summarize the posterior distribution. We assessed convergence by inspecting trace plots and Gelman-Rubin diagnostics (Gelman and Rubin 1992). To assess goodness-of-fit, we generated posterior predictive distributions for two summary discrepancy measures: the mean and standard deviation (SD) of growth increments across all individuals and capture intervals (Gelman et al. 1996, Chambert et al. 2014). We calculated one-sided (left-tail) posterior predictive P -values for each measure, with values near 0.5 indicating

adequate model fit and values near 0 or 1 indicating poor model fit. To assess sensitivity of estimates to prior specifications, we ran the final model used for inference after increasing the upper bounds of uniform priors for β_0 , $\sigma_{\Delta L}$, $\sigma_{\infty,F}$, and $\sigma_{\infty,M}$ by a factor of two, widening the priors for $\bar{L}_{\infty,F}$ and $\bar{L}_{\infty,M}$ to include values up to 80 mm, and increasing the standard deviation of each normal prior by a factor of two.

RESULTS

Model assessment

For the range of values we explored, estimates of characteristic growth rate (k), mean asymptotic length (\bar{L}_{∞}), and date of maximum growth (t_s) from our model were largely unbiased, with mean percent relative bias ranging from -0.2% to 1.7% (Appendix D: Table D1). Variance parameters, however, were overestimated consistently (Appendix D: Table D1). Even when growth was constant throughout a year, our model provided reliable estimates of \bar{L}_{∞} and k , with mean percent relative bias $<2\%$. When growth fluctuated seasonally, our model outperformed a model where growth was assumed constant, as expected. When fit to data where growth fluctuated seasonally, a model that assumed growth to be constant overestimated k (Appendix D: Table D1) and overestimated the time required to reach sexual maturity (40 mm) by 49% (7 weeks; Fig. 3.1).

Growth of canyon treefrogs

We marked 1852 treefrogs, 404 of which (22%) we recaptured at least once. Of the 189 individuals recaptured that we identified as females, we recaptured 85% once, 13%

twice, and 3% three or more times (mean = 1.2 recaptures/female, range=1–7). Of the 186 recaptured males, we recaptured 76% once, 19% twice, and 5% three or more times (mean = 1.3 recaptures/male, range=1–5). We surveyed four stream reaches 223 times in total (mean no. surveys/reach/year = 27.9, range = 26–30) and observed a bimodal pattern in annual reproduction and recruitment (Fig. 3.2). Duration of the larval period ranged from 6–12 weeks. For eggs oviposited in early spring (eggs observed on 41% of surveys between 16 Mar and 24 Apr), most post-metamorphic individuals emerged just prior to the onset of summer monsoon rains (metamorphs observed on 46% of surveys between 1 Jun and 14 Jul). For eggs oviposited at the beginning of monsoons (eggs observed on 58% of surveys between 27 Jun and 31 Jul), most individuals emerged in early fall (metamorphs observed on 98% of surveys between 24 Aug and 17 Oct).

Growth of treefrogs fluctuated seasonally (Δ DIC for a non-seasonal model = 58.5). Because there was strong evidence that treefrogs stopped growing in winter (between late December and March), we fixed the magnitude of seasonal oscillations in the growth rate (C) to 1 in our final model (>77% of samples from the posterior distribution of C were >0.90). We found that mean asymptotic size varied with sex and growth rates varied with sex and year (Δ DIC for models that excluded any of these effects ≥ 2.7 ; Table 3.1). Specifically, females grew faster than males (mean difference in characteristic growth rate = 0.52 yr^{-1}) and reached larger asymptotic sizes ($\bar{L}_{\infty,F} - \bar{L}_{\infty,M} = 5.1 \text{ mm}$; Table 3.2). In addition, individuals of both sexes grew faster in water year 2015 than in other years (Table 3.2). Projections of post-metamorphic growth indicated that treefrogs typically reached 90% of asymptotic length 5–11 months after metamorphosis (Fig. 3.3). Time to reach asymptotic length varied somewhat with sex, cohort, and year (Fig. 3.3). Only

11% of females and 22% of males we captured had an SVL within 1 mm of or greater than mean asymptotic length, indicating low rates of post-metamorphic survival.

All diagnostic measures for the final model we used for inference about growth of canyon treefrogs indicated adequate model fit, including posterior predictive P -values of 0.30 and 0.70 for mean and SD discrepancy measures, respectively. There was little evidence of autocorrelation within chains after thinning iterations by 20. Gelman-Rubin statistics for all parameters were <1.1 , indicating convergence of Markov chains. Estimates of parameters were largely insensitive to prior specification; on average, posterior means differed by 2.1% (range = 0.0–11.3%) when we assumed different priors.

DISCUSSION

Sophisticated models have been developed to characterize somatic growth and transition rates of fish and other aquatic organisms (e.g., Robins et al. 2006, Zhang et al. 2009, Dzul et al. 2017), but models for terrestrial vertebrates are uncommon, particularly for species that are not harvested, such as amphibians. For many species, information on growth is lacking because wild animals are difficult to age reliably in the field. Our model, however, provides a framework for estimating growth based on repeated measurements of body size from individuals of unknown age, data collected commonly during studies that use capture-recapture methods.

With growing evidence of seasonal fluctuations or interruptions in growth of fish and other taxa, multiple approaches have been developed to incorporate seasonality into models of somatic growth, including sinusoidal models (Pitcher and Macdonald 1973, Somers 1988), polynomial regression (Brown 1988), Gaussian-process models

(Sigourney et al. 2012), and log-linear models (Dzul et al. 2017). We adopted a sinusoidal approach, which is phenomenological and does not require specifying mechanisms that might govern seasonal fluctuations in growth. If environmental conditions thought to be associated with growth were measured across seasons at the local scale, a mechanistic model could be used to assess the relative influence of environmental factors on seasonal growth patterns (e.g., Sigourney et al. 2012, Dzul et al. 2017). When these auxiliary data are unavailable, however, our model provides an approach to estimate growth while accounting for seasonal variation, a likely circumstance for organisms that inhabit an array of dynamic environments.

Accounting for seasonal fluctuations in growth can have strong effects on inferences, particularly when growth-related parameters are used to estimate the rate of population change or to predict population responses to future environmental changes. For relatively short-lived species that reproduce more than once per year, for example, time to sexual maturity might vary appreciably among cohorts that develop under different sets of environmental conditions, a pattern we observed in canyon treefrogs (Figs. 3.2 and 3.3). Accounting for seasonal fluctuations in growth may also be necessary to estimate rates of population change or turnover reliably for univoltine or semelparous species that inhabit environments with strong seasonal signals. For these species, seasonal models provide unbiased estimates of growth rates during the active season whereas non-seasonal models provide estimates of growth rates averaged across active and non-active periods. We found that models that failed to account for existing seasonal fluctuations in growth overestimated growth rates by up to 38%, increasing the probability of bias in estimates

of the time to reach sexual maturity or a particular body size that is physiologically or ecologically important (Fig. 3.1).

Beyond the seasonal component, our approach incorporates several features that improve upon conventional von Bertalanffy models for growth. Unlike traditional approaches, the hierarchical structure of our model accommodates multiple recaptures of individuals over time, which can be especially important when the number of recaptured individuals is small. Second, we modeled individual heterogeneity in asymptotic size, which reduces bias in estimates of growth parameters (Appendix D: Table D1; Eveson et al. 2007, Zhang et al. 2009). Third, a state-space formulation allows us to estimate growth while accounting explicitly for measurement error, which is likely to be appreciable for post-metamorphic amphibians (Hayek et al. 2001). This feature was particularly appealing for canyon treefrogs, which can lose >25% of their body mass throughout the day while basking (Snyder and Hammerson 1993).

Like all approaches, ours has limitations. Although our model provided unbiased estimates of key parameters (asymptotic size, growth rate, and date of maximum growth), variance components were overestimated (Appendix D), a pattern similar to that observed in studies of growth in other species (Zhang et al. 2009). Variance parameters are not usually of direct ecological interest, but these biases limit the ability to interpret or compare estimates of variance components across studies. Should variance be a focal parameter in future applications of the model, additional simulations could be used to explore potential sources of bias and identify methods to reduce it.

Our approach extends the von Bertalanffy growth model, which is the framework used most commonly to characterize growth of post-metamorphic amphibians; therefore,

our estimates of growth and asymptotic size are comparable with those from previous studies. For example, our estimates of growth parameters (Table 3.2) are similar to those based on 313 canyon treefrogs from a canyon approximately 90 km NE of our study area ($\hat{L}_{\infty,F} = 50.7$, $\hat{L}_{\infty,M} = 46.4$, $\hat{k} = 1.8\text{--}3.0$; Wylie 1981). This suggests that like other species in the Hylidae family, canyon treefrogs in southern Arizona have rapid rates of post-metamorphic growth, reaching sizes consistent with sexual maturity (approx. 40 mm; Wylie 1981) in <1 year (Jameson 1956, Moravec 1990, Hamer and Mahony 2007; Fig. 3.3). Our estimates, however, contrast with the suggestion that canyon treefrogs in Colorado wait until their third year to breed (Hammerson 1999). This could be explained by differences in elevation or temperature, factors often associated with geographic variation in post-metamorphic growth and other demographic rates (Duellman and Trueb 1986, Liao and Lu 2010).

Similar to most anurans, canyon treefrogs are sexual size dimorphic, with females reaching larger asymptotic sizes than males (Duellman and Trueb 1986). Interestingly, females in our population also grew faster than males, which could allow them to breed in the spring (Mar–Apr) following their first winter, regardless of whether they metamorphosed in late spring (Jun–Jul) or fall (Sep–Oct) of the previous year (Fig. 3.3). Males took 2–6 months longer than females to reach sexual maturity, therefore most males that metamorphosed in fall likely did not breed until the following summer (Jul; Fig. 3.3). There may be strong selection for fast growth in female treefrogs given that low rates of survival limit the number of lifetime breeding opportunities and clutch size is associated positively with female body size (Wylie 1981, Duellman and Trueb 1986).

In addition to differences in growth between sexes, growth of treefrogs varied both within and among years. Growth ceased during winter months, when individuals retreated to rock crevices, presumably to avoid cold ambient and water temperatures (Hammerson 1999), and peaked during the monsoon season in early August (Fig. 3.3). Further, both sexes grew at higher rates in 2015 than in other years (Table 3.2), which may have reflected variation in water availability. Regional precipitation was well above average in water year 2015 (121% of the 30-year average) and well below average in 2014 (67%). Estimated growth rates were lowest between October 2015 and June 2016, however, when precipitation was somewhat higher than the 30-year average (117%).

Fast growth and low survival of adults (ERZ, *unpublished data*) suggest high rates of population turnover in canyon treefrogs. Although this combination of life-history traits may not be unusual for hylid frogs (Jameson 1956, Kluge 1981, Hamer and Mahony 2007), it contrasts with other amphibians in the Sky Island region, including several toad species that can live 2–13 years after metamorphosis and forego breeding when environmental conditions are unfavorable (Tinsley and Tocque 1995, Sullivan and Fernandez 1999). Comparisons of life-history traits among closely-related or co-occurring species and inferences about population dynamics like these for canyon treefrogs are made possible because of intensive capture-recapture efforts. Maximizing the information gained from such surveys to estimate somatic growth in addition to survival is not only a good use of resources, but also a way to provide novel insights about factors driving population change and to inform future management efforts for species of conservation concern.

TABLE 3.1. Deviance information criterion (DIC) for models of growth in canyon treefrogs that evaluated the effect of sex on asymptotic size, L_∞ , and the effects of sex and year (1 Oct–30 Sept) on characteristic growth rate, k . All models allowed for individual heterogeneity in L_∞ and within-year, seasonal oscillations in k .

L_∞	k	No. parameters	DIC
Sex	Sex + year	11	1977.52
Sex	Year	10	1980.21
Sex	Sex	9	2001.63
Sex	--	8	2000.74
--	Sex + year	9	2003.17
--	Year	8	2083.46
--	Sex	7	2021.33
--	--	6	2086.67

TABLE 3.2. Mean, standard deviation (SD), and 95% credible intervals (CRI) of posterior distributions for parameters in a seasonal, von Bertalanffy model of growth for canyon treefrogs captured in the Rincon Mountains, Arizona, USA, 2014-2016. We fixed C , the magnitude of seasonal oscillations, equal to one to allow growth to cease seasonally.

Parameter	Description	Mean	SD	95% CRI
$\bar{L}_{\infty,F}$	Mean asymptotic length of females (mm)	50.98	0.59	49.93 – 52.25
$\bar{L}_{\infty,M}$	Mean asymptotic length of males (mm)	45.87	0.53	44.92 – 46.96
$k_{2014,F}$	Growth of females, Apr 2014–Sep 2014	2.52	0.36	1.86 – 3.26
$k_{2015,F}$	Growth of females, Oct 2014–Sep 2015	3.30	0.34	2.66 – 4.00
$k_{2016,F}$	Growth of females, Oct 2015–Jun 2016	1.85	0.28	1.35 – 2.45
$k_{2014,M}$	Growth of males, Apr 2014–Sep 2014	2.00	0.39	1.28 – 2.82
$k_{2015,M}$	Growth of males, Oct 2014–Sep 2015	2.78	0.36	2.11 – 3.52
$k_{2016,M}$	Growth of males, Oct 2015–Jun 2016	1.33	0.35	0.71 – 2.06
t_s	Day of year with maximum growth	220.01	4.91	209.99 – 229.36
$\sigma_{\infty,F}$	SD of female asymptotic lengths (mm)	1.14	0.63	0.11 – 2.42
$\sigma_{\infty,M}$	SD of male asymptotic lengths (mm)	0.85	0.57	0.05 – 2.12
$\sigma_{\Delta L}$	Measurement error (mm)	1.67	0.06	1.55 – 1.80

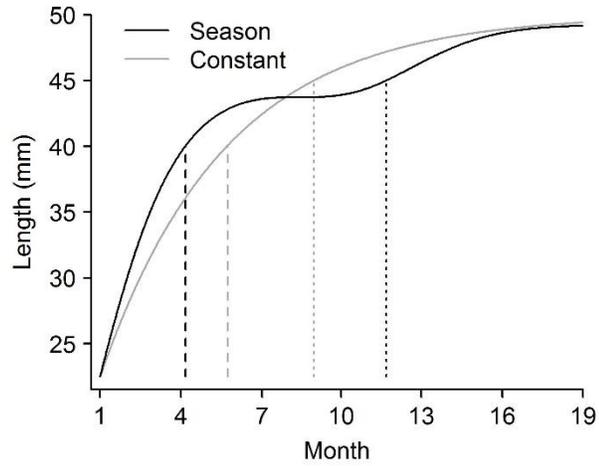


FIGURE 3.1. Predicted growth of individuals based on a model that allowed growth to vary seasonally (solid black line) and a model that assumed constant growth (solid gray line). Length measurements were simulated for 600 individuals assuming growth rates decreased to zero during some period of the year. Vertical dashed lines indicate the time at which an individual is predicted to reach sexual maturity (40 mm) based on each of the two models. Vertical dotted lines indicate the time at which an individual is predicted to reach 90% of mean asymptotic size. Additional details about the simulations appear in Appendix D.

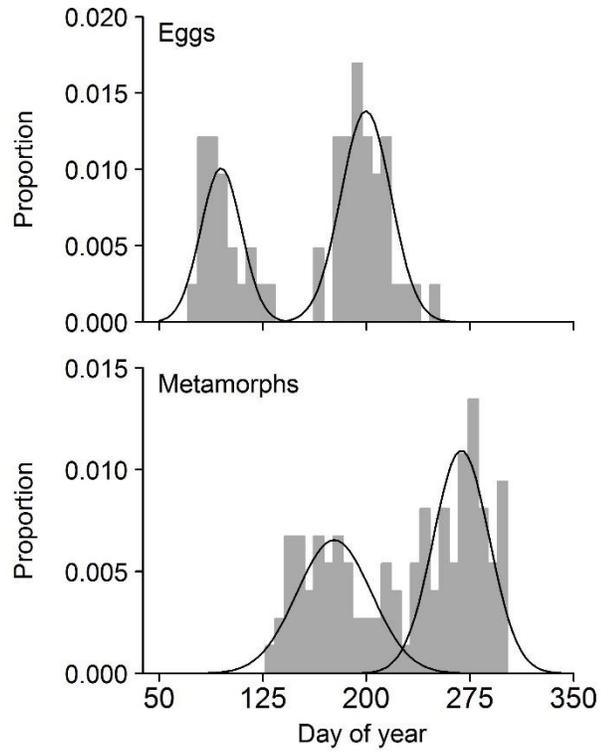


FIGURE 3.2. Proportion of surveys, across all reaches and years, when we observed canyon treefrog eggs (top) or metamorphs (bottom) by date (gray bars). Black lines represent components of a normal mixture distribution fit to the frequency data.

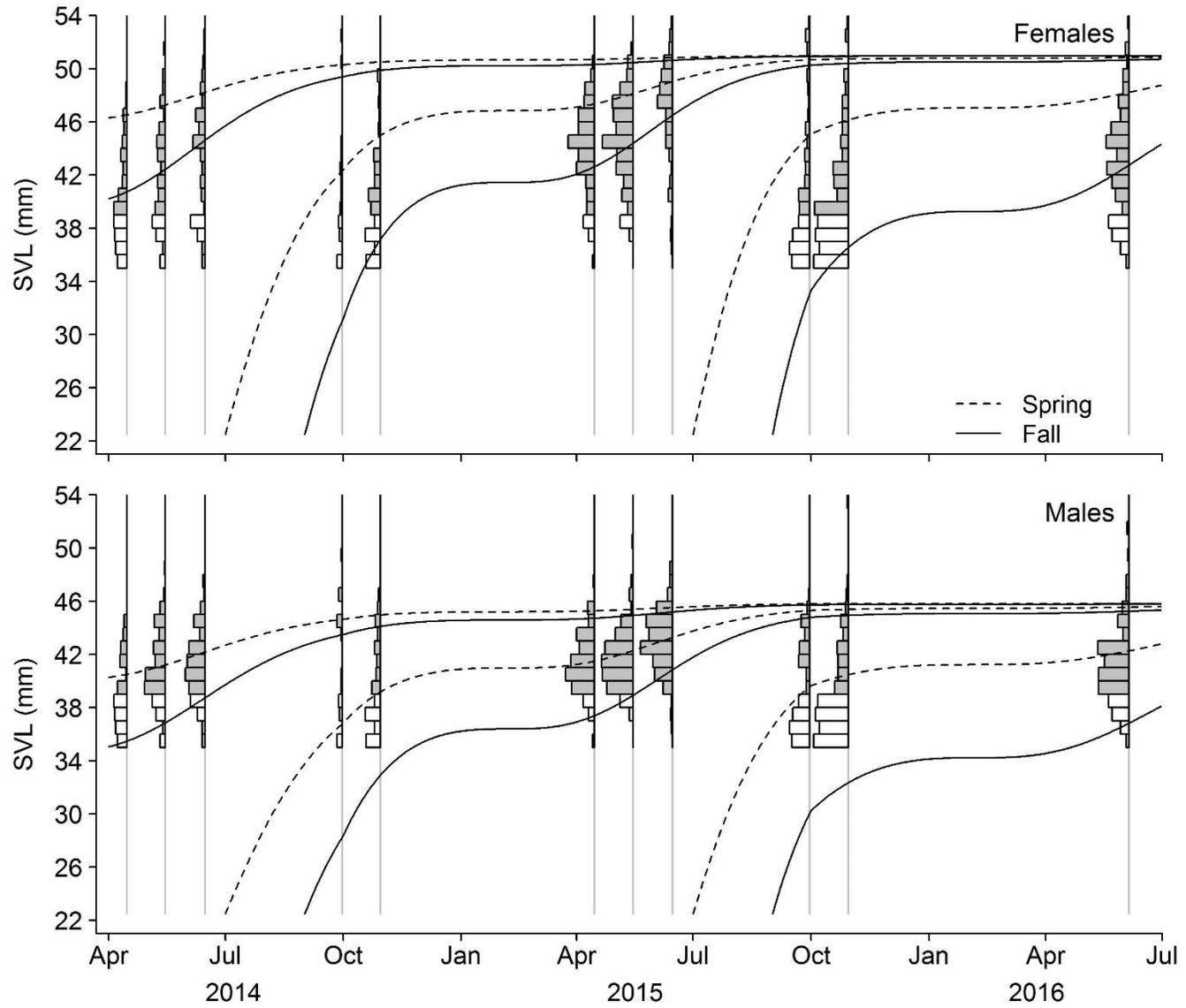


FIGURE 3.3. Predicted growth of post-metamorphic female and male canyon treefrogs emerging from larval stages with an SVL of 22.5 mm in late spring (1 Jul) and late summer (1 Sep), 2013-2015. Predictions are based on a seasonal, growth-interval form of the von Bertalanffy model, where asymptotic length differed between males and females and growth rates varied with sex and year (see Table 3.2 for parameter estimates). Predicted growth is overlaid on length-frequency histograms for treefrogs captured at each survey occasion. Filled bars represent length frequencies of females (top) and males (bottom); open bars represent length frequencies for individuals of unknown sex.

APPENDIX A: EVALUATING THE RELATIONSHIP BETWEEN DROUGHT INDICES AND SURFACE WATER AVAILABILITY

METHODS

We explored whether drought indices explained variation in availability of surface water in mid-elevation reaches of arid mountain canyons. Generally, surface-water levels were lowest between 16 May and 15 July (hereafter, late spring) and in November and December (early winter). Therefore, we related surface-water availability during each of these periods to downscaled estimates of Palmer Drought Severity Index (PDSI). We measured surface-water levels in May, June, July, and November during VES for leopard frogs and used measurements from a separate but related study for December.

Between 1996 and 2017, we surveyed repeatedly eight canyons in the Rincon Mountains, Arizona, USA during late spring and early winter; canyons were often surveyed more than once during each of these periods. For each canyon, we calculated the minimum proportion of pools that held water during each late spring and early winter period after excluding any surveys when observers visited only a small section of the survey reach (<7 pools). We used logistic regression to relate these proportions to PDSI values averaged over the preceding three-, six-, or twelve-month period; we included indicator variables for canyon and season (late spring versus early winter) in all models.

RESULTS

Surface-water availability (i.e., the minimum proportion of pools with water each season) was associated positively with PDSI after accounting for canyon and season

(Table A1). PDSI values averaged over a six-month period explained more variation in surface-water availability than three- or twelve-month means (Table A1). On average, the odds a pool held water increased by 22% (95% CI = 16–28%) for each one unit increase in six-month PDSI.

TABLE A1. Comparison of logistic regression models exploring variation in the minimum proportion of pools with water in arid mountain canyons as a function of drought (Palmer Drought Severity Index; PDSI), season (May–Jul or Nov–Dec), and geographic location (canyon). PDSI values were averaged over the preceding 3, 6, or 12 months (3mo.PDSI, 6mo.PDSI, and 12mo.PDSI, respectively).

Model	No. parameters	AIC ^a	Δ AIC ^b
water ~ 6mo.PDSI + canyon + season	10	1032.64	0.00
water ~ 3mo.PDSI + canyon + season	10	1035.90	3.27
water ~ 12mo.PDSI + canyon + season	10	1039.89	7.25
water ~ canyon + season	9	1090.31	57.67

^a AIC = Akaike information criterion

^b Δ AIC = AIC relative to the most parsimonious model

**APPENDIX B: VARIATION IN DETECTION PROBABILITY OF LOWLAND
LEOPARD FROGS ON VISUAL ENCOUNTER SURVEYS AS A FUNCTION OF
COVARIATES**

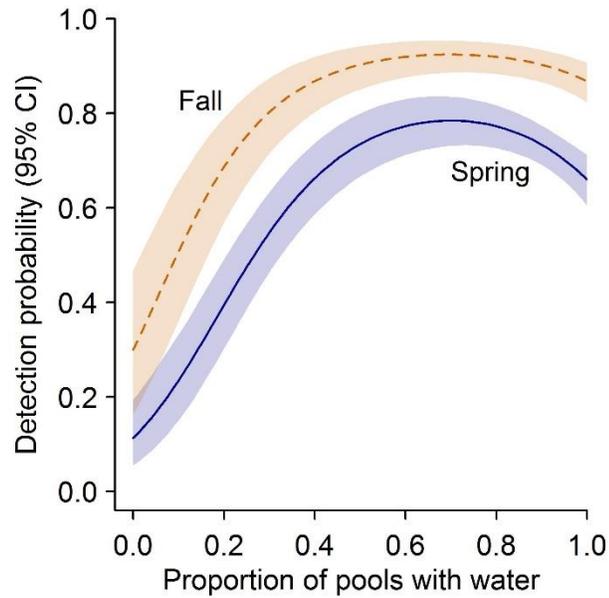


FIGURE B1. Probability of experienced observers detecting ≥ 1 post-metamorphic lowland leopard frogs as a function of surface-water availability during visual encounter surveys in spring (16 May–15 Jul) and fall (1 Oct–30 Nov), 1996–2017.

APPENDIX C: ACCOUNTING FOR BIAS IN ESTIMATES OF SURVIVAL OF LOWLAND LEOPARD FROGS

One of the fundamental assumptions underlying capture-recapture methods is that marks are not lost, overlooked, or misidentified (Williams et al. 2002). This assumption can be violated, however, when photographic data are used to identify and “recapture” individuals. If false rejection errors occur (here, failing to recognize that two partial spot maps are associated with the same frog), the number of encounter histories will exceed the number of individuals observed, resulting in estimates of survival that are negatively biased (Morrison et al. 2011). Although false acceptance errors might occur (here, incorrectly assuming features were from the same frog when in fact, they were part of spot patterns from two different frogs), these types of errors tend to be rare (Morrison et al. 2011; ERZ, *unpublished data*), therefore we did not account explicitly for this potential source of bias.

METHODS

We identified a range of strategies to address potential bias associated with false rejection errors. First, we could assume false rejection errors occurred rarely and elect not to account for such errors (i.e., use all encounter histories, based on all survey occasions and photosets). Although a tenuous assumption, most capture-recapture studies that rely on photographic data have adopted this strategy, ignoring the potential for bias (but see Morrison et al. 2011, Hiby et al. 2013, McClintock et al. 2013). Second, we could restrict analyses to only those encounter histories associated with individuals

whose spot patterns were mapped completely (i.e., features mapped over all three body regions). Although this strategy might reduce or even eliminate identification errors, sample sizes would be reduced and estimates of survival could nevertheless be biased if the individuals associated with those encounter histories were not representative of the larger population. Third, we could censor the initial observation of all individuals and partial spot maps, thereby excluding capture histories with a single encounter event. This approach was developed by Morrison et al. (2011) to address false rejection errors resulting from low-quality photographic images and was based on the assumption that low-quality images are likely to result in superfluous histories, each with a single encounter. When false rejection errors result from incomplete information rather than poor image quality, as in our study, censoring initial encounters may reduce but not eliminate this potential bias, as partial spot maps could be encountered more than once and retained in analyses. In addition to the three alternatives listed above, we investigated whether methods developed recently for “bilateral” data (Wilson et al. 1999, Corkrey et al. 2008, Link et al. 2010, Hiby et al. 2013, McClintock et al. 2013) could be extended to photographic studies where identification was based on patterns or markings on three regions of the body (dorsum, left flank, right flank). We determined that for our study, with three body regions and >240 survey occasions, model likelihoods would be prohibitively complex, therefore we did not pursue this alternative.

To compare how methods to account for bias could affect parameter estimates, we implemented each of the three strategies detailed above to estimate survival of post-metamorphic leopard frogs. Specifically, we created three sets of encounter histories: 1) histories for all individuals and partial spot maps that included all observations

(uncensored), 2) histories for only those individuals whose spot patterns were mapped completely, including all observations of each individual (uncensored), and 3) histories for all individuals and partial spot maps, excluding the initial observation (censored; Table C1). For each set of encounter histories, we estimated apparent monthly survival based on a null model (i.e., constant survival and recapture probability) and a model that allowed survival to vary with surface-water availability, temperature, dew point, and perimeter groundcover and allowed recapture probability to vary with surface-water availability, temperature, humidity, wind, perimeter groundcover, and year (see the Methods section in Chapter 2 for descriptions of covariates).

RESULTS AND DISCUSSION

As expected, estimates of survival based on censored encounter histories were slightly higher and less precise than estimates based on uncensored encounter histories of all individuals and partial spot maps (Table C1). Estimates based on censored histories were 4% lower than estimates based on only those individuals whose spot patterns were mapped completely. Methods used to account for bias did not seem to affect inferences about the factors governing variation in survival over space and time, as regression coefficients from analyses that used censored encounter histories were similar to regression coefficients from both analyses that used uncensored encounter histories (Table C1).

Although our use of in-situ photographs introduced the possibility of identification errors, we viewed these costs as reasonable given that non-invasive methods allowed us to survey frogs multiple times per year, providing valuable insights about the factors that

govern seasonal variation in survival of lowland leopard frogs. Among the strategies that could be used to account for these errors, censoring methods reduced potential sources of bias while incurring minimal costs associated with precision of parameter estimates.

Although surely imperfect, this approach seemed preferable to those that ignored known sources of bias or used only a subset of individuals that may not have been representative of the larger population.

TABLE C1. Parameter estimates from models evaluating post-metamorphic survival of lowland leopard frogs based on 1) uncensored encounter histories for all individuals and partial spot maps, 2) uncensored encounter histories for only those individuals whose spot patterns that were mapped completely, and 3) censored encounter histories for all individuals and partial spot maps. We report estimates of monthly apparent survival, $\hat{\phi}$, and associated coefficients of variation (CV) from a null model, and regression coefficients (β) on the logit-scale, relating monthly apparent survival to surface-water availability (Water), temperature, dew point, and perimeter groundcover from a more general model. We provide 95% confidence intervals for each parameter estimate.

	All histories, uncensored	Histories for individuals with completely-mapped spot patterns only, uncensored	All histories, censored
No. encounter histories	352	215	205
$\hat{\phi}$	0.81 (0.79 to 0.83)	0.86 (0.84 to 0.88)	0.82 (0.80 to 0.85)
CV($\hat{\phi}$)	1.4%	1.3%	1.6%
β .Water	0.17 (-0.17 to 0.51)	0.28 (-0.15 to 0.70)	0.19 (-0.25 to 0.63)
β .Water ²	-0.31 (-0.53 to -0.10)	-0.28 (-0.53 to -0.03)	-0.36 (-0.63 to -0.10)
β .Temperature	0.33 (-0.05 to 0.70)	0.42 (-0.02 to 0.86)	0.58 (0.06 to 1.11)
β .Dew point	-0.38 (-0.78 to 0.01)	-0.49 (-0.95 to -0.03)	-0.69 (-1.24 to -0.14)
β .Groundcover	0.01 (-0.13 to 0.15)	0.09 (-0.07 to 0.26)	-0.05 (-0.23 to 0.13)

APPENDIX D: SIMULATIONS TO ASSESS BIAS OF PARAMETER ESTIMATES IN GROWTH MODELS

METHODS

We simulated data to evaluate the reliability of the growth model and to characterize bias of parameter estimates. We assumed all individuals captured were females and did not include covariates on growth parameters (e.g., year effects) to simplify comparisons of estimates from a model that included seasonal fluctuations in growth with estimates from a model that did not allow seasonal fluctuations in growth.

We assumed captures occurred each month between March and October for two consecutive years (16 total occasions) and 40 new females were marked on each of the first 15 occasions, resulting in a total of 600 individuals. Length at first capture ranged from 35 to 54 mm, with values ≥ 50 mm observed rarely. To ensure all individuals had ≥ 2 length measurements in a given year, we assumed all individuals were recaptured during the survey immediately after they were marked. After the first recapture, we simulated recapture data based on an annual survival rate of 0.50 and recapture rate of 0.70. We simulated length measurements during each recapture assuming seasonal fluctuations in growth with $\bar{L}_\infty = 50$ mm, $\sigma_\infty = 1$ mm, $k = 2 \text{ yr}^{-1}$, $t_s = 0.62$ (15 Aug), $C = 1$, and $\sigma_{\Delta L} = 1$ mm (Table D1).

For each dataset, we estimated \bar{L}_∞ , σ_∞ , k , t_s , and $\sigma_{\Delta L}$ from a seasonal model where C was fixed to one (eqn 3.1) and in addition, estimated \bar{L}_∞ , σ_∞ , k , and $\sigma_{\Delta L}$ from a model where growth was assumed constant (eqn 3.4). We used the same priors as those used in the analysis of the canyon treefrog data. For each simulated dataset and model used for

estimation, we ran three Markov chains for 6000 iterations. After discarding the first 1000 iterations as burn-in we retained 1 of every 5 iterations to summarize the posterior distribution. Gelman-Rubin statistics for all parameters were ≤ 1.1 . For each parameter estimate associated with a simulated data set, we calculated relative bias by subtracting the true value from the posterior mean and dividing by the true value.

Finally, to assess the value of modeling individual heterogeneity in asymptotic length, we estimated L_∞ , k , t_s , and $\sigma_{\Delta L}$ for the same 100 simulated data sets using a model that assumed no variation in L_∞ among individuals. To assess whether the seasonal model was robust to misspecification, we simulated 100 new datasets where growth rate was constant throughout the year and estimated \bar{L}_∞ , σ_∞ , k , t_s , C , and $\sigma_{\Delta L}$ from a seasonal growth model.

RESULTS

For the range of values we simulated, estimates of characteristic growth rate (k), mean asymptotic length (\bar{L}_∞), and date of maximum growth (t_s) from our model had low bias (mean percent relative bias ranged from -0.2% to 1.7% ; Table D1). Variance parameters, however, were consistently overestimated. On average, measurement error, $\sigma_{\Delta L}$, was overestimated by 14% and estimates of variance associated with individual heterogeneity in asymptotic length, σ_∞ , were 29% greater than simulated values. Despite relatively high bias in variance parameters, estimation of individual heterogeneity was beneficial given that models without this component resulted in negatively biased estimates of k , the parameter of primary interest (Table D1). Importantly, when simulated growth varied seasonally, a model that assumed constant

growth overestimated k (Table D1), overestimated the time required to reach sexual maturity (40 mm) by 7 weeks, and underestimated the time required to reach 90% of asymptotic length by >11 weeks (Fig. 3.1).

Even when simulated growth was constant throughout a year, our model provided reliable estimates of \bar{L}_∞ and k (mean percent relative bias <2%). In these scenarios, posterior distributions of C were heavily skewed towards zero (97% of distribution <0.1), indicating little evidence for seasonal fluctuations in growth rates, as expected.

TABLE D1. Results of simulations used to assess bias of parameter estimates from growth models when simulated growth rates fluctuated seasonally and asymptotic length varied among individuals. Parameters were estimated from three models: 1) a model that allowed for seasonal growth and individual heterogeneity (truth), 2) a model that allowed for seasonal growth but no individual heterogeneity, and 3) a model with constant growth rates and individual heterogeneity. For each estimating model, we present the mean of parameter estimates and mean percent relative bias (%RB) across 100 simulated datasets.

Parameter	Sim. value	Season, heterogeneity		Season, no heterogeneity		Constant, heterogeneity	
		Mean	%RB	Mean	%RB	Mean	%RB
\bar{L}_∞	50	49.93	-0.14	50.09	0.19	49.62	-0.76
k	2	2.03	1.67	1.92	-4.17	2.56	28.17
t_s	0.62	0.62	-0.22	0.62	-0.46		
σ_∞	1	1.29	28.71			1.37	37.40
$\sigma_{\Delta L}$	1	1.14	13.60	1.22	22.15	1.29	29.14

APPENDIX E: EXAMPLE JAGS CODE FOR A SEASONAL MODEL OF GROWTH

Data used in the model:

nind: number of frogs
 ncap: vector with the number of captures of each frog
 nunk: number of frogs of unknown sex
 L: matrix [dimensions = nind*max(ncap)] with measured length of each frog on each occasion it was captured. Sorted with frogs of unknown sex in the first nunk rows.
 growthinc: matrix [nind*(max(ncap)-1)] with measured growth of frogs during each capture interval.
 tyear: matrix [nind*max(ncap)] with capture dates for each frog, calculated in fractions of a year.
 int.y: matrix [nind*(max(ncap)-1)] with length of capture intervals for each frog, calculated in fractions of a year.
 sex: vector listing the sex of each frog (1=male, 0=female, NA=unknown), with NAs listed first.
 wy15: matrix [nind*max(ncap)] indicating whether capture of each frog occurred in water year 2015 (1 = 2015, 0 = 2014 or 2016)
 wy16: matrix [nind*max(ncap)] indicating whether capture of each frog occurred in water year 2016 (1 = 2016, 0 = 2014 or 2015)

#--- JAGS model

```

model{
  for(i in 1:nind){
    for(j in 2:ncap[i]){
      growthinc[i,j-1] ~ dnorm(growth_mu[i,j-1],meas_tau)
      growth_mu[i,j-1] <-
        (Linf[i]-L[i,j-1])* (1-exp(-(k[i,j-1]*ints.y[i,j-1] -
          C*k[i,j-1]/(2*pi)*sin(2*pi*(tyear[i,j-1] - ts)) +
          C*k[i,j-1]/(2*pi)*sin(2*pi*(tyear[i,j-1] +
          ints.y[i,j-1]-ts))))
      k[i,j-1] <- b0 + b1.male*sex[i] + b2.2015*wy15[i,j-1] +
        b3.2016*wy16[i,j-1]
    } #j
    Linf[i] ~ dnorm(Linf_mu[sex[i]+1],Linf_tau[sex[i]+1])
  } #i

  for(w in 1:nunk){
    sex[w] ~ dbern(0.5)
  } #w

```

```
for(s in 1:2){
  Linf_mu[s] ~ dunif(40,60)
  Linf_sd[s] ~ dunif(0,10)
  Linf_tau[s] <- 1/(Linf_sd[s]*Linf_sd[s])
} #s

b0 ~ dunif(0,5)
b1.male ~ dnorm(0,1)
b2.2015 ~ dnorm(0,1)
b3.2016 ~ dnorm(0,1)

pi <- 3.14159265359
ts ~ dunif(0,1)
C ~ dunif(0,1)

meas_sd ~ dunif(0,10)
meas_tau <- 1/(meas_sd*meas_sd)
} #model
```

REFERENCES

- Abatzoglou, J. T., D. J. McEvoy, and K. T. Redmond. 2017. The west wide drought tracker: drought monitoring at fine spatial scales. *Bulletin of the American Meteorological Society* 98:1815–1820.
- Adams, M. J., D. A. W. Miller, E. Muths, P. S. Corn, E. H. C. Grant, L. L. Bailey, G. M. Fellers, R. N. Fisher, W. J. Sadinski, H. Waddle, and S. C. Walls. 2013. Trends in amphibian occupancy in the United States. *PLoS ONE* 8:e64347.
- Anderson, T. L., B. H. Ousterhout, W. E. Peterman, D. L. Drake, and R. D. Semlitsch. 2015. Life history differences influence the impacts of drought on two pond-breeding salamanders. *Ecological Applications* 25:1896–1910.
- Bailey, L. L. 2004. Evaluating elastomer marking and photo identification methods for terrestrial salamanders: marking effects and observer bias. *Herpetological Review* 35:38–41.
- Baker, K. D. 2010. Disease and natural history of canyon treefrogs (*Hyla arenicolor*). University of Arizona.
- Balling, R., and G. Goodrich. 2010. Increasing drought in the American Southwest? A continental perspective using a spatial analytical evaluation of recent trends. *Physical Geography* 31:293–306.
- Benard, M. F. 2015. Warmer winters reduce frog fecundity and shift breeding phenology, which consequently alters larval development and metamorphic timing. *Global Change Biology* 21:1058–1065.
- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23:85–97.
- Biek, R., W. C. Funk, B. A. Maxell, and L. S. Mills. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology* 16:728–734.
- Blackwell, E. A., R. A. Angus, G. R. Cline, and K. R. Marion. 2003. Natural growth rates of *Ambystoma maculatum* in Alabama. *Journal of Herpetology* 37:608–612.
- Bled, F., J. A. Royle, and E. Cam. 2011. Hierarchical modeling of an invasive spread: the Eurasian collared-dove *Streptopelia decaocto* in the United States. *Ecological Applications* 21:290–302.
- Boulanger, J., S. Himmer, and C. Swan. 2004. Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. *Canadian Journal of Zoology* 82:1267–1277.

- Bowers, J. E., and S. P. McLaughlin. 1987. Flora and vegetation of the Rincon Mountains, Pima County, Arizona. *Desert Plants* 8:51–94.
- Bradford, D. F. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. *Journal of Herpetology* 25:174–177.
- Bradford, D. F., J. R. Jaeger, and R. D. Jennings. 2004. Population status and distribution of a decimated amphibian, the relict leopard frog (*Rana onca*). *The Southwestern Naturalist* 49:218–228.
- Broms, K. M., M. B. Hooten, D. S. Johnson, R. Altwegg, and L. L. Conquest. 2016. Dynamic occupancy models for explicit colonization processes. *Ecology* 97:194–204.
- Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67:148–164.
- Brown, D. E. 1982. Biotic communities of the American Southwest - United States and Mexico. *Desert Plants* 4:1–342.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.
- Brown, J. R. 1988. Multivariate analyses of the role of environmental factors in seasonal and site-related growth variation in the Pacific oyster *Crassostrea gigas*. *Marine Ecology Progress Series* 45:225–236.
- Carr, L. W., and L. Fahrig. 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15:1071–1078.
- Caswell, H. 2001. *Matrix population models: construction, analysis and interpretation*. Sinauer Associates, Sunderland, MA.
- Caughley, G., and A. Gunn. 1996. *Conservation biology in theory and practice*. Blackwell Science, Cambridge, MA.
- Cayuela, H., D. Arsovski, E. Bonnaire, R. Duguet, P. Joly, and A. Besnard. 2016. The impact of severe drought on survival, fecundity, and population persistence in an endangered amphibian. *Ecosphere* 7:e01246.
- Chambert, T., J. J. Rotella, and M. D. Higgs. 2014. Use of posterior predictive checks as an inferential tool for investigating individual heterogeneity in animal population vital rates. *Ecology and Evolution* 4:1389–1397.
- Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack. 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *Journal of Applied Ecology* 52:1325–1333.

- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Church, D. R., L. L. Bailey, H. M. Wilbur, W. L. Kendall, and J. E. Hines. 2007. Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* 88:891–903.
- Clarkson, R. W., and J. C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southeastern California. *Southwestern Naturalist* 34:531–538.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- Collins, J. P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9:89–98.
- Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1:e1400082.
- Corkrey, R., S. Brooks, D. Lusseau, K. Parsons, J. W. Durban, P. S. Hammond, and P. M. Thompson. 2008. A Bayesian capture–recapture population model with simultaneous estimation of heterogeneity. *Journal of the American Statistical Association* 103:948–960.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412–1423.
- Dahm, C. N., M. A. Baker, D. I. Moore, and J. R. Thibault. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology* 48:1219–1231.
- Daszak, P., D. E. Scott, A. M. Kilpatrick, C. Faggioni, J. W. Gibbons, and D. Porter. 2005. Amphibian population declines at Savannah River Site are linked to climate, not chytridiomycosis. *Ecology* 86:3232–3237.
- DiRenzo, G. V., C. Che-Castaldo, A. Rugenski, R. Brenes, M. R. Whiles, C. M. Pringle, S. S. Kilham, and K. R. Lips. 2017. Disassembly of a tadpole community by a multi-host fungal pathogen with limited evidence of recovery. *Ecological Applications* 27:309–320.
- Duellman, W. E., and L. Trueb. 1986. *Biology of amphibians*. McGraw-Hill, New York, NY.
- Dunham, J. B., A. E. Rosenberger, C. H. Luce, and B. E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10:335–346.

- Dzul, M. C., C. B. Yackulic, J. Korman, M. D. Yard, and J. D. Muehlbauer. 2017. Incorporating temporal heterogeneity in environmental conditions into a somatic growth model. *Canadian Journal of Fisheries and Aquatic Sciences* 74:316–326.
- Eaton, M. J., P. T. Hughes, J. E. Hines, and J. D. Nichols. 2014. Testing metapopulation concepts: effects of patch characteristics and neighborhood occupancy on the dynamics of an endangered lagomorph. *Oikos* 123:662–676.
- Eden, C. J., H. H. Whiteman, L. Duobinis-Gray, and S. A. Wissinger. 2007. Accuracy assessment of skeletochronology in the Arizona tiger salamander (*Ambystoma tigrinum nebulosum*). *Copeia* 2007:471–477.
- Ehrlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters* 18:303–314.
- Eveson, J. P., T. Polacheck, and G. M. Laslett. 2007. Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. *Canadian Journal of Fisheries and Aquatic Sciences* 64:602–617.
- Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.
- Ferner, J. W. 2010. Measuring and marking post-metamorphic amphibians. Pages 123–141 in C. K. Dodd, editor. *Amphibian ecology and conservation: a handbook of techniques*. Oxford University Press, New York, NY.
- Ferrari, S., and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. *Journal of Applied Statistics* 31:799–815.
- Ficetola, G. F., and F. De Bernardi. 2006. Trade-off between larval development rate and post-metamorphic traits in the frog *Rana latastei*. *Evolutionary Ecology* 20:143–158.
- Forrest, M. J., and M. A. Schlaepfer. 2011. Nothing a hot bath won't cure: infection rates of amphibian chytrid fungus correlate negatively with water temperature under natural field settings. *PLoS ONE* 6:e28444.
- Fortuna, M. A., C. Gómez-Rodríguez, and J. Bascompte. 2006. Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society of London B* 273:1429–1434.
- Franken, R. J., and D. S. Hik. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *Journal of Animal Ecology* 73:889–896.
- Frazer, N. B., and L. M. Ehrhart. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. *Copeia* 1985:73–79.

- Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.
- Gehlbach, F. R. 1965. Herpetology of the Zuni Mountains region, northwestern New Mexico. *Proceedings of the United States National Museum* 116:243–322.
- Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis* 1:515–534.
- Gelman, A., X.-L. Meng, and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica* 6:733–760.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Goode, J. R., C. H. Luce, and J. M. Buffington. 2012. Enhanced sediment delivery in a changing climate in semi-arid mountain basins: implications for water resource management and aquatic habitat in the northern Rocky Mountains. *Geomorphology* 139–140:1–15.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos larvae with notes on identification. *Herpetologica* 16:183–190.
- Grafe, T. U., S. K. Kaminsky, J. H. Bitz, H. Lüssow, and K. E. Linsenmair. 2004. Demographic dynamics of the afro-tropical pig-nosed frog, *Hemisus marmoratus*: effects of climate and predation on survival and recruitment. *Oecologia* 141:40–46.
- Grimm, N. B., A. Chacon, C. N. Dahm, S. W. Hostetler, O. T. Lind, P. L. Starkweather, and W. W. Wurtsbaugh. 1997. Sensitivity of aquatic ecosystems to climatic and anthropogenic changes: the Basin and Range, American Southwest and Mexico. *Hydrological Processes* 11:1023–1041.
- Grimm, N. B., and S. G. Fisher. 1992. Responses of arid-land streams to changing climate. Pages 211–233 in P. Firth and S. G. Fisher, editors. *Global Climate Change and Freshwater Ecosystems*. Springer-Verlag, New York, NY.
- Hall, D., and R. J. Steidl. 2007. Movements, activity, and spacing of Sonoran mud turtles (*Kinosternon sonoriense*) in interrupted mountain streams. *Copeia* 2007:403–412.
- Hamer, A. J., and M. J. Mahony. 2007. Life history of an endangered amphibian challenges the declining species paradigm. *Australian Journal of Zoology* 55:79–88.
- Hammerson, G. A. 1999. *Amphibians and reptiles in Colorado*. 2nd edition. University Press of Colorado, Niwot, CO.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.

- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* 10:578–590.
- Harkey, G. A., and R. D. Semlitsch. 1988. Effects of temperature on growth, development, and color polymorphism in the ornate chorus frog *Pseudacris ornata*. *Copeia* 1988:1001–1007.
- Harper, E. B., T. A. G. Rittenhouse, and R. D. Semlitsch. 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology* 22:1205–1215.
- Harrison, P. J., I. Hanski, and O. Ovaskainen. 2011. Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. *Ecological Monographs* 81:581–598.
- Hayek, L.-A. C., W. R. Heyer, and C. Gascon. 2001. Frog morphometrics: a cautionary tale. *Alytes* 18:153–177.
- Heard, G. W., M. A. McCarthy, M. P. Scroggie, J. B. Baumgartner, and K. M. Parris. 2013. A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Diversity and Distributions* 19:555–566.
- Hemelaar, A. 1988. Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. *Journal of Herpetology* 22:369–388.
- Hendrickson, D. A., and W. L. Minckley. 1985. Cienegas: vanishing climax communities of the American Southwest. *Desert Plants* 6:130–176.
- Hiby, L., W. D. Paterson, P. Redman, J. Watkins, S. D. Twiss, and P. Pomeroy. 2013. Analysis of photo-id data allowing for missed matches and individuals identified from opposite sides. *Methods in Ecology and Evolution* 4:252–259.
- Hodgson, J. A., A. Moilanen, and C. D. Thomas. 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. *Ecology* 90:1608–1619.
- Holmberg, J., B. Norman, and Z. Arzoumanian. 2008. Robust, comparable population metrics through collaborative photo-monitoring of whale sharks *Rhincodon Typus*. *Ecological Applications* 18:222–233.
- Hossack, B. R., M. J. Adams, C. A. Pearl, K. W. Wilson, E. L. Bull, K. Lohr, D. Patla, D. S. Pilliod, J. M. Jones, K. K. Wheeler, S. P. McKay, and P. S. Corn. 2013a. Roles of patch characteristics, drought frequency, and restoration in long-term trends of a widespread amphibian. *Conservation Biology* 27:1410–1420.

- Hossack, B. R., W. H. Lowe, and P. S. Corn. 2013b. Rapid increases and time-lagged declines in amphibian occupancy after wildfire. *Conservation Biology* 27:219–228.
- Howell, P. E., B. R. Hossack, E. Muths, B. H. Sigafus, and R. B. Chandler. 2016. Survival estimates for reintroduced populations of the Chiricahua leopard frog (*Lithobates chiricahuensis*). *Copeia* 104:824–830.
- Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences* 111:13894–13899.
- Jameson, D. L. 1956. Growth, dispersal and survival of the Pacific tree frog. *Copeia* 1956:25–29.
- Jiao, Y., L. Rogers-Bennett, I. Taniguchi, J. Butler, and P. Crone. 2010. Incorporating temporal variation in the growth of red abalone (*Haliotis rufescens*) using hierarchical Bayesian growth models. *Canadian Journal of Fisheries and Aquatic Sciences* 67:730–742.
- Kagarise Sherman, C., and M. L. Morton. 1993. Population declines of Yosemite toads in the eastern Sierra Nevada of California. *Journal of Herpetology* 27:186–198.
- Kellner, K. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1.4.4.
- Keppel, G., K. P. Van Niel, G. W. Wardell-Johnson, C. J. Yates, M. Byrne, L. Mucina, A. G. T. Schut, S. D. Hopper, and S. E. Franklin. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* 21:393–404.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, MA.
- Kluge, A. G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscellaneous Publications of the Museum of Zoology University of Michigan* 160:1–170.
- Knowlton, J. L., and C. H. Graham. 2010. Using behavioral landscape ecology to predict species' responses to land-use and climate change. *Biological Conservation* 143:1342–1354.
- Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA.
- Langtimm, C. A., C. A. Beck, H. H. Edwards, K. J. Fick-Child, B. B. Ackerman, S. L. Barton, and W. C. Hartley. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. *Marine Mammal Science* 20:438–463.

- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lee, D. E., J. B. Bettaso, M. L. Bond, R. W. Bradley, J. R. Tietz, and P. M. Warzybok. 2012. Growth, age at maturity, and age-specific survival of the arboreal salamander (*Aneides lugubris*) on southeast Farallon Island, California. *Journal of Herpetology* 46:64–71.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Lewontin, R. C. 1965. Selection of colonizing ability. Pages 79–94 in H. G. Baker and G. L. Stebbins, editors. *The genetics of colonizing species*. Academic Press, New York, NY.
- Liao, W. B., and X. Lu. 2010. Age structure and body size of the Chuanxi tree frog *Hyla annectans chuanxiensis* from two different elevations in Sichuan (China). *Zoologischer Anzeiger* 248:255–263.
- Link, W. A., J. Yoshizaki, L. L. Bailey, and K. H. Pollock. 2010. Uncovering a latent multinomial: analysis of mark-recapture data with misidentification. *Biometrics* 66:178–185.
- Martof, B. 1956. Growth and development of the green frog, *Rana clamitans*, under natural conditions. *American Midland Naturalist* 55:101–117.
- Marucco, F., D. H. Pletscher, L. Boitani, M. K. Schwartz, K. L. Pilgrim, and J.-D. Lebreton. 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the western Alps. *Journal of Applied Ecology* 46:1003–1010.
- McClintock, B. T., P. B. Conn, R. S. Alonso, and K. R. Crooks. 2013. Integrated modeling of bilateral photo-identification data in mark-recapture analyses. *Ecology* 94:1464–1471.
- McLaughlin, S. P., and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. *Ecology* 63:246–248.
- McMenamin, S. K., E. A. Hadly, and C. K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences* 105:16988–16993.
- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454:100–103.

- Miller, D. A. W., C. S. Brehme, J. E. Hines, J. D. Nichols, and R. N. Fisher. 2012. Joint estimation of habitat dynamics and species interactions: disturbance reduces co-occurrence of non-native predators with an endangered toad. *Journal of Animal Ecology* 81:1288–1297.
- Moravec, J. 1990. Postmetamorphic growth in the European treefrog (*Hyla arborea*). *Acta Universitatis Carolinae-Biologica* 34:359–370.
- Moritz, S., and T. Bartz-Beielstein. 2017. imputeTS: time series missing value imputation in R. *The R Journal* 9:207–218.
- Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V. Haridas, C. L. Boggs, M. S. Boyce, E. M. Bruna, D. R. Church, T. Coulson, D. F. Doak, S. Forsyth, J.-M. Gaillard, C. C. Horvitz, S. Kalisz, B. E. Kendall, T. M. Knight, C. T. Lee, and E. S. Menges. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89:19–25.
- Morrison, T. A., J. Yoshizaki, J. D. Nichols, and D. T. Bolger. 2011. Estimating survival in photographic capture-recapture studies: overcoming misidentification error. *Methods in Ecology and Evolution* 2:454–463.
- Muths, E., P. S. Corn, A. P. Pessier, and D. E. Green. 2003. Evidence for disease-related amphibian decline in Colorado. *Biological Conservation* 110:357–365.
- Nair, T., J. B. Thorbjarnarson, P. Aust, and J. Krishnaswamy. 2012. Rigorous gharial population estimation in the Chambal: implications for conservation and management of a globally threatened crocodylian. *Journal of Applied Ecology* 49:1046–1054.
- Northrup, J. M., and B. D. Gerber. 2018. A comment on priors for Bayesian occupancy models. *PLoS ONE* 13:e0192819.
- O'Brien, T. G., M. F. Kinnaird, A. Nurcahyo, M. Prasetyaningrum, and M. Iqbal. 2003. Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. *Animal Conservation* 6:115–121.
- Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity in female wood ducks. *Evolutionary Ecology Research* 4:563–576.
- Painter, C. W. 2005. *Hyla arenicolor* Cope. Canyon treefrog. Pages 447–448 in M. J. Lannoo, editor. *Amphibian declines: the conservation status of United States species*. University of California Press, Berkeley, CA.
- Parker, J. T. C. 2006. Post-wildlife sedimentation in Saguaro National Park, Rincon Mountain District, and effects on lowland leopard frog habitat. *Scientific Investigations Report 2006-5235*. U.S. Geological Survey, Reston, VA.

- Parmesan, C. N. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37:636–637.
- Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892–895.
- Peterson, E. E., J. M. Ver Hoef, D. J. Isaak, J. A. Falke, M. J. Fortin, C. E. Jordan, K. McNyset, P. Monestiez, A. S. Ruesch, A. Sengupta, N. Som, E. A. Steel, D. M. Theobald, C. E. Torgersen, and S. J. Wenger. 2013. Modelling dendritic ecological networks in space: an integrated network perspective. *Ecology Letters* 16:707–719.
- Pilliod, D. S., R. S. Arkle, J. M. Robertson, M. A. Murphy, and W. C. Funk. 2015. Effects of changing climate on aquatic habitat and connectivity for remnant populations of a wide-ranging frog species in an arid landscape. *Ecology and Evolution* 5:3979–3994.
- Pilliod, D. S., E. Muths, R. D. Scherer, P. E. Bartelt, P. S. Corn, B. R. Hossack, B. A. Lambert, R. McCaffery, and C. Gaughan. 2010. Effects of amphibian chytrid fungus on individual survival probability in wild boreal toads. *Conservation Biology* 24:1259–1267.
- Pitcher, T. J., and P. D. M. Macdonald. 1973. Two models for seasonal growth in fishes. *Journal of Applied Ecology* 10:599–606.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vienna, Austria.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ray, A. M., W. R. Gould, B. R. Hossack, A. J. Sepulveda, D. P. Thoma, D. A. Patla, R. Daley, and R. Al-Chokhachy. 2016. Influence of climate drivers on colonization and extinction dynamics of wetland-dependent species. *Ecosphere* 7:e01409.
- Reading, C. J. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* 151:125–131.
- Relyea, R. A. 2004. Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology* 85:172–179.
- Risk, B. B., P. de Valpine, and S. R. Beissinger. 2011. A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. *Ecology* 92:462–474.

- Robins, J., D. Mayer, J. Staunton-Smith, I. Halliday, B. Sawynok, and M. Sellin. 2006. Variable growth rates of the tropical estuarine fish barramundi *Lates calcarifer* (Bloch) under different freshwater flow conditions. *Journal of Fish Biology* 69:379–391.
- Robinson, R. A., S. R. Baillie, and H. Q. P. Crick. 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* 149:357–364.
- Rowe, C. L., and W. A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* 102:397–403.
- Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823.
- Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:241–247.
- Sartorius, S. S., and P. C. Rosen. 2000. Breeding phenology of the lowland leopard frog (*Rana yavapaiensis*): implications for conservation and ecology. *Southwestern Naturalist* 45:267–273.
- Savage, A. E., M. J. Sredl, and K. R. Zamudio. 2011. Disease dynamics vary spatially and temporally in a North American amphibian. *Biological Conservation* 144:1910–1915.
- Scheele, B. C., D. A. Driscoll, J. Fischer, and D. A. Hunter. 2012. Decline of an endangered amphibian during an extreme climatic event. *Ecosphere* 3:101.
- Schlaepfer, M. A., M. J. Sredl, P. C. Rosen, and M. J. Ryan. 2007. High prevalence of *Batrachochytrium dendrobatidis* in wild populations of lowland leopard frogs *Rana yavapaiensis* in Arizona. *EcoHealth* 4:421–427.
- Schnute, J., and D. Fournier. 1980. A new approach to length–frequency analysis: growth structure. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1337–1351.
- Schwarzkopf, L., and R. A. Alford. 2002. Nomadic movement in tropical toads. *Oikos* 96:492–506.
- Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181–1184.
- Semlitsch, R. D., and J. P. Caldwell. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. *Ecology* 63:905–911.

- Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184–192.
- Sibly, R. M., and J. Hone. 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London B* 357:1153–1170.
- Sigourney, D. B., S. B. Munch, and B. H. Letcher. 2012. Combining a Bayesian nonparametric method with a hierarchical framework to estimate individual and temporal variation in growth. *Ecological Modelling* 247:125–134.
- Sinsch, U. 2015. Review: skeletochronological assessment of demographic life-history traits in amphibians. *Herpetological Journal* 25:5–13.
- Skelly, D. K. 1992. Field evidence for a cost of behavioral antipredator response in a larval amphibian. *Ecology* 73:704–708.
- Snyder, G. K., and G. A. Hammerson. 1993. Interrelationships between water economy and thermoregulation in the canyon tree-frog *Hyla arenicolor*. *Journal of Arid Environments* 25:321–329.
- Somers, I. F. 1988. On a seasonally oscillating growth function. *Fishbyte* 6:8–11.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* 64:583–639.
- Spotila, J. R., and E. N. Berman. 1976. Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comparative Biochemistry and Physiology A* 55:407–411.
- Sredl, M. J. 2005. *Rana yavapaiensis*. Pages 596–599 in M. Lannoo, editor. *Amphibian declines: the conservation status of United States species*. University of California Press, Berkeley, CA.
- Sredl, M. J., J. M. Howland, J. E. Wallace, and L. S. Saylor. 1997. Status and distribution of Arizona's native ranid frogs. Pages 37–89 in M. J. Sredl, editor. *Ranid frog conservation and management*. Technical report 121. Nongame and Endangered Wildlife Program, Arizona Game and Fish Department, Phoenix, AZ.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York, NY.
- Stewart, J. A. E., D. H. Wright, and K. A. Heckman. 2017. Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the northern Sierra Nevada, California, USA. *PLoS ONE* 12:e0181834.

- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Sullivan, B. K., and P. J. Fernandez. 1999. Breeding activity, estimated age-structure, and growth in Sonoran Desert anurans. *Herpetologica* 55:334–343.
- Sutherland, C. S., D. A. Elston, and X. Lambin. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. *Ecology* 95:3149–3160.
- Tang, M., Y. Jiao, and J. W. Jones. 2014. A hierarchical Bayesian approach for estimating freshwater mussel growth based on tag-recapture data. *Fisheries Research* 149:24–32.
- Tingley, R., and R. Shine. 2011. Desiccation risk drives the spatial ecology of an invasive anuran (*Rhinella marina*) in the Australian semi-desert. *PLoS ONE* 6:e25979.
- Tinsley, R. C., and K. Tocque. 1995. The population dynamics of a desert anuran, *Scaphiopus couchii*. *Australian Journal of Ecology* 20:376–384.
- Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proceedings of the Royal Society B* 278:2191–2197.
- Turner, F. B. 1960. Postmetamorphic growth in anurans. *American Midland Naturalist* 64:327–338.
- Valentine-Darby, P., L. Baril, K. Struthers, C. Filippone, D. Swann, A. Mathis, and N. Chambers. 2017. Saguaro National Park: natural resource condition assessment NPS/SODN/NRR-2017/1364. National Park Service, Fort Collins, CO.
- Wallace, J. E., R. J. Steidl, and D. E. Swann. 2010. Habitat characteristics of lowland leopard frogs in mountain canyons of southeastern Arizona. *Journal of Wildlife Management* 74:808–815.
- Walls, S., W. Barichivich, and M. Brown. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–418.
- Weiss, J. L., C. L. Castro, and J. T. Overpeck. 2009. Distinguishing pronounced droughts in the southwestern United States: seasonality and effects of warmer temperatures. *Journal of Climate* 22:5918–5932.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *The American Naturalist* 128:319–341.

- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Werner, E. E., R. A. Relyea, K. L. Yurewicz, D. K. Skelly, and C. J. Davis. 2009. Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. *Ecological Monographs* 79:503–521.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Whitfield, S. M., K. R. Lips, and M. A. Donnelly. 2016. Amphibian decline and conservation in Central America. *Copeia* 104:351–379.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA.
- Wilson, B., P. S. Hammond, and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Witte, C. L., M. J. Sredl, A. S. Kane, and L. L. Hungerford. 2008. Epidemiologic analysis of factors associated with local disappearances of native ranid frogs in Arizona. *Conservation Biology* 22:375–383.
- Wylie, S. R. 1981. Effects of basking on the biology of the canyon treefrog, *Hyla arenicolor* Cope. Dissertation. Arizona State University, Tempe, AZ.
- Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. To predict the niche, model colonization and extinction. *Ecology* 96:16–23.
- Yackulic, C. B., J. Reid, R. Davis, J. E. Hines, J. D. Nichols, and E. Forsman. 2012. Neighborhood and habitat effects on vital rates: expansion of the Barred Owl in the Oregon Coast Ranges. *Ecology* 93:1953–1966.
- Yoshizaki, J. 2007. Use of natural tags in closed population capture-recapture studies: modeling misidentification. Dissertation. North Carolina State University, Raleigh, NC.
- Zhang, Z., J. Lessard, and A. Campbell. 2009. Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth parameters from tag-recapture data. *Fisheries Research* 95:289–295.

Zylstra, E. R., R. J. Steidl, D. E. Swann, and K. Ratzlaff. 2015. Hydrologic variability governs population dynamics of a vulnerable amphibian in an arid environment. PLoS ONE 10:e0125670.