Demographic Approaches to Assessing Climate Change Impact: An Application to Pond-Breeding Frogs and Shifting Hydropatterns

John H. Matthews, W. Chris Funk, and Cameron K. Ghalambor

Applications of conservation science to aquatic ecosystems have traditionally focused on water quality and quantity issues, the establishment of protected areas, the need for restoring impaired or reduced hydrological function (including flow regime), and the improvement of connectivity that has been damaged by freshwater infrastructure (Brönmark and Hansson 2002; Brinson and Malvarez 2002). All of these issues will remain critically important in the future and in the face of climate change. However, anthropogenic climate change represents two new threats. First, traditional freshwater conservation practice assumes climate “stationarity” (Milly et al. 2008), which means that interventions risk producing poor results without reevaluation in light of realized and potential effects. Second, freshwater species have a diminished capacity to respond autonomously to climate change-induced shifts as a result of extensive human modifications of these ecosystems that are not climate-related (Matthews et al. 2009; Matthews and Wickel 2009). Indeed, management responses to climate change, such as building more “clean energy” hydropower facilities or increasing irrigation demands as a result of lower soil moistures, are likely to produce synergistic effects between historic threats and emerging climate conditions (Le Quesne et al. 2010).

How will freshwater species respond to these changes? Amphibians hold a special significance with regard to this question. Given their wide distribution globally and the ability of many species to connect both terrestrial and aquatic ecosystems through their life histories, amphibians may be especially vulnerable to climate change impacts in both sets of landscapes, and some researchers suggest that they may be the most threatened group of vertebrates globally (Stuart et al. 2004; IUCN et al. 2008), particularly as a result of climate change (Corn 2005; Pounds et al. 2006; McMenamin et al. 2008).

In this chapter, we focus on the gap between ecosystem-level shifts driven by climate change and the implications for population dynamics, connectivity, and management. A key assumption in this analysis is that amphibians may be sensitive to climate-change–related threats due to the
coupling between many species’ life histories and aquatic hydropattern, which is the “normal” cycling of high and low water in an annual period (typically represented by an annual hydrograph; Jackson 2006). Here, we will describe the importance of hydropattern as a key variable in freshwater ecosystems, discuss how variation in historic hydropatterns shape evolved and plastic reproductive strategies, describe a framework for how hydropattern may be shifting globally as a result of climate change, present a demographic model to examine the effects of hydropattern shifts on pond-breeding amphibians relative to management options to offset these impacts, posit the evolutionary implications of hydropattern shifts, and finally propose management approaches for amphibians and aquatic ecosystems that may encompass both traditional and climate-induced threats. In this chapter we attempt to demonstrate that demographic modeling combined with sufficient ecosystem and species knowledge can assist in the design of targeted conservation management interventions.

**Shifting Hydropattern: An Emerging Focus for Amphibian Conservation**

Phenology and demography are linked in many species. Recent research on fresh waters points to the critical role of hydropattern (for standing water systems) and flow regime (for flowing water systems) in determining a wide range of species, communities, and ecosystem qualities. Hydropattern is determined in a particular region or ecosystem through a wide variety of factors, such as surface-to-volume ratio, flow hydraulics, and geomorphology. However, climate plays an especially critical role as hydropattern is determined by precipitation and groundwater inflows (including seasonality, intensity, quantity) and outflows (especially evapotranspiration or ET, reflecting air temperature and humidity: Winter and Woo 1990; Brinson 1993; Jackson 2006).

While air temperature is a critical variable when discussing terrestrial
ecosystems, the relationship between air and water temperature is complex. Since liquid water has a greater thermal mass than the atmosphere, water temperatures may not be shifting in conjunction with air temperatures in some regions and/or some types of systems (Poole et al. 2004). Indeed, hydropattern-driven volume changes, such as changes in salinity, pH, and time until complete drying of a given water body (Williams 2006; Matthews 2011), are likely to play a more important role in water quality (Allen and Ingram 2002; Karl and Trenberth 2003; Lambert et al. 2004).

**Historic Hydropatterns and the Evolved and Plastic Reproductive Strategies of Amphibians**

Amphibians exhibit a diverse range of reproductive strategies that often reflect the historic hydropatterns and associated selective pressures under which they evolved. These evolved strategies are observed as the mean differences between populations and species in key life-history traits such as the number and size of offspring, the length of the larval period, and the age and size at maturity (reviewed in Morrison and Hero 2003). These life-history differences are correlated with environmental gradients, such as altitude, latitude, and hydropattern, that reflect variation in important ecological factors including predation risk, length of the breeding season, temperature, food availability, and the probability of pond desiccation (e.g., Wilber 1997; Altweg and Reyer 2003; Morrison and Hero 2003; Rose 2005; see below). For example, at higher latitudes and altitudes where the breeding season is short, temperatures are cool, and breeding ponds have longer hydroperiods, amphibians tend to produce smaller clutches of larger eggs, have longer larval periods, and take longer to mature despite being under selection for rapid growth to compensate for the relatively short and cool breeding season (Berven 1982a, b; Morrison and Hero 2003).

These same life-history traits also show extensive phenotypic plasticity in response to these ecological variables, and the degree of plasticity also varies between populations and species (e.g., Leips and Travis 1994; McCollum and VanBuskirk 1996; Denver et al. 1998; Laurila and Kujasalo 1999). For example, amphibians breeding in ponds with variable predation risk in time and space exhibit greater predator-induced plasticity in morphology and growth rate, presumably as an adaptive strategy to cope with the unpredictable nature of predation risk (Lardner 2000). Thus, as hydroperiods shift in response to climate change, amphibian species and populations may be more or less adapted to coping with environmental change depending on where they fall along these environment-
tal gradients. Relatively little research has been done to identify specific life-history traits that would alter populations susceptibility to climate change, but it is reasonable to expect that populations that have historically experienced stable hydropatterns will be most vulnerable to disruption of the inflow and outflow of water.

For example, some amphibian species, such as spadefoot toads (gena Scaphiopus and Spea), have evolved striking patterns of phenotypic plasticity in their growth rates, ages, sizes at maturity, foraging modes as a means of dealing with highly variable hydropatterns (reviewed in Doughty and Reznick 2004). Yet there is also variation in these plastic responses that reflects the historic hydropatterns of a population or species. Further, the degree of plasticity in growth and stage of development in spadefoot toads increases with how ephemeral their hydropattern is (Morey and Reznick 2000). Again, the implications of this variation in plasticity for climate change remain unknown, but with regards to increasing severity and frequency of extreme events that alter hydropatterns, a reasonable hypothesis is that species and populations from ephemeral environments may be more resilient than their counterparts from more stable environments because they are more plastic.

A Framework for Describing Impacts on Amphibian Populations and Life-History Patterns

Many trends suggest that hydropatterns are shifting globally, perhaps even in the majority of freshwater ecosystems (Carney et al. this volume). However, the literature describing climate change interactions between hydropattern and amphibians is limited. Studies have tended to focus on what might be considered primary, direct climate change impacts, as in physiological tolerance studies (e.g., of phenological or range shifts: Beebee 2002; Parra-Olea et al. 2005), rather than on secondary or tertiary climate change impacts, as in studies of population demographics, interspecies relationships, community assemblages, and ecosystem tipping points—topics generally associated with multivariate and often highly uncertain processes.1 Our purpose here is not to review the literature on the effects of climate change on amphibians, but rather to present new perspectives and modeling approaches on how phenology and studies of

1. Much of the discussion in recent years of climate change impact on amphibians has raged over the causes of observed global amphibian declines, such as over the relative importance of climate shifts on the distribution and abundance of invasive species or diseases (e.g., Pounds et al. 2006; Lips et al. 2008). In most cases, “the” global amphibian decline seems likely to be multifactorial rather than from a single cause, and we will avoid these debates in this analysis.
ecosystem-level impacts, landscape connectivity, and climate change can be integrated to understand the effects of climate change on amphibian demography. We refer the reader to recent reviews for a broad overview of the effects of climate change on amphibians (e.g., Corn 2005; Collins and Crump 2009).

Are shifts in hydropattern a current threat to amphibians? The climate science literature documents widespread impacts on hydropattern-relevant variables. Precipitation patterns have been shifting worldwide since at least 1945 (Dore 2005). Globally, annual precipitation is increasing (Wentz 2007), although there is much variation in regional and local precipitation patterns. In some areas, such as the Murray-Darling Basin of Australia, rates of evapotranspiration change are outpacing or reinforcing shifts in precipitation (Murphy and Timbal 2008). Thus, even when annual precipitation amounts may be increasing, given shifts in other climate variables, there may be a net decrease in surface water for aquatic species.

Given that key life-history events are key to hydropattern, how will climate change impact amphibian demographic patterns? Here we describe general geographic patterns of hydropattern alteration, and how the mode of climate change can influence hydropattern and amphibian demographic patterns.

At temperate and boreal latitudes, and at high altitudes in tropical and subtropical regions, hydropatterns are influenced by the timing and form of precipitation and ambient air temperature (Magnuson et al. 1997). Most freshwater ecosystems in these areas include a period of ice cover and water temperatures that do not sustain active movement and development for most amphibian species. In almost all temperate zones, ice-free periods are lengthening and more winter precipitation is falling as rain rather than snow, thus resulting in a reduced snowpack and a longer warm period (Magnuson et al. 1997; IPCC 2008). In many regions, summer temperatures and/or evapotranspiration rates are also increasing, thus raising the rate of outflows. For some water bodies, this may result in a transition from a long-hydropattern state (a permanent or perennial system) into a short-hydropattern state (an ephemeral, temporary, or intermittent system). Given the influence of water volume on water quality, not all water need leave a system to render it unviable for aquatic species: water temperatures are more likely to match high air temperatures at low volumes, dissolved oxygen rates can fall as temperatures increase, and pH and salinity can increase rapidly as solute concentration increases (Oviatt 1997; Poff et al. 2002; Issar 2003; Matthews 2011).

As suggested above, trophic structure can also shift dramatically in
response to changes in state from short- to long-hydropattern regimes. At temperate and tropical latitudes, for instance, long-hydropattern systems tend to be dominated by vertebrate fish predators, while short-hydropattern systems are often dominated by invertebrate predators such as aquatic insects (e.g., Heenar and M’Closkey 1997; Hero et al. 1998; Williams 2006). Regional shifts between long and short hydropatterns are likely to have profound impact on community assemblages and survivorship of amphibians.

In contrast, monsoonal precipitation patterns dominate influences on hydropattern at tropical and subtropical latitudes, as intra-annual temperatures do not vary as widely there as they do in temperate and boreal regions. Generally speaking, hydropatterns in these regions will be most sensitive to changes in monsoon timing, which can easily result in shifts between long (permanent) and short (ephemeral) hydropattern states. Although air temperature shifts are predicted to be more dramatic at mid-

Interestingly, these observations may also be relevant to species that are considered semiaquatic or dependent on very humid but nominally terrestrial ecosystems. Particularly in tropical rainforests and cloud forests, many amphibians have direct development, in which eggs are laid in leaf litter or on leaves; larval development occurs within the egg, and individuals hatch as miniature versions of adults (Duellman and Trueb 1994). These habitats are characterized by high humidity and abundant moisture even in the absence of a fluid environment. In effect, these species exist within a terrestrial “humidity envelope,” so that they are subjected to pressures similar to those experienced by fully aquatic amphibian species. Indeed, high-elevation tropical amphibians in these habitats may be already in substantial decline due to the drying of the terrestrial humidity envelope (e.g., Pounds et al. 1999; Rovito et al. 2009).

While examination of broad latitudinal patterns is critical to understanding global amphibian demographic impacts from climate change, the mode through which regional or local climate shifts are expressed is also important to consider. Perhaps the three most important modes of climate change are shifts in “mean” climate conditions (e.g., annual precipitation increases), shifts in seasonality (e.g., more rain in winter, later monsoon arrival), and shifts in climate extremes (in effect, the climate variance around the mean, such as more intense tropical cyclones or more long droughts; see table 4.1 for an overview of all three modes;
Table 4.1. Modes of climate change and implications for ecosystems and management responses

<table>
<thead>
<tr>
<th>Mode of climate shift</th>
<th>Relevant spatial and temporal scale</th>
<th>Implications for ecosystems</th>
<th>Implications for management</th>
<th>Evolutionary ecology impacts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shifts in “mean” climate</td>
<td>Basin and seasonal/annual; slow change in “normal” weather patterns</td>
<td>Persistent and usually slow movement of climate; probably the least harmful form of climate change for most species and ecosystems</td>
<td>Type of change most often predicted by circulation models, but not often shown in climate history</td>
<td>Unidirectional selection</td>
</tr>
<tr>
<td>Change in climate seasonality</td>
<td>Whole basin, monthly or below; seasonality changes already widespread</td>
<td>Flow regime and hydropattern shifts</td>
<td>Management for old or new flow regime extremely difficult to predict; best detected through retrospective analyses</td>
<td>Selection for changes in the timing of phenological events such as breeding and development time</td>
</tr>
<tr>
<td>More extreme weather</td>
<td>Basin to local, mostly subannual</td>
<td>Major changes in precipitation/evapotranspiration intensity, and very hot/cold days that shock ecosystems for brief periods, destabilizing ecosystem processes and local species and populations</td>
<td>Water quality variability increasing due to intense precipitation and high evapotranspiration rates (ET) and temperature shocks</td>
<td>Bottlenecks, plasticity, microevolution</td>
</tr>
</tbody>
</table>

Le Quesne et al. 2010). Note that these three modes are not mutually exclusive and in many localities all three modes of change are occurring simultaneously (IPCC 2008).

Understanding the mode of change is important to understanding the climate pressures and potential for adaptive responses to those pressures. Gradual shifts in mean climate conditions, for instance, are probably the least acute of the three modes for amphibian populations over short time scales (roughly, decades to centuries). From an evolutionary perspective, a shift in mean climate is equivalent to persistent directional selection. However, not all shifts in mean climate are likely to be gradual. As dis-
cussed above, the paleoecological literature shows ample evidence that a cluster of climate variables describing a particular climate state or “plateaus” can cross thresholds or tipping points that result in abrupt transitions to new climate states. Many glacial-interglacial transitions, for instance, spanned only a few decades (Issar 2003; Anderson et al. 2007). To date, few state-level changes appear to have occurred as a result of anthropogenic climate change. Three possible large-scale candidates described in the current literature are alterations in ocean currents off the Pacific Northwest coast of North America (Grantham et al. 2004), the widespread disappearance of subtropical and tropical snowpacks and glaciers (Thompson et al. 2006), and rapid change in the precipitation-evapotranspiration regime in southeastern Australia (Murphy and Timbal 2008).

Shifts in seasonality present a different set of pressures, particularly for community-level interactions and life-history stages. Seasonal changes such as earlier springs, later winters, and increases in the number of frost-free days also are occurring (Magnuson et al. 1997; Schindler 1998). Monsoon timing is shifting in the tropics (Bueh et al. 2003; Mirza and Ahmad 2005), melting dates for snowpack are advancing (Nolin and Daly 2006; IPCC 2007), and ice-free periods for lakes and rivers are increasing in length as freeze dates recede and breakup dates advance (Prowse et al. 2006).

Phenological mismatches between species (e.g., butterfly-plant, parasite-host) and between triggering cues and significant life-history events are likely with seasonality shifts. In the latter case, dependence on cues that are proxies for climate variables (such as photoperiod) can present a significant “signaling” problem for an organism (Parmesan and Yohe 2003; Parmesan 2006). From an ecological perspective the ability to sense and appropriately respond to these cues is likely to occur initially through adaptive phenotypic plasticity, or the capacity of individuals to track environmental changes through altered developmental, physiological, and behavioral changes. How well amphibians can track phenological changes will in turn determine the strength of selection and the capacity for evolutionary changes to occur (Ghalambor et al. 2007). Given the importance of hydropattern signaling for amphibians and the responsiveness of hydropatterns to alterations in the precipitation-evapotranspiration regime, shifts in seasonality are likely to be a critical factor in shaping amphibian responses to climate change.

Likewise, changes in the frequency and severity of climate extremes can have a powerful impact on populations and communities if these shifts alter disturbance regimes. Weather extremes have also been increasing in
frequency globally (Groismann et al. 1999; Easterling et al. 2000); they have been shown to have a powerful influence on populations and community assemblages (Parmesan et al. 2000; McLaughlin et al. 2003; Tews et al. this volume). Precipitation intensity is growing in many regions, impacting runoff, erosion, nutrient loading, and groundwater recharge processes (Zhang and Nearing 2005; Beighley et al. 2008). Greater climate variability is increasing the frequency of floods and droughts (IPCC 2007). Extreme events represent episodes of selection that in the short term may cause mass mortality and reproductive failure, and in the long term may impact the genetic structure of populations and the interactions between community members. Ultimately, these changes in extreme severity and frequency modify the ecological disturbance regime that over decades or centuries can alter key ecosystem qualities.

Demographic Modeling of Climate Change Impacts

A recent IPCC technical report (2008) on water and climate identified small, shallow lentic systems, such as ponds and other wetlands used by many amphibian species, as the most climate-change–threatened type of habitat globally, due to their rapid response to even minimal shifts in climate characteristics, with their low volume making them more likely to change from permanent to ephemeral (or from less ephemeral to more ephemeral). They are probably also one of the types of systems least likely to be monitored to observe these impacts.

Climate change can affect lentic-breeding amphibians directly, by reducing their survival and fecundity, or indirectly, by altering their habitats (figure 4.1). Much climate change research focuses on direct effects on fitness, although many species, including amphibians, are more likely to first be impacted by habitat changes (Collins and Crump 2009). Moreover, climate change can impact breeding, foraging, and/or overwintering habitats that are used by amphibians in different life-history stages (figure 4.1). These habitat changes, in turn, can reduce survival and fecundity rates, thereby reducing population growth rates and increasing extinction probabilities. Thus, predicting the effects of climate change on amphibian populations requires an understanding of which habitats will be impacted and how these changes will affect amphibian vital (birth and death) rates.

Here, we provide an example of how population projection matrix models can be used to assess the effects of climate change and management actions on the growth and extinction probabilities of amphibian populations. Similar modeling approaches have been used to assess the effects of shifting hydropattern, precipitation, and climate on the demog-
Figure 4.1. Conceptual diagram of the direct effects (on different life-history stages) and indirect effects (mediated through habitat changes) of climate change on pond-breeding amphibians. Solid arrows indicate life-history transitions; dashed arrows indicate climate change impacts.

We used projection matrix models to examine the effects of reduced...
tadpole survival ($S_t$) caused by reduced hydroperiods predicted under climate change on $\lambda$ and $P$, of amphibian populations. We had two specific questions. First, how will various scenarios of reduced hydroperiod affect $\lambda$ and $P$? Second, how effective are different management strategies at offsetting the effects of reductions in $S_t$ caused by shorter hydroperiods? Our goal, however, is not to make accurate predictions for a given population, but to demonstrate how projection matrix models can be used to address these questions for amphibians put at risk by climate change.

Our focal species for this analysis was the Columbia spotted frog (*Rana luteiventris*) in the northern Rocky Mountains of Montana. Columbia spotted frogs (hereafter referred to as CSFs) are a widely distributed pond-breeding species found in the Great Basin of Nevada, Utah, Idaho, and Oregon as well as northward into eastern Washington, northern Idaho, western Montana, northwestern Wyoming, western Alberta, British Columbia, and the southernmost reaches of the Yukon Territory. CSFs have a typical temperate-zone pond-breeding frog life history in that the adults lay eggs in the early spring, embryos hatch one to two weeks later, and tadpoles develop in ponds and metamorphose in the summer (figure 4.1; Stebbins 2003). These frogs become sexually mature in two or more years, depending on sex, latitude, altitude, and other local environmental conditions (Bull 2005).

Our analysis focuses on a low-elevation population of CSFs in Keeler Creek in the Cabinet Mountains of northwestern Montana. This population consists of eight breeding ponds (primarily beaver ponds) adjacent to Keeler Creek and connected to it by small inlet and outlet streams (Funk et al. 2005a). The breeding ponds are separated from each other by a maximum straight-line distance of 7 km. Genetic analysis using microsatellite loci showed that these eight ponds represent a single random mating population that is genetically distinct from nearby populations (Funk et al. 2005b).

We use CSFs from Keeler Creek as our focal population for this analysis for three main reasons. First, CSFs in the northern Rocky Mountains may be negatively impacted by climate change due to shortening in the length of the regional hydroperiod regime. Climate change is predicted not only to increase temperatures and therefore evapotranspiration, but also to reduce spring snowpack in the northern Rocky Mountains (Karl et al. 2009). This combination of increasing evapotranspiration and decreasing snowpack is predicted to result in shorter high-water periods (i.e., earlier drying) for ponds used by CSFs for breeding, since snowmelt is the main source of water in these ponds. Second, WCF collected detailed
demographic data for CSFs in Keeler Creek between 2000 and 2003 as part of a dispersal study (Funk et al. 2005a), allowing us to parameterize a matrix model that quantitatively describes the demography of this population. Finally, during this demographic study, WCF observed CSF breeding ponds in Keeler Creek drying out completely before tadpoles were able to metamorphose, demonstrating that pond drying potentially already impacts this population, and providing a baseline estimate of the probability of pond drying prior to metamorphosis.

We constructed a female-based, post-birth pulse Lefkovitch matrix model (Burgman et al. 1993; Caswell 2000) with annual projection intervals representing a population with a life history consisting of three stages: prejuvenile (embryo, tadpole, and overwintering metamorph), juvenile, and reproductive adult. The matrix for this life history is

\[
\begin{bmatrix}
0 & [S_j \times \Psi_{ja} \times P_i \times C] & [S_a \times P_i \times C] \\
[S_e \times S_t \times S_j^{0.67}] & [S_j \times (1 - \Psi_{ja})] & 0 \\
0 & [S_j \times \Psi_{ja}] & [S_a]
\end{bmatrix}
\]

where \( S_e = \) embryo survival, \( S_t = \) tadpole survival, \( S_j = \) juvenile survival, \( S_a = \) adult survival, \( \Psi_{ja} = \) the probability that a juvenile becomes an adult (given that the juvenile has survived), \( P_i = \) the probability of laying eggs, and \( C = \) clutch size. \( S_j \) is taken to the power of 0.67 in the transition from prejuveniles to juveniles (matrix element \( a_{21} \)), to account for the fact that new juveniles metamorphose at the end of the summer and therefore only have to survive eight-twelfths (0.67) of a year until the next census. This matrix is the same as the one used in Biek et al. (2002) for temperate-zone pond-breeding frogs.

We parameterized our matrix model using vital rate means and temporal variances estimated for the low-elevation Keeler Creek population (table 4.2). \( S_j, S_t, \) and \( \Psi_{ja} \) were estimated in 2000, 2001, and 2002 using capture-mark-recapture (CMR) analysis (Funk et al. 2005a). Females were considered adults once they reached 50 mm snout-vent length, the minimum size of breeding females observed in this population. The probability of laying eggs (\( P \)) was assumed to be 1.00. This is likely a reasonable assumption for low-elevation CSFs. Most adult females were clearly gravid by the end of the summer and many were found breeding in consecutive years, suggesting that low-elevation females typically breed every year.

Clutch size (\( C \)) was estimated using a modified version of the sub-
Table 4.2. Vital rate estimates used in projection matrix model for Columbia spotted frogs from lower Keeler Creek, Montana

<table>
<thead>
<tr>
<th>Vital rate symbol</th>
<th>Vital rate description</th>
<th>Mean</th>
<th>Temporal process variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_e$</td>
<td>Embryo survival</td>
<td>0.9810</td>
<td>0.0006</td>
</tr>
<tr>
<td>$S_t$</td>
<td>Tadpole survival</td>
<td>0.0191</td>
<td>0.0000</td>
</tr>
<tr>
<td>$S_j$</td>
<td>Juvenile survival</td>
<td>0.4700</td>
<td>0.0570</td>
</tr>
<tr>
<td>$S_a$</td>
<td>Adult survival</td>
<td>0.7800</td>
<td>0.0470</td>
</tr>
<tr>
<td>$P_l$</td>
<td>Probability of laying eggs</td>
<td>1.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>$C$</td>
<td>Clutch size</td>
<td>434</td>
<td>1302</td>
</tr>
<tr>
<td>$\Psi_{ja}$</td>
<td>Probability of juvenile becoming adult</td>
<td>0.1000</td>
<td>0.0029</td>
</tr>
</tbody>
</table>

Sampling-volume displacement method of Werner et al. (1999). In this method (1) the egg mass (clutch) volume is measured with a 1-liter beaker using volume displacement; (2) the volume of three different egg mass subsamples is measured with a 250 ml graduated cylinder; (3) the number of eggs in each subsample is counted; and (4) the average ratio of the number of eggs per milliliter for the three subsamples is used to estimate the number of eggs in the entire clutch. Counts of entire egg masses showed that this method provides accurate estimates of clutch size (Maxell and Funk, unpublished data). Clutch size estimates were divided by two to estimate the number of female embryos, assuming an equal sex ratio. Clutch sizes were estimated for 33, 45, and 61 egg masses in the low-elevation Keeler Creek population in 2001, 2002, and 2003, respectively.

Observations at the beginning of the study revealed that embryo survival approached 1.00 unless an entire clutch was stranded due to desiccation, in which case embryo survival was 0.00. Embryo survival ($S_e$) for a given breeding pond was thus estimated as the proportion of egg masses that did not dry out due to stranding. $S_e$ was estimated at each breeding pond in 2001, 2002, and 2003.

Tadpole survival ($S_t$) was estimated for each pond as the estimated number of metamorphs (tadpoles that successfully metamorphosed into froglets) divided by the estimated number of hatchlings (embryos that hatched). The number of hatchlings was estimated as the number of egg masses $\times C \times S_e$. The number of metamorphs was estimated using Chapman’s unbiased version of the Lincoln-Petersen closed-population CMR estimator of abundance (Seber 1982) and dividing by two to estimate the number of female embryos.
number of female metamorphs. $S_t$ was also estimated at each breeding pond in 2001, 2002, and 2003.

In some years, ponds dried before any tadpoles metamorphosed due to a short hydroperiod. We defined $P_{dry}$ as the probability of a pond drying before tadpoles were able to metamorphose. We estimated $P_{dry}$ in 2001, 2002, and 2003 as the number of ponds that dried before metamorphosis divided by the total number of ponds in the population (eight). Ponds that dried before metamorphosis were not included in estimates of $S_t$ so that baseline tadpole mortality ($1-S_t$) could be modeling separately from tadpole mortality caused by short hydroperiods.

For each vital rate, process variance among years (temporal variance) was estimated using White’s (2000) method, which removes sampling variance from total variance to estimate process variance. Using process variance rather than total variance is important to avoid over-estimating $P_e$. We used Morris and Doak’s (2002) program (white.m) in Matlab R2008b to estimate process variance. For our starting population size vector we assumed 100 adult females and a stable stage distribution.

We used stochastic projection matrix model simulations to estimate stochastic population growth rates ($\lambda$), the number of adult females at the end of simulations (only including simulated populations that did not decrease below the quasi-extinction threshold), and quasi-extinction probabilities ($P_{qe}$) under various hydroperiod and management scenarios for a single CSF breeding pond in the low-elevation Keeler Creek population. We defined $P_{qe}$ as the probability of falling below a predefined threshold population size (10 adult females). Our matrix simulations are based on those of Morris and Doak (2002) as implemented in their Matlab program vitalsim.m. In our model, however, we did not include vital rate correlations, autocorrelations, or cross-correlations, as there are insufficient data to reliably estimate these parameters for CSFs.

We modeled projected reductions in hydroperiods in our simulations by incorporating a probability of complete reproductive failure for a given year ($S_t = 0$) due to pond drying before metamorphosis. Specifically, $P_{dry}$ for each year of the simulation was determined by randomly drawing from a beta distribution of $P_{dry}$. The beta distribution of $P_{dry}$ was determined from the mean and variance observed in the low-elevation Keeler Creek population from 2001 to 2003. If $P_{dry} \geq$ a uniform random number, then $S_t = 0$ for that year. If $P_{dry} <$ the uniform random number, then $S_t$ was chosen from the baseline $S_t$ beta distribution. To model an increasing probability of $P_{dry}$ over the next 40 years, the mean of the beta distribution was increased. For example, in a scenario of a 50% increase in $P_{dry}$ over the next 40 years and a baseline $P_{dry}$ of 0.20, mean $P_{dry}$ would be 0.25.

Demographic Approaches to Assessing Impact | 71
in year 20 \([= 0.20 \times (1 + (20 \times (0.50/40)))\)]. For each scenario, we ran five independent runs of 5,000 iterations each for 40 years. Our Matlab code is available from WCF upon request.

Climate change projections for the northwest United States (which includes Keeler Creek) predict a 10% to 30% decrease in spring snowpack by mid-century and a 1.7 to 5.6°C increase in temperature by the end of the century (Karl et al. 2009). The impact of these climatic changes on hydroperiods of the ephemeral, semipermanent, and permanent ponds used by CSFs for breeding is unknown, although a conservative estimate is that these changes in climate will result in a reduction in hydroperiod equivalent to the reduction in snowpack (10%–30%) since snowmelt is the main source of water in these ponds.

Also uncertain is the relationship between hydroperiod length and the probability of a pond drying before CSF tadpoles metamorphose \(P_{dry}\) as defined above). Field observations by WCF show that in many cases, CSF tadpoles metamorphose “just in time,” within a few days before ponds dry out completely. This leads to the prediction that a small reduction in hydroperiod length may result in a large increase in \(P_{dry}\). Thus we hypothesize that the relationship between \(P_{dry}\) and hydroperiod length is sigmoidal, with small reductions in hydroperiod resulting in dramatic increases in \(P_{dry}\) (figure 4.2).

Accordingly, we considered climate change scenarios with large increases in \(P_{dry}\) over the next 40 years of 50%, 100%, and 200%. We feel that these are reasonable possibilities for lower Keeler Creek. We also ran simulations with no probability of pond drying before metamorphosis, and with the current, baseline \(P_{dry}\) for comparison. In addition, we modeled the effects of three different management scenarios to counteract the negative effects of a 100% increase in \(P_{dry}\). First, we simulated the effects of introducing 10, 50, 100, or 200 metamorphs from a different source population to the focal population once every five years. In Keeler Creek and other nearby CSF populations, WCF observed considerable variation in recruitment among ponds from 2001 to 2003. Thus, in any given year, there were usually some ponds with high recruitment that could serve as source populations for translocations. Translocations would therefore be a relatively straightforward management option. Second, we considered the effects of increasing connectivity so that five metamorphs immigrate to the focal population each year. One possible method of increasing connectivity for amphibians is the construction of road underpasses to facilitate movement between populations on opposite sides of roads (Lesbarreres et al. 2004). Finally, we examined the effects of increasing
Figure 4.2. Hypothesized relationship between the probability of pond drying before tadpoles can metamorphose ($P_{dry}$) and hydroperiod length. In the example shown, a small future reduction in hydroperiod results in a 200% increase in $P_{dry}$.

Output from Demographic Models

The projection matrix model simulations indicate that reproductive failure due to pond drying is predicted to have a significant negative impact on population growth rates and population persistence (table 4.3; figure 4.3). With the current rate of pond drying ($P_{dry} = 0.1984$), the stochastic population growth ($\lambda_s$) is 4.3% lower than it would be without any pond drying. The final number of adults is 74% lower with current pond drying compared to what it would be with no pond drying. The probability of quasi-extinction ($P_{qe}$) is also 214% higher with the current rate of pond drying than with no drying. With the current rate of pond drying, $\lambda_s$ is slightly greater than one, thus indicating that the population is growing at a slow rate. With increases in $P_{dry}$ over the next 40 years, however, population growth dips below one, indicating a population de-
Table 4.3. Results of projection matrix model simulations for Columbia spotted frogs from lower Keeler Creek, Montana, under different climate change and management scenarios. $P_{\text{dry}}$ = baseline probability of a pond drying before tadpoles can metamorphose; $\text{Inc}P_{\text{dry}}$ = proportional increase in $P_{\text{dry}}$ over the next 40 years due to climate change; $N_{\text{met}}$ = number of metamorphs introduced or immigrating; MetFreq = frequency with which metamorphs are introduced or immigrate; $\text{Inc}S_{j}$ = increase in juvenile survival through management actions; $\lambda_{s}$ = stochastic growth rate for a given scenario; number of adults = number of adult females after 40 years for simulated populations that have remained above the quasi-extinction threshold of 10 or fewer adults. Means and 95% confidence intervals (CIs) are based on five independent runs of 5,000 iterations per run for each scenario.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Impacts</th>
<th>Management</th>
<th>$\lambda_{s}$</th>
<th>Number of adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$P_{\text{dry}}$</td>
<td>$\text{Inc}P_{\text{dry}}$</td>
<td>$N_{\text{met}}$</td>
<td>MetFreq</td>
</tr>
<tr>
<td>No pond drying</td>
<td>0.00</td>
<td>0.00</td>
<td>0 N.A.</td>
<td>0.00</td>
</tr>
<tr>
<td>Baseline (current) pond drying</td>
<td>0.1984</td>
<td>0.00</td>
<td>0 N.A.</td>
<td>0.00</td>
</tr>
<tr>
<td>50% increase in pond drying</td>
<td>0.1984</td>
<td>0.50</td>
<td>0 N.A.</td>
<td>0.00</td>
</tr>
<tr>
<td>100% increase in pond drying</td>
<td>0.1984</td>
<td>1.00</td>
<td>0 N.A.</td>
<td>0.00</td>
</tr>
<tr>
<td>200% increase in pond drying</td>
<td>0.1984</td>
<td>2.00</td>
<td>0 N.A.</td>
<td>0.00</td>
</tr>
<tr>
<td>Introduce 10 metamorphs every 5 years</td>
<td>0.1984</td>
<td>1.00</td>
<td>10 Every 5 years</td>
<td>0.00</td>
</tr>
<tr>
<td>Introduce 50 metamorphs every 5 years</td>
<td>0.1984</td>
<td>1.00</td>
<td>50 Every 5 years</td>
<td>0.00</td>
</tr>
<tr>
<td>Introduce 100 metamorphs every 5 years</td>
<td>0.1984</td>
<td>1.00</td>
<td>100 Every 5 years</td>
<td>0.00</td>
</tr>
<tr>
<td>Introduce 200 metamorphs every 5 years</td>
<td>0.1984</td>
<td>1.00</td>
<td>200 Every 5 years</td>
<td>0.00</td>
</tr>
<tr>
<td>Increase connectivity</td>
<td>0.1984</td>
<td>1.00</td>
<td>5 Every year</td>
<td>0.00</td>
</tr>
<tr>
<td>Increase juvenile survival by 10%</td>
<td>0.1984</td>
<td>1.00</td>
<td>0 N.A.</td>
<td>0.10</td>
</tr>
</tbody>
</table>

*For the metamorph introduction and increased connectivity management scenarios, estimates of $\lambda_{s}$ are expected to approximate 1, because when there is a fixed introduction of a given number of individuals to a population that otherwise has $\lambda_{s} < 1$, the population will be stable (D. F. Doak, personal communication).
Figure 4.3. Cumulative distribution of quasi-extinction probability ($P_{qe}$) for scenarios with different probabilities of pond drying before tadpoles can metamorphose ($P_{dry}$). The five different runs for the “no pond drying” scenario are shown as an example of the amount of variability typically observed among runs.

cline. The number of adults is predicted to decrease 31%, 50%, and 73%, and $P_{qe}$ is predicted to increase 14%, 45%, and 118% over the current level in 40 years with a 50%, 100%, and 200% increase in $P_{dry}$, respectively.

The three management scenarios counteract the negative effects of a 100% increase in $P_{dry}$ to varying degrees (table 4.3; figure 4.4). A relatively ineffective management scenario is increased connectivity resulting in five juvenile immigrants per year. This strategy only increases $\lambda_s$ by 0.8% and reduces $P_{qe}$ in 40 years by 13%. It has essentially no effect on the final number of adults. The second most effective management strategy is introduction of metamorphs once every five years. For example, introduction of 100 metamorphs once every five years increases $\lambda_s$ by 1.7%, increases the number of adults by 6.2%, and reduces $P_{qe}$ by 34%. The most effective option is increasing juvenile survival by 10%, which results in an increase in $\lambda_s$ of 4.4%, an increase in the number of adults of 212%, and a reduction in $P_{qe}$ by 63%.
These projection matrix model simulations show that, despite generally low sensitivity of $\lambda$ to variation in $S_t$ for pond-breeding frogs (Biek et al. 2002), periodic mass mortality of tadpoles due to pond drying can have a significant negative impact on $\lambda$, the final number of adults, and $P_{qe}$ for CSFs in the low-elevation Keeler Creek population. Moreover, although historical $P_{dry}$ is unknown, $\lambda$, and the final number of adults are substantially lower and $P_{qe}$ is much higher with the current rate of $P_{dry}$ than in the case of $P_{dry} = 0$, thus suggesting that this population may already be impacted by pond drying. Indeed, McMenamin et al. (2008) have recently found evidence that CSFs and two other amphibian species have declined in Yellowstone National Park in the last 16 years due at least in part to pond desiccation. Increases in $P_{dry}$ will only exacerbate the predicted impact on the lower Keeler Creek population of CSFs. A large increase in $P_{dry}$ is required, however, for a significant impact on this population. A 50% increase in $P_{dry}$ is predicted to have a minimal effect on $\lambda$, the number of
adults, and \( P_{qe} \). But impacts on \( \lambda_s \), the number of adults, and \( P_{qe} \) increase substantially if \( P_{dry} \) increases by 100% or 200% in 40 years.

Fortunately, the simulations also demonstrate that management actions can buffer this population from the negative impacts of brief high-water periods and earlier drying, although different strategies vary substantially in their effectiveness. If all of these management actions were equally feasible and cost the same, then increasing \( S_j \) would clearly be the best option because it would increase \( \lambda_s \) and the number of adults and decrease \( P_{qe} \) the most. For a given species and population, however, some strategies may not be possible at all, or some may be more expensive than others. In a real management situation, feasibility and cost-effectiveness clearly should be included in the analysis.

There are several data and model limitations in the current analysis. The first data limitation is that our vital rate estimates are based on data from a limited number of years (four years for this population). This is often the case with projection matrix models. Second, although climate change models clearly show that hydroperiods in the northern Rocky Mountains will become shorter, the magnitude of this reduction is uncertain. Third, the relationship between \( P_{dry} \) and hydroperiod length is unknown although, as explained earlier, the observation that many tadpoles metamorphose a few days before complete desiccation of ponds suggests that a short reduction in hydroperiod may result in a large increase in \( P_{dry} \). Finally, the effect of climate change on other vital rates is unknown for CSFs. For example, Scherer et al. (2008) found that adult survival of boreal toads (Bufo boreas) in Colorado was positively related to winter temperatures. Similarly, McCaffery and Maxell (2010) found a positive relationship between survival and winter temperatures and between breeding probabilities and winter temperatures in high-elevation populations of CSFs in the Bitterroot Mountains of Montana. Thus, increased temperatures from climate change may also have some positive effects on amphibian populations.

Our simulations are limited in that they do not include vital rate correlations, autocorrelations, cross-correlations, density dependence, or demographic stochasticity, all of which could change our predictions. Collecting additional years of data will allow proper estimation of these parameters. A second limitation is that the models do not incorporate plasticity or evolution, which we recognize can buffer populations over shorter and longer time periods (see above). For example, tadpoles may be able to develop and complete metamorphosis faster, either through phenotypic plasticity within generations or by adaptation to selection im-

Demographic Approaches to Assessing Impact | 77
posed by shorter hydropериods across generations. Furthermore, populations may vary in their capacity to exhibit plasticity or in their response to selection, thus making it difficult for us to make universal generalizations. Any demographic model that does not include plasticity or adaptation is likely to predict a greater impact than a model that does include these factors, thus resulting in somewhat “pessimistic” results.

Several gaps in the current understanding of climate change and amphibian demography need to be filled before population models can accurately predict climate change impacts and the effectiveness of management actions for amphibians. First, much more research is needed to understand future hydropériod changes of amphibian breeding ponds, the relationship between $P_{dry}$ and hydropériod, and the effect of climate change on multiple vital rates. Second, long-term demographic studies are needed to estimate vital rates, vital rate correlations, autocorrelations, and cross-correlations, and also to understand the importance of other demographic processes, such as density dependence, in amphibian population dynamics. Third, demographic studies should be conducted on amphibian species with different reproductive modes and life histories to determine the variation in their responses to climate change. In addition, amphibian demographic research and amphibian management should be conducted in an adaptive management framework in which model predictions are tested, data is collected to improve those predictions, and management practices are adjusted on the basis of the improved models (Bakker and Doak 2009).

**Recommendations for Management**

Perhaps the most important contribution of the modeling efforts presented here is the implication that physiological ecology approaches to climate change, such as bioclimate envelope modeling, are likely to be insufficient for capturing the complex suite of climate variables that describe hydropattern. The phenological mismatches induced by advancing drying times present a severe, unforgiving threat for many amphibians in an aquatic stage. Thus, observational data for regional drying trends is critical to determine whether permanent ecosystems are becoming intermittent, or whether intermittent systems are becoming more frequently intermittent. Such an assessment can identify habitats, regions, and individual water bodies that may be at special risk from climate change, even in the absence of more detailed natural history information or high-confidence global circulation model downscaling to discern trends in precipitation impacts (Matthews and Wickel 2009).

Closely related to this is the need for a formal consideration of connect-
tivity within a network of aquatic ecosystems (cf. Cross et al. this volume). Ideally, demographic modeling can provide guidance about the critical or sensitive stages of amphibian life history to guide management interventions. For instance, are there “traditional” barriers to dispersal between habitat patches, such as water infrastructure? Is climate change altering these barriers—for example, is it increasing the frequency of terrestrial fires? Likewise, can water infrastructure be managed to buffer shifts in hydroperiod for critically endangered habitat or species, and to buffer ecosystems from some climate change impacts (Le Quesne et al. 2010)? By extension, the importance of including an area of management focus large enough to encompass significant microclimate variation could be useful in preventing more frequent extreme weather events from eliminating multiple populations from a network and disrupting their connectivity over large areas.

Over longer time scales, amphibian management should also consider the evolutionary implications of shifts in mean climate and seasonality, both of which are likely to be experienced as directional selection. What are the limits to adaptation and phenotypic plasticity in responses to climatic change (see Austin et al. this volume)? Is there evidence of potential critical mismatches in phenology between other members of the trophic network or the climate-regulated portions of the disturbance regime? Does change appear to advance much faster than species can respond? Is there genetic evidence for multigenerational connectivity between disjunct populations? A decision framework has recently been proposed for assisted migration (Hoegh-Goldberg et al. 2008; Popescu and Hunter, this volume); it may be necessary to consider this for taxa, such as amphibians, that inhabit isolated habitat patches embedded in semiarid landscapes, with little potential for autonomous connectivity.

Here we have focused on the importance of hydropattern as an aspect of freshwater ecosystems that are rapidly shifting in response to anthropogenic climate change, especially as a function of shifts in the timing and amount of precipitation. Hydropattern has a critical relationship with the life-history patterns of many amphibians, particularly pond-dwelling species. Shifts in ponds from long to short hydropattern regimes are likely to be especially dire for amphibian populations that have been acclimated to relatively stable hydrological conditions. Matrix modeling is one method for untangling the relative impacts of climate change from other demographic influences, such as loss of connectivity, and it can be helpful in pursuing sound, adaptive management interventions. Ideally, matrix modeling can assist resource managers in trying to explore future impacts. However, some amphibian species demonstrate complex reactions
to shifting hydropatterns; and species- or population-specific research that focuses on estimates of major demographic variables, evolutionary implications of demographic changes across population networks, and the possibility of phenotypically plastic interactions with hydropattern should also be considered.

**LITERATURE CITED**


Hero, J. M., C. Gascon, and W. E. Magnusson. 1998. Direct and indirect effects of


82 | Chapter Four


